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The management and ecology of Oncorhynchus spp. and other estuarine-dependent native California fishes in artificially and naturally disconnected aquascapes

Author

Huber, Eric

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The management and ecology of *Oncorhynchus* spp. and other estuarine-dependent native California fishes in artificially and naturally disconnected aquascapes

by

Eric Huber

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Committee in charge:
Professor Stephanie M. Carlson, Chair
Professor Vincent H. Resh
Professor Mark T. Stacey

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ABSTRACT

The management and ecology of *Oncorhynchus* spp. and other estuarine-dependent native California fishes in artificially and naturally disconnected aquascapes

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In this dissertation I investigate the impacts of artificial and natural watershed disconnection on the management and ecology of valued native California fishes. I explore the subject at regional and local scales and pay particular attention to the consequences of river discontinua on juvenile rearing and habitat use patterns for multiple populations of Pacific salmonids with conservation and economic importance. Scientific inquiry in my study systems was initially motivated by the intention to comprehend the potential direct and indirect links between connectivity loss and collapsed hatchery-supported Chinook salmon (*Oncorhynchus tshawytscha*) commercial and recreational fisheries and recurring widespread animal mass mortality events involving the take of threatened *O. mykiss* at one of California's few remaining estuary-saltmarsh habitat complexes. My research coincided with a severe and historic drought and the timing offers a special opportunity to better understand the potential effects of climate change on salmon hatchery management and estuarine fish ecology in California.

From the 1940s to the 1970s, salmon hatcheries were constructed in the foothill zones of California's Sacramento and San Joaquin river watersheds in order to mitigate for lost spawning and rearing habitat upstream of large impassable dams. While initially intended to reduce harvesting pressure on wild stocks, hatchery-produced Central Valley fall run Chinook salmon (CVFRCS) now dominate the population complex and comprise the majority of the California and Southern Oregon commercial salmon fishery. The population collapsed from 2006-2009 and the commercial and recreational fisheries were completely closed in 2007 and 2008 for the first time in their 90 year histories. The proximate cause for the collapse was warm water temperatures and low food abundances in the nearshore zone when smolts exited the Golden Gate in 2005. However, the environmental conditions were not unprecedented and, given that hatchery salmon currently sustain the fisheries, a closer inspection of hatchery management practices was warranted. Surprisingly, basic hatchery release data was largely in hard copy form at the time of the collapse and, thus, largely inaccessible to scientists until June 2015 when my second chapter and accompanying electronic database were published in the San Francisco Estuary and Watershed Science online journal.

In chapter two I synthesize information from 139 state hatchery annual reports and pre-existing state and federal electronic records and present an analysis of temporal trends for the

total number of CVFRCS released and release timing, size, and location from 1946-2012. I find that over two billion juvenile CVFRCS salmon were released during the 67-year period and increased optimization of incubation and rearing hatchery 'habitats' over time permitted distinct shifts in management practices. Individuals have been trucked and planted off-site in the San Francisco Estuary (SFE) with increasing frequency since the early 1980s in a literal effort to circumvent poor rearing and survival conditions in the Sacramento and San Joaquin rivers and delta. Since 2000-2001 there has been a dramatic shift towards planting fish in very large quantities at similar times, sizes, and locations. Indeed, approximately half or more of the total number of fish currently released annually from all hatcheries combined are springtime releases of "advanced smolts" in the SFE. This rapidly growing life history type was not observed before the mid-1980s and advancements in medical, feed, filtration, circulation, heating, aeration, and other technologies help facilitate its production. Borrowing from economic theory, my results indicate that CVFRCS population resiliency may have been compromised in recent years by reduced diversity of release life history types (akin to "assets" in a financial portfolio). Continued restoration of inland habitats in conjunction with a re-diversification of release phenotypes would enhance system biocomplexity and theoretically reduce risks to the fishing industry by providing more stable supplies of adult fish for market and recreational purposes.

Intermittent estuaries (IEs) are a special estuarine type characterized by the temporary formation of a coastal sandbar at the river mouth which produces shifts between fully open (complete tidal exchange), partially open (muted tidal exchange), and closed (no tidal exchange) ecosystem states. These highly variable and complicated ecosystems are commonly encountered in small to medium sized watersheds in regions possessing wet/dry seasonality and energetic wave climates such as those found in South Africa, Australia, and North America's Pacific Coast. During the closed state, trapped salts combined with the loss of powerful tidal mixing forces produces density-stratification in the water column and increased hydraulic residence times. The enhanced benthic-pelagic coupling processes can deplete dissolved oxygen levels in the estuary and, depending on season, lagoon waters can either be much warmer or cooler than adjacent ocean waters. Water volume generally increases during the closed state, however, and there is a pressing need to better understand how fishes respond to water quality and habitat quantity tradeoffs, especially during drought periods when sandbar-closed conditions persist for longer durations.

Longitudinal studies that determine fish assemblage and population changes over time in response to drought-induced sandbar regime shifts are especially lacking in the published literature and assemblage studies in California IEs north of Point Conception, where a biogeographical split exists, are nearly nonexistent. In chapter three I present fisheries data from 27 months of continuous mid-month sampling at a large Central California IE (Pescadero Creek Estuary, San Mateo County, CA, USA) experiencing regular breach-induced fish kills caused by widespread anoxia. My sampling commenced three months before the official onset of drought and conditions become progressively drier over time. I find that the Pescadero IE fish assemblage exhibits marked seasonality and is characterized by low species diversity and high species dominance. After 19 months of drought the system shifted from one open or partially open for approximately 75% of the year to one closed for 75% of the time or more. Small-sized estuarine residents possessing rapid life cycles and protracted repeat spawning life histories appear to benefit most from prolonged sandbar closure. Not surprisingly, marine migrant species that utilize the IE for rearing, spawning, predator refuge, or a combination of these factors were most negatively impacted by marine disconnection. Standardized catches of *O. mykiss* remained elevated during summer months regardless of ecosystem condition. An acute breach-induced fish kill on 11-November, 2011 terminated the steelhead rearing period and produced high levels of species turnover. However, the assemblage rebounded to normal levels two to three months post-kill once water quality in the estuary was restored by repeated tidal exchanges. Overall, I observe strong regularity of seasonal icthyoassemblage shifts despite dramatic changes to the estuarine habitat over time. This observation is almost certainly due to specialized physiological adaptations of commonly encountered fishes to widely fluctuating environmental conditions.

Oncorhynchus mykiss was the most dominant species sampled overall and, while summertime standardized catch rates for *O. mykiss* remained elevated during all three years, the somatic growth rate analyses I present in chapter four suggests that juveniles likely experienced sublethal stress after one year of drought. Through the combined use of mark-recapture methods and a newly presented scale pattern microanalysis technique, I demonstrate that juvenile *O. mykiss* summertime body growth rates were fastest when the Pescadero IE was fully or partially open in 2011 and 2012 and slowest when it was completely closed in 2013. While growth of the 2013 cohort was probably limited in part by density-dependent effects, the lagoon nevertheless provided abundant aquatic habitat during a period when upstream habitats were heavily degraded. The novel scale method offers an appealing non-lethal alternative to other biochronological techniques and, thus, is especially suited for conservation-listed fishes. The method has most utility for detecting broad-scale differences in individual growth patterns and life history trajectories and may serve as a useful bioassessment procedure. My analysis reveals that the "twice smolting" phenotype is likely a popular and successful life history strategy for Pescadero steelhead as a result of rapid estuarine growth rates and migration opportunities during favorable environmental conditions.

In chapter five I utilize recent advances in sophisticated acoustic telemetry technology in order to elucidate fine-scale microhabitat use and movement patterns in the Pescadero IE for multiple steelhead from the 2013 rearing cohort. I observe that vertical and lateral habitat compression is correlated to degraded water quality both at depth and upstream in the estuary. The fish exhibited strict preferences for shallow (<1.5 m) and protected microhabitats where the sandy substrate/food production zone occurred within the lighted and oxygenated freshwater epilimnion. Fish use of the upper estuary declined linearly when mean daily water temperatures surpassed 18.0ºC and dissolved oxygen concentrations declined below 7.0 ppm. The concentration of individuals in restricted zones of suitable water quality likely contributes to the density-dependent growth effects observed in chapter four. Efforts that alleviate anoxia and hypoxia in lagoon waters should increase the total amount of aquatic habitat available to steelhead and other fishes in California IEs and increase fish production. Strategic addition of complex large woody debris structure near preferred microhabitats could improve habitat conditions immediately. Efforts that prevent breach-induced fish kills from occurring until early winter when double smolts have moved upstream would maintain life history diversity and, thus, enhance population resiliency.

In summary, by synthesizing and analyzing pre-existing and field-obtained long-term data sets, I am able to elucidate important aspects of the historical, community, population, and behavioral ecology of native California fishes with high economic and conservation value. The analyses presented in this dissertation can help inform management decisions during an anticipated period of rapid and extreme environmental change.

This dissertation is dedicated to Gordon Becker

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ACKNOWLEDGMENTS

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I am grateful for my academic advisor, Dr. Stephanie Carlson, for providing me with the opportunities to attend UC Berkeley's Dept. of Environmental Science, Policy, and Management (ESPM) doctoral program and perform important research. Dr. Carlson's guidance helped me navigate through the challenging academic process and this dissertation would not have been possible without her scientific expertise and financial support which helped me formulate and organize my research plan and accomplish my objectives.

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CURRICULUM VITAE

Eric R. Huber, Ph.D.
200 Manning St. #29A, Hudson, MA 01749
eric.r.huber@gmail.com
(508) 446-5433

EDUCATION

2010-2018	**University of California, Berkeley, Dept. of Environmental Science, Policy and Management (ESPM), Ph.D.** *Dissertation title:* The management and ecology of *Oncorhynchus* spp. and other estuarine-dependent native California fishes in artificially and naturally disconnected aquascapes. GPA: 3.8
2003-2006	**University of California, Davis, Graduate Group in Ecology, M.S.** *Thesis title:* Food limitations in nature intensify sublethal thermal stress experienced by juvenile steelhead trout (*Oncorhynchus mykiss*): current estimates and future predictions. GPA: 4.0
1994-1999	**University of California, Berkeley, B.A. (Integrative Biology), minor (Forestry)**. GPA: 3.4

PROFESSIONAL EXPERIENCE (RESEARCH – AQUATIC ECOLOGY)

2016	**Fish Biologist** for FISHBIO, Chico, CA
2010-2014	**Graduate Student Researcher** for Dr. Stephanie Carlson, UC Berkeley, Carlson Fish Ecology Laboratory (8 semesters total)
2012-2013	**Private Contractor** for Center for Ecosystem Management and Restoration (CEMAR), Oakland, CA
2007-2008	**Research Associate** for Dr. David Herbst, UC Santa Barbara, Aquatic Research and Bioassessment at the Sierra Nevada Aquatic Research Laboratory
2006	**Laboratory Technician** for Dr. Charles Goldman, UC Davis, Tahoe Research Group
2003-2006	**Graduate Student Researcher** for Dr. Michael Johnson, UC Davis, Aquatic Ecosystems Analysis Laboratory (8 quarters total)
2001-2003	**Post Undergraduate Researcher** for Dr. Michael Johnson, UC Davis, Aquatic Ecosystems Analysis Laboratory

PROFESSIONAL EXPERIENCE (MANAGEMENT)

2008-2010	**Fish Ecology Laboratory Manager** for Dr. Stephanie Carlson, UC Berkeley, ESPM

PROFESSIONAL EXPERIENCE (TEACHING AND MENTORING)

2017	**Graduate Student Instructor** for Ms. Sayaka Araki (EPS 117): Geomorphology (fall semester)
2017	**Graduate Student Instructor** for Drs. Alan Goldstein and Mary Firestone (ESPM 15): Introduction to Environmental Science (spring semester)
2015	**Graduate Student Instructor** for Dr. Federico Castillo (ESPM 102C): Resource Economics and Management (spring semester)

2013-2014	**Undergraduate Mentor** for Hannah Tokuno, UC Berkeley, ESPM *Topics:* fish scale pattern analysis, estuarine fish sampling
2012-2014	**Senior Thesis Mentor** for Zane Rankin, UC Berkeley, ESPM *Thesis title:* Evolutionary pressure of a fish kill: reconstructing steelhead trout (*Oncorhynchus mykiss*) life history using scale and otolith microanalysis
2013	**Undergraduate Mentor** for Thu-Quynh Phan, UC Berkeley, ESPM *Topics:* large database management, estuarine fish sampling
2011	**Graduate Student Instructor** for Dr. Stephanie Carlson (ESPM 115C): Fish Ecology (fall semester)
2009-2010	**Senior Thesis Mentor** for Kathryn Watson, UC Berkeley, ESPM *Thesis title:* The influence of absolute size and growth rate on outmigration timing in coho salmon (*Oncorhynchus kisutch*) smolts
2008-2009	**Undergraduate Mentor** for Matthew Young, UC Berkeley, ESPM *Topic:* large database management

PROFESSIONAL EXPERIENCE (RESEARCH – OTHER)

2000	**Research Assistant** for Drs. Jiquan Chen and Siyan Ma, Michigan Technological University, Landscape Ecology and Ecosystem Science Laboratory
1999-2000	**Research Assistant** for Dr. Julian Hadley, Harvard University, Harvard Forest
1999	**Laboratory Technician** for Franciscan Estate Winery, St. Helena, CA
1999	**Research Assistant** for Dr. Steven Beissinger, UC Berkeley, Dept. of ESPM
1998	**Research Assistant** for Dr. F.S. “Terry” Chapin III, University of Alaska Fairbanks, Institute of Arctic Biology and Dept. of Biology and Wildlife
1997-1998	**Work Study Laboratory Assistant** for Dr. Wilhelm Gruissem, UC Berkeley, Dept. of Plant and Microbial Biology

AWARDS AND FELLOWSHIPS

2016	**Best Blogger Award**, FISHBIO, Chico, CA
2014	**Graduate Student Continuing Fellowship**, Dept. of ESPM, UC Berkeley
2014	**Graduate Student Summer Grant**, Dept. of ESPM, UC Berkeley
2013-2014	**Graduate Student Travel Grant**, Dept. of ESPM, UC Berkeley
2010-2011	**Graduate Student Travel Grant**, Dept. of ESPM, UC Berkeley
2005	**Block Grant Award**, Graduate Group in Ecology, UC Davis
2003-2004	**Graduate Student Fellowship**, University of California Toxic Substances Research and Training Program
1998	**Dean’s Honor List for College of Letters and Science**, UC Berkeley
1994-1998	**Federal Pell Grant**, U.S. Department of Education

INVITED SEMINARS AND LECTURES

2016	**Aquatic biota and habitat in and around Bidwell Park.** Guest lecture for Osher Lifelong Learning Institute at CSU, Chico, CA, April 2016.
2015	**Are fish hatcheries a socio-ecological benefit or cost? Case study: Central Valley California fall Chinook (king) salmon hatcheries**. Guest lecture for Resource Economics and Management (ESPM 102C), Berkeley, CA, February 2015.

2014	**Pescadero steelhead trout ecology**. Invited seminar for Pescadero Estuary Confab, Long Marine Laboratory, Santa Cruz, CA, August 2014.
2014	**Pescadero steelhead trout ecology**. Invited seminar for Pescadero Science Panel Workshop, Berkeley, CA, March 2014.
2013	**Pescadero steelhead trout ecology**. Invited seminar for Pescadero Science Panel webinar, Berkeley, CA, December 2013.
2012	**Intermittent estuary fish ecology: Pescadero Marsh case study**. Guest lecture for Fish Ecology (ESPM 115C), Berkeley, CA, October 2012.

PUBLICATIONS (PEER-REVIEWED)

2015	Huber, E.R. and Carlson, S.M. 2015. **Temporal trends in hatchery releases of fall-run Chinook salmon in California's Central Valley**. San Francisco Estuary and Watershed Science 13(2): article 3.
2015	Fey, S.B., Siepielski, A.M., Nusslé, S., Cervantes-Yoshida, K., Hwan, J.L., Huber, E.R., Fey, M.J., Catenazzi, A., and Carlson, S.M. 2015. **Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events**. Proceedings of the National Academy of Sciences USA 112: 1083-1088.

PUBLICATIONS (OTHER)

2015	Largier, J.L, Aiello, I.W. Jacobs, D., Lacy, J., Pallud, C., Stacey, M.T., Carlson, S.M., Huber, E., and Bowles, C.M. 2015. **Report of Pescadero Lagoon Science Panel**. 48 pages.
2011	Huber, E., Post, C., and Kayed, S. 2011. **Relationship between juvenile steelhead survival and winter habitat availability**. Water Resources Collections and Archives, University of California.
2006	Huber, E.R. 2006. **Food limitations in nature intensify sublethal thermal stress experienced by juvenile steelhead trout (*Oncorhynchus mykiss*): current estimates and future predictions**. M.S. Thesis, University of California, Davis, Davis, CA.
2002	Johnson, M. L., Pasternack, G., Florsheim, J., Werner, I., Smith, T.B., Bowen, L., Turner, M., Viers, J., Steinmetz, J., Constantine, J., Huber, E.R., and Jordal, O. **The impact of abiotic and biotic stressors on salmonids in the Navarro River watershed**, Vols I-III. Report CTSW-RT-02-040 to the Division of Environmental Analysis, California Department of Transportation, Interagency Agreement Nos 43A0014 and 43A0073.

CONFERENCE TALKS

2015	**California drought causes apparent loss of steelhead estuarine nursery habitat**. American Fisheries Society (California-Nevada Chapter) annual meeting, Santa Cruz, CA.
2013	**Sink or swim: steelhead performance in a coastal marsh-bar built estuary wetland complex**. American Fisheries Society (California-Nevada Chapter) annual meeting, Davis, CA.
2012	**Fish assemblage shifts track ecosystem states in a Central California intermittent estuary**. Ecological Society of America annual meeting, Portland, OR.

2012	**Sink or swim: steelhead performance in a coastal marsh-bar built estuary wetland complex**. Annual Salmonid Restoration Conference, Davis, CA.
2011	**Temporal trends in hatchery releases of California Central Valley fall run Chinook salmon**. American Fisheries Society annual meeting, Seattle, WA.
2011	**Relationship between juvenile steelhead survival and winter habitat availability**. UC Berkeley California Hydrology Symposium, Berkeley, CA.
2009	**Chinook salmon in San Francisco Bay streams: A consequence of management practices?** Ecological Society of America annual meeting, Albuquerque, NM.
2004	**Sr:Ca ratios in juvenile *Oncorhynchus mykiss* otoliths provide an understanding about levels of anadromous broodstock in a population**. American Fisheries Society (California-Nevada Chapter) annual meeting, Sacramento, CA.

CONFERENCE POSTERS

2005	**Using otolith microanalysis to understand the timing and extent of Chinook salmon and steelhead exposures to contaminants in California's Bay Delta**. University of California Toxic Substances Research & Teaching Program (UCTSR&TP) 18th Annual Research Symposium, San Diego, CA.
2004	**Otolith microchemistry provides an understanding of Pacific salmon (*Oncorhynchus spp.*) migration patterns**. University of California Toxic Substances Research & Teaching Program (UCTSR&TP) 17th Annual Research Symposium, San Diego, CA.

CHAPTER 1

INTRODUCTION AND MOTIVATION

Introduction and motivation

Lotic ecosystems are highly integrated by nature and disruptions to fluvial processes can induce strong environmental and biological responses and necessitate extensive resource management interventions. For example, construction of large impassable dams may require the creation of salmon hatcheries to mitigate for lost upstream spawning and rearing habitats. In California's Great Central Valley, five Chinook salmon (*Oncorhynchus tshawytscha*) hatcheries were constructed from the 1940s to 1970s as components of monumental federal and state water projects. Over the years, hatchery-reared Central Valley fall run Chinook salmon (CVFRCS) have supplanted natural-origin fish as the dominant race supporting the California and Southern Oregon commercial salmon fishery (Kormos et al. 2012, Palmer-Zwahlen and Kormos 2013; 2015). From 2006-2009 the CVFRCS population complex experienced a large-scale collapse that resulted in complete commercial and recreational fishery closures in 2008 and 2009 for the first time in their approximate 90 year histories (McEvoy 1990, Lindley et al. 2009). Approximately 5,000 to 23,000 jobs and a half to two billion dollars were lost to the state's economy as a result of the collapse (Schwarzenegger 2008; 2009) and the emergency fishery closures required the provision of 170 million dollars in federal disaster aid from 2008-2010 (Upton 2013). A panel of experts determined that elevated water temperatures and low food availability when smolts first entered the nearshore zone in 2005 caused the population collapse (Lindley et al. 2009). However, the poor springtime ocean conditions were not unprecedented which suggests that additional factors may have also contributed to the collapse.

Given importance of artificial propagation for the sustainability to the California's commercial and recreational salmon fisheries, historical information about total number of CVFRCS released and release timing, size, and location was surprisingly inaccessible to scientists at the time of the fishery closures. In chapter two I synthesize information from 139 state hatchery annual reports and pre-existing state and federal electronic databases and analyze shifting temporal trends in hatchery release practices from 1946-2012 (Huber and Carlson 2015). I find that over two billion juvenile salmon were released during the 67-year period and that individuals have been planted off-site in the San Francisco Estuary (SFE) with increasing frequency since the early 1980s in a literal effort to circumvent poor survival conditions in freshwater habitats. Since the turn of the 21st century there has been a dramatic shift towards releasing fish at similar sizes and times in either the upper Sacramento River near the Coleman National Fish Hatchery or directly into the SFE near the Carquinez Straight. A life history type not observed earlier in the time series now comprises nearly all of the SFE releases: springtime releases of large ocean-ready "advanced smolts". Similar to a diversified financial investment portfolio, increased phenotypic diversity of released fish would enhance biocomplexity and theoretically permit fisheries to remain resilient and provide more stable adult returns to consumers and hatcheries.

Intermittent estuaries (IEs) are a special estuarine type commonly encountered in small to medium sized watersheds in regions with energetic ocean wave climates and seasonal aridity such as that existing along South Africa's eastern seaboard where they are called "temporarily open/closed estuaries (TOCE)", southeast Australia where they are known as "wet and dry tropical/subtropical estuaries" or "intermittently closed and open lake lagoons (ICOLL)", India and Sri Lanka where they are called "seasonally open tidal inlets/coastal lagoons", and the Mediterranean climate region of North America's Pacific coast where they are also called "bar-built estuaries" (Perissinotto et al. 2010, Heady et al. 2014). Regardless of the name given, these highly variable and complicated ecosystems alternate between open (full tidal exchange), partially open (muted tidal exchange), and closed (no tidal exchange) estuarine states depending on the presence or absence of a coastal sandbar at the river mouth and the sandbar's size in relation to fluctuations in ocean water surface elevations.

Of California's 350 estuaries, 86% are considered "intermittent" (Heady et al. 2014). Despite their abundance and ubiquity throughout the state, California IE fish ecology remains largely under-studied. Smith (1990) initially demonstrated the importance of coastal California lagoons for juvenile steelhead (*O. mykiss*) and other native fishes. Since then, nearly all peer-reviewed investigations of California IE fish ecology concerns juvenile steelhead use of a relatively small Central Coast IE during the closed estuarine state (Scott Creek Estuary, Santa Cruz County, CA, USA). While these illuminating studies have elucidated critical aspects of steelhead lagoon ecology, more information from disparate systems is needed, especially for distressed systems during periods of environmental extremes and shifting ecosystem states. The current state of knowledge in California contrasts that for South Africa where TOCEs comprise 71% of the country's 258 functional estuaries and published fisheries science information exists for over one hundred of them (Perissinotto et al. 2010).

The NOAA Scott Creek steelhead studies demonstrate that extended rearing and rapid body growth rates in coastal lagoons enhances subsequent marine survival (Bond et al. 2008, Hayes et al. 2008) and promotes life history diversity (Hayes et al. 2011) which, together, helps promote population sustainability. However, predation pressure in these "high-risk-high-reward" ecosystems is considered high (Satterthwaite et al. 2012, Osterback et al. 2013) and both chronic and acute degradation of lagoon water quality may impair nursery function or cause it to cease altogether (Smith 1990, Jankovitz 2015, Largier et al. 2015). Experts are concerned that climate change will cause lagoon waters to become too stagnant, warm, and oxygen-poor for rearing juvenile salmonids and recommend restoration of essential estuarine habitats in order to prevent the extermination of coastal California populations (Moyle et al. 2017).

In chapters three, four, and five I provide community, population, and behavioral ecology information for fishes residing in a large Central California Coast IE (Pescadero Creek Estuary, San Mateo County, CA, USA). The California Coastal Commission considers Pescadero to be one of the two "most critical estuarine and wetland resources in the Central Coast region". The beach-estuary-marsh complex provides rare and critical habitat for numerous conservation-listed fishes, amphibians, reptiles, and birds and serves as a critical stop-over grounds for birds migrating along the Pacific Flyway. Since completion of a large scale restoration project in the mid-1990s, recurring breach-induced animal mass mortality events have occurred in Pescadero and the signs of ecosystem distress are a particular concern to conservation managers and other stakeholders (Largier et al. 2015).

In chapter three, I present an analysis of 27 months of continuous mid-month fish sampling data and relate population and community metrics to water quality parameters and other relevant habitat features. My fish sampling commenced in July 2011, three months before the official onset of a severe five year drought and the research timing provides a rare and important opportunity to better understand and predict system responses to extreme climate. Overall, I find that the Pescadero IE icthyoassemblage was composed of relatively few species capable of tolerating widely fluctuating physico-chemical conditions. The specialized physiological adaptations of commonly encountered fishes confers a high degree of assemblage resiliency to dramatic environmental changes. Assemblage structure was highly seasonal and heavily dominated by *O. mykiss*, especially during summer when standardized catches peaked. Marine migrant topsmelt (*Atherinops affinis)* were the second most dominant species, especially during winter when *O. mykiss* were largely nonexistent and strong outflows and storm swells promoted marine connectivity and movement opportunities between habitats. Threespine stickleback (*Gasterosteus aculeatus*) and endemic and endangered tidewater goby (*Eucyclogobius newberryi*) appear to benefit most from prolonged drought-induced sandbar closure periods. Both species are short-lived estuarine residents tolerant of heavily degraded water quality and capable of repeat and protracted spawning. These life history attributes likely enabled rapid population expansion during environmentally perturbed periods. Not surprisingly, marine-origin species like starry flounder (*Platichthys stellatus*) and shiner surfperch (*Cymatogaster aggregata*) were most negatively impacted by extended sandbar presence. Standardized catches of steelhead (*O. mykiss*) during summer remained elevated during both open and closed estuarine states as a result of their remarkable phenotypic plasticity and strong osmoregulatory capacities in particular. A breach-induced fish kill caused by widespread anoxia on 11-November, 2011 terminated the steelhead rearing period and produced high levels of species turnover. However, the assemblage structure approached levels observed during non-kill years after two to three months post-kill when favorable estuarine water quality was restored by repeated tidal flushing.

In chapter four I investigate the growth performance of juvenile steelhead during all three estuarine states using a combination of mark-recapture and scale pattern microanalysis methods. The newly presented scale technique builds on recent laboratory research (Beakes et al. 2014) and permits assignment of calendar dates to individual scale circuli based on sample date, circulus spacing, and water temperature. I find that juvenile steelhead grew two to three times faster during summers 2011 and 2012 when the IE was open or partially open than in summer 2013 when it was completely closed for two to five months. These observations indicate that, while standardized catches of *O. mykiss* remained elevated, nursery function impairment was likely caused by ongoing drought. The novel scale method provides an appealing non-lethal opportunity to elucidate growth trends for conservation-listed *O. mykiss* and can be especially useful for rapid bioassessment purposes and reconstruction of individual life histories.

In chapter five, I determine fine-scale juvenile *O. mykiss* habitat use and movement patterns for 15 weeks during the 2013 slow growth rearing period. I observe that steelhead utilize a small portion of the overall wetted habitat, especially at night when fish appear less territorial and adopt more schooling behaviors. The habitat compression is almost certainly caused by degraded water quality at depth and upstream in the estuary and the crowding probably contributes to the density-dependent growth effects described in chapter four. Juvenile steelhead express strong preference for shallow, sandy, and protected microhabitats where the benthic substrate occurs within the buoyant, lighted, and oxygenated freshwater epilimnion. Ecosystem management actions that reduce hypoxia and anoxia in the lagoon should increase the total amount of functional lagoon habitat available to steelhead and other fishes. Habitat quality in the cover-poor estuary can be improved immediately by the strategic addition of complex large woody debris structure in close proximity to preferred microhabitats. Efforts that prevent fish kills from occurring until late fall or early winter after double smolts (Hayes et al. 2011) have moved upstream will maintain biocomplexity and, thus, minimize the negative consequences of acute ecosystem function loss on the Pescadero *O. mykiss* population.

In summary, while the nature of watershed disconnection and the degree of human intervention in both my study systems varies, commonalities nonetheless are observed. Both hydropower dams and coastal sandbars radically alter *Oncorhynchus* spp. rearing conditions and exert strong controls on patterns of life history expression, estuarine occupancy, and marine entry. Ecological shock is observed in both systems in the forms of a collapsed fishery or recurring animal mass mortality events. Resource management solutions in both systems is hindered by a lack of access to basic scientific information and the rigorous analyses of abundant empirical data presented in this dissertation can help managers make more informed decisions. Given the pace of habitat destruction and the expected impacts of climate change, the need for more informed environmental stewardship is urgent.

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CHAPTER 2

TEMPORAL TRENDS IN HATCHERY RELEASES OF FALL-RUN CHINOOK SALMON IN CALIFORNIA'S CENTRAL VALLEY

Temporal trends in hatchery releases of fall-run Chinook salmon in California's Central Valley

Eric R. Huber
Department of Environmental Science, Policy, and Management, University of California, Berkeley 94720

Stephanie M. Carlson
Department of Environmental Science, Policy, and Management, University of California, Berkeley 94720

Abstract: The Central Valley fall-run Chinook salmon (*Oncorhynchus tshawytscha*) is the dominant population complex supporting the California and Southern Oregon commercial salmon fishery. The stock is largely dominated by hatchery production and has shown high variability in adult returns, suggesting that hatchery practices are critical to the long-term sustainability of the fishery. We compiled information from numerous sources to synthesize trends in the number, location, size, and timing of fall-run Chinook salmon released from the five Central Valley hatcheries between 1946 and 2012. Approximately 2 billion fish were released during this period, nearly half of which were released from the single federally-operated hatchery. Juveniles have been planted off-site in the estuary with increasing frequency since the early 1980s, particularly by state-operated hatcheries. Approximately 78% of all releases occurred between January and June, including ~25% in April and ~20% in May. Release timing and size trends differed among hatcheries and were correlated. For example, the Coleman and Nimbus hatcheries tended to release small fish (<5 g, on average) early in the year, while the Feather, Mokelumne, and Merced hatcheries tended to release larger fish (>10 g, on average) later in the year. Moreover, sizes-at-release (by month) have increased since the 1980s, leading to the emergence of a new life history type that now comprises nearly all of the estuary releases: springtime releases of large ocean-ready "advanced smolts". We collapsed release timing and size data into a single index of life history diversity and our results indicate a reduction in juvenile life history diversity, with decreased variability in release number, timing, and size through time. Together, these results indicate a reduction in the diversity of life history types represented in the fall-run hatchery releases, which may be a factor contributing to the decreased stability of the Central Valley fall-run stock complex.

Keywords: *Oncorhynchus tshawytscha*, San Francisco Estuary, Sacramento-San Joaquin Delta, artificial propagation, stocking, growth, life history, phenotypic diversity, portfolio effect

Introduction

Habitat loss and large-scale harvest of valuable animals and plants often requires extensive supplementation of artificially-propagated individuals in order to sustain the services they provide to humans (Laikre et al. 2010). An example is the post-World War II release of hundreds of billions of hatchery-reared Pacific salmonids across much of their Pacific Rim distribution (Mahnken et al. 1998). In the face of major habitat destruction and population declines (Lichatowich 2001), constraints on habitat restoration efforts (Bond and Lake 2003), and human nutritional preferences (FAO 2014), salmonid hatcheries satisfy important societal demands (NRC 1996) while providing a potentially valuable conservation tool (Naish et al. 2008).

Despite the benefits of fish hatcheries, the long term sustainability of such technological fixes has been questioned (e.g., Fraser 2008). Reasons include overfishing of wild fish in mixed stock fisheries (Nehlsen et al. 1991), negative behavioral and ecological interactions between hatchery and wild fish (Rand et al. 2012), and/or detrimental genetic effects (Reisenbichler and Rubin 1999; Araki et al. 2007). Indeed, the debate over the value of fish hatcheries for Pacific salmon is contentious (Ruckelshaus et al. 2002) with arguments in both their defense (e.g., Brannon et al. 2004) and opposition (e.g., Myers et al. 2004).

California's Central Valley Chinook salmon have received extensive attention because of their economic, environmental, and cultural importance (see reviews by Yoshiyama et al. 1998 and Williams 2006). The region represents the southern-most extent of the species' range, which spans approximately 40 degrees latitude and 100 degrees longitude across a diverse array of habitats including high and low elevation streams, floodplains, marshes, estuaries, bays, nearshore, and offshore oceanic habitats throughout the Northeast Pacific Ocean region (Augerot et al. 2005). The stock complex is characterized by an unprecedented degree of life history diversity: it is the only Chinook salmon complex containing four distinct runs named for the time of year when they return to freshwater as adults: winter, fall, late fall, and spring (reviewed by Williams 2006). NMFS has classified these four runs into three Evolutionary Significant Units (ESUs) for purposes of management based on genetic and life history similarities. Abundances (Fisher 1994; Yoshiyama et al. 1998) and life history diversity (Gustafson et al. 2007) of Central Valley Chinook salmon have been greatly reduced since Euro-American settlement due to interacting anthropogenic (Yoshiyama et al. 1998) and natural (Lindley et al. 2009) factors. The winter and spring run ESUs are considered endangered and threatened under the federal Endangered Species Act, respectively, and the fall/late fall run ESU is classified as a federal and state Species of Concern (Myers et al. 1998).

Central Valley fall-run Chinook salmon (CVFRCS) breed and rear in low elevation mainstem rivers (Moyle 2002). Adults migrate upstream from June-December and spawn in gravel-bed streams from late September-December (Yoshiyama et al. 1998). Juveniles emerge from the gravel in the spring and spend a limited amount of time in their natal rivers before moving to downriver nursery habitats before moving out to the ocean (Moyle 2002; Williams 2012). While they are regarded as ocean-type Chinook, Williams (2012) makes the distinction between fry migrants that travel directly to brackish water in the bays to rear and fry migrants that migrate to the Delta and rear there for an extended period (weeks to months) before continuing downriver to the bays, emphasizing that together these are the most common juvenile life history patterns among CVFRCS. Emigration of fall-run juveniles from natal sites to downriver nursery grounds extends from December to July with maximum activity occurring from February to June.

In addition to natural reproduction in Central Valley rivers, many fall-run Chinook now breed in one of five production hatcheries in California's Central Valley. Like other salmon hatcheries, these hatcheries have several shared goals and practices, including collecting adult fish, selecting broodstock, spawning fish, rearing eggs through the juvenile life stage, and releasing these fish. The larger Central Valley fall-run population complex receives significant hatchery contributions (Johnson et al. 2012; Kormos et al. 2012; Palmer-Zwahlen et al. 2013), and fishery catches are largely supported by hatchery production (Barnett-Johnson et al. 2007).

The CVFRCS is the dominant stock supporting the California and Southern Oregon coastal fishery (California HSRG 2012).

Recent research has revealed that the CVFRCS stock complex is genetically homogenized (Williamson and May 2005), likely due, in part, to hatchery release practices (Garza et al. 2008). Specifically, hatchery fish released off-site are straying into basins with and without hatcheries, at rates approximately eight times greater (Sholes and Hallock 1979; Dettman et al. 1987; Cramer 1991; JHRC 2001; Lasko 2014; Kormos et al. 2012; Palmer-Zwahlen et al. 2013) than background rates in this system of 5-10% for hatchery fish released on-site (Cramer 1991). Site infidelity is a concern for both hatchery managers because of concerns about meeting broodstock quotas (JHRC 2001; California HSRG 2012) and for conservationists because it could be eroding local adaptations (Lindley et al. 2009) and masking population declines for wild fish (Johnson et al. 2012). Moreover, the constituent populations within the fall-run complex exhibit synchronous adult dynamics, which results in little buffering capacity and only a weak 'portfolio effect' (Carlson and Satterthwaite 2011). Similar to a portfolio of financial stocks, when individual fish populations exhibit diverse life histories and vary somewhat independently in their dynamics, the larger complex of populations is buffered against environmental variation (Hilborn et al. 2003, Schindler et al. 2010). While a weak portfolio effect remains in the CVFRCS stock complex, it has degraded through time (Carlson and Sattterthwaite 2011), probably due in part to habitat loss and degradation as well as the influence of hatcheries.

In 2007-2008, the CVFRCS stock complex suffered a large-scale collapse that resulted in emergency commercial and recreational fishery closures (Lindley et al. 2009) and the provision of $170 million in federal disaster relief aid from 2008-2010 (Upton 2013) in order to mitigate the societal harm caused by this ecological shock. California state government records indicate that 5,000 to 23,000 jobs and 0.5 to 2 billion dollars to the state's economy in 2008 and 2009 were lost as a result of the fishery collapse (Schwarzenegger 2008; 2009). Following the fishery closures in 2008 and 2009, the U.S. Congress approved funds to form the California Hatchery Scientific Review Group (California HSRG) in 2010 to synthesize information about hatchery operations and objectives following the model established by groups operating in Puget Sound and coastal Washington (HSRG 2004) and the Columbia River (HSRG 2009). The recently released review offered several key recommendations for improved management of California's anadromous fish hatcheries, which included the need to make full use of pre-existing data sets for more scientifically-informed management decisions (California HSRG 2012).

In order to improve transparency and contribute to more informed science and management efforts, we undertook a synthesis of 67 years of hatchery production and release data in California's Central Valley. Our first objective was to illuminate the temporal trends in fall Chinook releases, including a focus on (1) number released, (2) release location, (3) release size, and (4) release timing. A second objective was to explore patterns in life history diversity of hatchery releases through time. By highlighting patterns and improving data access, our hope is that this effort will inform future research and management decisions.

Materials and methods

Study site - CVFRCS all originate in the heavily modified foothill streams and valley floor rivers of the Sacramento and San Joaquin watersheds. To mitigate for lost breeding and rearing habitat due to dam construction, mitigation hatcheries were constructed. There are five main hatcheries propagating fall-run Chinook salmon, including the Coleman National Fish Hatchery on Battle Creek, Nimbus Fish Hatchery on the American River, Feather River Hatchery, Mokelumne River Fish Hatchery, and the Merced River Fish Facility. The Coleman, Nimbus, and Feather hatcheries are in the northern Sacramento watershed whereas the Mokelumne and Merced hatcheries are in the southern San Joaquin watershed. The Coleman Hatchery is operated by the US Fish and Wildlife Service (USFWS) while the Nimbus, Feather, Mokelumne, and Merced hatcheries are operated by the California Department of Fish and Wildlife (CDFW; formerly named the California Department of Fish and Game, CDFG).

Release data - We compiled information from 139 annual reports provided by the four state-operated hatcheries: Feather (34 reports, 1968-2001), Nimbus (47 reports, 1956-2002), Mokelumne (37 reports, 1964-2001), and Merced (21 reports, 1971-2001) hatcheries. From 2002-2012 for the Feather, Mokelumne, and Merced hatcheries and 2003-2012 for the Nimbus Hatchery, an electronic database compiled by CDFW and provided by David Krueger (dave.krueger@wildlife.ca.gov) was used instead of annual reports. At the time of writing, state hatchery data were considered in "draft" or non-finalized form from 2012 back to 1992 for the Feather, 1993 for the Nimbus and Mokelumne, and 1995 for the Merced hatchery. According to one hatchery manager, any changes between the "draft" and "final" report stage are likely to be very minor (e.g., on the order of 10s of fish, Anna Kastner, personal communication). Zero releases occurred in 1975 (disease outbreak) and 1980 (low female escapement) for the Merced Hatchery. Additionally, no release data were available for the Merced Hatchery from 1991-1994 due to hatchery closure and renovation. All data from 1946-2012 for the Coleman Hatchery were obtained from an electronic database provided by Kevin Niemela (kevin_niemela@fws.gov). We compiled release data from all five hatcheries into a single aggregate database (Appendix I includes a description of the metadata; Appendix II includes the complete database can be found at *[include link here]*).

Regardless of the source of data, the basic reporting unit was a cohort of fish released together at a given location over a specific period of time (hereafter referred to as a "release group"). Typically, each release group was associated with information about brood year, total number of fish released, location of release, mean weight-at-release, and release time of year. Annual state hatchery reports spanned two calendar years from July 1 in year t to June 30 in year t + 1. When fish of a given cohort were released before and after the June 30 cutoff for reporting, data were pooled from multiple annual reports. For an extremely limited number of cases, the release time range spanned greater than 365 days. When this occurred, the release group was assigned to the year when the majority of releases occurred. In a small number of cases involving volitional releases from hatcheries, the number of fish released per release group was not reported. Instead, estimates of total egg production and egg-to-fry survival rates were reported. In these instances, estimates of total fish released per release group were made by multiplying total egg production by egg-to-fry survival rate estimates. This phenomenon only occurred during the very early stages of hatchery operation and represents a very small proportion (0.37%) of the total releases of fall-run Chinook from the Central Valley hatcheries.

The release locations were reported at different levels of detail using non-standardized nomenclature. Consequently, only a coarse-level release location analysis is provided in this investigation: those fish released in the San Francisco Estuary (defined here as releases downstream of Chipps Island: latitude 38.055198; longitude -121.911904) and those released upstream of this point. Inland releases made upstream of impassable dams were not included in the analysis, nor were those used for laboratory work (0.31% of total releases).

Fish weights were reported in most cases (90% of total releases) and expressed as a single mean fish mass for the release group. When a range of weights were reported, the range midpoint was calculated and applied to the release group. In order to improve the relevance of size data and facilitate comparisons with other studies, weights were converted to fork lengths (FLs) by the following relationship generated by data downloaded from the Regional Mark Processing Center (RMPC, http://www.rmpc.org/) for hatchery CVFRCS, including data from 1,578 release groups with lengths and weights reported from 1981-2013 (79 mm mean, 36-217 mm range, R^2=0.95):

$$\ln(\text{FL, mm}) = 0.313 \bullet \ln(\text{WEIGHT, g}) + 3.840$$

The start month and end month for a given release group was usually the same but occasionally a range of months were reported (7.8% of total releases) and in other cases only release year was reported (9.5% of total releases). Because of these irregularities, release timing data were restricted to cases when the release start and end months were the same (82.7% of total releases). We focused on release month because information about release day-of-month was limited through much of the early and middle parts of the dataset.

To calculate the dispersion in release size and timing, we calculated the yearly population standard deviation (SD) for releases from each hatchery and all hatcheries combined as:

$$\text{Population SD} = \text{sqrt}(\Sigma(p_i \bullet (X_i - X_{avg})^2)$$

where p_i equals the number of fish in release group *i* divided by the total number of fish released per year with size or month-of-release reported, X_i equals the size or month-of-release of fish in release group *i,* and X_{avg} equals the average size or average month-of-release of fish per year (calculated as the weighted mean across all release groups).

To examine temporal trends in release variability, we then examined the coefficient of variation (CV) for release number, size, and timing. For release number, we calculated decadal CVs by dividing 10-year standard deviations by corresponding means for each hatchery and all hatcheries combined. The CV for release size and timing is the population SD divided by the average size or average month-of-release per year for all hatcheries combined.

Life history designations and life history diversity - We classified the life histories of released fish according to size-classes determined from information provided by the state hatchery annual reports and by Williams (2012). “Fry” were defined as fish with estimated fork lengths <55 mm; “fingerlings (or parr)”: ≥55 to <70 mm; “smolts”: ≥70 to <87.5 mm; “advanced (or ocean-ready) smolts”: ≥87.5 to <140 mm; and “yearlings”: ≥140 mm. The 87.5 mm cutoff for the smolts and advanced smolts was based on two factors: (1) it approximates the average size of ocean entry for CVFRCS (Williams 2012, originally derived from Lindley et al. 2009), and (2) it represented the estimated fork length attributed to a 7.56 $\text{g}\cdot\text{fish}^{-1}$ (60 $\text{fish}\cdot\text{lb}^{-1}$), which was emphasized in the annual reports as a distinct release type.

Timing and size data were collapsed into a single life history diversity index developed for juvenile Chinook salmon (“Early Life History Index (ELHD)”, Johnson et al. 2014) that combines elements of fish abundance, trait richness (i.e., number of traits), and trait evenness (i.e., relative frequency of each trait). Johnson et al. 2014 developed the index to characterize the diversity of life histories observed among juvenile Chinook originating from the Columbia

River system, with a goal of developing a quantitative index that could be used to assess trends in life history diversity through time (e.g., before and after a restoration effort) or to compare life history diversity through space. The index incorporates both morphological (e.g., size class) and behavioral (e.g., release month) attributes and offers a quantitative and standardized method to evaluate these often-measured and ecologically-relevant juvenile Chinook salmon life history traits across broad spatial and temporal scales. Johnson et al. (2014) describe three different calculations for the ELHD index that place different emphases on time-size trait combinations. We used the first-order diversity estimator index (^{1}ELHD) recommended by the authors because of its insensitivity to rare or abundant trait combinations. We presented the normalized index ($^1\mathrm{ELHD}_{\mathrm{norm}}$) because it converts the index to an easily comprehendible range (0-1), with values representing the proportion of total possible release time-size class combinations:

$$^1\mathrm{ELHD}_{\mathrm{norm}} = (\exp(-\Sigma p_i \bullet \ln(p_i)))/T$$

where p_i is the proportion of the total abundance for the i^{th} month-size class combination and T is the total number of month-size class combinations. Since there are 12 months in a year and 5 size classes investigated in this study, the total number of possible time-size combinations was 60. Since not all size classes are expected to be released each month (e.g., a 55 mm or smaller fry is not expected to migrate downstream in August), a more realistic value of $T = 17$ was chosen for this study (see Results), which reflects actual month-size combinations observed among the hatchery releases.

All statistical analyses were performed with JMP® software version 8.0 (SAS Institute Inc., Cary, NC, USA) and effects were considered significant at $\alpha = 0.05$.

Results

Number released - Using the data compiled from the CDFW annual reports and CDFW and USFWS databases, we calculated the number of fall-run Chinook produced in Central Valley hatcheries across years 1946-2012. Just over two billion hatchery-reared fall-run Chinook salmon were released during this period, representing 253 hatchery-year combinations (Figure 1F). Approximately half (52.4%) of these fish ($n = 1.05 \bullet 10^6$) were released from the federal hatchery at Battle Creek (Coleman). Amongst the state hatcheries, the Nimbus Hatchery was numerically dominant in terms of total releases ($n = 455 \bullet 10^6$, representing 22.6% of total releases), followed by the Feather ($n = 352 \bullet 10^6$, 17.5%), Mokelumne ($n = 127 \bullet 10^6$, 6.3%), and Merced ($n = 22 \bullet 10^6$, 1.1%) hatcheries (Table 1).

The release number trends for the individual hatcheries showed different patterns (Figures 1A-E, Table 1). Coleman Hatchery releases (mean = $15.8 \bullet 10^6$; median = $13.4 \bullet 10^6$; CV = 0.53; Figure 1A) were highly variable from inception through the 1970s and have stabilized since then. Releases from the Feather Hatchery were relatively consistent through time (mean = $7.9 \bullet 10^6$; median = $8.2 \bullet 10^6$; CV = 0.39; Figure 1C). Mokelumne releases increased over time and were highly variable (mean = $2.7 \bullet 10^6$; median = $2.2 \bullet 10^6$; CV = 0.91; Figure 1D) due, in part, to facility remodeling in 2002. Releases from the Nimbus and Merced hatcheries were somewhat bimodal, with peaks occurring in the mid-1960s and early 1980s for the Nimbus Hatchery (mean = $8.1 \bullet 10^6$; median = $5.8 \bullet 10^6$; CV = 0.67; Figure 1B) and the mid-1990s and mid-2000s for the Merced Hatchery (mean = $0.6 \bullet 10^6$; median = $0.4 \bullet 10^6$; CV = 0.83; Figure 1E).

Release location - Approximately 20.8% of all releases in the time series occurred downstream of Chipps Island in the San Francisco Estuary ($n=418 \bullet 10^6$, Figure 1F), with breakdowns by hatchery presented in Table 1. The first planting in the estuary happened in 1964 but large scale planting in the estuary did not begin until 1981 when 16.9% of all releases were deposited in the estuary (previous yearly high was 3.2%). From 1981-2012; an average of $13.0 \bullet 10^6$fish were released in the estuary per year ($\min = 6.4 \bullet 10^6$; $\max=20.4 \bullet 10^6$; median=$13.3 \bullet 10^6$; CV=0.25; Figure 1F). The Feather Hatchery released the most fish outside the freshwater environment ($n = 217.7 \bullet 10^6$, Figure 1C), followed by Nimbus ($n = 125.5 \bullet 10^6$, Figure 1B), Mokelumne ($n = 55.7 \bullet 10^6$, Figure 1D), Coleman ($n = 17.7 \bullet 10^6$, Figure 1A), and Merced ($n = 1.0 \bullet 10^6$, Figure 1E) hatcheries.

Size-at-release - The average release size of all hatcheries combined was 5.9 g, equivalent to ~81 mm fork length (see Methods, Figure 2F). Release sizes were bimodal, with the Coleman (Figure 2A) and Nimbus (Figure 2B) hatcheries mainly releasing small fish (mean = 3.9 g or 71 mm and 4.9 g or 77 mm, respectively, Table 1). The Feather (mean = 10.7 g or 98 mm, Figure 2C), Mokelumne (mean = 13.4 g or 105 mm, Figure 2D), and Merced (mean = 12.7 g or 103 mm, Figure 2E) hatcheries released larger fish overall (Table 1). On average, Coleman (Figure 2A), Nimbus (Figure 2B), and Feather (Figure 2C) hatcheries released similarly-sized fish over time, while the Mokelumne (Figure 2D) and Merced (Figure 2E) hatcheries released smaller fish over time.

Release timing - The month with the greatest number of total released fish was April (24.7% of total releases), followed by May (20.4%), June (14.8%), March (11.6%), February (10.0%), January (4.5%), July (4.3%), October (3.1%), August (2.2%), September (2.1%), December (1.4%), and November (0.8%) (Figure 3). The average release month of all hatcheries combined was 4.7 which is equivalent to calendar day 22-April (Figure 3F). The Coleman (average month 4.4 or calendar day 11-April, Figure 3A) and Nimbus (average month 4.6 or 19-April Figure 3B) hatcheries tended to release fish earlier in the year than the Feather (average month 5.4 or 13-May, Figure 3C), Mokelumne (average month 5.5 or 16-May, Figure 3D), and Merced (average month 5.3 or 11-May, Figure 3E) hatcheries (Table 1). Overall, release timing was unimodal, with a skewed peak of later-year releases occurring during the 1960s and gradually trending towards earlier releases over time (Figure 3F). From 2000-2012 nearly all releases occurred in the months of April (51.2% of all fish released), May (30.4%), and June (18.4%) (Figure 3F).

Temporal trends in variability of releases - To further evaluate release trends, we investigated the relationship between variability (measured at coefficient of variation, CV) versus year for release number (Figure 4A), release size (Figure 4B), and release timing (Figure 4B). In all cases, we found that variability has decreased (Figures 4A,B). For total releases over 10-year periods, the trends declined for all hatcheries (Figure 4A). Similarly, there have been reductions in release month variation ($R^2=0.30$, $P<0.0001$) and release size variation ($R^2=0.38$, $P<0.0001$) through time (Figure 4B), and these were correlated ($R^2=0.82$, $P<0.0001$).

Life-history-at-release - Fry, smolts, and advanced smolts represented the dominant life history types released by CVFRCS hatcheries (Figure 5, Table 1). Over time, the releases of smolts and advanced smolts have steadily increased whereas fry, fingerling, and yearling releases have largely ceased (Figure 5). The Coleman hatchery released the majority of their fish as fry (42.9% of total releases for the hatchery) and smolts (39.0%). The Nimbus hatchery has had a balanced release of fry (41.8%), advanced smolts (30.0%), and smolts (24.6%) over the entire time series. The majority of Feather releases were advanced smolts (55.8%) followed by smolts (21.3%), whereas the majority of Merced releases were smolts (61.4%) followed by advanced smolts (21.4%). The Mokelumne Hatchery released most of their fish as advanced smolts (75.9%). From 2000-2012 smolts and advanced smolts averaged $16.1 \bullet 10^6$ (52%) and $14.0 \bullet 10^6$ (45%) fish released per year from all hatcheries combined, respectively, whereas fry ($0.3 \bullet 10^6 \cdot yr^{-1}$, 0.9%), fingerling ($0.5 \bullet 10^6 \cdot yr^{-1}$, 1.7%), and yearling ($0.07 \bullet 10^6 \cdot yr^{-1}$, 0.2%) releases averaged far less during the same period.

Generally, fry were released from January to March (87% of total fry releases), fingerlings from March to May (89% of total fingerling releases), smolts from April to June (93% of total smolt releases), advanced smolts from April to July (80% of total advanced smolt releases), and yearlings from October to January (86% of total yearling releases) producing the 17 dominant size class-month combinations used for the life history diversity index calculation (see Materials and Methods).

The early life history diversity of releases based on index values (i.e., $^1ELHD_{norm}$) was found to be unimodal and symmetrical and could be described by a second order polynomial fit ($y = -0.0003x^2 + 1.2823x - 1271.5$, $R^2=0.62$) with peak release diversity occurring in the 1980s (Figure 6). Values from 1949 to 1956 were excluded due to poor release timing information (only 0.03% of fish released during this period had the same start and end release months). Maximum diversity values occurred in 1983 and 1993 ($^1ELHD_{norm} = 0.66$ for both years). Minimum diversity occurred in 1946 and 1947 ($^1ELHD_{norm} = 0.08$ for both years) when most fish were released as fry from the Coleman Hatchery, approximately 300 km upstream of Chipps Island. Average annual $^1ELHD_{norm}$ values and CVs (in parentheses) for the 5 decades from 1960-2009 were 0.29 (0.25), 0.44 (0.24), 0.52 (0.12), 0.46 (0.19), and 0.27 (0.12), respectively.

Discussion

Here we present an overview of the main trends in hatchery releases of Central Valley fall-run Chinook salmon from hatchery inception through 2012. Through compilation of a suite of datasets, we were able to ask questions about temporal patterns in hatchery releases, including juvenile release numbers, locations, sizes, timing, and life history stages.

Our analysis revealed several patterns in release abundance over time, including differences both among and within hatcheries. For example, total releases from the two dominant producers, Coleman and Nimbus hatcheries, have declined over time whereas those from the Feather, Mokelumne, and Merced have increased (Figure 1). Variation in the total release number has declined steadily over time for all hatcheries (Figure 4A), particularly as release strategies have stabilized in recent years. The vast majority of fish have been and continue to be released from three of the five hatcheries propagating CVFRCS (Coleman [~53%], Nimbus [~23%], and Feather [~18%]), and these hatcheries have different release strategies, which has implications for the larger fall-run stock complex (discussed below).

Fish sizes-at-release were low from the 1940s to mid-1960s (Figure 2F), reflecting the popular practice of releasing fry directly from the Coleman (Figure 2A) and Nimbus (Figure 2B) hatcheries at the time. Average size-at-release has decreased since the 1960s at the Mokelumne (Figure 2D) and Merced (Figure 2E) hatcheries due largely to termination of yearling releases at the San Joaquin hatcheries. In contrast, average size-at-release has remained relatively more consistent since the 1960s at the Coleman (Figure 2A), Nimbus (Figure 2B), and Feather (Figure 2C) hatcheries, although both the Coleman and Nimbus hatcheries show a recent uptick in release size and stabilization of release size beginning in the late 1990s. Similar to trends in release number, the variability in size-at-release has decreased over time for all five hatcheries combined (Figure 4B), particularly since 2000 (Figures 2A, 4B).

There is an apparent pattern of releases occurring later in the year from the 1940s to the 1960s (Figure 3F), but this may be partially biased by data reporting, which cannot account for fish outmigrating volitionally from spawning channels (a practice that largely ceased in the 1960s according to state annual reports). Data reporting has become more reliable since the 1970s, and there is an overall trend of earlier releases since then, with most releases occurring during the spring (Figure 3F). Among other factors, these patterns may reflect insufficient flows earlier in the year to allow outmigration of poor swimming fry and freshwater thermal barriers later in the year for older and larger fish. Some of the shifts in release timing are related to shifts in release size (e.g., cessation of yearling releases from the San Joaquin hatcheries is associated with shifts from fall to late-spring releases) as well as release location, which we discuss below.

While not an original objective, one observation regarding size-at-release was an increase in size-at-release month over time (Figure 7A). This has led to an apparent "substitution of growth for time" effect as fish released in April in recent years are approximately the same average size as those released in May in the late 1980s/early 1990s and in June in the late 1970s (Figure 7A). Ultimately, this resulted in a new life history release type that emerged in the early 1980s and has steadily increased in frequency since then: April, May, and June releases of ocean-ready "advanced smolts" (Figure 7B). This phenotype comprised 16%, 24%, and 35% of total fish released from all hatcheries for years 1980-1989, 1990-1999, and 2000-2009, respectively (Figure 7B). Furthermore, April, May, and June releases of advanced smolts between 87.5 mm and 100 mm FL comprised a steadily increasing proportion of total estuarine plants since 1980 (Figure 7C). Assuming that spawning and emergence schedules have remained largely unaltered, this trend may reflect improvements in hatchery practices (e.g., better feed, improved immunology, density and temperature controls) and/or efforts to target the largest and fastest growing fish for earlier releases. There may also be domestication selection for rapidly growing fish, which has been shown to occur in other artificially propagated salmonids (Fleming et al. 2002). Regardless of the mechanism(s), variables related both to ecological *state* (e.g., variable release size and month patterns, Figures 2A-F, 3A-F) and *process* (i.e., increasing size-at-release month patterns, Figure 7A) have been changing for hatchery-produced Central Valley fall-run Chinook over the course of 67 years (~20 salmon generations) of hatchery management. Through future research, we aim to better understand the consequences of these changes on adult demographic properties and the dynamics of the stock complex.

Causes of the trends - A full exploration of changes in hatchery practices and policies that have influenced the production trends is beyond the scope of this paper but are likely many, including shifting hatchery management strategies intended to boost juvenile survival rates and maximize the average contribution of a given program to ocean fisheries, aquacultural and economic constraints such as limited hatchery rearing capacity and the relatively high costs and risks associated with producing older and larger fish, environmental stochasticity (e.g., droughts), as well as technological advancements (e.g., disease and avian depredation controls) (e.g., Brown 2006, Lufkin 1991, as well as detailed information in the annual hatchery reports).

Some of the more striking shifts in release patterns that we highlight in figures 1-3 are fairly well understood, including shifts in production goals and biomass allocations (e.g., many small vs. fewer larger fish). For example, the Coleman National Fish Hatchery production goals originally included ~40 million 1.5-2 inch fish (fry) and 2 million 5-7 inch fish (yearlings) (Cope and Slater 1957, Scott Hamelberg, personal communication). Studies conducted in the 1960s and 1970s revealed that smolts released in the spring survived at higher rates than fry released in the fall (USFWS 1982), which led to a shift away from fry releases over time towards a release of smolts, as presented in the 1987 Coleman NFH Station Development Plan (USFWS 1987, Scott Hamelberg, personal communication). This shift is readily apparent when considering the recent stabilization in numbers, size, and timing of releases from CNFH (Figures 1A, 2A, and 3A). Kevin Niemela (USFWS) additionally emphasized that the shift toward smolt releases began earlier (in the mid-1960s) and that fry production in the 1980s and 1990s from Coleman could be considered 'added production', that is, production on top of the established smolt production.

As another example from one of the state-operated hatcheries, release patterns from the Feather River Hatchery have stabilized since the mid-1990s. Around this time, new target numbers were finalized (6 million mitigation fish + 1-2 million enhancement fish, Anna Kastner, personal communication). This timing also coincides with a shift towards planting fish directly in the estuary, which was associated with shifts towards releasing fish at ~85mm (i.e., 60 fish$\cdot$lb^{-1}, Figure 2B) a size that is typically reached by April to mid-May, hence releases concentrated during this time (Figure 3B) (Anna Kastner, personal communication).

More generally, since the early 1980s there has been an increasing trend of planting fall-run Chinook directly into the San Francisco Estuary (Figure 1) to avoid exposing fish to undesirable conditions in the degraded freshwater environments (JHRC 2001; Newman and Rice 2002, Figure 1). Three state hatcheries – Nimbus (Figure 1B), Feather (Figure 1C), and Mokelumne (Figure 1D) – have planted the most fish in the estuary. Such “off-site” releases present a conundrum for both hatchery and conservation managers. Recent improvements in marking strategies have indicated that smolts released in the estuary, especially advanced smolts from the Feather Hatchery acclimated to net pens, contribute disproportionately more to fishery catches and hatchery returns (Kormos et al. 2012; Palmer-Zwahlen et al. 2013). However, these same fish are straying at rates up to eight times greater (Kormos et al. 2012; Palmer-Zwahlen et al. 2013) than the background rates of 5-10% estimated for CVFRCS hatchery fish that were released “on-site” at the hatchery (Cramer 1991). Given that both Feather and Nimbus hatcheries are large producers that currently release a large fraction of fish off-site (Figure 1), these two hatcheries are likely generating a disproportionate number of strays, including strays to systems without hatcheries. Indeed, recent evidence from the constant fractional marking program suggests that these hatcheries do contribute a high number of strays to non-hatchery streams (Kormos et al. 2012; Palmer-Zwahlen et al. 2013). In contrast, the Coleman National Fish Hatchery, produces many more fish but tends to release these fish on-site, which leads to considerably lower out of basin straying (Kormos et al. 2012; Palmer-Zwahlen et al. 2013). Important exceptions were off-site releases from Coleman during the recent stock collapse (see the recent uptick in off-site releases in Figure 1A), which resulted in high rates of out of basin straying of Coleman fish (Palmer-Zwahlen et al. 2013). We can expect the recent off-site releases of Coleman fish in response to the current drought will have the same effect. These patterns are all consistent with strong positive relationships observed between straying rate and distance trucked (Dettman et al. 1987; Cramer 1991; JHRC 2001;

Lasko 2014), and our current understanding of salmon homing mechanisms in which salmon are thought to sequentially imprint on freshwater as they move downstream (Dittman and Quinn 1996). This matter deserves serious management attention because local adaptations (Utter 2004) and the ability to adapt to future environmental changes (Ghalambor et al. 2007) can be rapidly altered by excessive immigration of individuals from different genetic stocks and/or selective environments (Myers et al. 1998), which could reduce the resiliency of this stock complex, a topic we discuss further in the next section.

Implications - Life history diversity enhances stock stability via a portfolio effect that provides enhanced resiliency to fluctuating environmental conditions (Hilborn et al. 2003; Schindler et al. 2010; Carlson and Satterthwaite 2011). Based on the premise that life history diversity improves resilience, salmon recovery plans often include restoration activities to increase life history diversity (e.g., in the Columbia River system, NMFS 2011, Johnson et al. 2014).It therefore reasons that life history diversity of hatchery fish has implications for stock performance, particularly when the complex is dominated by hatchery fish like the Central Valley fall-run complex (Barnett-Johnson et al. 2007; Johnson et al. 2012; Kormos et al. 2012; Palmer-Zwahlen et al. 2013). Indeed, Hankin (1990) reported that the Chinook salmon population structure from Klamath River and southern Oregon hatcheries is strongly related to life histories of hatchery releases. More generally, size- and month-of-release of juvenile fish eventually affects important adult demographic properties such as average age, size-at-age, and maturation schedule – all of which can influence dynamics and stability of the stock complex.

Our analysis of size-class based life history types revealed distinct temporal patterns (Figure 5). Fry, smolts, and advanced smolts were the numerically dominant life history stages released by all hatcheries, with recent shifts towards releases of smolts and advanced smolts (Figure 5). The practice of releasing fry, fingerlings, and yearlings largely ceased during the late 1980s and early 1990s (Figure 5). Using an index to characterize life history diversity of the hatchery releases ($^1\mathrm{EHHD}_{\mathrm{norm}}$, Johnson et al. 2014), we found that the current life history diversity-at-release is about half of the maximum measured in the 1980s and is similar to levels measured early in the time series (Figure 6). It should be noted that, until the 1960s, only the Coleman and Nimbus hatcheries were operational, which limits direct comparisons between early and modern management schemes. Also noteworthy is that the early life history index (ELHD) of Johnson et al. (2014) does not account for shifting release types over time, such as we have documented in this system (e.g., March releases of fry from hatcheries early in the time series was equivalent to June releases of advanced smolts in the estuary later on). Upstream releases of small sized fish have more potential to diversify into different phenotypes before reaching the San Francisco Bay and Pacific Ocean than ocean-ready, larger fish deposited in the estuary (Myers et al. 1998; Healey 1991). Therefore, the *true* life history diversity of ocean-arriving fish was likely higher for a given $^1\mathrm{EHHD}_{\mathrm{norm}}$ index value early in the time series compared to more recent values (Figure 6) because of the increasing trend of downstream releases over time (Figure 1).

Beyond the changes in release practices and life history diversity of fall-run hatchery releases, it is also worth considering the importance of the average contribution and variability in adult returns from each hatchery. Doak et al. (1998) emphasize that stock complexes are better buffered when abundances of constituent populations are more even, and releases are very uneven among the different hatcheries (Figure 1). Moreover, within hatchery populations, there is likely a positive relationship between average contribution rate and its variability. From a management perspective, high average contribution is desirable, but high variability is not – so there is a trade-off here that warrants closer attention by both hatchery and fishery managers. Ideally, hatchery releases from all five Central Valley hatcheries producing fall-run Chinook would be coordinated amongst themselves and managed in concert with other aspects of the fishery, such as harvest rates, in order to consciously balance the harvest level, variability, and sustainability of this system.

Conclusions

We compiled and synthesized information on hatchery releases of fall-run Chinook salmon from California's Central Valley from various sources to create a single database of hatchery releases, representing 253 hatchery-year combinations (Appendix II available at *[include link here]*). These data are now available to the broader community interested in considering the role of hatchery practices in Central Valley fall-run Chinook dynamics. As a first step towards exploring these patterns, we examined trends in hatchery release practices through time. We found that variation in release number, location, size, and timing of hatchery CVFRCS releases has decreased over time in significant and consistent ways. In particular, the years of 1999-2012 were characterized by strong ecological homogenization of the fall-run hatchery release life history portfolio (Figure 6). Coincident with the recent drop in early life history diversity has been the multiple fishery closures and increasingly variable returns of adults to Central Valley hatcheries and non-hatchery spawning grounds (Lindley et al. 2009, Carlson and Satterthwaite 2011, PFMC 2014) – an apparent relationship that warrants closer inspection. There are several management actions that could allow for more complete expression of life history diversity in this stock complex. For naturally-produced fish, examples include the designation of salmon sanctuaries to protect wild populations where they still exist and the continued restoration of freshwater and brackish water habitats, especially those that re-introduce habitat complexity allowing for a greater expression of juvenile phenotypes. For hatchery-produced fish, one possibility is to directly manipulate the phenotypes of hatchery releases to artificially generate diversity within hatchery releases (e.g., by staggering time at release). Another option is to release fish closer to the hatchery so that, like their natural counterparts, they are exposed to habitat complexity that generates phenotypic diversity during their outmigration. Indeed, when fish are released far downstream from natal sources, especially at crowded densities, they have less exposure to an array of energetically profitable nursery habitats, including intermittent (Limm and Marchetti 2009) and gravel-bed (Chapman and Bjornn 1969) streams, floodplains (Jeffres et al. 2008), and wetlands (Healey 1980; Roegner et al. 2010) that allow for a fuller range of genetic and phenotypic expression within populations (Myers et al. 1998). Moreover, releasing high densities of ocean-ready fish may increase the vulnerability to match-mismatch dynamics when these fish enter the ocean (Satterthwaite et al. 2014). Consequently, population resilience and persistence is presumably under greater threat when fish are released in large numbers at restricted times, sizes, and locations, a common current practice at all of the Central Valley fall-run Chinook salmon hatcheries.

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Table 1. Summary table with all the mean and calculated values for each hatchery.

	Coleman	Feather	Nimbus	Mokelumne	Merced
Range of release years included in database	1946-2012	1968-2012	1957-2012	1964- 2012	1971-2012
Number of release years	67	45	56	49	42
Total number of fish released (millions)	1,053	352	455	127	22
Mean number of fish released (millions)	15.8	7.9	8.1	2.7	0.6
Median number of fish released (millions)	13.4	8.2	5.8	2.2	0.4
Percentage of fish released from a given hatchery	52.4	17.5	22.6	6.3	1.1
CV in number released across years	0.53	0.39	0.67	0.91	0.83
Total number released to estuary (millions)	17.7	217.7	125.5	55.7	1
Mean size at release (g)	3.9	10.7	4.9	13.4	12.7
Mean time of release	11-April	13-May	19-April	16-May	11-May
Mean proportion of each life stage released					
(i) fry	42.9	13.4	41.8	1.2	1.2
(ii) fingerlings	8.4	4.3	2.6	0.8	4.3
(iii) smolts	39.0	21.3	24.6	14.5	61.4
(iv) advanced smolts	8.9	55.8	30.0	75.9	21.4
(v) yearlings	0.8	5.2	1.1	7.6	11.6

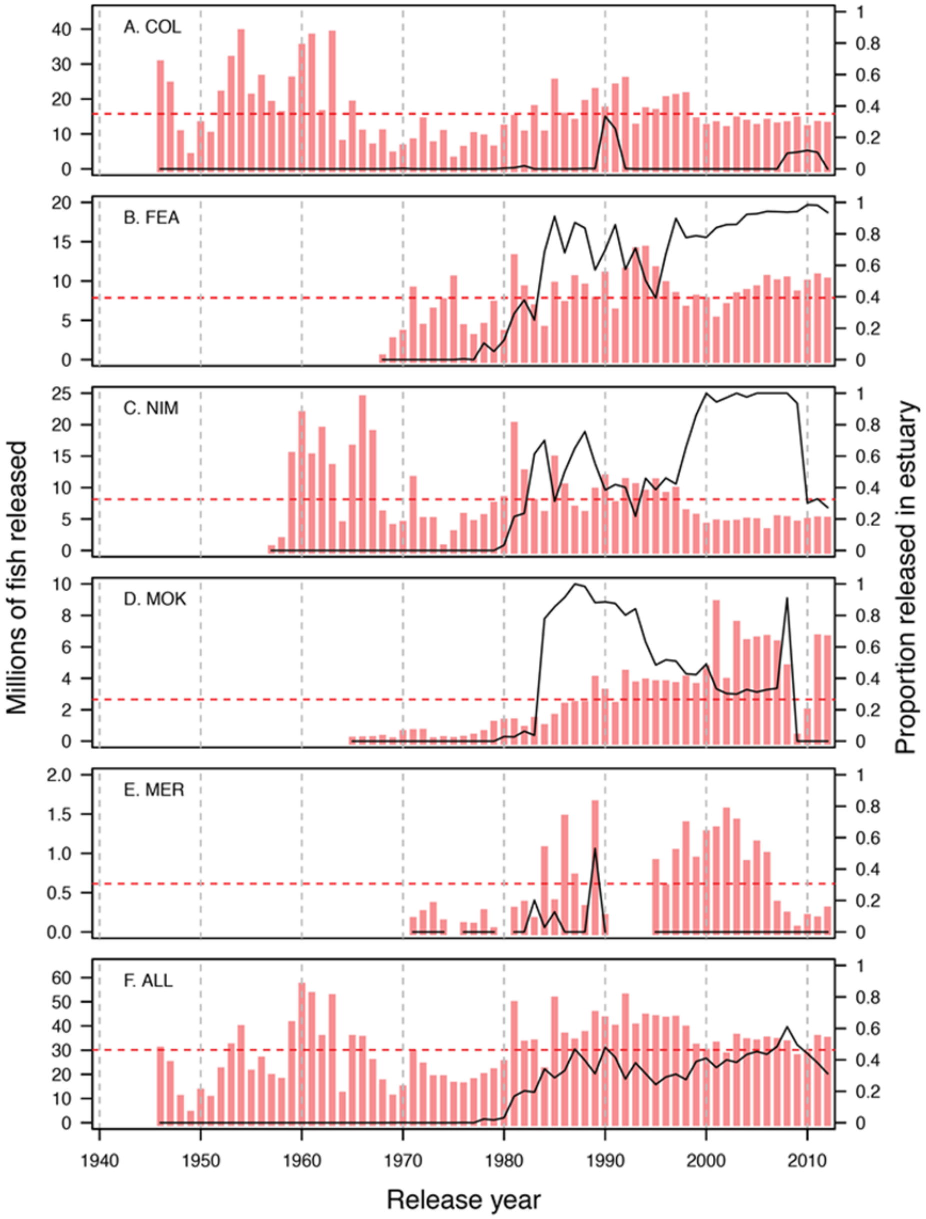

Figure 1. Annual fall-run Chinook salmon released from five of California's hatcheries that produce Central Valley fall-run Chinook salmon (A–E), including data for all five hatcheries (F) combined. Red bars are millions of fish released (left Y-axis) and the black line represents the proportion of the total number of releases that occur downstream of Chipps Island (right Y-axis). The dashed horizontal line on each panel indicates the mean number of releases over the entire release period. Panels show data from these five hatcheries: (A) Coleman, (B) Feather, (C) Nimbus, (D) Mokelumne, and (E) Merced. Panel (F) shows data for all five hatcheries combined.

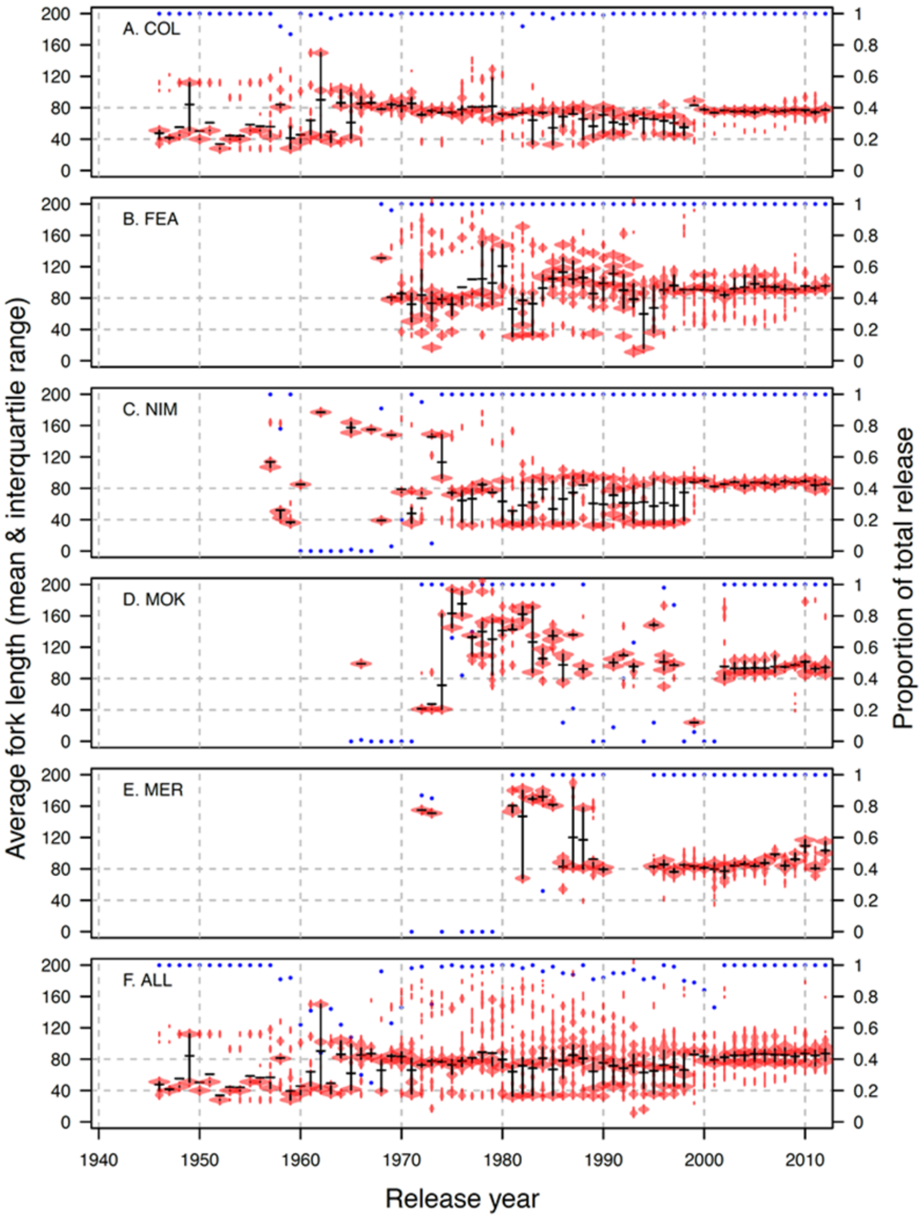

Figure 2. Annual fork length-at-release (left Y-axis) and interquartile range (black cross, dash represents the mean and whiskers represent the IQR)—with violin plot in red to show the associated density distribution—and the proportion of total yearly releases per year (right Y-axis) with size data reported (blue circle). Panels show data for five different hatcheries: (A) Coleman, (B) Feather, (C) Nimbus, (D) Mokelumne, and (E) Merced. Panel (F) shows data for all five hatcheries combined.

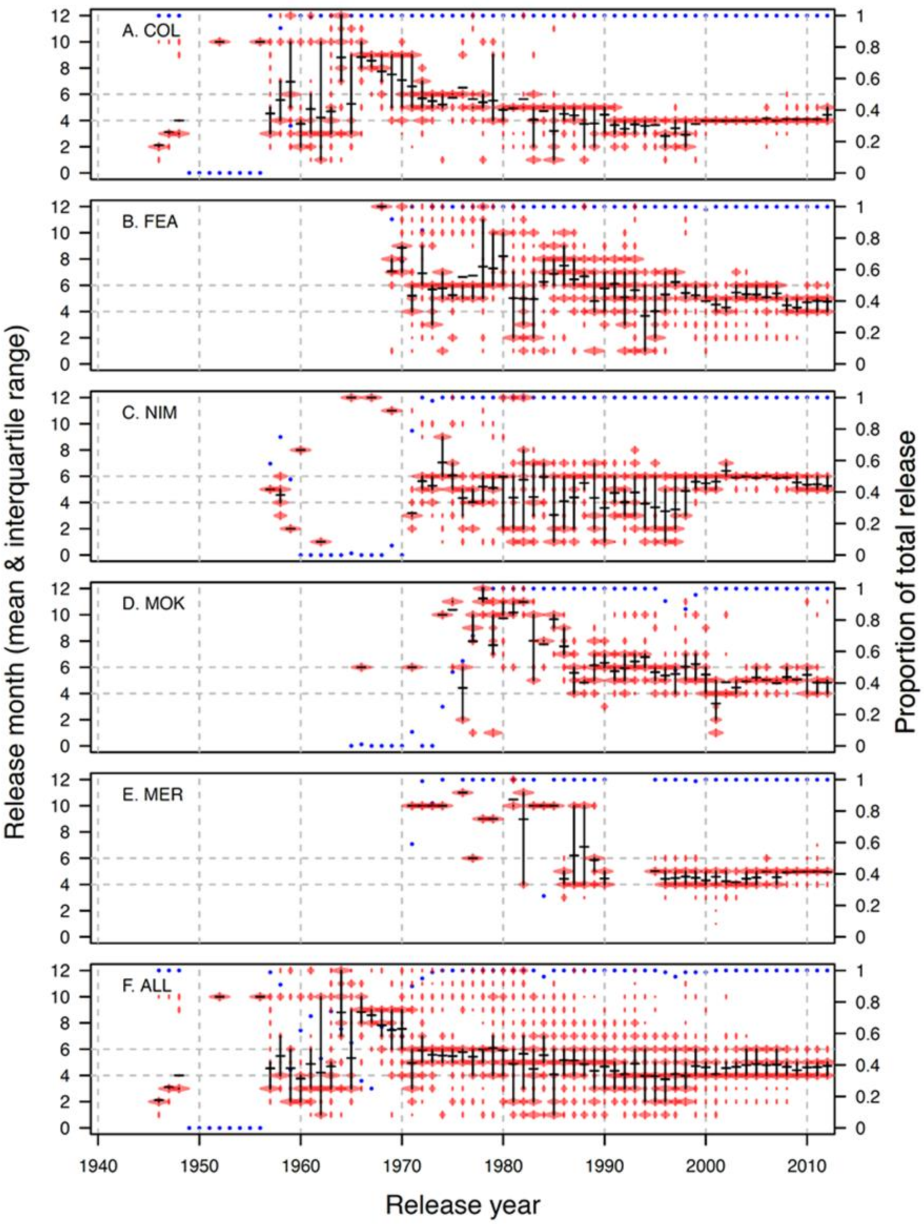

Figure 3. Annual release month (left Y-axis) including mean and interquartile range (black cross, dash represents the mean and whiskers represent the IQR)—with violin plot in red to show the associated density distribution—and the proportion of total release per year (right Y-axis), with data reported at the monthly scale (blue circle). Panels show data for five different hatcheries: (A) Coleman, (B) Feather, (C) Nimbus, (D) Mokelumne, and (E) Merced. Panel (F) shows data for all five hatcheries combined.

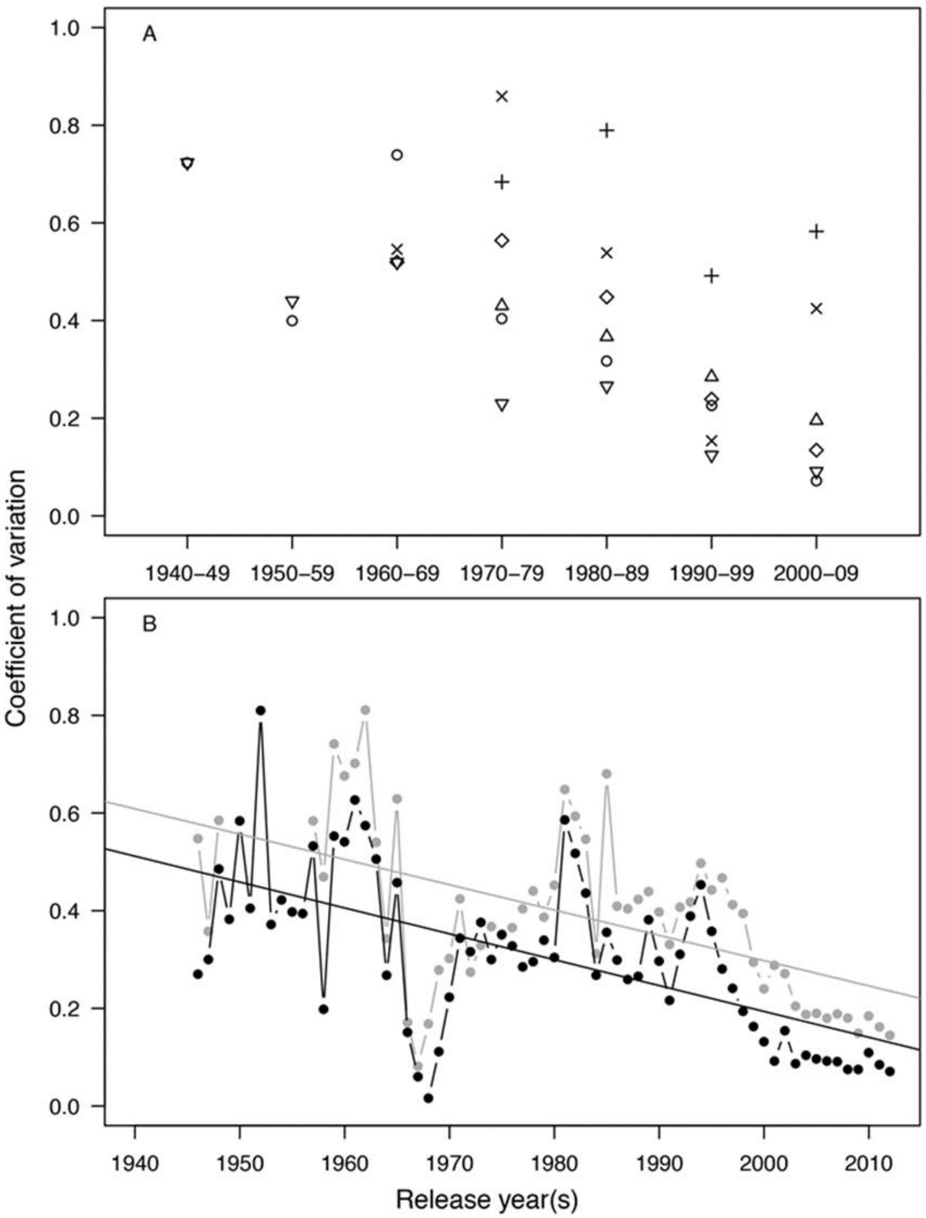

Figure 4. Portfolio reductions of key release traits, expressed as declining coefficient of variation (CV) trends for (A) decadal release number for the Coleman (O), Nimbus (◊), Feather (Δ), Mokelumne (×), Merced (+), and all (∇) hatcheries, and (B) fork length-at-release (black dots and black line) and month-at-release (grey dots and grey line) for all hatchery data combined. In panel A, data were included beginning for the first decade when release information was available for the majority of years within the decade.

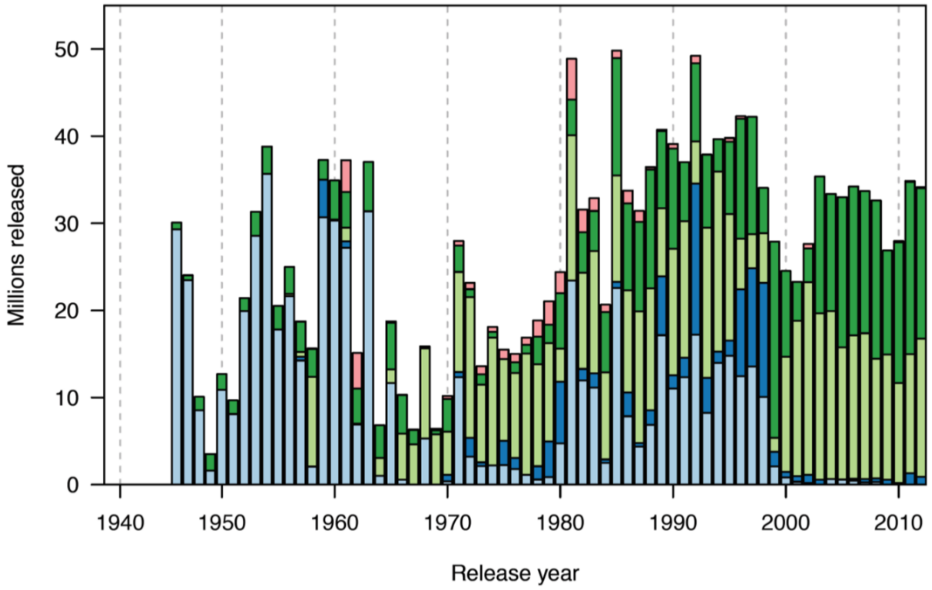

Figure 5. Release life-history types, presented as total released per type across all years and hatcheries. Life-history types are based on size (fry: <55 mm, light blue bar; fingerlings: ≥55 to <70 mm, dark blue bar; smolts: ≥70 to <87.5 mm, light green bar; advanced smolts: ≥87.5 to <140 mm, dark green bar; yearlings: ≥ 140 mm, pink bar). Note that the discrepancies between figure 1 and figure 5 are due to the decision rule to only include fish whose release begin and end months are the same for life history analyses presented in this plot.

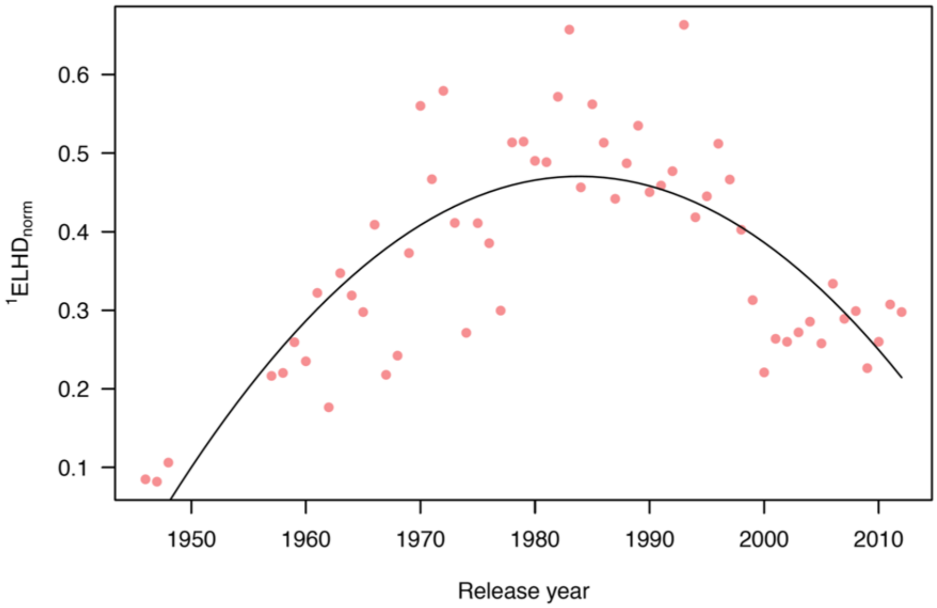

Figure 6. Release portfolio as expressed by a life-history diversity index (1ELHDnorm, see "Materials and Methods") developed for juvenile Chinook salmon (pink circles). The first-order normalized diversity estimator incorporates release month and size data and expresses values as a proportion of total possible release month–fish size combinations. The overall trend is unimodal and symmetrical with release diversity peaking in the 1980s (best described as a second-order polynomial fit, $y = -0.0003x^2 + 1.2823x - 1271.5$, black line).

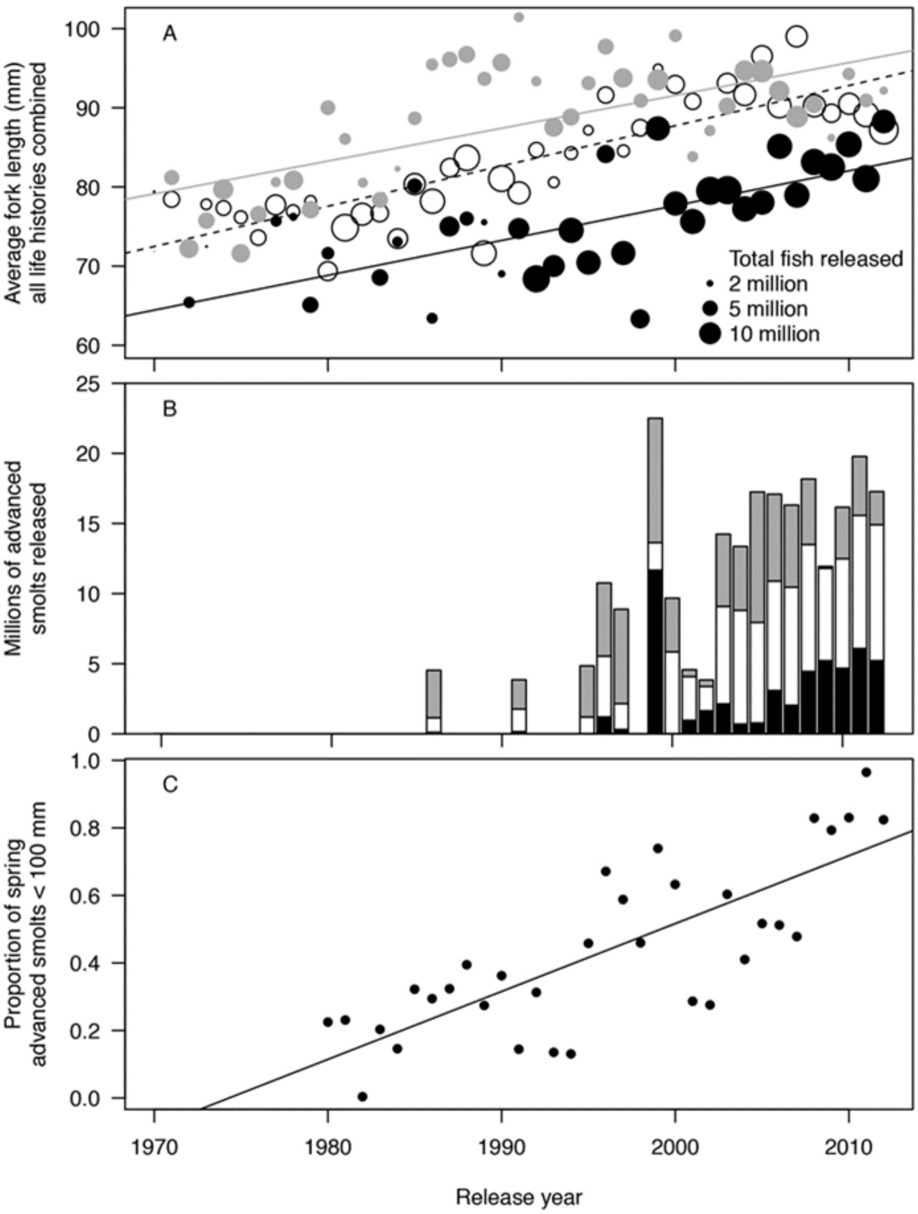

Figure 7. (A) Average fork lengths for April (black circles and trendline, $y = 0.0811x + 2.7614$, $R^2 = 0.43$, $P < 0.001$); May (white circles and dashed trendline, $y = 0.1273x + 3.7744$, $R^2 = 0.70$, $P < 0.001$); and June (grey circles and trendline, $y = 0.1051x + 5.5073$, $R^2 = 0.39$, $P < 0.001$) from 1970 to 2012. Circle sizes represent relative differences in monthly total release numbers. (B) Advanced (i.e., ocean-ready) smolt releases in April (black stacked bar), May (white stacked bar), and June (grey stacked bar) for all hatcheries combined across all years. (C) Increasing temporal trend of the proportion of total estuary plants comprised of spring (i.e., April, May, and June) releases of advanced smolts between 87.5 mm and 100 mm FL (with series year used instead of calendar year, $y = 0.0206x + 0.0774$, $R^2 = 0.64$, $P < 0.001$).

Appendix I. Metadata for the hatchery release database. Appendix II contains the release database as an excel file that can be found at: escholarship.org/uc/item/7237t9xn#supplemental

Field	**Description**
ID	The first number represents a hatchery code (1-5, corresponding to the five hatcheries listed below). The second number (i.e., following the dash) represents individual release groups from a given hatchery.
Hatchery	One of five hatcheries propagating fall-run Chinook salmon within the Central Valley: Coleman National Fish Hatchery, Nimbus Hatchery, Feather River Hatchery, Mokelumne River Hatchery, Merced River Fish Hatchery.
Data-source	One of four sources: electronic database supplied by the USFWS, RMIS, annual report for one of the four state-operated hatcheries, electronic database provided by CDFW
Brood Year	The calendar year when the parents of these fish spawned.
Year Release Start	Start year for a given release group.
Month Release Start	Start month for a given release group.
Day of Month Release Start	Start day of the month for a given release group.
Year Release End	End year for a given release group.
Month Release End	End month for a given release group.
Day of Month Release End	End day of the month for a given release group.
Total Number Released	Total number of fish released for a given release group.
Avg. Fish Weight (g)	Release weights were reported as a single mean fish mass for the release group. In a small number of cases (usually early in the time series), a range of weights were reported. The range mid-point is presented in these cases.
Release County	County of release for the release group.
Release Location	Coarse scale release location information associated for the release group. Empty cells reflect those cases where this information was not reported.
Release Site	Finer scale release location information associated for the release group. Empty cells reflect those cases where this information was not reported.

CHAPTER 3

FISH ASSEMBLAGE COMPOSITION, STRUCTURE, AND CHANGE IN A CENTRAL CALIFORNIA INTERMITTENT ESTUARY DURING SEVERE DROUGHT

Fish assemblage composition, structure, and change in a Central California intermittent estuary during severe drought

Abstract: Here, I present analysis of 27 months of continuous monthly fish sampling and environmental data from an understudied Central California intermittent estuary (Pescadero estuary) experiencing quasi-annual fish kills associated with sandbar breaching. A severe drought commenced four months after the study's initiation and led to heightened ecosystem disconnection between the estuary and marine environment. A total of 15 anadromous, marine-origin, freshwater-origin, and estuarine resident species were sampled. The four most common species comprised 97.0% of the total numerical abundance. Steelhead (*Oncorhynchus mykiss*) dominated the catch in terms of numerical abundance (41.1%) and biomass abundance (89.9%). Significant effects of month, summer year, and sampling location on the fish assemblage were detected and distinct seasonal species groupings or fish guilds are observed: 1. the "anadromous" guild dominated by *O. mykiss* during summertime when photoperiods are long and water temperatures are warmest, 2. the "marine migrant" guild represented by dominant topsmelt (*Atherinops affinis*) during the winter when days are short and temperatures are coldest, and 3. the "estuarine resident" guild dominated by either Pacific staghorn sculpin (*Leptocottus armatus*) during the open ecosystem state or threespine stickleback (*Gasterosteus aculeatus*) during prolonged sandbar-closed conditions when mean water surface elevations and temperatures are higher. Unlike the marine migrant guild, the anadromous guild is characterized by elevated species richness, species dominance, and Morisita assemblage similarity levels and low apparent species turnover rates. Post-kill effects include reduced assemblage similarity, increased species turnover, rapid declines in biomass abundance, and a sharp increase of seine hauls yielding zero fish catch. The assemblage rebounded to normal levels approximately three months after the mass mortality event. Summertime abundances of threespine stickleback and tidewater goby (*Eucyclogobius newberryi*) increased over time as the drought progressed whereas abundances of marine-origin starry flounder (*Platichthys stellatus*) and shiner perch (*Cymatogaster aggregata*) exhibited sharp declines. Despite temporary losses of ecosystem function, the Pescadero intermittent estuary provides critical nursery and reproductive habitat for a variety of native species, including endemic and endangered and *E. newberryi* and threatened *O. mykiss*.

Keywords: Intermittent estuary, fish assemblage, drought, fish kill, water quality, biophysical coupling, shifting ecosystem states, California

Introduction

Estuaries are amongst the most dynamic and productive ecosystems on earth (Haedrich and Hall 1976). The mixing of river and ocean waters produce large spatial and temporal variations in environmental conditions and concentrate nutrients and organic matter from both fluvial and marine sources. Eurytopic fishes adapted to the highly fluctuating salinity, temperature, dissolved oxygen, turbidity, and other factors benefit from the rich growth opportunities and predatory refugia provided by shallow and protected coastal inlets (Kennish 1990). Five general types of fishes are typically found in estuaries: 1. Estuarine resident species that either breed exclusively in estuaries or may also breed in marine or fresh waters, 2. Euryhaline marine fishes that usually reproduce at sea and produce juveniles with variable degrees of estuarine dependence, ranging from obligate nursery requirements to occasional opportunistic visits, 3. Non-dependent marine species, 4. Euryhaline freshwater species that may either breed in fresh or brackish water habitats, 5. Catadromous species that use estuaries as migration corridors and, in some cases, for extended residence (Whitfield and Marais 1999). All types may represent an assemblage at any time but the relative abundances of each often change depending on season, environmental conditions, and location within the estuary (Kennish 1990).

Intermittent estuaries are a unique type that evaded early definitions of estuaries requiring a "free connection with the open sea" (Pritchard 1967, Day 1981). Intermittent estuaries are known by many names including temporary open/closed estuaries (TOCE), intermittently closed/open lakes and lagoons (ICOLL) and closed, blind, or bar-built estuaries. Regardless of the name given, intermittent estuaries are characterized by the ephemeral formation of a sandbar across the sea mouth which severs marine connectivity. Intermittent estuaries typically occur in small- to medium-sized watersheds in regions experiencing energetic wave climates and seasonal rainfall patterns such as portions of South Africa, Australia, New Zealand, India, Sri Lanka, Spain, Portugal, Chile, Brazil, Uruguay, and the west coast of North America. Sandbar condition is controlled by the opposing forces of wave- and incoming tide-driven sediment delivery to the mouth which builds the frontal berm. Intermittent estuaries thus shift between fully open (spring and neap tidal mixing), partially open (spring tidal mixing only), and fully closed (no tidal mixing) ecosystem states which increases the estuary's physico-chemical complexity (Perissinotto et al. 2010). Persistent salinity stratification, extended bottom-water residence time, and deep water anoxia from elevated biological or chemical oxygen demands are common features of the closed ecosystem state (Schumann et al. 1999, Allanson and Winter 1999). While migration opportunities for aquatic organisms are restricted by the sandbar, the nursery function may be enhanced (Bond et al. 2008, Hayes et al. 2008). Sandbar breaching eventually occurs when water levels rise above the frontal berm and an outflow channel forms. Breaching causes dramatic changes to estuarine water quality and quantity and breach-induced fish kills have been documented in intermittent estuaries (Becker et al. 2009), including regular events at the study site presented here (Sloan 2006, Largier et al. 2015) from chemical oxygen demand (Smith 2009) caused by re-suspension of sulfide precipitates (Richards and Pallud 2016).

Despite intermittent systems comprising 79% of the California's 380 bays and estuaries (Heady et al. 2014), icthyofaunal studies in California intermittent estuaries are surprisingly rare, especially north of Point Conception where a biogeographical split occurs (Allen et al. 2006). Peer-reviewed studies north of Point Conception have focused almost exclusively on a single species (*Oncorhynchus mykiss*) from a small watershed (Scott Creek) during the spring and summer closed estuarine state (e.g., Bond et al. 2008, Hayes et al. 2008, 2011). These illuminating studies demonstrate the intermittent estuary's critical nursery function for a threatened and iconic California native fish species. More information, however, is needed about the icthyofauna in these understudied ecosystems. In particular, analyses of long-term abundance patterns of multiple fish assemblage members over time in response to shifting environmental conditions is needed (Allen et al. 2006).

The primary objective of this study is to obtain continuous monthly fish assemblage and environmental data over a multiple year period from a northern California intermittent estuary. Research questions include: Which species comprise the estuarine fish assemblage? What are the numerical and biomass abundances of commonly encountered assemblage members? Can life history properties of common species be identified by spatiotemporal abundance and size trends? How does assemblage composition and structure change over time and space? Can associated biological, physical, and chemical drivers of assemblage state and change be identified? How do breach-induced fish kills affect assemblage state and change?

Methods

Study site - The Pescadero intermittent estuary intermittent estuary is located at California's Central Coast, approximately 60 km south of San Francisco (Fig. 1). It represents the largest estuary-coastal marsh wetland complex for approximately 125 km between Elkhorn Slough to the south and San Francisco Bay to the north. Two major basins comprise the 212 km^2 watershed: Pescadero Creek (155 km^2) and Butano Creek (57 km^2) catchments. Both originate in the heavily forested Santa Cruz mountains and converge in the upper estuary (Fig. 1). Total watershed relief is 830 m and mean annual precipitation is 84 cm. Ninety percent of the precipitation occurs between December and April. Estimated maximum and minimum runoff occurred in years 1941 (144,000 ac-ft) and 1977 (1,200 ac-ft), respectively, and average yearly runoff is 50,864 ac-ft (Curry et al. 1985). Sandbar formation is highly seasonal and generally forms during the dry period of the region's Mediterranean-like climate. At full closure, the lagoon's volume, surface area, and mean depth are approximately $1.2 \cdot 10^6$ m^3, $1.0 \cdot 10^6$ m^2, and 1.2 m, respectively. When open, the Pescadero intermittent estuary is microtidal and subject to diurnal tidal fluxes possessing a 12.4 hour period. Sandbar breaching usually occurs during the early rainy season and full sandbar blowout has been associated with 16 acute widespread organism kills between the 1996 and 2013 water years (WYs). Recreational fishing in the estuary was permitted for *Oncorhynchus mykiss* from 1-December 2011 to 7-March 2012 for three days per week but not during 2012-13 season because of severe drought and the continued presence of the sandbar at the sea mouth which restricted adult in-migration.

Environmental data -Freshwater inflows were measured by a water stage recorder (USGS 11162500) in Pescadero Creek, approximately 8 km upstream of the estuary at an elevation of 19 m above sea level and draining approximately 56% of the total watershed area. Since actual inflows into the estuary are unknown, I present freshwater discharge data as unitless "flow departures". Flow departures are calculated by dividing $\log_{10}$-transformed mean daily discharge by the corresponding $\log_{10}$-transformed median value for the given calendar date (period of record: WY 1952-WY 2013).

Estuary water surface elevations (WSEs) were measured hourly by a pressure sensor (RBR XR-420 CTD) positioned in the middle of the study reach from 14-July 2011 to 20-May 2013. During the closure period from 21-May 2013 to 13-September 2013 WSEs were periodically measured using a staff gauge attached to a bridge pier approximately 100 m upstream of the sea mouth. Daily WSE ranges during this period are assumed to be 2 cm and missing mean daily WSE values are estimated by polynomial regression. Water surface elevation data are converted to meters using the NAVD88 vertical datum (GEOID 2009 model) and summarized as mean daily WSE, minimum daily WSE, maximum daily WSE, and daily WSE range. Sample month mouth condition is determined from mean monthly daily WSE ranges: closed (<0.03 m), partially open (0.03 m-0.30 m), and open (>0.30 m). Total number of days closed per month is based on observer records for sandbar formation and breaching events.

Measurements of salinity, water temperature, and dissolved oxygen levels were made at multiple locations throughout the study reach during late morning and afternoon hours at 25 cm depth increments from the water surface to the benthic substrate using a YSI Pro handheld multiparameter meter or a YSI DO200 handheld dissolved oxygen meter. Water quality monitoring was performed opportunistically depending on instrument and personnel availability and safety considerations. Water quality parameters are summarized as depth-averaged values for the upper (≤150 cm depth) portions of the water column. Lower (>150 cm depth) water column physico-chemical conditions are not presented because of widespread hypoxic and anoxic deep water conditions which fish are assumed to avoid.

In order to scale environmental data to biological data, physico-chemical measurements are presented as mean monthly values for measurements made between mid-month fish sampling events for the given month (including fish sampling days) and the first day after fish sampling for the previous month. Environmental data also summarized as overall seasonal means which are the mean values of three monthly means. Winter months are from January to March, spring from April to June, summer from July to September, and fall from October to December. The summer season is emphasized here because it is the period of peak biological activity and, unlike the other seasons, more than two years of data exist for summer months.

Fish sampling - Mid-month beach seine fish sampling events were conducted during daylight hours from July 2011 to September 2013. Depending on timing with concurrent studies, fishes were sampled for 1, 2, 3, or 5 days per month. The beach seine was swept from the left to right bank (Fig. 1) by a team composed of two people holding the seine poles vertically in the water and four or more workers pulling them towards the shoreline with ropes. From July 2011 until April 2013 a 30.5 m X 1.8 m (9.5 mm mesh) beach seine with a 1.8 m X 1.8 m (6.4 mm mesh) bunt was used to sample fishes. From May 2013 to September 2013 a 30.5 m X 3.0 m (9.5 mm mesh) seine with a 3.0 m X 3.0 m (9.5 mm mesh) bunt was used instead because of increased water depths and amendments to the state fish sampling permit which required larger bunt mesh diameter. A total of six equally-spaced seine haul sampling zones spanning a combined distance of approximately 500 m from the estuary mouth to the Pescadero Creek-Butano Creek confluence (Fig. 1) were sampled each month. The lowest three zones are relatively wide and shallow (Fig. 1) whereas the upper three zones are narrower and deeper (Fig. 1). During the fully closed ecosystem state, maximum and minimum haul distances were approximately 150 m (zone 2 Fig. 1) and 50 m (zone 6, Fig. 1), respectively. During the fully open state, maximum and minimum haul distances were approximately 50 m (zone 1, Fig. 1) and 20 m (zone 4, Fig. 1), respectively. Attempts were made to sample all six zones each month but occasionally this was impossible because of inadequate haul-out conditions or the widespread proliferation of benthic algae which loaded the seine too heavily.

All fishes were identified to the species taxonomic level and enumerated before being returned alive to the environment after a proper recovery period in live wells. If time permitted, fishes were also measured for lengths and a subset of those were measured for mass if weather conditions were suitable. Fork lengths (FLs) were measured for species possessing a forked caudal fin and total lengths (TLs) are measured for all other species. Missing masses for individual fish are estimated from length-weight regressions when only length data are available. For *O. mykiss*, separate length-weight regressions are generated for sub-adults (<450 mm fork length) and adults (≥450 mm FL) because many adult-sized fish were captured soon after spawning and possessed reduced bodily condition. Unmeasured fish are assigned the mean length and mass for the given sample month. All abundance and biomass data are standardized as catch-per-unit-effort which is the numerical abundance ($CPUE_a$) or total biomass ($CPUE_b$) of each species or all species combined captured per seine haul. Mean fish sizes are calculated by dividing mean monthly CPUE_b by CPUE_a for each species. Because of upstream-downstream differences in biological composition, both mean CPUE_a and CPUE_b data per month are presented for each sampling zone (Fig. 1) in addition to overall study reach means calculated from the means for sampling zones 1-6.

Assemblage structure - Assemblage structure is described by species richness, species dominance, and non-metric multidimensional scaling (NMDS) ordination analysis (ter Braak and Prentice 1988, Kwak and Peterson 2007). Percent dominance is calculated using both the standardized numerical abundance and biomass data. The formula used for percent dominance (*D*) is:

$$D=100\cdot\sum p_i$$

> where: p_i=proportion of the study reach mean CPUE_a or CPUE_b for all species combined composed of CPUE_a or CPUE_b of the *i*th species. Two percent dominance values are calculated for both the single (i=1) and top two (i=2) most numerically abundant or biomass abundant species.

Non-metric multidimensional scaling analysis (ter Braak and Prentice 1988) was implemented using PAST version 3.05 (Hammer et al. 2001). Only standardized numerical abundance data are used for NMDS ordination. Prior to ordination, species CPUE_a data for each sample month-haul zone combination were $\log_{10}(x+1)$ transformed in order to reduce the influence of dominant taxa on ordination (Clark and Green 1988). Species appearing in less than 5% of monthly fish samples were excluded from multivariate analyses because of their minor influence on the results and their potential to confound statistical interpretations (Gauch 1982). The Euclidean similarity resemblance measure was used because of high degrees of species dominance (see below; Wolda 1981). In order to determine the set of coordinates on the NMDS plot that most closely resembles the original resemblance matrix in multiple dimensions, 9,999 iterations were conducted. Stress values, which indicate the divergence of the Euclidean association matrix from the original sample-by-sample similarity matrix (Kruskal 1964), are reported to assess the ordination's "goodness of fit". Lower stress values indicate better fit and values greater than 0.20 are considered random (Clarke 1993). If a two-dimensional ordination produces a stress value greater than 0.20 then a three dimensional ordination is used instead to properly represent the data.

Assemblage change - Fish assemblage change is quantified by both Morisita similarity index (Morisita 1959) and apparent species turnover rate (Diamond and May 1977) and described by NMDS behavior in species-space (sensu Matthews et al. 2013). Morisita indices are calculated using PAST version 3.05 (Hammer et al. 2001). Morisita index measures proportion similarity between two assemblages using absolute abundance data instead of relative abundances and is recommended when absolute abundance data are available (Wolda 1981). Zero values represent no species in common whereas a value of one indicates identical species composition. Here, I calculate Morisita indices using $\log_{10}(x+1)$ transformed CPUE_a values for common species, defined as those occurring in 5% more of all monthly samples. The Morisita index value for each sample month-haul zone combination represents the similarity of the given sample month-haul zone combination compared to all other sample month-haul zone combinations. Morisita similarity indices are summarized and presented as overall means and standard errors based on month-zone values for each haul zone, calendar month, and summer season.

Unlike the Morisita index calculations, apparent species turnover rates account for both common and rare species and treat all species equally if they are sampled at least once during a given month in any of the six sampling zones (Fig. 1). The formula (Diamond and May 1977) used to calculate apparent species turnover rate (T) is:

$$T=(I+E)/(S_1+S_2)$$

> where: I and E are the number of species that immigrated or were extirpated between consecutive sampling months for all haul zones combined and S_1 and S_2 are the number of species present in each sample month for all haul zones combined.

Ordination behavior in species-space is described according to NMDS axes trajectory paths. Hypothetical temporal movement patterns can be non-directional, directional, or directional with return and transitions within each of the three patterns can be either gradual or abrupt (see Matthews et al. 2013, their Fig. 1). However, it is likely that assemblages in nature exhibit a combination of these idealized behaviors at different times (Matthews et al. 2013).

Two-way permutational multivariate analyses of variance (PERMANOVA, Anderson 2001) using the Euclidean similarity measure is used to test two null hypotheses: 1. month (12 levels), sampling zone (6 levels), and the interaction between month and sampling zone do not affect fish assemblage structure, and 2. year (3 levels), sampling zone (6 levels), and the interaction between year and sampling zone do not affect fish assemblage structure. The second analysis is restricted to the summer months because more than two years of data exist for July, August, and September. A total of 9,999 iterations are conducted to obtain P-values and results are considered significant at the $\alpha=0.05$.

If significant differences are detected by two-way PERMANOVA, the species assemblage data are subject to similarity percentage analysis (SIMPER, Clarke 1993) in order to identify the species most responsible for the observed differences between sample groups. The SIMPER method calculates the average contribution of each species to the overall similarity between samples. Samples are pooled and all possible pairs of sample month-haul zone and sample year-haul zone were compared pairwise using the Euclidean distances. Key species groups are defined as those accounting for 90% or more of the cumulative similarity. Both PERMANOVA testing and SIMPER analysis are conducted using PAST version 3.05 (Hammer et al. 2001).

In order to identify associated biotic and abiotic drivers of assemblage state and change, monthly summarizations of ordination axes scores, Morisita similarity indices, apparent species turnover rates, species CPUE data, and environmental data are subject to linear Pearson r correlation analysis using PAST version 3.05 (Hammer et al. 2001). Mean NMDS axes scores, mean Morisita indices, and apparent species turnover rates represent dependent variables; independent variables include $\log_{10}$-transformed study reach mean CPUE_a values for common species and monthly means of flow departure, mean daily WSE, minimum daily WSE, maximum daily WSE, daily WSE range, salinity, water temperature, dissolved oxygen, and photoperiod. Correlations are considered significant at the $\alpha=0.05$ level.

Results

Environmental data - Overall mean flow departure for the 27 monthly means from July 2011 to September 2013 was 0.92 (Table 2). Mean monthly flow departure was greater than or equal to one from July 2011 to November 2011 ($\bar{x}$ =1.6), April 2012 to June 2012 ($\bar{x}$ =1.1), and December 2012 to January 2013 ($\bar{x}$ =1.7). Mean monthly flow departure was less than one from December 2011 to March 2012 ($\bar{x}$ =0.7), July 2012 to November 2012 ($\bar{x}$ =0.8), and February 2013 to September 2013 ($\bar{x}$ =0.4) (Table 2). Minimum (-0.2) and maximum (2.0) mean monthly flow departures occurred in September 2013 and October 2011, respectively (Table 2).

Data gaps for physico-chemical measurements occurred for multiple reasons including instrument non-availability, instrument malfunction, or unsafe monitoring conditions. Estuary WSE data are available for all months except July 2011 and February 2013 and mouth condition during those months was assessed according to observer records. The ecosystem state was closed for 7 sample months, partially open for 9 months, and open for 11 months. The equation used to estimate mean daily WSE (m) for May 2013 to September 2013 is: $\text{WSE}=2.55\cdot10^{-7}x^3-1.10\cdot10^{-4}x^2+1.38\cdot10^{-2}x+2.13$ (R^2=0.98, *df*=13; period of record: 26-Apr 2013 [x=1] to 8-Feb 2014 [x=289]). Overall mean WSE, calculated from the 25 monthly means, was 1.97 m (Fig. 2). Minimum (1.39 m) and maximum (2.63 m) mean monthly WSEs occurred in August 2011 November in 2011, respectively (Fig. 2). The overall mean WSE daily range was 0.35 m (Fig. 2). Minimum (0.02 m) and maximum (0.97 m) measured mean monthly daily WSE ranges occurred in January 2012 and May 2012, respectively (Fig. 2). Mean summertime WSE levels (and mean daily range) were 1.70 m (0.53 m) in 2011, 1.51 m (0.45 m) in 2012, and 2.49 m (0.02 m) in 2013 (Fig. 2).

Nine sandbar breaches (and total WSE decline) occurred during the period on 11-Nov 2011 (2.22 m), 22-Jan 2012 (1.46 m), 21-Feb 2012 (1.05 m), 3-Mar 2012 (1.02 m), 24-Oct 2012 (0.39 m), 30-Nov 2012 (1.27 m), 26-Feb 2013 (0.73 m), 9-Mar 2013 (0.23 m), and 8-Apr 2013 (0.92 m). An acute and widespread animal mass mortality event occurred during the November 2011 sandbar breach. The October 2012 event was a managed breach intended to alleviate harmful water quality conditions for federal ESA-listed threatened Central California Coast *O. mykiss* (NOAA 2013).

Salinity data are missing for January, February, March, June, and December 2012 (Fig. 2). Overall mean salinity, calculated from the 22 monthly means, was 11.2 ppt (Fig. 2). Minimum (1.8 ppt) and maximum (26.3 ppt) mean monthly salinities occurred in July 2013 and December 2011, respectively (Fig. 2). Salinity was fresh-brackish during winter ($\bar{x}$ =8.5 ppt) and spring ($\bar{x}$ =5.7 ppt) seasons and brackish during summer ($\bar{x}$ =13.6 ppt) and fall ($\bar{x}$ =13.4 ppt) (Fig. 2) seasons. Summertime salinity was brackish in 2011 ($\bar{x}$ =17.2 ppt) and 2012 ($\bar{x}$ =21.5 ppt) and fresh in 2013 ($\bar{x}$ =2.0 ppt) (Fig. 2). Overall, lower estuary (haul sampling zones 1 and 2, Fig. 1) salinities were 43% greater than levels in the upper estuary (zones 5 and 6, Fig. 1) and the difference during the open sandbar state (19%) was less than the partially open (51%) and closed (45%) ecosystem states.

Water temperature data are available for all months except June and December 2012 (Fig. 2). Overall mean water temperature, calculated from the 25 monthly means, was 15.1°C (Fig. 2). Minimum mean monthly water temperature (8.2°C) was measured in January 2013 and maximum mean monthly water temperature (21.8°C) was measured in September 2013 (Fig. 2). Mean water temperatures for winter, spring, summer, and fall were 10.5°C, 15.3°C, 17.7°C, and 15.6°C, respectively (Fig. 2). Mean summertime water temperatures were warmer in 2013 (20.1°C) than in 2011 (15.9°C) and 2012 (16.2°C) (Fig. 2). Overall, upper estuary (sampling zones 1 and 2, Fig. 1) water temperatures were 6% greater than lower estuary (sampling zones 5 and 6, Fig. 1) temperatures; the difference was more pronounced during the partially open state (11%) than the open state (6%). During the closed ecosystem state, temperatures were 3% lower in the upper estuary compared to the lower estuary.

Dissolved oxygen data are available for all months except June and December 2012 (Fig. 2). Overall mean dissolved oxygen levels, calculated from the 25 monthly means, was 8.4 mg·L^{-1}. Minimum (5.4 mg·L^{-1}) and maximum (11.2 mg·L^{-1}) mean monthly dissolved oxygen levels were measured in August 2012 and January 2012, respectively (Fig. 2). Dissolved oxygen levels declined consistently from winter ($\bar{x}$ =10.4 mg·L^{-1}) to spring ($\bar{x}$ =8.8 mg·L^{-1}), summer ($\bar{x}$ =7.5 mg·L^{-1}), and fall ($\bar{x}$ =7.1 mg·L^{-1}) seasons (Fig. 2). Summertime dissolved oxygen levels were normoxic for each of the three years ($\bar{x}$ =8.0 mg/L in 2011, 7.3 mg/L in 2012, 7.1 mg/L in 2013) (Fig. 2). Overall, upper estuary (haul sampling zones 1 and 2, Fig. 1) dissolved oxygen levels were 6% greater than those measured in the lower estuary (zones 5 and 6, Fig. 1); the difference was more pronounced during the open state (10%) than the partially open (2%) and closed (5%) ecosystem states.

Fish sampling - A total of 18,142 fish weighing approximately 851 total kg were captured by 410 seine hauls between July 2011 and September 2013. The relationships between measured fish lengths and masses used to estimate missing fish masses are presented in Table 1. Eight common species were encountered in more than 5% of the monthly samples and represent 99.9% of the total catch in terms of numerical abundance: steelhead/rainbow trout (*Oncorhynchus mykiss*) dominated the catch in terms of study reach mean CPUEa across the 27 month study period ($\bar{x}$ =20.7 fish·haul^{-1}) followed by topsmelt (*Atherinops affinis*, $\bar{x}$ =11.2 fish·haul^{-1}), Pacific staghorn sculpin (*Leptocottus armatus*, $\bar{x}$ =8.6 fish·haul^{-1}), threespine stickleback (*Gasterosteus aculeatus*, $\bar{x}$ =8.3 fish·haul^{-1}), prickly sculpin (*Cottus asper*, $\bar{x}$ =0.8 fish·haul^{-1}), starry flounder (*Platichthys stellatus*, $\bar{x}$ =0.3 fish·haul^{-1}), tidewater goby (*Eucyclogobius newberryi*, $\bar{x}$ =0.2 fish·haul^{-1}), and shiner perch (*Cymatogaster aggregata*, $\bar{x}$ =0.1 fish·haul^{-1}) (Table 2). *Oncorhynchus mykiss* also dominated the catch in terms of standardized biomass abundance (study reach mean CPUE$_b$=2001.8 g·haul^{-1}) followed by *A. affinis* ($\bar{x}$ =129.1 g·haul^{-1}), *P. stellatus* ($\bar{x}$ =74.6 g·haul^{-1}), *L. armatus* ($\bar{x}$ =24.0 g·haul^{-1}), *G. aculeatus* ($\bar{x}$ =8.1 g·haul^{-1}), *C. aggregata* ($\bar{x}$ =3.5 g·haul^{-1}), and *C. asper* ($\bar{x}$ =1.7 g·haul^{-1}) (Table 2). Rare species sampled include saddleback gunnel (*Pholis ornate*; n$_{tot}$=14), English sole (*Parophrys vetulus*; n$_{tot}$=4), striped bass (*Morone saxatilis*; n$_{tot}$=3), bonehead sculpin (*Artedius notospilotus*; n$_{tot}$=2), redtail surfperch (*Amphistichus rhodoterus*; n$_{tot}$=1), rock prickleback (*Xiphister mucosus*; n$_{tot}$=1), and walleye surfperch (*Hyperprosopon argenteum*; n$_{tot}$=1).

Spatiotemporal size and abundance trends - Mean fish size was greater in the lower three sampling sites compared to the upper three sampling sites (Fig. 1) for *O. mykiss* ($\bar{x}_{lower}$=112.6 g·fish^{-1}, $\bar{x}_{upper}$=104.2 g·fish^{-1}, Fig. 3a), *A. affinis* ($\bar{x}_{lower}$=10.4 g·fish^{-1}, $\bar{x}_{upper}$=9.7 g·fish^{-1}, Fig. 3b), *C. asper* ($\bar{x}_{lower}$=3.0 g·fish^{-1}, $\bar{x}_{upper}$=1.6 g·fish^{-1}, Fig. 3e), *P. stellatus* ($\bar{x}_{lower}$=215.2 g·fish^{-1}, $\bar{x}_{upper}$=161.9 g·fish^{-1},215.2, 161.9, Fig. 3f). The opposite was observed for *L. armatus* ($\bar{x}_{lower}$=2.3 g·fish^{-1}, $\bar{x}_{upper}$=2.7 g·fish^{-1}, Fig. 3c). Mean size for *G. aculeatus* was equal in the lower three and upper three sampling zones ($\bar{x}$=0.9 g·fish^{-1}, Fig. 3d).

Mean CPUEa was greater in the lower three sampling sites compared to the upper three sampling sites (Fig. 1) for *A. affinis* ($\bar{x}_{lower}$=19.0 fish·haul^{-1}, $\bar{x}_{upper}$=5.6 fish·haul^{-1}, Fig. 3b), *L. armatus* ($\bar{x}_{lower}$=13.4 fish·haul^{-1}, $\bar{x}_{upper}$=4.5 fish·haul^{-1}, Fig. 3c), *P. stellatus* ($\bar{x}_{lower}$=0.5 fish·haul^{-1}, $\bar{x}_{upper}$=0.1 fish·haul^{-1}, Fig. 3f), *E. newberryi* ($\bar{x}_{lower}$=0.3 fish·haul^{-1}, $\bar{x}_{upper}$=0.2 fish·haul^{-1}, Fig.

3g), and *C. aggregata* ($\bar{x}_{\text{lower}}$=0.2 fish·haul^{-1}, $\bar{x}_{\text{upper}}$=<0.1 fish·haul^{-1}, Fig. 3h). Mean CPUEa was greater in the upper three sampling sites compared to the lower three sampling sites (Fig. 1) for *O. mykiss* ($\bar{x}_{\text{lower}}$=10.5 fish·haul^{-1}, $\bar{x}_{\text{upper}}$=26.2 fish·haul^{-1}, Fig. 3a), *G. aculeatus* ($\bar{x}_{\text{lower}}$=7.4 fish·haul^{-1}, $\bar{x}_{\text{upper}}$=10.2 fish·haul^{-1}, Fig. 3d), and *C. asper* ($\bar{x}_{\text{lower}}$=0.3 fish·haul^{-1}, $\bar{x}_{\text{upper}}$=1.1 fish·haul^{-1}, Fig. 3e).

Study reach mean *O. mykiss* sizes were temporally bimodal with expression of a major peak from March to May ($\bar{x}$ =417.9 g·fish^{-1}, Fig. 4a) and a minor peak from November to December ($\bar{x}$ =270.6 g·fish^{-1}, Fig. 4a). *Atherinops affinis* mean sizes were largest from January to June ($\bar{x}$ =18.2 g·fish^{-1}, Fig. 4b) and smallest from August to December ($\bar{x}$ =6.7 g·fish^{-1}, Fig. 4b). Mean *L. armatus* sizes increased consistently from February ($\bar{x}$ =1.3 g·fish^{-1}, Fig. 4c) to October ($\bar{x}$ =7.6 g·fish^{-1}, Fig. 4c). *Gasterosteus aculeatus* mean sizes were relatively small from October to February ($\bar{x}$ =0.9 g·fish^{-1}, Fig. 4d) and relatively large from March to September ($\bar{x}$ =1.3 g·fish^{-1}, Fig. 4d). *Cottus asper* mean sizes were largest in April ($\bar{x}$ =15.4 g·fish^{-1}, Fig. 4e) and decreased considerably in May ($\bar{x}$ =5.0 g·fish^{-1}, Fig. 4e) before remaining low from June to December ($\bar{x}$ =1.6 g·fish^{-1}, Fig. 4e). *Platichthys stellatus* mean sizes were relatively small from December to May ($\bar{x}$ =108.6 g·fish^{-1}, Fig. 4f) and much larger from June to November ($\bar{x}$ =303.0 g·fish^{-1}, Fig. 4f). Mean *C. aggregata* size was relatively large in April, June, and July ($\bar{x}$ =28.8 g·fish^{-1}, Fig 4h) and relatively low from August to October ($\bar{x}$ =15.1 g·fish^{-1}, Fig 4h).

Study reach mean CPUE$_a$ values varied seasonally with elevated levels occurring for variable time periods depending on the species. Mean CPUE$_a$ was greatest during the winter and early spring periods for *L. armatus* (March-May $\bar{x}$=22.0 fish·haul^{-1}, Fig. 4c), *E. newberryi* (March-May $\bar{x}$ =0.5 fish·haul^{-1}, Fig. 4g), *G. aculeatus* (April $\bar{x}$ =45.0 fish·haul^{-1}, Fig. 4d), and *A. affinis* (February-March $\bar{x}$ =41.3 fish·haul^{-1}, Fig. 4b). *Oncorhynchus mykiss* standardized numerical abundance was greatest from May to October ($\bar{x}$ =33.0 fish·haul^{-1}, Fig. 4a) and peaked in July ($\bar{x}$ =72.4 fish·haul^{-1}, Fig. 4a). *Platichthys stellatus* abundance was greatest from June to July ($\bar{x}$ =1.1 fish·haul^{-1}, Fig.4f) and, for *C. asper*, from August to October ($\bar{x}$ =2.2 fish·haul^{-1}, Fig. 4e). The study reach mean CPUE$_a$ from March to October for the eight common species combined was 62.6 fish·haul^{-1} and was comprised almost entirely of *O. mykiss* ($\bar{x}$ =26.0 fish·haul^{-1}, Fig. 4a), *L. armatus* ($\bar{x}$ =12.7 fish·haul^{-1}, Fig. 4c), *A. affinis* ($\bar{x}$ =11.7 fish·haul^{-1}, Fig. 4b) and *G. aculeatus* ($\bar{x}$ =10.1 fish·haul^{-1}, Fig. 4d). The study reach mean CPUE$_a$ from November to February for the eight common species combined was only 18.3 fish·haul^{-1} and was comprised almost entirely of *A. affinis* ($\bar{x}$ =12.3 fish·haul^{-1}, Fig. 4b) and *G. aculeatus* ($\bar{x}$ =4.6 fish·haul^{-1}, Fig. 4d). Zero monthly catch occurred for *A. affinis* (July, Fig. 4b), *L. armatus* (January, Fig. 4c), *C. asper* (January, February, Fig. 4e), *E. newberryi* (January, February, November, Fig. 4g), and C. *aggregata* (November to March, May, Fig. 4h).

Year 2011 represented the largest summertime study reach mean fish size for *C. aggregata* ($\bar{x}$ =19.3 g·fish^{-1}, Fig. 5h) and smallest size for *O. mykiss* ($\bar{x}$ =56.4 g·fish^{-1}, Fig. 5a) and *P. stellatus* ($\bar{x}$ =34.0 g·fish^{-1}, Fig. 5f). Summer size was largest in 2012 for *O. mykiss* ($\bar{x}$ =200.5 g·fish^{-1}, Fig. 5a) and *G. aculeatus* ($\bar{x}$ =1.7 g·fish^{-1}, Fig. 5d) and smallest for *A. affinis* ($\bar{x}$ =2.2 g·fish^{-1}, Fig. 5b), *L. armatus* ($\bar{x}$ =4.0 g·fish^{-1}g, Fig. 5c), *C. asper* ($\bar{x}$ =1.1 g·fish^{-1}, Fig. 5e), and *C. aggregata* ($\bar{x}$ =18.3 g·fish^{-1}, Fig. 5h). Sizes were largest in summer 2013 for *A. affinis* ($\bar{x}$ =9.5 g·fish^{-1}, Fig. 5b), *L. armatus* ($\bar{x}$ =7.6 g·fish^{-1}, Fig. 5c), *C. asper* ($\bar{x}$ =4.1 g·fish^{-1}, Fig. 5e), and *P. stellatus* ($\bar{x}$ =448.2 g·fish^{-1}, Fig. 5f) and smallest for *G. aculeatus* ($\bar{x}$ =1.0 g·fish^{-1}, Fig. 5d).

Mean summertime study reach CPUE_{a} values were greatest in 2011 for *O. mykiss* ($\bar{x}$ =61.6 fish·haul^{-1}, Fig. 5a) and *P. stellatus* ($\bar{x}$ =0.9 fish·haul^{-1}, Fig. 5f), and lowest for *A. affinis* (zero fish·haul^{-1}, Fig. 5b), *G. aculeatus* ($\bar{x}$ =0.3 fish·haul^{-1}, Fig. 5d), and *E. newberryi* (zero fish·haul^{-1}, Fig. 5g). Overall summertime standardized abundances in 2012 were greatest for *A. affinis* ($\bar{x}$ =16.9 fish·haul^{-1}, Fig. 5b), *L. armatus* ($\bar{x}$ =13.9 fish·haul^{-1}, Fig. 5c), and *C. asper* ($\bar{x}$ =3.3 fish·haul^{-1}, Fig. 5e) and lowest for *O. mykiss* ($\bar{x}$ =13.9, Fig. 5a). Year 2013 represented the greatest summertime abundances for *G. aculeatus* ($\bar{x}$ =23.0 fish·haul^{-1}, Fig. 5d) and *E. newberryi* ($\bar{x}$ =0.5 fish·haul^{-1}, Fig. 5g) and the lowest abundances for *L. armatus* ($\bar{x}$ =0.7 fish·haul^{-1}, Fig. 5c), *C. asper* ($\bar{x}$ =0.6 fish·haul^{-1}, Fig. 5e), *P. stellatus* ($\bar{x}$ =0.2 fish·haul^{-1}, Fig. 5f), and *C. aggregata* (zero fish·haul^{-1}, Fig. 5h).

Assemblage structure - Fifteen total fish species were sampled over the 27 month study period. Maximum species richness (n=10 spp) occurred in April 2013 and minimum richness (n=1 sp) occurred twice in April 2011 and January 2012. Mean (±SE) richness is 6.0 (±0.4) species·month^{-1} and greatest during spring ($\bar{x}$±SE=7.3±0.7), least during winter ($\bar{x}$±SE=4.3±1.0) and intermediate during summer ($\bar{x}$±SE=6.8±0.6) and fall ($\bar{x}$±SE=5.2±1.1) seasons. The relationship between species richness (*S*) and calendar month is best described by second order polynomial regression: $S = -0.13 * \text{mo}^2 + 1.71 * \text{mo} + 1.55$ (R^2=0.65). According to this model, maximum species richness (S_{max}=7.4 species) is predicted to occur in the third week of July. Summertime species richness was greatest in 2012 ($\bar{x}$±SE=8.7±0.3), lowest in 2011 ($\bar{x}$±SE=5.7±0.3), and intermediate in 2013 ($\bar{x}$±SE=6.0±1.0). Compared to open or partially open sandbar states, species richness declines by 80% during winter when fully closed. The effect of closure on species richness is less pronounced during summer (16% decline), fall (5% decline), and spring (5% decline). When non-kill sandbar breaching events precede sampling, species richness is 171% and 10% higher in winter and spring, respectively. Four species were sampled several days after the breach-induced fish kill in November 2011 compared to seven species sampled during the same time of year in 2012 when no fish kill occurred.

Mean monthly species dominance values for the most numerically abundant and top two most numerically abundant species are 75% (range: 42%-100%) and 91% (range: 70%-100%), respectively (Table 2). In any given sample month, four different species (*O. mykiss*, *A. affinis, L. armatus, G. aculeatus*) represented the numerically dominant catch and six different species (*O. mykiss, A. affinis, L. armatus*, *G. aculeatus*, *C. asper, P. stellatus*) represented the second most numerically dominant monthly catch (Table 2). Mean species dominance values for the single most numerically abundant species are above average during fall ($\bar{x}$ =76%) and winter ($\bar{x}$ =85%) and below average during spring ($\bar{x}$ =70%) and summer ($\bar{x}$ =72%). The relationship between species dominance for the most numerically abundant species (D_{1n}) and calendar month is best described by second order polynomial regression: $D_{\text{1n}} = 0.51 * \text{mo}^2 - 7.54 * \text{mo} + 91.19$ (R^2=0.37). According to this model, minimum species dominance in terms of numerical abundance ($D_{\text{1n(max)}}$=69%) is predicted to occur during the second week of August.

Mean monthly species dominance values for the most biomass abundant and top two most biomass abundant species are 86% (range: 49%-100%) and 97% (range: 87%-100%), respectively (Table 2). In terms of biomass abundance, three species (*O. mykiss, A. affinis, G. aculeatus*) represented the dominant monthly catch and five species (*O. mykiss, A. affinis, L. armatus, G. aculeatus, P. stellatus*) represented the second most dominant monthly catch (Table 2). Mean species dominance values for the single most biomass abundant species are average in winter ($\bar{x}$ =86%), below average in fall ($\bar{x}$ =72%) and above during spring

($\bar{x}$ =90%) and summer ($\bar{x}$ =94%). The relationship between species dominance for the most biomass abundant species (D_{1b}) and calendar month is best described by second order polynomial regression: D_{1b} = -0.63*mo^2 + 6.68*mo + 76.10 (R^2=0.64). According to this model, maximum species dominance in terms of biomass abundance ($D_{1b(max)}$=94%) is predicted to occur during the second week of June.

A data matrix consisting of 145 rows with log$_{10}$-transformed monthly mean CPUE$_a$ values for the eight common species in each haul sampling zone (Fig. 1) was subjected to NMDS ordination analysis. Seventeen sample month-haul sample zone combinations are missing because of insufficient sampling conditions (see above). Two dimensional ordination analysis produced a stress value of 0.24. Therefore, three dimensional ordination was used instead (3D stress=0.18, Fig. 6a). Study reach mean NMDS axis 1 scores are sinusoidal over time (Fig. 6a). Study reach mean axis 2 scores decline temporally and those for ordination axis 3 are high during mid-investigation and low during early and late study periods (Fig. 6a).

Assemblage change - The overall mean Morisita similarity index is 0.38 for all sample months and sample zones combined (Fig. 6b). Mean Morisita similarity indices increase from downstream to upstream; lowest values occur at zone one ($\bar{x}$±SE=0.30±0.03, Figs. 1, 7a) and maximum values were observed at zone five ($\bar{x}$±SE=0.45±0.03, Figs. 1, 7a). The linear relationship between the six sampling zones (independent variable) and Morisita similarity index (dependent variable) is significant and positive (R^2=0.83, p<0.05, df=5) with a 3% increase in assemblage similarity for every 100 m of linear distance moved upstream (Fig. 7a).

Maximum and minimum mean monthly assemblage similarity occurred in June 2013 ($\bar{x}$ =0.54) and January 2012 ($\bar{x}$ =0.03), respectively (Fig. 6b). Mean Morisita similarity indices are low during fall ($\bar{x}$±SE=0.32±0.03, Fig. 7b) and winter ($\bar{x}$±SE=0.28±0.03, Fig. 7b) and elevated during spring ($\bar{x}$±SE=0.47±0.02, Fig. 7b) and summer ($\bar{x}$±SE=0.44±0.02, Fig. 7b). The relationship between Morisita similarity index (M) and calendar month (Fig. 7e) is best described by second order polynomial regression: M = -9.71·10^{-3}*mo^2 + 0.13*mo + 6.03·10^{-2} (R^2=0.91). According to this non-linear relationship, maximum similarity (M_{max}=0.50) is predicted to occur during the last week in July. Mean summertime Morisita index values increase from year 2011 ($\bar{x}$±SE=0.41±0.03, Fig. 7c) to 2012 ($\bar{x}$±SE=0.45±0.04, Fig. 7c) to 2013 ($\bar{x}$ ±SE=0.46±0.02, Fig. 7c). Compared to open or partially open sandbar states, Morisita similarity index declines by 90% in winter and increases by 18%, 7%, and 65%during spring, summer, and fall, respectively, when fully closed. When non-kill sandbar breaching events precede mid-month sampling, Morisita similarity index is 151% greater in winter and 12% lower in spring. Similarity for November 2011 ($\bar{x}$ =0.23, Fig. 6b), one week after the breach-induced fish kill, was 49% less than that observed during the same time of year in 2012 ($\bar{x}$ =0.45, Fig. 6b) when no breach or fish kill occurred.

Mean (±SE) apparent species turnover rates for all sample months is 0.30 (±0.04) (Fig. 6b). Maximum (T=0.71) and minimum (T=zero) turnover rates occurred in October 2011 and June 2013, respectively (Fig. 6b). Mean apparent species turnover rates are elevated during fall ($\bar{x}$±SE=0.36±0.10) and winter ($\bar{x}$±SE=0.48±0.06, Fig. 7e) and low during spring ($\bar{x}$±SE=0.18±0.04) and summer ($\bar{x}$±SE=0.20±0.03). The relationship between apparent species turnover rates (T) and calendar month is best described by second order polynomial regression: T = -9.34·10^{-3}*mo^2 - 0.14*mo + 0.68 (R^2=0.58). According to this non-linear relationship, minimum turnover (T_{min}=0.19) is predicted to occur during the third week of August. Mean summertime apparent species turnover rates increase slightly from year 2011 ($\bar{x}$±SE=0.18±0.09) to 2012 ($\bar{x}$±SE=0.19±0.05) and again from 2012 to 2013 ($\bar{x}$

±SE=0.22±0.02). When fully closed, apparent species turnover rates increase by 49%, 20%, and 22% during winter, summer, and fall, respectively, compared to open or partially open mouth conditions. In contrast, turnover rates during spring months are greater during partially open or open ecosystem states ($\bar{x}$ =0.21) compared to closed conditions ($\bar{x}$ =zero). Turnover rates are 132% higher during spring and 7% less during winter when non-kill breaching events precede fish surveys. Apparent species turnover rates after the fish kill in November 2011 (T=0.60) is 104% greater than that measured for November 2012 (T=0.29) when no breach or fish kill preceded sampling (Fig. 6b).

Ordination trajectory in species space according to NMDS axes 1 and 3 is directional and consists of relatively abrupt (haul sampling zone transitions 1 to 2, 2 to 3, and 4 to 5) and gradual (zone transitions 3 to 4, and 5 to 6) changes (Figs. 1, 7d). Temporal ordination behavior is directional with return and includes both gradual changes from September to January and saltatory shifts from February to August (Fig. 7e). Summer season multivariate behavior consists of idiosyncratic saltatory shifts that appear non-directional based on the very limited data (Fig. 7f). The shift from 2012 to 2013 is more abrupt than the shift from 2011 to 2012 (Fig. 7c).

According to two-way PERMANOVA, significant effects of month (p<0.001, *df*=11, *pseudo-F*=4.42) and sample zone (p<0.05, *df*=5, *pseudo-F*=1.6) on monthly fish assemblages are observed but not the interaction between month and sample zone (p>0.05, *df*=55, *pseudo-F*=0.26). According to SIMPER analysis, the species contributing most to the monthly differences are *O. mykiss* (29%), *A. affinis* (26%), *L. armatus* (20%), and *G. aculeatus* (18%). Also according to two-way PERMANOVA, a significant effect of summer year (p<0.001, *df*=2, *pseudo-F*=5.50) and haul zone (p<0.05, *df*=5, *pseudo-F*=1.21) on summertime fish assemblages is also observed but not the interaction between the two factors (p>0.05, *df*=10, *pseudo-F*=-0.17). The species contributing most to the annual differences according to SIMPER analysis are *O. mykiss* (27%), *G. aculeatus* (25%), *A. affinis* (19%), *L. armatus* (18%), and *C. asper* (7%).

Significant relationships between each ordination axis and associated biological and environmental parameters are plotted in three dimensions using Pearson r values as coordinates for ease of visual display (Fig. 8; sensu Desmond et al. 2002, their Fig. 6). The $\log_{10}$-transformed study reach mean monthly CPUE_a values for *O. mykiss* (r=0.87), *P. stellatus* (r=0.65), *L. armatus* (r=0.50), *C. aggregata* (r=0.43), and *A. affinis* (r=-0.72) are significantly correlated to mean monthly NMDS axis 1 scores (Fig. 8). Amongst the environmental factors significantly correlated to axis 1 mean values are photoperiod (r=0.80) and water temperature (r=0.45) (Fig. 8). Log_{10}-transformed study reach mean monthly CPUE_a values for *A. affinis* (r=0.63), *L. armatus* (r=0.42), *C. asper* (r=0.59), and *E. newberryi* (r=0.46) are biological variables significantly correlated to mean monthly ordination axis 2 scores (Fig. 8). Flow departure (r=-0.41) is the only environmental factor significantly correlated to axis 2 scores (Fig. 8). Log_{10}-transformed study reach mean monthly CPUE_a values for *L. armatus* (r=-0.70) and *G. aculeatus* (r=0.57) are significantly correlated to mean monthly NMDS axis 3 scores (Fig. 8). The environmental variables significantly correlated to axis 3 scores are days closed (r=0.72), water temperature (r=0.45), and mean overall (r=0.52), mean maximum (r=0.51), and mean minimum (r=0.42) WSEs (Fig. 8).

The biological variables significantly associated with study reach mean monthly Morisita similarity indices are $\log_{10}$-transformed study reach mean monthly CPUE_a values for *O. mykiss* (r=0.77), *P. stellatus* (r=0.44), and *A. affinis* (r=-0.43). Amongst the abiotic variables significantly correlated with study reach mean monthly Morisita index values are photoperiod (r=0.60), water temperature (r=0.53), and dissolved oxygen (r=-0.51). The biological variables significantly associated with monthly apparent species turnover rates are $\log_{10}$-tranformed study reach mean monthly CPUEa values for *O. mykiss* (r=-0.43), *P. stellatus* (r=-0.56), *C. aggregata* (r=-0.47), and *C. asper* (r=-0.40). The environmental variables significantly correlated to monthly apparent species turnover rates are photoperiod (r=-0.56), water temperature (r=-0.44), and maximum WSE (r=0.42).

Discussion

The Pescadero intermittent estuary fish assemblage is characterized by low species richness, high levels of species dominance, and distinct temporal abundance and size trends that produce seasonal species groupings that are modified according to interannual differences in the coastal sandbar regime and other environmental conditions. This 27 month continuous study commenced shortly before the onset of severe drought which provides a rare opportunity to understand the effects of environmental extremes on the ecology of California fishes in intermittent estuaries. Also, the availability of pre- and post- animal mass mortality event data are rare (Fey et al. 2015) and the breach-induced fish kill that occurred four months into the study presents another unusual scientific opportunity to assess the biological impacts of ecological shock.

Fifteen total fish species were sampled during this study. Low species richness is a common property of temperate estuary icthyofauna because unstable abiotic conditions require specialized physiological adaptations to rapidly fluctuating salinities, water temperatures, dissolved oxygen levels, turbidities, and other factors (Kennish 1990). While the Pescadero estuary is among the largest intermittent lagoonal estuaries in the region, its relatively small size compared to other brackish habitats in the state contributes to the low species richness. Allen et al. (2006) present a robust linear relationship between species richness (independent variable) and habitat area (dependent variable) for 15 California bays and estuaries and the Continental Shelf. Based on their model, the Pescadero lagoon is predicted to support 22 total species which is 47% more than the total described here and 5% more than the total reported by Smith (1990) for Pescadero lagoon fish surveys conducted periodically throughout the mid to late 1980s using a combination of gill nets and beach seines of variable dimensions and mesh sizes. While low fish species richness is a common feature in estuaries, unusually low diversity indicates a stressed fish fauna (Whitfield and Elliott 2002). It is not possible to determine if the reduced species richness observed here compared to the three decades before is the result of habitat degradation over time or an artifact of sampling gear bias (Murphy and Willis 1996). Breach-induced fish kills, however, were first reported in 1995 soon after the completion of substantial physical modifications to the estuary-marsh complex (reviewed by Smith 2009) and have recurred nearly every year since then which indicates that the ecosystem is currently distressed and experiences periodic loss of ecosystem function (Largier et al. 2015).

Eight common species were encountered in more than 5% of the monthly samples (Table 2) and, together, represent 99.9% of the total catch in terms of numerical abundance. All eight species share similar life history characteristics; each species is either bentho-pelagic (*O. mykiss, A. affinis, G. aculeatus, C. aggregata*) or demersal (*P. stellatus, L. armatus, C. asper, E. newberryi*) (Moyle 2002). All are euryhaline and prefer the shallow water protected habitats, such as those found in estuaries (Moyle 2002). Each species favors feeding on small crustaceans belonging to the family Pericaridae but are capable of switching to aquatic insects as a food source when lagoons form and salinities freshen (Robinson 1993, Martin 1995, Moyle 2002). Except for anadromous *M. saxatilis*, the rarely encountered species are all facultative marine fishes. Not surprisingly, 85% of the total individuals representing rare species were captured during periods of open or partially-open sandbar conditions with the majority being captured during summer (54% of total) followed by spring (23%), fall (15%), and winter (8%). All species sampled in the Pescadero estuary are native to California except for *M. saxatilis* which was introduced to the state from the east coast during the late 19th century (Moyle 2002).

Especially high levels of species dominance are observed in terms of both numerical and biomass abundance. Based on the overall mean for mean monthly study reach CPUE_a values, the four most abundant species in Pescadero intermittent estuary account for 97.0% of the total numerical abundance and include *O. mykiss* (41.1% of total abundance), *A. affinis* (22.3%), *L. armatus* (17.0%), and *G. aculeatus* (116.5%) (Table 2). In terms of the overall mean for mean monthly study reach CPUE_b values across the study period, *O. mykiss* alone accounts for 89.3% of the total biomass abundance followed by *A. affinis* (5.8%), *P. stellatus* (3.3%), and *L. armatus* (1.1%) (Table 2). Species dominance is a typical property of estuarine fish assemblages because relatively few species are adapted to the unstable environmental conditions and those that possess specialized physiological adaptations benefit from the presence of abundant and high quality food resources (Kennish 1990). Consequently, dominant species tend to utilize estuaries for nursery purposes (Kennish 1990). The overwhelming dominance of *O. mykiss* in the system, particularly in terms of biomass, is the result of several physiological, ecological, and evolutionary factors that include specialized chloride cells on gill surfaces for osmoregulation, large asymptotic body sizes, superior competitive abilities, the facultative use of estuaries for nursery purposes, and the obligate use of estuaries for both juveniles and adults as migration corridors (Moyle 2002, Hayes et al. 2008, Bond et al. 2008). Indeed, Central California Coast *O. mykiss* growth in intermittent estuaries can be as much as 80 times greater than that occurring upstream in freshwater (Hayes et al. 2008). Lagoon-rearing *O. mykiss* exhibit greater fitness than non-lagoon rearing fish (Bond et al. 2008) and it is possible that increased selection for extended estuarine nursery use has occurred over time as upstream habitats continue to degrade.

Relatively high numerical abundance, biomass abundance, species richness and Morisita assemblage similarity indices (Fig. 7b) and relatively low apparent species turnover rates occur during spring and summer. Together, the seasonal properties of the Pescadero intermittent estuary fish fauna produce the highly regular circular pattern of mean monthly ordination scores in “species space” (Fig. 7e). Maximum (July 2011 $\bar{x} = 172.8$ fish·haul^{-1}) and minimum (January 2013 $\bar{x} = 2.2$ fish·haul^{-1}) study reach mean CPUE_a values for all species combined varied by a factor of 79 (Table 2) and maximum (May 2012 $\bar{x} = 8781.3$ g·haul^{-1}) and minimum (January 2012 $\bar{x} = 17.1$ g·haul^{-1}) study reach mean CPUE_b values for all species combined varied by a factor of 514 (Table 2)! Study reach mean CPUE_a values for all species combined during summer ($\bar{x} = 70.1$ fish·haul^{-1}) is 3.0, 1.5, and 1.3 times greater than standardized numerical abundances during fall, winter, and spring, respectively (Table 2). Study reach mean CPUE_b for all species combined during spring ($\bar{x} = 3432.6$ g·haul^{-1}) is 4.1, 2.4, and 1.2 times greater than biomass abundances in fall, winter, and summer, respectively (Table 2). The elevated abundance of competitively superior *O. mykiss* during the spring and summer nursery period (Fig. 4a) likely limits species turnover rates which are more than two times less during those seasons compared to fall and winter. Assemblage similarity levels are more than 50% higher in spring and summer compared to fall and winter and are driven by the seasonal abundance trends of *O. mykiss* (Fig. 4a), the most dominant species in the assemblage. The distinct seasonal fish composition trends observed here are consistent with most studies of estuarine icthyofauna in both California (Allen et al. 2006) and elsewhere (Kennish 1990). These observations suggest that photoperiod and temperature are paramount factors that influence assemblage dynamics in temperate estuaries, including intermittent systems along California's coast. Environmental conditions are relatively stable and predictable during the productive spring and summer seasons of California's Mediterranean climate. Long photoperiods, warm temperatures, and the lack of storm-related disturbances favor high primary and secondary production rates.

Temporal trends of mean body sizes for commonly encountered fishes provide insight into the species' life history patterns and the Pescadero estuary's biological functions. Study reach mean *O. mykiss* size peaks in March ($\bar{x}$ =588.8 g or 365 mm FL, Table 1, Fig. 4a) before declining until July ($\bar{x}$ =61.9 g or 175 mm FL, Table 1, Fig. 4a). Mean *O. mykiss* size then increases steadily from July to December at an apparent growth rate of 41.8 g·month^{-1} (R^2=0.78, *df*=5, Fig. 4a) or 21 mm·month^{-1} (R^2=0.83, *df*=5, Table 1, Fig. 4a) according to linear regression analysis of mean monthly sizes. Observations of early spring mean size maxima can be attributed to two successful life history strategies regularly expressed by Central California Coast *O. mykiss*: iteroparity (Shapovalov and Taft 1954) and double smolting (Hayes et al. 2011). During periods of adequate marine connectivity, post-spawned adults (Shapovalov and Taft 1954) and large "twice smolts" (Hayes et al. 2011) rapidly migrate through the estuary from late winter to early spring. If permitted to exit, the large fish are replaced by smaller *O. mykiss* that continue to recruit to the estuary until early summer (Shapovalov and Taft 1954). Individuals belonging to the new cohort class continue to grow rapidly throughout the summer and fall if water quality conditions remain favorable (Hayes et al. 2008). For *A. affinis,* the second most dominant Pescadero fish species, mean sizes are largest during the first half (January-June $\bar{x}$ =18.2 g or 131 mm FL, Table 1, Fig. 4b) and lowest during the second half (August-December $\bar{x}$ =6.7 g or 96 mm FL, Table 1, Fig. 4b) of the year. In California, *A. affinis* fractionally spawn on benthic algae when estuarine water temperatures range from approximately 13-27°C and salinities are approximately 30 ppt (Moyle 2002). While they are capable of spawning from March to October, near marine salinities are usually not available in the Pescadero estuary after mid-summer sandbar formation. Juvenile *A. affinis* are omnivorous and feed on a combination of algae, detritus, and benthic invertebrates during fall and winter rearing periods (Moyle 2002). In contrast to *A. affinis, L. armatus* mean size increases consistently from February ($\bar{x}$ =1.3 g or 50 mm FL, Table 1, Fig. 4c) to October ($\bar{x}$ =7.6 g or 87 mm FL, Table 1, Fig. 4c) at an apparent growth rate of 0.8 g·month^{-1} (R^2=0.97, *df*=8, Fig. 4c) or 5 mm·month^{-1} (R^2=0.96, *df*=8, Table 1, Fig. 4c) according to linear regression analysis of mean monthly sizes. These observations are consistent with reproduction and rearing schedules for the estuarine resident species (Moyle 2002). *Leptocottus armatus* reproduction peaks during January and February in California when adequate salinities are available because embryos cannot tolerate salinities less than 10 ppt (Moyle 2002). Juvenile *L. armatus* rear in California estuaries from spring to fall and usually mature at age-1 (Moyle 2002). Small size and persistent expression of the low plate morphotype indicate that the Pescadero *G. aculeatus* population is comprised of non-migratory estuarine residents (Moyle 2002). The largest *G. aculeatus* measured for size was 74 mm TL and the mean total length of 21 males exhibiting breeding coloration from May to September was 56 mm±2.7 mm SD (range: 50-61 mm). The relationship between *G. aculeatus* size (g) and calendar month is best described by second order polynomial regression: size = $-1.88{\cdot}10^{-2}{*}mo^2 + 0.22{*}mo + 0.70$ (R^2=0.40, df=11). According to this relationship, minimum size (0.7 g or 42 mm TL, Table 1, Fig. 4d) is expected to occur in mid-December and maximum size (1.4 g or 52 mm TL, Table 1, Fig. 4d) is expected to occur during the last week of June. These properties suggest that Pescadero *G. aculeatus*, like others in the region, can mature in less than a year and spawn over a protracted time period (Snyder 1991, Moyle 2002). *Cottus asper* adults move downstream from lower reaches of rivers and streams to spawn in intertidal areas at the upper limits of estuaries from February to June with peaks occurring during April and May (Moyle 2002). Consistent with spring spawning behavior and subsequent rearing of age-0 fish in the estuary, *C. asper* sizes peaked in April ($\bar{x}$ =15.4 g or 108 mm TL, Table 1, Fig. 4e) and declined rapidly and remained low from late spring to fall (June-December $\bar{x}$ =1.6 g or 54 mm TL, Table 1, Fig. 4e). Apparent growth rate estimates for *P. stellatus*, a marine migrant species, are consistent with observations that peak spawning in the nearshore zone occurs during December and January and juvenile rearing occurs from spring to summer in Pacific Coast estuaries (Moyle 2002). According to linear regression analysis of mean monthly body sizes, *P. stellatus* apparent growth rates are approximately 34.2 $g{\cdot}month^{-1}$ (R^2=0.56, *df*=9, Fig. 4f) or 15 $mm{\cdot}month^{-1}$ (R^2=0.59, *df*=9, Table 1, Fig. 4f) from February to November. Viviparous *C. aggregata*, another marine migrant, give birth to live young from spring to summer in estuaries before returning to the ocean. The temporal size trends observed in the Pescadero estuary for *C. aggregata* (Fig. 4h) are consistent with reproductive and juvenile rearing schedules observed elsewhere (Moyle 2002). Mean monthly *C. aggregata* size declined consistently from a maximum of 32.0 g or 114 mm FL in April (Table 1, Fig. 4h) to a minimum of 10.1 g or 76 mm FL in September (Fig. 4h) as adults exited the estuary and juveniles remained in the system during the spring and summer for nursery period.

Temporal species abundance patterns are highly seasonal. The maximum abundance for seven of the eight common species occurred during spring or summer and minimum abundance for six species occurred during fall or winter (Figs. 4a-h). The species with the greatest difference between study reach mean $CPUE_a$ values in spring and summer compared to fall and winter was *O. mykiss* (851% greater in spring and summer; convention hereafter, Fig. 4a), followed by *P. stellatus* (567%, Fig. 4f), *C. aggregata* (567%, Fig. 4h), *G. aculeatus* (164%, Fig. 4d), *L. armatus* (141%, Fig. 4c), *C. asper* (125%, Fig. 4e), and *E. newberryi* (70%. Fig. 4g). *Atherinops affinis* represents the only exception; standardized abundances were 85% *less* in spring and summer compared to fall and winter (Fig. 4b). The abundance trends for *O. mykiss*, *P. stellatus*, *C. aggregata*, and *C. asper* reflect facultative nursery use of the estuary during the productive spring and summer months. Both *L. armatus* and *G. aculeatus* are estuarine resident species and the numerical abundance maxima in spring and summer occurs during post-spawning periods when numerical abundances are greatest. *Atherinops affinis* is a poorly competitive schooling marine species capable of tolerating low temperatures and may favor winter residency for predator avoidance and increased movement opportunities between the estuary and ocean.

Mean body size was largest in the two sampling zones closest to the ocean for six of the seven common Pescadero estuary fish species measured for size. Similar body size spatial patterns are expressed for nearly all common Pescadero intermittent estuary fish species (Figs. 1, 3a-h). Salinities were much higher in the lowest two zones and these findings are consistent with observations that salinity tolerances of estuarine fish species are age or size-dependent (reviewed by Varsamos et al. 2005). *Gasterosteus aculeatus* represents the only exception; overall, the largest-sized individuals ($\bar{x}$ =1.0 g) were sampled from the uppermost zone at a mean size only 10% larger than those sampled from zone two (Figs. 1, 3d). At this size, *G. aculeatus* are sexually mature and it is possible that the large sizes observed upstream results from the location's close proximity to flooded marshlands during the closed ecosystem state (Fig. 1) which provides favorable spawning and rearing habitat (see below; Moyle 2002).

The dissimilar species numerical abundance patterns in space (Figs. 3a-h) most likely result from a combination of species-specific natal origins and habitat preferences. Generally, salinities are much greater and water temperatures are slightly lower at downstream sites, particularly during periods of heightened marine connectivity. Study reach mean CPUE_a in the lower three sampling sites is greater than that in the upper three sites (Fig. 1) for *C. aggregata* (488% difference; convention hereafter, Fig. 3h) followed by *P. stellatus* (272%, Fig. 3f), *Atherinops affinis* (237%, Fig. 3b), and *L. armatus* (199%, Fig. 3c). All are marine-origin or estuarine resident species that prefer brackish-marine salinities (Moyle 2002). Alternatively, mean abundance in the upper three sampling sites is greater than mean abundance in the lower three sites (Fig. 1) for *C. asper* (323%; convention hereafter, Fig. 3e) followed by *O. mykiss* (150%, Fig. 3a), and *G. aculeatus* (38%, Fig. 3d). All three species spawn in freshwater or the upper limits of estuaries and oftentimes rear in estuaries (Moyle 2002, Bond et al. 2008, Hayes et al. 2008). *Gasterosteus aculeatus*, in particular, prefers clear shallow slow water zones with emergent vegetation for spawning and rearing (Moyle 2002) such as those found in the flooded marshlands adjacent to the upper sampling sites (Fig. 1) during the sandbar-closed ecosystem state. The deeper habitat provided in the upper sites (Fig. 1) favors large-bodied *O. mykiss* individuals (Everest and Chapman 1972), particularly during sandbar-open conditions when WSEs are lower overall (Fig. 2). Standardized numerical abundance of *E. newberryi* (Fig. 3g) is 79% greater in the lower three sites compared to the upper three sites (Fig. 1) which is unexpected because the estuary resident species prefers salinities less than 10 ppt. The majority of gobies, however, were captured during the closed ($\bar{x}$ =0.30 fish·haul^{-1}) and partially open ($\bar{x}$ =0.36 fish·haul^{-1}) ecosystem states compared to the open state ($\bar{x}$ =0.07 fish·haul^{-1}) and longitudinal salinity gradients in the estuary are dampened by the partial or complete presence of the coastal sandbar. It is also possible that the elevated downstream abundance of *E. newberryi* is partially attributed to sampling bias (Murphy and Willis 1996). By far, the greatest levels of benthic algae were observed in the shallow lower estuary in late spring and summer during partially open and closed conditions. The effective mesh size of the beach seine was reduced by the clogged algae which increased the likelihood of sampling small-bodied *E. newberryi* at the lower sites (Murphy and Willis 1996).

While unforeseen at the study's onset, the severe drought that officially commenced during WY 2012 and continued beyond the investigation's termination presents a special post-hoc opportunity to investigate the impacts of extreme climatic shifts on California intermittent estuary fish assemblages. Mean summertime flow departure in 2011, 2012, and 2013 declined from 1.6 to 0.8 to 0.1, respectively (Table 2) and the declining inflows induced ecosystem state shifts. Mean daily WSE (and daily range) was 1.70 m (0.53 m) in summer 2011, 1.51 m (0.45 m) in summer 2012, and 2.49 m (0.02 m) in summer 2013 (Fig. 2). Permutational hypothesis testing indicates that the Pescadero fish assemblage differed significantly between summer years and haul sampling zones (Fig. 1) and that the annual and spatial differences are consistent regardless of changes to the main effects. The species most responsible for the differences, in order of importance, were *O. mykiss*, *G. aculeatus*, *A. affinis*, *L. armatus* (18%), and *C. asper* (7%). The summertime *O. mykiss* standardized numerical abundance pattern (Fig. 5a) was unique amongst all common Pescadero estuary fish species; study reach mean CPUE$_a$ in summer 2012 ($\bar{x}$ =13.9 fish·haul^{-1}) was 4.4 and 4.3 times less than summer 2011 and 2012 values, respectively (Fig. 5a). The abundance pattern may result from strong size-based intraspecific competition effects (Moyle 2002); mean *O. mykiss* body size during summer 2012 ($\bar{x}$ =200.5 g·fish^{-1} or 256 mm FL, Table 1) was 3.6 and 3.2 times greater than mean masses in summers 2011 and 2013, respectively. Indeed, cannibalism by adult-sized *O. mykiss* was documented in 2012; a 485 mm FL sized fish captured on 20-July, 2012 contained four passive integrated transponder (PIT) tags in its stomach from fish tagged the previous day at fork lengths of 138, 140, 147, and 153 mm. In contrast to *O. mykiss*, standardized numerical abundances of *A. affinis* (Fig. 5b), *L. armatus* (Fig. 5c), and *C. asper* (Fig. 5e) peaked in summer 2012 when the estuary was partially open to the sea (Fig. 2). Partial tidal exchange during summer 2012 (Fig. 2) likely provided more favorable reproductive conditions for *A. affinis* for multiple reasons including, 1. opportunities for pre-spawning adult estuarine entry, 2. maintenance of elevated salinity levels, and 3. promotion of benthic algal bed formation. Besides allowing for optimum spawning conditions for *A. affinis*, the muted tidal mixing during summer 2012 (Fig. 2) enhanced the estuary's summertime nursery functions for demersal *L. armatus* and *C. asper* by maintaining adequate hypolimnetic water quality conditions and allowing predatory refugia from benthic algal cover. During summer 2011, movement opportunities between the estuary and ocean were available but algal beds probably did not develop because of strong tidal scour. Widespread benthic algae was present in 2013 but the completely closed conditions prevented movement opportunities and the lack of strong mixing forces produced hypoxic and anoxic bottom waters. Summertime numerical abundances of *G. aculeatus* (Fig. 5d) and *E. newberryi* (Fig. 5g) increased consistently over the three year period. Both *G. aculeatus* and *E. newberryi* are poor-swimming short-lived estuarine residents capable of rapid population increases during favorable environmental conditions (Moyle 2002). Reduced tidal water and freshwater currents during successive summer seasons possibly permitted downstream range expansion for both species. Also, increased flooding of adjacent marshlands (Fig. 1) by prolonged closure and high WSEs in 2013 (Fig. 2) created more favorable spawning habitat for *G. aculeatus* and *E. newberryi* in both space and time. The increased abundances should be interpreted as conservative estimates because both *G. aculeatus* and *E. newberryi* are small-bodied and a beach seine with a larger bunt mesh size than that used during summer 2011 and 2012 was used during summer 2013 in order to minimize handling of endangered *E. newberryi*. In contrast to the estuarine residents, summertime study reach mean CPUE$_a$ values for marine *P. stellatus* (Fig. 5f) and *C. aggregata* (Fig. 5h) declined steadily as the drought progressed. Also, while invertebrates are not included in the analyses presented here, it is also worth noting that the abundance of Dungeness crab (*Metacarcinus magister*) in the Pescadero estuary appears highly sensitive to sandbar-closed conditions. Extremely high summertime *M. magister* abundances were noted in summer 2011 but not enumerated. Study reach mean CPUE$_a$ values for July, August, and September 2012 were 11.5 crabs·haul^{-1}, 83.7 crabs·haul^{-1}, and 5.3 crabs·haul^{-1}, respectively. However, zero *M. magister* were sampled during the 2013 summer months. The decreased ecosystem connectivity during successive summers (Fig. 2) curtailed movement of marine fish species into the estuary during sandbar-closed periods and low bottom-water salinity and dissolved oxygen levels likely impaired *M. magister* habitat.

Despite pronounced environmental differences across summers, summertime Morisita assemblage similarity only increased by 3.1% from 2011 to 2012 and 1.3% from 2012 to 2013 (Fig. 7f). Summertime apparent species turnover rates also increased slightly over the three year period by 0.9% and 3.4% from 2011 to 2012 and 2012 to 2013, respectively. Temporal behavior of mean summertime ordination axes in species space (Fig. 7f) indicates that the 2011 assemblage is more advanced seasonally than the 2012 assemblage and that the 2013 summertime assemblage is the most anomalous of the three years (Figs. 7e, f). Stability of the basic structure of estuarine fish communities despite unstable physical conditions is commonly observed and results from several factors including the dominance of relatively few eurytopic species and predictable seasonal migration patterns (Kennish 1990). Anadromous *O. mykiss* dominates the summertime catch in terms of both standardized numerical abundance (65%) and biomass abundance (94%). The overwhelming dominance of *O. mykiss* during summer in the Pescadero estuary (Table 2), when juvenile recruitment to the nursery from upstream sources is mostly complete (Fig. 4a), is the single most important factor stabilizing the summertime assemblage as the drought progressed despite declining inflows and increased sandbar-closed conditions (Fig. 2).

A major goal of this analysis is to test for the influence of temporal and spatial factors on the estuarine fish assemblage. Two-way PERMANOVA hypothesis testing indicates that significant fish assemblage differences exist for calendar month and sampling zone (Fig. 1) and that the differences are consistent regardless of changes to the main factors. According to SIMPER analysis, the species most responsible for the assemblage differences, in order of importance, are *O. mykiss*, *A. affinis*, *L. armatus*, and *G. aculeatus*. One of these four species represented the most numerically dominant catch for any given sample month (Table 2). Consequently, the Pescadero intermittent estuary assemblage can conveniently be partitioned into separate species groupings or guilds based on life history characteristics of the four different dominant species: 1. the "anadromous guild" dominated by *O. mykiss* (n=12 mos, Table 2), 2. the "marine migrant guild" dominated by *A. affinis* (n=7 mos, Table 2), and 3. the "estuarine resident guild" dominated by either *L. armatus* (n=5 mos, Table 2) or *G. aculeatus* (n=3 mos, Table 2). For ease of visual display, significant Pearson r correlation values (positive or negative) between NMDS axes scores and biological and environmental variables are plotted as vectors in Fig. 8. In addition to *O. mykiss* (Figs. 4a, 8), the anadromous guild is represented by three additional sub-dominant species during long summertime days when water temperatures are elevated (Fig.2): *L. armatus* (Figs. 4c, 8), *P. stellatus* (Figs. 4f, 8), and *C. aggregata* (Figs. 4h, 8). The anadromous guild is characterized by large numerical and biomass abundances for all species combined (Table 2), elevated species richness and assemblage similarity (Figs. 6b, 7e), and low apparent species turnover rates (Fig. 6b). In contrast, the marine migrant guild, dominated by *A. affinis,* prevails during short winter days when water temperatures are cold (Figs. 2, 4b, 8). As mentioned previously, winter is a period of low numerical and biomass abundances for all species combined (Table 2), reduced species richness and assemblage similarity (Figs. 6b, 7e), and elevated apparent species turnover rates (Fig. 6b). The estuarine resident guild is represented by either *L. armatus* or *G. aculeatus* depending on season and sandbar status. *Leptocottus armatus* (Table 2, Figs. 4c, 8) is favored during the open ecosystem state in winter or spring whereas *G. aculeatus* (Table 2, Figs. 4d, 8) is favored during extended sandbar closed state in winter, spring or fall when water surface elevations and water temperatures are elevated (Fig. 2). *Atherinops affinis, E. newberryi*, and

C. asper are favored when freshwater inflows are atypically low for the given time of year (Table 2, Fig. 8).

Nine sandbar breaches occurred during the study period including one that triggered an acute and widespread fish kill from anoxia on 11-November, 2011. The availability of both pre- and post-animal mass mortality data is rare (Fey et al. 2015; exceptions include Becker et al. 2009) and the regularly occurring breach-induced fish kills in the Pescadero estuary offer an extraordinary opportunity to understand the abrupt and complete loss of ecosystem function on the fish assemblage. Fish mortalities included federal ESA-threatened Central California Coast *O. mykiss*, *A. affinis*, *G. aculeatus*, and *C. asper*. Many thousands of dead gammarid amphipods (*Corophium spinicorne*, *Eogammarus ramellus*) were also observed along the estuary's margins. Post-kill effects include reduced assemblage similarity levels (Fig. 6b), increased apparent species turnover rates (Fig. 6b), sharp declines in biomass abundance (Table 2), and a spike of seine hauls yielding zero fish catch. Mean Morisita similarity indices declined from 0.41 three weeks before the kill in mid-October 2011 to 0.23 one week after the kill event in mid-November 2011 (Fig. 6b). Mean assemblage similarity continued to decline to 0.15 in December 2011 and 0.03 in January 2012 before rebounding to more typical winter levels in February 2012 (Fig. 6b). Mean Morisita assemblage similarity and mean apparent species turnover rates from November to January are 58% less and 22% greater in 2011-2012, respectively, compared to the same time period in 2012-2013 when no kill was observed (Fig. 6b). Study reach mean $CPUE_b$ values for all species combined in October 2011 was 1.9 times greater than standardized biomass in October 2012. (Table 2). However, mean standardized biomass abundances for all species combined from November 2011 (one week post-kill) to December 2012 were 4.2 times less than mean biomass abundances for the same three month period in 2012-2013 when no kill occurred (Table 2). Furthermore, of the 29 total hauls yielding zero catch of any fish species during the 27 month study period, 86% of them occurred in November and December 2011. Not until mid-February did biomass abundances for all species combined in 2012 resemble those in 2013 (Table 2). Water quality conditions returned to more favorable conditions approximately two weeks after the kill which suggests an assemblage response lag of approximately 2.5 months behind environmental conditions when mass mortality events are associated with sandbar breaching. Individual species responded to the kill in dissimilar ways with some actually benefitting. Species that use the Pescadero intermittent estuary for nursery purposes were most negatively impacted by the breach-induced fish kill whereas residents that are poor competitors or marine migrants that require ecosystem connection appear to benefit from the dystrophic event. *Oncorhynchus mykiss* study reach mean $CPUE_a$ and $CPUE_b$ values declined by factors of 46 and 22, respectively, from October 2011 to November 2011 (Table 2). On the other hand, *A. affinis* and *G. aculeatus* study reach mean $CPUE_a$ values were 27.7 fish·haul^{-1} and 14.0 fish·haul^{-1}, respectively, in November 2011 after zero *A. affinis* and *G. aculeatus* were captured in eight seine hauls during October 2011 sampling (Table 2). Becker et al. (2009) report similar fish community responses to a breach-induced fish kill from anoxia in the Surrey River intermittent estuary (Victoria, Australia). However, the biological response in the Surrey River estuary appears to be much slower than that observed in the Pescadero estuary. Becker et al. (2009) report that relatively few marine migrants and estuarine residents were captured in the estuary three months following the dystrophic event. However, residents re-established their territories throughout the Surrey River estuary after six months post-kill. The authors attribute the assemblage response to the ability of fish to move to move and evade poor water quality zones in addition to life history characteristics that enable rapid population recovery such as high fecundity, fast growth, and short lifespans.

In summary, the Pescadero intermittent estuary an extensive estuary-coastal marsh wetland complex and provides critical rearing, reproductive, and migratory habitat for a variety of native anadromous, estuarine, and marine species including endemic and federal ESA-endangered *E. newberryi* and federal ESA-threatened Central California Coast *O. mykiss*. The Pescadero icthyofauna is marked by distinct seasonality with peak species richness, assemblage similarity, species turnover, numerical abundance, and biomass abundance occurring in spring and summer. The assemblage alternates between guilds dominated by *O. mykiss* during summer and another dominated by *A. affinis* during winter. After approximately 19 months of drought, the ecosystem shifted from a predominately open estuary to a closed lagoon. Disconnection between the estuary and ocean by the coastal sandbar favored small-bodied euryhaline-freshwater estuarine residents with short life cycles and protracted spawning periods and disfavored euryhaline-marine estuarine residents and marine migrant species. While the Pescadero estuary provides important ecosystem services, a history of nearly annual breach-induced fish kills since the mid-1990s indicates that the system is vulnerable to acute loss of ecosystem function. Impacts of one such mass mortality event observed here include termination of the estuary's nursery function and a pronounced decline in numerical and, especially, biomass abundances of all fish species combined. After approximately three months post-kill, assemblage characteristics rebounded to regular levels. More extreme climatic shifts, like those observed during this 27 month continuous study, are expected to be more common during the 21st century and future management decisions can be informed by the scientific information presented here.

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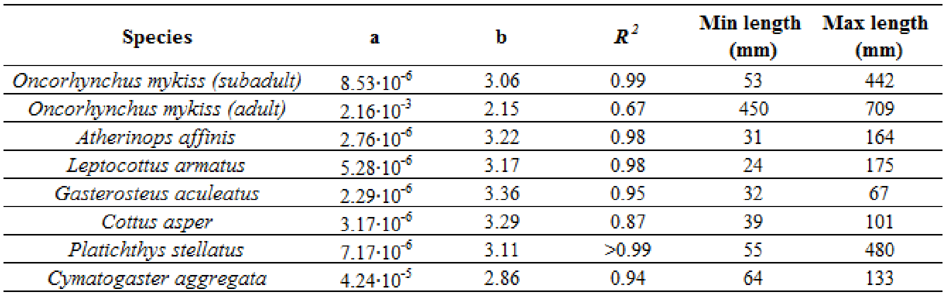
Table 1. Equation parameters for power functions ($g=a\cdot mm^{b}$) used to estimate individual fish masses (g) from body length measurements (mm) of commonly encountered fish species Goodness-of-fit R^2 values, minimum, and maximum lengths also presented. Total lengths are measured for species without a forked caudal fin (*L. armatus*, *G. aculeatus*, *C. asper*, and *P. stellatus*) and fork lengths measured for species possessing a forked caudal fin (*O. mykiss*, *A. affinis, C. aggregata*). Separate functions are presented for sub-adult (<450 mm FL) and adult-sized (≥450 mm FL) *O. mykiss* because of general poor condition for post-spawned adults.



Species	**a**	**b**	R^2	**Min length (mm)**	**Max length (mm)**
Oncorhynchus mykiss (subadult)	$8.53\cdot10^{-6}$	3.06	0.99	53	442
Oncorhynchus mykiss (adult)	$2.16\cdot10^{-3}$	2.15	0.67	450	709
Atherinops affinis	$2.76\cdot10^{-6}$	3.22	0.98	31	164
Leptocottus armatus	$5.28\cdot10^{-6}$	3.17	0.98	24	175
Gasterosteus aculeatus	$2.29\cdot10^{-6}$	3.36	0.95	32	67
Cottus asper	$3.17\cdot10^{-6}$	3.29	0.87	39	101
Platichthys stellatus	$7.17\cdot10^{-6}$	3.11	>0.99	55	480
Cymatogaster aggregata	$4.24\cdot10^{-5}$	2.86	0.94	64	133

Table 2. Study reach mean catch-per-unit-effort according to numerical abundance ($CPUE_a$, before “/”) and biomass abundance ($CPUE_b$, after “/”) for commonly encountered fish species according to study month. The most numerically dominant and second most numerically dominant species and associated values are presented. Flow departure and sandbar status are also indicated (O=open, C=closed, P=partial, $b_{(k)}$=breach with associated fish kill precedes sampling, $b_{(nk)}$=breach with no kill precedes sampling).

Year	Month	Mouth condition	Flow departure	Dominant species	2nd dominant species	Pct dominance (1 sp)	Pct dominance (2 spp)	*Oncorhynchus mykiss*	*Atherinops affinis*	*Leptocottus armatus*	*Gasterosteus aculeatus*	*Cottus asper*	*Platichthys stellatus*	*Eucyclogobius newberryi*	*Cymatogaster aggregata*	All
2011	Jul	O	1.4	*O. mykiss/O. mykiss*	*L. armatus/P. stellatus*	85/96	98/98	147.0/6044.9	0/0	22.1/97.2	0.2/0.2	0/0	2.2/115.1	0/-	1.3/41.7	172.8/6299.1
2011	Aug	O	1.7	*O. mykiss/O. mykiss*	*C. asper/L. armatus*	97/100	98/100	19.0/821.0	0/0	0.1/0.6	0.2/0.2	0.2/0.2	<0.1/0.3	0/-	0/0	19.5/822.3
2011	Sep	P	1.6	*O. mykiss/O. mykiss*	*L. armatus/L. armatus*	64/97	d	18.7/1589.0	0/0	5.3/31.2	0.6/1.3	3.9/7.9	0.6/9.4	0/-	0.2/1.3	29.3/1640.1
2011	Oct	C	2.0	*O. mykiss/O. mykiss*	-/-	100/100	-/-	18.4/2264.7	0/0	0/0	0/0	0/0	0/0	0/-	0/0	18.4/2264.7
2011	Nov	$P_{b(k)}$	1.4	*A. affinis/A. affinis*	*G. aculeatus/O. mykiss*	66/49	99/87	0.4/103.9	27.7/133.4	0/0	14.0/15.9	0/0	0.1/17.4	0/-	0/0	42.2/270.6
2011	Dec	O	0.9	*G. aculeatus/O. mykiss*	*O. mykiss/P. stellatus*	85/63	93/91	0.2/18.5	0.1/0.4	0.1/0.4	2.2/1.8	0/0	0.1/8.2	0/-	0/0	2.7/29.3
2012	Jan	C	0.6	*G. aculeatus/G. aculeatus*	-/-	100/100	-/-	0/0	0/0	0/0	17.3/17.1	0/0	0/0	0/-	0/0	17.3/17.1
2012	Feb	$P_{b(nk)}$	0.6	*L. armatus/O. mykiss*	*A. affinis/A. affinis*	60/86	91/95	0.5/144.7	1.9/14.9	3.7/4.8	0.1/0.1	0/0	0.1/3.1	0/-	0/0	6.3/167.6
2012	Mar	$P_{b(nk)}$	0.6	*L. armatus/O. mykiss*	*O. mykiss/L. armatus*	82/91	90/98	4.7/1332.6	0/0	50.3/98.3	2.9/4.1	2.0/6.4	0.3/28.9	1.3/-	0/0	61.5/1471.1
2012	Apr	O	1.3	*L. armatus/O. mykiss*	*O. mykiss/P. stellatus*	63/94	77/98	1.4/1077.3	0/0	6.4/9.4	1.4/3.1	0.3/8.2	0.3/43.6	0.2/-	0.1/3.2	10.1/1144.9
2012	May	O	1.1	*O. mykiss/O. mykiss*	*L. armatus/P. stellatus*	74/99	99/99	22.0/8733.0	0.3/7.2	7.4/16.3	0.2/0.1	0/0	0.1/24.7	0/-	0/0	30.0/8781.3
2012	Jun	O	1.0	*O. mykiss/O. mykiss*	*L. armatus/P. stellatus*	63/95	95/99	36.3/5303.9	0.1/3.1	18.5/56.2	0.8/1.3	<0.1/0.3	1.0/208.6	0.2/-	1.1/29.5	58.0/5603.0
2012	Jul	O	0.9	*O. mykiss/O. mykiss*	*L. armatus/P. stellatus*	76/98	88/99	28.2/2074.1	0/0	4.5/15.1	3.6/5.7	0.3/0.6	0.2/25.1	0/-	0.2/4.6	37.0/2125.2
2012	Aug	O	0.8	*L. armatus/O. mykiss*	*A. affinis/P. stellatus*	48/78	75/97	9.5/2023.6	18.3/9.9	32.3/61.9	1.9/2.7	3.3/1.9	1.1/499.9	0.3/-	0.1/1.8	66.8/2602.1
2012	Sep	P	0.7	*A. affinis/O. mykiss*	*C. asper/A. affinis*	67/85	80/93	4.1/1290.8	32.5/124.1	5.0/34.3	0.1/0.2	6.3/5.1	0.2/49.9	0.2/-	0.4/5.5	48.8/1510.0
2012	Oct	C	0.6	*A. affinis/O. mykiss*	*O. mykiss/A. affinis*	64/72	81/96	6.5/868.9	24.9/283.7	1.8/13.6	2.2/1.8	2.7/2.4	0.1/29.3	0.3/-	0.4/6.9	38.9/1206.8
2012	Nov	$P_{b(nk)}$	0.9	*A. affinis/O. mykiss*	*O. mykiss/P. stellatus*	42/87	70/95	2.5/828.4	3.8/44.0	0.2/1.2	2.3/1.3	0.1/0.1	0.1/71.7	0/-	0/0	9.0/946.7
2012	Dec	$O_{b(nk)}$	1.8	*A. affinis/A. affinis*	*G. aculeatus/O. mykiss*	96/58	98/100	0.3/119.6	26.9/167.5	0/0	0.6/0.3	0.1/0.1	0/0	0.1/-	0/0	28.0/287.6
2013	Jan	O	1.5	*O. mykiss/O. mykiss*	*P. stellatus/P. stellatus*	86/76	95/98	1.9/80.9	0.1/2.8	0/0	0/0	0/0	0.2/23.3	0/-	0/0	2.2/107.0
2013	Feb	O	0.8	*A. affinis/A. affinis*	*G. aculeatus/O. mykiss*	99/99	100/99	0.1/1.0	38.1/240.1	0/0	0.4/0.4	0/0	0/0	0/-	0/0	38.6/241.5
2013	Mar	$P_{b(nk)}$	0.6	*A. affinis/O. mykiss*	*G. aculeatus/A. affinis*	85/63	94/99	4.7/4202.2	125.3/2421.9	4.8/2.7	12.7/11.7	0.3/0.4	0/0	0.3/-	0/0	148.1/6639.1
2013	Apr	$P_{b(nk)}$	0.6	*G. aculeatus/O. mykiss*	*L. armatus/G. aculeatus*	76/86	89/93	10.7/932.5	1.2/20.0	15.3/34.8	88.6/73.8	0.4/1.4	0.1/22.9	0.5/-	0/0	116.8/1085.7
2013	May	P	0.6	*L. armatus/O. mykiss*	*O. mykiss/L. armatus*	69/90	95/99	18.0/1375.4	0.2/0.5	47.8/135.1	1.3/1.5	0.2/1.0	0.5/15.0	0.9/-	0/0	68.9/1529.0
2013	Jun	C	0.5	*O. mykiss/O. mykiss*	*L. armatus/P. stellatus*	77/77	89/99	22.5/1896.9	0.1/1.9	3.4/18.9	1.7/3.1	0.2/0.3	1.4/531.6	0.2/-	0/0	29.5/2452.8
2013	Jul	C	0.5	*O. mykiss/O. mykiss*	*G. aculeatus/P. stellatus*	69/92	94/99	42.0/2984.1	0/0	2.1/15.2	15.4/14.2	0.3/0.8	0.5/244.2	0.2/-	0/0	60.5/3258.6
2013	Aug	C	0.1	*O. mykiss/O. mykiss*	*G. aculeatus/G. aculeatus*	58/97	97/98	54.3/3343.5	1.1/10.5	0.1/0.8	36.9/41.1	0.6/2.8	0.1/40.8	0.7/-	0/0	93.8/3439.9
2013	Sep	C	-0.2	*O. mykiss/O. mykiss*	*G. aculeatus/G. aculeatus*	82/100	98/100	84.3/4593.3	0/0	0/0	16.7/15.1	1.0/5.1	0/0	0.7/-	0/0	102.7/4613.9

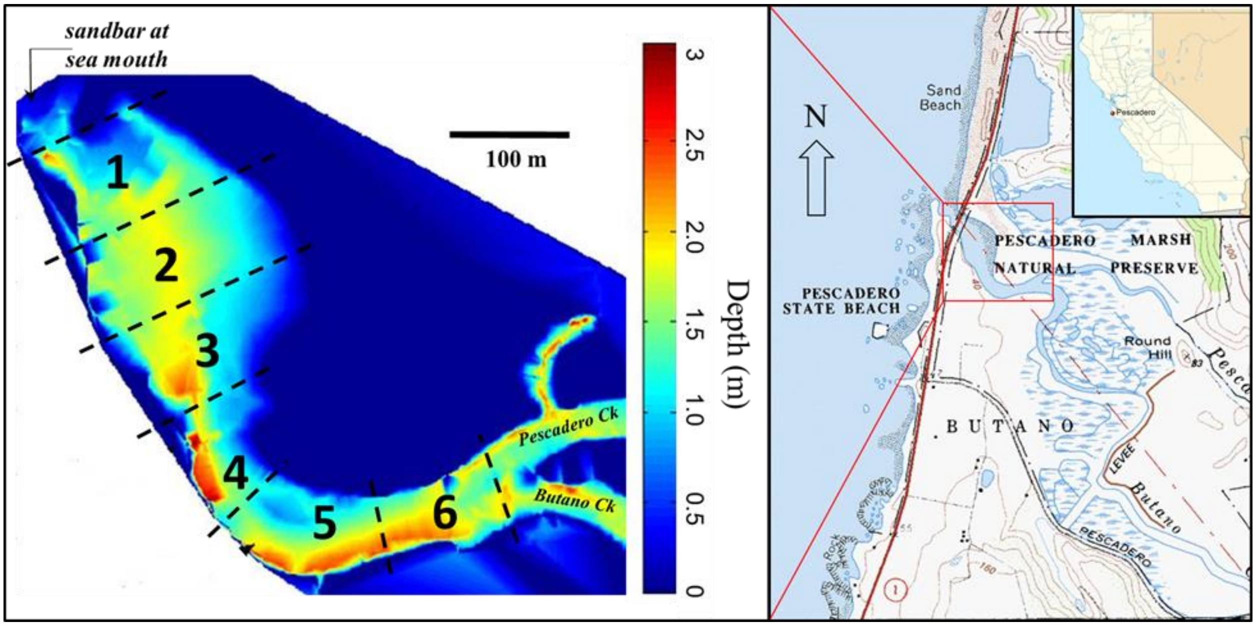


Figure 1. Location of the Pescadero intermittent estuary study site in Central California, USA, approximately 60 km south of San Francisco. The study reach is divided into six equally-spaced seine haul sampling zones. Bathymetry data are from October 2010 when the estuary was in a sandbar-closed ecosystem state.

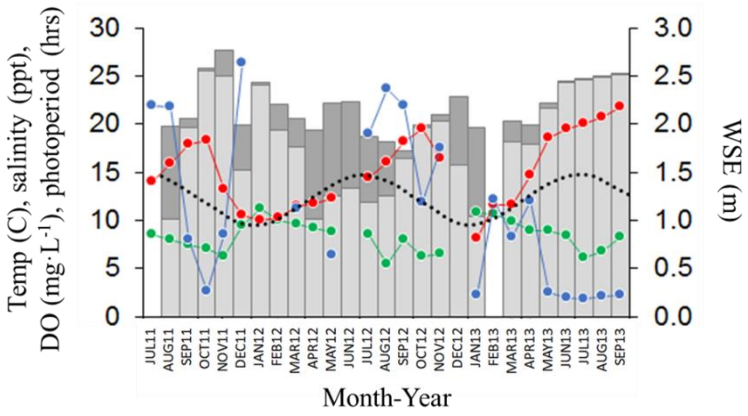
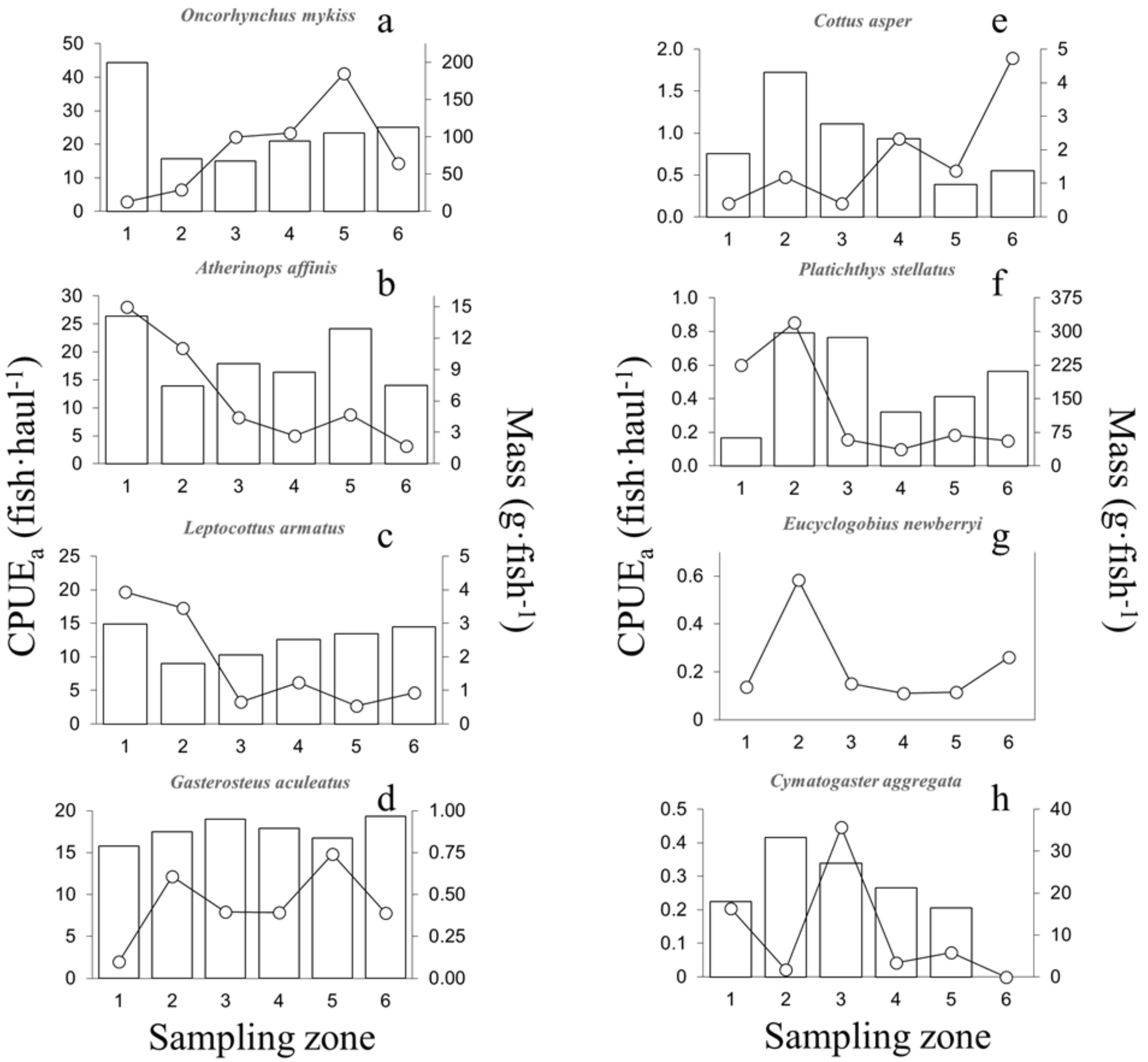
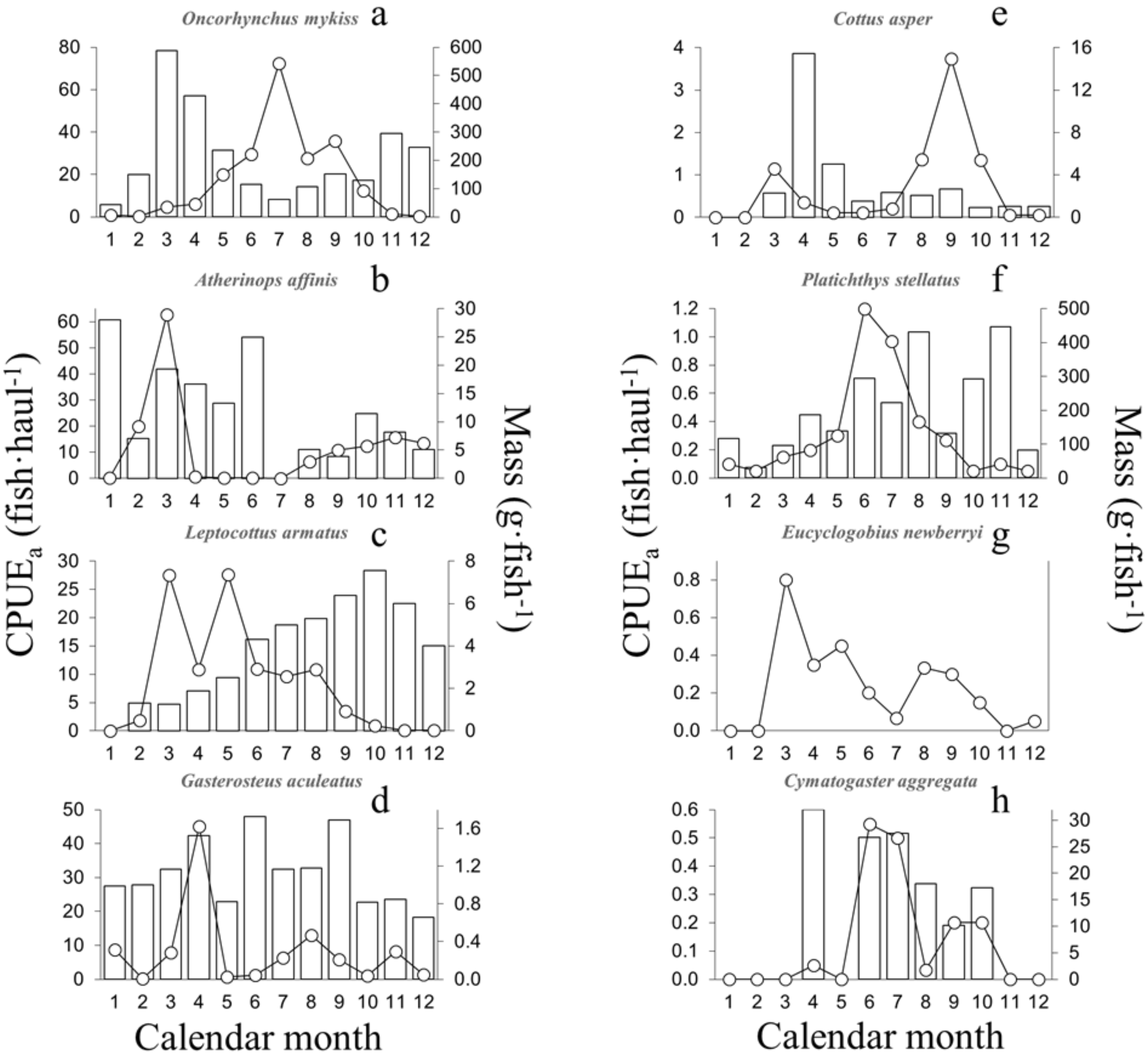


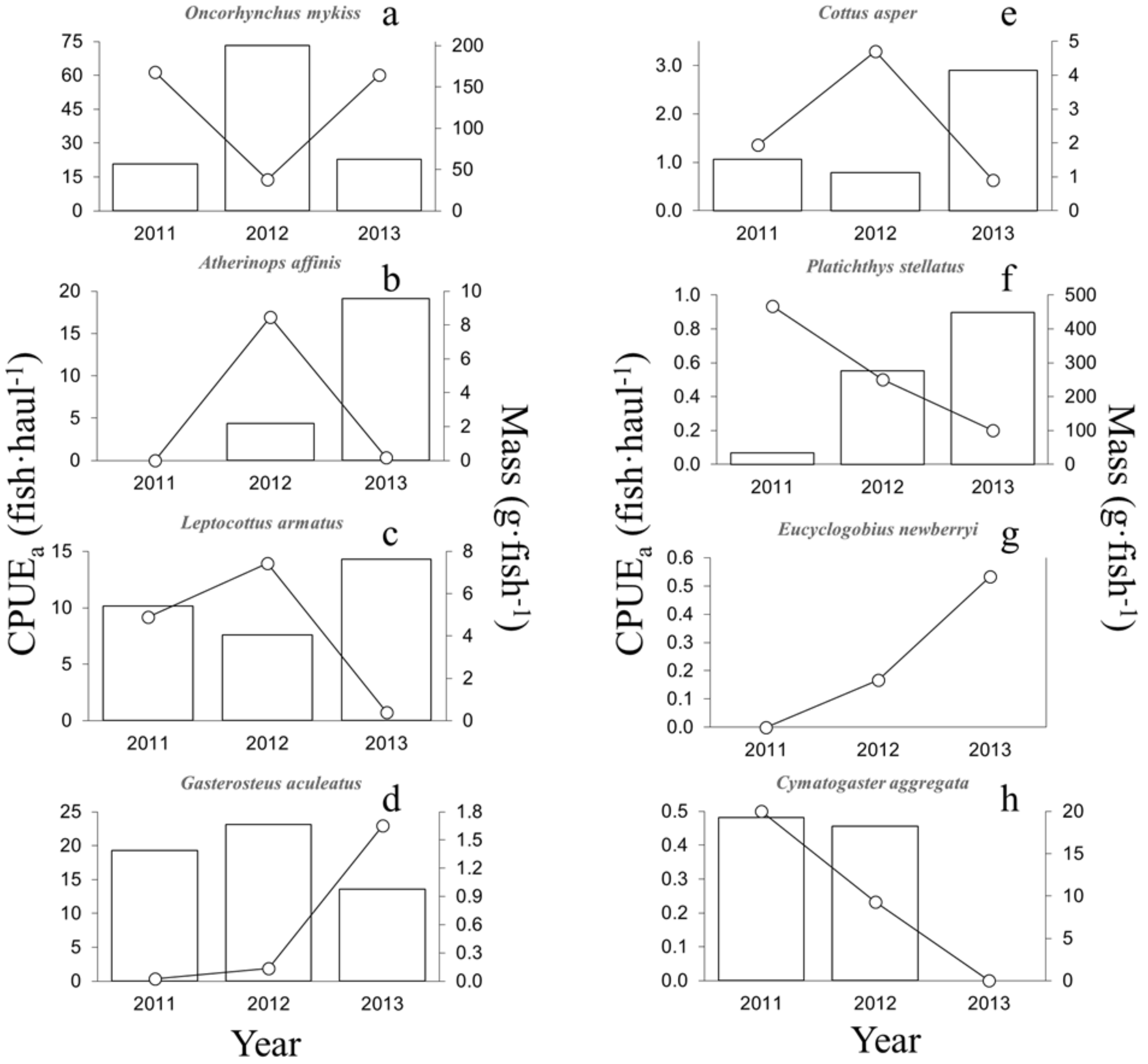
Figure 2. Mean monthly upper water column (≤150 cm depth) temperature (°C, red), salinity (ppt, blue), and dissolved oxygen (mg/L, green) measurements. Mean monthly photoperiod (hours, black dots), minimum water surface elevation (WSE, light grey bars), and maximum WSE (dark grey bars) are also presented.



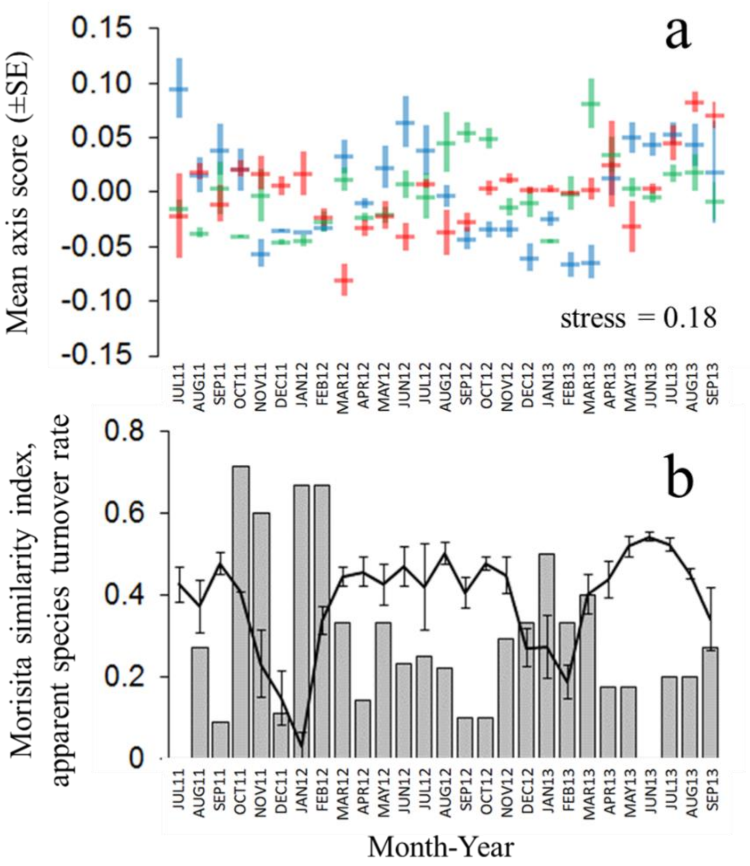
Figures 3a-h. Study reach mean catch-per-unit-effort according to numerical abundance (lines) and mean fish mass (bars) for commonly encountered Pescadero intermittent estuary fish species according to seine haul sampling zones.



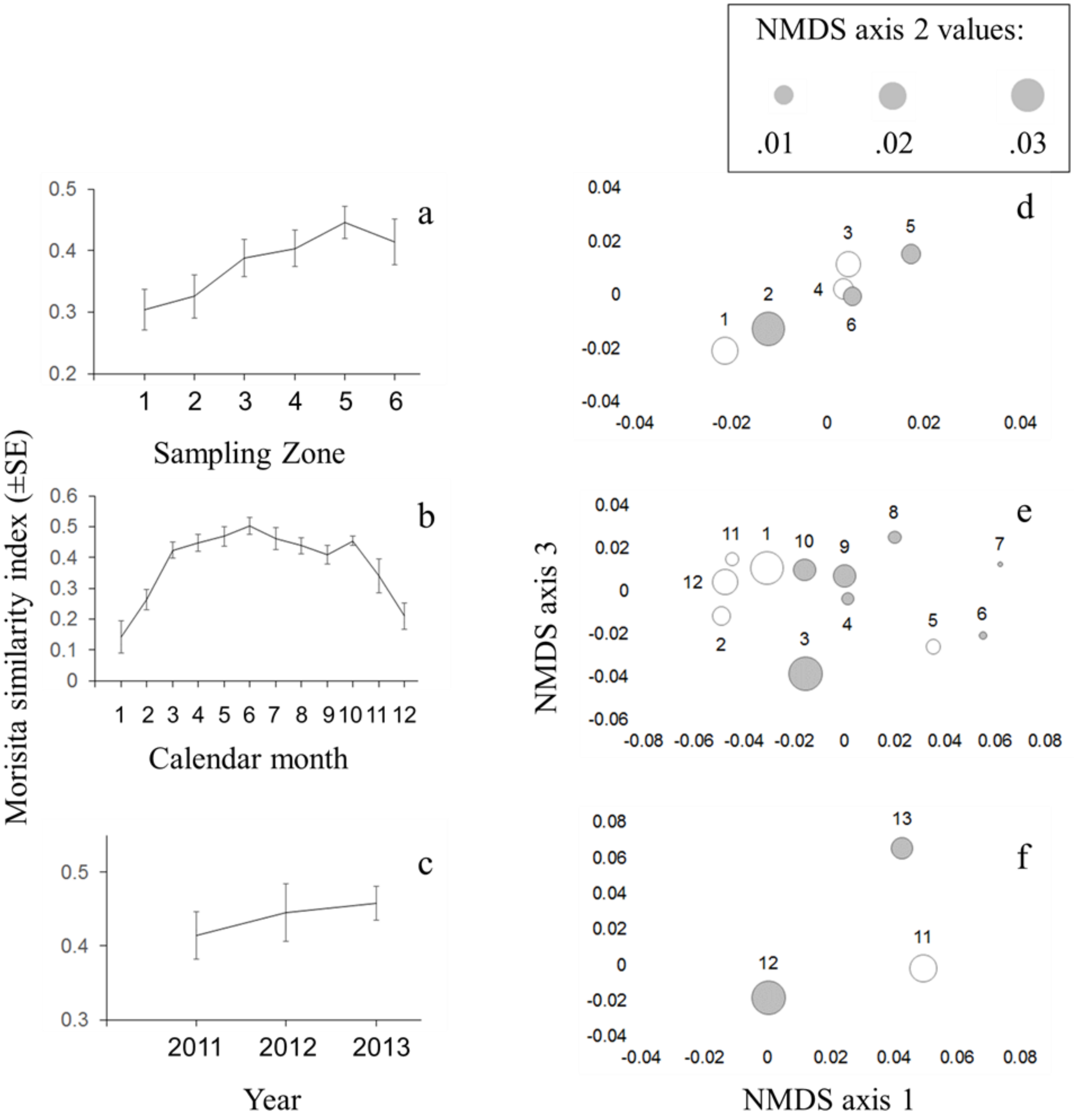
Figures 4a-h. Study reach mean catch-per-unit-effort according to numerical abundance (lines) and mean fish mass (g, bars) for commonly encountered Pescadero intermittent estuary fish species according to sample month.



Figures 5a-h. Mean summertime (July-September) study reach mean catch-per-unit-effort according to numerical abundance (lines) and mean fish mass (bars) for commonly encountered Pescadero intermittent estuary fish species from 2011-2013.



Figures 6a-b. Mean monthly three dimensional non-metric multi-dimensional scaling (NMDS) axes scores are shown in panel ‘a’ (blue: axis 1, red: axis 2, green: axis 3). Mean monthly Morisita similarity indices (line) and apparent species turnover rates (bars) are shown in panel ‘b’.



Figures 7a-f. Mean Morisita similarity indices according to seine haul sampling zone (panel ‘a’),calendar month (panel ‘b’), and summer year (panel ‘c’) are presented. Mean three dimensional non-metric multi-dimensional (NMDS) axes scores according to seine haul sampling zone (panel ‘d’), calendar month (panel ‘e’), and summer year (panel ‘f’) are also shown.

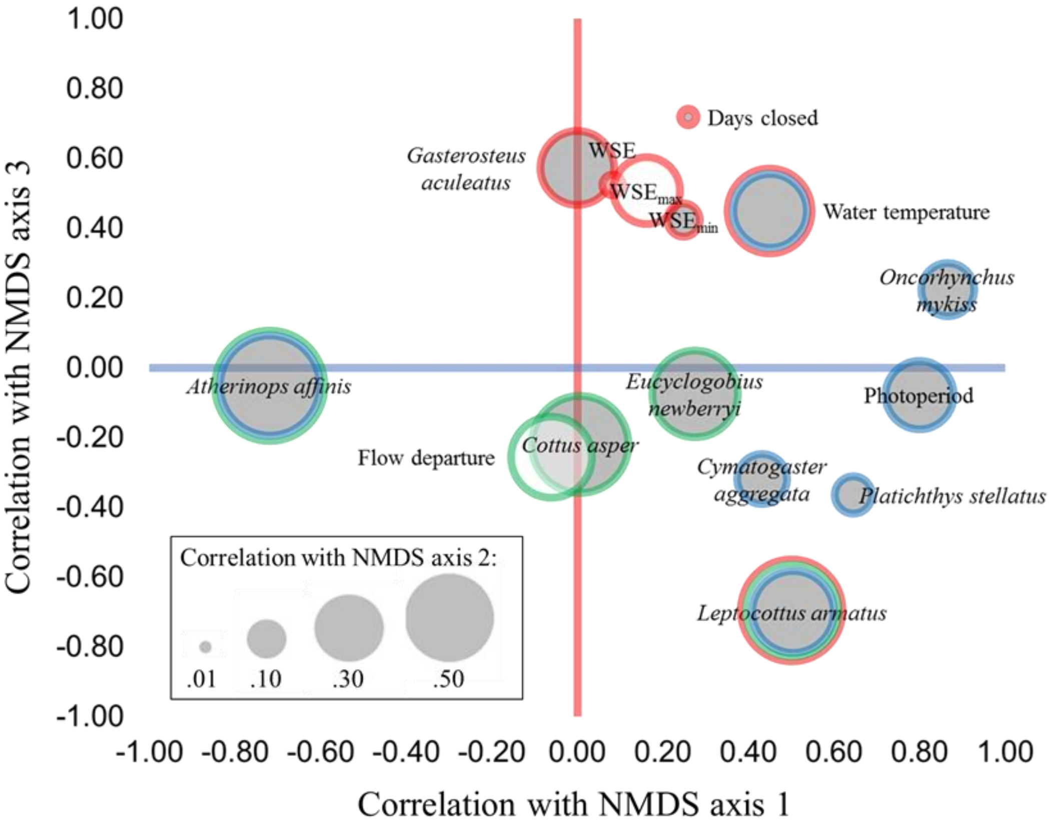


Figure 8. Pearson r correlations between non-metric multi-dimensional scaling (NMDS) axes scores and commonly encountered Pescadero intermittent estuary fish species or environmental variables. Color-coding indicates significant (*p*<0.05) correlations (blue: axis 1, green: axis 2, red: axis 3).

CHAPTER 4

JUVENILE STEELHEAD (*Oncorhynchus mykiss*) BODY GROWTH PATTERNS IN A CALIFORNIA INTERMITTENT ESTUARY DURING SEVERE DROUGHT AND SHIFTING ECOSYSTEM STATES

Juvenile steelhead (Oncorhynchus mykiss) body growth patterns in a California intermittent estuary during severe drought and shifting ecosystem states

Abstract: Fish life history expression is largely determined by growth performance and novel non-lethal techniques to reconstruct fine-scale growth trajectories of individual fish can benefit fisheries scientists and conservation managers. A new and simple method to assign dates to *Oncorhynchus mykiss* scale circuli and estimate growth and life histories is presented based on *scale radius-fish fork length* and *circuli spacing-measured body growth rate* relationships. Model development and results are validated using scales sampled from mark-recaptured fish. The results closely agree with those from a recently published laboratory study that discovered circuli spacing-growth rate relationships are mediated by water temperatures. This long-term investigation occurred shortly before and during severe drought which offers a special opportunity to understand the effects of climatic extremes on fish growth performance and life history expression. Several common life history types are detected based on shared growth histories and prolonged ocean disconnection appears to constrain *O. mykiss* life history decisions in the estuary. However, the extended lagoonal phase provides abundant aquatic habitat during extremely dry periods when freshwater rearing conditions are unfavorable. By using mark-recapture techniques to inform scale pattern analyses, far more insight about California *O. mykiss* estuarine ecology is gained than would be possible by using either method in isolation.

Keywords: biochronology, circuli, growth rate, ecosystem connectivity, bar-built estuary, temporary open/closed estuary (TOCE), intermittently closed/open lake and lagoon (ICOLL)

Introduction

Fish fitness and population and community dynamics are largely governed by patterns of individual growth performance (Wainwright 1994). Variable growth patterns promote population phenotypic expression (Hayes et al. 2008, Mangel and Satterthwaite 2008, Satterthwaite et al. 2009, 2010, 2012) and increased life history diversity enhances the resiliency of salmonid populations to fluctuating environmental conditions (Hilborn et al. 2003, Schindler et al. 2010, Moore et al. 2014). For salmonids, faster growing individuals possess enhanced osmoregulatory abilities (Wedemeyer et al. 1980), enabling more successful transitions from fresh to marine waters. Larger size confers survival advantages at sea (Healey 1982, Bond et al. 2008), particularly when ocean conditions are unfavorable (Holtby et al. 1990). Given the primary influence of physiology on fish ecology and population sustainability, new techniques that estimate fine-scale growth performance over time can benefit basic fisheries science and applied conservation management.

Fish growth is heavily influenced by environmental conditions and density-dependent biotic factors, especially temperature (Brett 1995) and competition for food and space resources (Bohlin et al. 2002, Vøllestad et al. 2002). Somatic growth is measured or estimated by several direct or indirect methods including mark and recapture techniques and the measurement of periodic growth increments preserved in calcified bony structures (Panfili et al. 2002). Commonly, marks with unique identifiers, such as passive integrated transponder (PIT) tags provide highly accurate data for individual fish but are costly and invasive and the temporal data resolution is oftentimes poor. Otoliths, while providing remarkably accurate records of daily growth, require lethal sampling and laborious preparation. Furthermore, detection of daily growth rings is only possible for the first year of life (Pannella 1971, 1974). Scales represent an appealing alternative calcified structure to otoliths because they are sampled non-lethally and are relatively inexpensive to analyze. Also, recent advancements in microscope camera technologies and freely available image analysis computer software permits far more data acquisition at reduced prices.

As early as the turn of the 20th century researchers noted that wider circuli spacing was associated with more rapid fish growth (reviewed by Jackson 2007). Since then, several studies have demonstrated that the circuli spacing increases with faster growth rate for salmonids (Bhatia 1931, Gray and Setna 1931, Bilton and Robins 1971, Healey 1982, Fisher and Pearcy 1990, 2005, Fukuwaka and Kaeriyama 1997, Beakes et al. 2014) and other teleosts (Doyle et al. 1987). Until recently, however, no studies explicitly tested how the relationship between circuli spacing and somatic growth rate varies according to temperatures and ration levels. Beakes et al. (2014) addressed the uncertainty by conducting a factorial laboratory study comprised of two ration treatments (high and low) and three temperature treatments (constant 8°C, 14°C, 20°C). The researchers discovered that the strong relationship between scale radii and body lengths for juvenile *Oncorhynchus mykiss* was independent of ration and temperature treatments but that temperature modulated the relationship between circuli spacing and somatic growth rates. The authors suggest that further ecological applications are possible, such as the effects of somatic growth and thermal regimes on scale development, provided environmental water temperatures are known.

The overall goal of this study is to explore the relationships between scale characteristics, somatic growth rates, and environmental temperatures for a population of mixed age *O. mykiss* sampled monthly from a relatively large Central California Coast intermittent lagoonal estuary over a multiple year period. My specific objectives are to: 1. Generate an empirical relationship between scale size and body size and use the model to back-calculate sizes-at-circuli; 2. Relate mark-recapture growth rate measurements to median circulus spacing for the period between tag and recapture and compare the results to Beakes et al. (2014); 3. Based on information obtained from objectives 1 & 2, assign estimated dates to scale circuli and reconstruct growth histories of individual fish; 4. Identify disparate life history types based on commonly expressed growth trajectories.

Intermittent estuaries are favorable sites for salmonid growth and life history studies reasons related to their roles as stop-over nursery habitats and migration corridors. Also known as “bar-built estuaries”, “lagoonal estuaries”, “temporary open/closed estuaries (TOCE)”, and “intermittently closed/open lakes and lagoons (ICOLL)”, these ecosystems are commonly encountered in small to medium-sized watersheds in regions with distinct wet/dry seasonality like portions of South Africa, Australia, and the west coasts of North and South America (Perissinotto et al. 2010). Regardless of the name given, these systems are characterized by the formation of a coastal sandbar which disconnects the estuary from the ocean for variable time which leads to profound changes in physical and chemical conditions. Amongst the natural and anthropogenic factors most influential on water quantity and quality are duration of mouth closure, hydraulic residence times, freshwater inflow levels, nutrient loading, and water abstractions (Perissinotto et al. 2010).

Current understanding of Central California Coast steelhead ecology derives from a combination of comprehensive research conducted historically in the Waddell Creek watershed (Shapovalov and Taft 1954), this study site (Pescadero estuary, Smith 1990, Robinson 1993, Martin 1995), and more recently in the Scott Creek watershed (e.g., Bond et al. 2008, Hayes et al. 2008, 2011, Satterthwaite et al. 2009, 2012). Juveniles rearing in the Scott Creek lagoon are amongst the fastest growing *O. mykiss* ever reported (Hayes et al. 2008) and fish may rear in the intermittent estuary for extended periods of time (1-10 months on average, Hayes et al. 2008). The rapid body growth is fueled by extremely high secondary production rates (Robinson 1993) that provide a fish with an abundant and high-quality food resource base (Martin 1995). During summer base-flow periods when upstream growth is slowest (Hayes et al. 2008), coastal lagoons provide abundant aquatic habitat with favorable water temperatures cooled by the coastal climate. The growth boosts enable fish to achieve threshold sizes that result in non-linear increases in ocean survival (Bond et al. 2008) and extended lagoon-rearing fish tend to have higher reproductive outputs than non-lagoon rearing individuals (Smith 1990, Bond et al. 2008). However, survival rates in intermittent estuaries can be poor (Satterthwaite et al. 2012) and widespread fish kills sometimes occur (Whitfield 1995), including repeated kills at the site studied here (Sloan 2006, Richards and Pallud 2016). Given the importance of these “high-risk-high-reward” habitats (Satterthwaite et al. 2012) to threatened and endangered populations of Coastal California steelhead and their ubiquity throughout the seasonally-dry region (Heady et al. 2014), more information is needed in order to better protect at-risk populations from further harm, particularly in systems experiencing recurring fish kills and other signs of ecosystem distress.

Methods

Study Site - The Pescadero intermittent lagoonal estuary (Fig. 1) is located in San Mateo County along California’s Central Coast, approximately 60 km south of San Francisco. It is associated with the most extensive coastal marsh complex for approximately 125 km between Elkhorn Slough to the south and San Francisco Bay to the north and provides critical habitat to several ESA-listed species including *O. mykiss*, tidewater goby (*Eucyclogobius newberryi*), San Francisco garter snake (*Thamnophis sirtalis tetrataenia*), red-legged frog (*Rana draytonii*), Western pond turtle (*Actinemys marmorata*), and Western snowy plover (*Charadrius nivosus*). The 212 km^2 watershed has two catchments: Pescadero Creek (155 km^2) and Butano Creek (57 km^2). Both originate in the heavily forested Santa Cruz mountains and converge in the upper estuary (Fig. 1). Total watershed relief is 830 m and mean annual precipitation is 84 cm. Approximately 90% of the precipitation falls between December and April. Coastal sandbar formation is highly seasonal and normally forms during the dry summertime period that characterizes the region’s Mediterranean climate. When open, the microtidal estuary is subject to diurnal tidal fluxes with a period of 12.4 hours. When full, the closed lagoon is approximately $1.0 \cdot 10^6$ m^2 in surface area and $1.2 \cdot 10^6$ m^3 in volume and mean and maximum depths are approximately 1.2 m and 3.5 m, respectively. Sandbar breaching usually occurs in the late fall or early winter and has been associated with 18 reported acute fish kills between 1995 and 2016 due to the chemical oxygen demand of iron sulfide flocculents entrained into the water column during drainage (Smith 2009, Largier et al. 2015, Richards and Pallud 2016).

Environmental Data - Water surface elevations (WSEs) were recorded hourly by a pressure sensor (RBR XR-420 CTD) positioned in the middle of the study site (sampling zone 4 or 5 in Fig. 1) from 14-Jul 2011 to 20-May 2013. During the sandbar-closed period from May 2013 to September 2013 WSEs were measured periodically from a staff gauge attached to a bridge pier near the mouth and missing daily values were interpolated by polynomial regression. Surface elevation data were converted to meters using the NAVD88 vertical datum

(GEOID 2009 model) and summarized as daily mean, minimum, and maximum WSEs. Mean values represent the mean of the minimum and maximum daily values. Water temperatures were measured hourly by automatic sensors (RBR XR-420 CTD, YSI 6600 Multi-Parameter Water Quality Sonde, or Hach Hydrolab MS5 Multi-Parameter Water Quality Sonde) positioned within 150 cm of the water surface in the middle of the study reach (zone 4 or 5 in Fig. 1) from 14-Jul 2011 until 9-Feb 2014. Temperature data are summarized as mean daily values and standard deviations. Occasionally data gaps occur due to instrument unavailability.

Fish Sampling - A total of six equally-spaced sample zones spanning a total distance of approximately 500 m from the estuary mouth to the river confluence (Fig. 1) were sampled mid-monthly with a beach seine during daylight hours. Continuous monthly sampling of all sample zones (conditions permitting) occurred from July 2011 to September 2013. Exploratory sampling of two sites also occurred in June 2010 and December 2013. During June 2010 and from July 2011 to April 2013, a 100'X6' beach seine (3/8" mesh) with a 6'X6' bunt (1/4" mesh) was used to sample fishes. From May 2013 to December 2013 100'X10' seine (3/8" mesh) with a 10'X10' bunt (3/8" mesh) was employed because of increased water depths and amendments to the state sampling permit. During the mark-recapture study months (July-November 2012; May-August 2013), 12-mm PIT tags (Oregon RFID) were implanted into the peritoneal cavity of CO_2-anaesthetized *O. mykiss*. The marking period consisted of two consecutive sampling days followed by two days of inactivity and one (sandbar-closed state) to three (sandbar-open state) days spent sampling recaptured individuals. All fishes were identified to the species taxonomic level and enumerated before being returned alive to the environment. A subset of *O. mykiss* was measured for fork lengths (FLs) and a subset of those was sampled for scales. Scales were removed from two to three scale rows above the left lateral line between the dorsal and anal fins (Scarnecchia 1979, zone 'A' in his Fig. 1) and stored in paper coin envelopes. Upon recapture, scales were removed from the fish's right side in order to avoid sampling regenerated scales. Incidental mortalities from two breach-induced fish kills that occurred on 11-Nov 2011 and 9-Feb 2014 in the estuary and adjacent marshlands were opportunistically sampled for scales. Additional *O. mykiss* scales were obtained from a subset of fish sampled from 26-Apr 2013 to 31-May 2013 at a migrant trap located in Pescadero Creek (37.2524°N, 122.3866°W), approximately 2 km upstream of the estuary.

Population size-The Lincoln-Petersen estimator (Seber 2002) is used to estimate *O. mykiss* estuary population sizes according to the following formula:

$$N = M \cdot C / R$$

where: N = estimate of total population size; M = total number of fish captured and marked on the marking period; C = total number of fish captured on the recapture period; R = number of fish captured on the marking period that were then recaptured on the recapture period. Confidence intervals (CIs) were calculated for the population size estimates following guidelines presented in Seber (2002).

Growth rate measurements - Tagged fish that were subsequently recaptured were re-measured for body size, allowing an assessment of individual growth rates during estuarine residency. Both absolute growth rates (AGR, $mm \cdot day^{-1}$) and specific growth rates (SGR, % $FL \cdot day^{-1}$) are presented here. The formulas used to calculate growth rates are:

$$AGR = (FL_{t+1} - FL_t)/(JD_{t+1} - JD_t)$$

$$SGR = 100\cdot((\ln(FL_{t+1})-\ln(FL_t))/(JD_{t+1}-JD_t)$$

where: FL = fork length (mm); JD = Julian day; t = time

Absolute and SGRs were calculated for each individual fish and then averaged for each month of study. Only fish that were marked in $month_t$ and recaptured in $month_{t+1}$ were used for somatic growth rate analysis.

Scale pattern analysis - Scales were removed from envelopes, cleaned in a 2.5% NaOH solution for 1-2 sec, and mounted in glycerin on a glass slide with a coverslip. Images of the most uniform non-regenerated scales were photographed by either a Canon EOS Rebel XS DSLR camera (Canon U.S.A., Inc.) or an AmScope 9MP digital camera (AmScope) mounted to the eyetube or eyepiece of a compound microscope. Magnified images (40X or 80X, Fig. 2) were imported into ImageJ version 1.48 (Rasband 2012). A micrometer was used to calculate pixel:distance ratios and calibrate the image analysis software. The PeakFinder Tool plug-in was used to automatically detect circuli followed by a visual inspection to correct potential errors made by the automated analysis (e.g., dust causing abrupt light-dark pixel shifts, Fig. 2). Scale characteristics (radius length, circuli number, circuli spacing) were measured along an axis 20° ventral to the anterior-posterior (i.e., long) axis that included the focus (Fig. 2). Circuli numbering commenced with the circuli closest to the scale focus and ended with the circuli closest to the scale's edge (Fig. 2). Scale radii represent the distance from the center of the focus (calculated as one half of its diameter along the 20° axis) to the outer edge of the scale. Fork lengths are estimated from scale radii by the regression method of back-calculation (Whitney and Carlander 1956):

$$FL_i = a\cdot(S_i) + b$$

where: FL = fork length (mm); S = scale radius (μm); i = time of back-calculation; a = slope of the liner regression between scale radius (independent variable) and fork length (dependent variable); b = regression intercept.

Growth rate modeling - The median circulus spacing of scales from recaptured fish from circuli numbers n_m to n_r is calculated, where n_m equals the total circuli count for scales sampled at PIT tagging and n_r equals the total circuli count for scales sampled at first recapture. A minimum of 28 days between marking and recapture is required for this analysis in order for multiple circuli to form. Median circuli widths are plotted against corresponding AGRs (sensu Beakes et al. 2014) and separate regression analyses are performed for non-overwinter and overwinter tag-recapture time periods because of the influence of water temperature on scale characteristics (Beakes et al. 2014).

Growth history reconstruction and validation - Calendar dates are assigned to individual circuli by dividing back-calculated body sizes-at-circuli (in mm) by the corresponding AGR estimates (in $mm\cdot day^{-1}$) and dating backwards from the outermost circulus (Fig. 2). The regression used to estimate somatic growth rate from circuli spacing (i.e. non-overwintering or overwintering model) is chosen according to the mean monthly water temperature for the given back-calculated date assigned to the circulus. The accuracy of growth history reconstructions is tested using scales sampled from recaptured *O. mykiss*; the back-calculated date associated with the back-calculated fork length that most closely matches the measured fork length at tagging is plotted against tagging date. If the slope is not significantly different from one, the method to reconstruct growth trajectories presented here is considered acceptable.

Statistical analyses - The ordinary least squares method is used for all regressions and a 95% confidence interval for the slope and intercept is calculated by bootstrapping with replacement from the pool of coordinates (n = 1999 iterations). For graphical displays, a 95% confidence interval (CI) band for the entire response line is presented (Working and Hotelling 1929). If the assumption of normal distribution of residuals is violated, a permutation *P* value based on bootstrapping is presented instead (n = 1999 replicates; sampling with replacement). The Breusch-Pagan statistic (Breusch and Pagan 1979) is used to test for heteroscedasticity of residuals and all hypothesis testing is considered significant at the $\alpha = 0.05$ level. For highly scattered raw data, locally weighted scatterplot smoothing (LOWESS, Cleveland 1979, 1981) with a smoothing parameter of 0.1 is used is used to clarify graphical presentations. This non-parametric procedure divides the space of the independent variable into different intervals according to the smoothing parameter and separate straight line regressions are fitted for each interval with a weighting function that decreases with distance. The smoothed point represents the fitted linear function at the original x coordinate. Mixture analysis is used to analyze frequency distribution modality. This method is a powerful maximum-likelihood technique for estimating measures of central tendency and variation (mean, standard deviation) for multiple groups of normal distributions based on a pooled univariate sample. The EM algorithm (Dempster et al. 1977) is used for the procedure and 20 automatic runs are conducted with new and random starting positions for the means of each iteration. The initial standard deviation is set to s/G, where s is the pooled standard deviation and G is the number of groups.

All statistical analyses are conducted using PAST, version 3.14 (Hammer et al. 2001).

Results

Environmental Data - The study coincided with the most severe drought on record which presents a unique opportunity to understand the effect of climate extremes on the estuarine ecology of California *O. mykiss*. The drought officially commenced water year (WY) 2012, approximately 2.5 months after the first month of continuous fish sampling in July 2011 and persisted beyond the end of the study period. Total outflow of Pescadero Creek, measured approximately 5 river km upstream of the estuary (USGS site no. 11162500), was 33,296 ac (WY 2011), 13,694 ac ft (WY 2012), 16,904 ac ft (WY 2013), and 1,839 ac ft (WY 2014). The prolonged drought induced an ecosystem state shift from a predominately open estuary (before May 2013) to a predominately closed lagoon (after and including May 2013) (Fig. 3a). The maximum WSE was recorded on 11-Nov 2012 (3.20 m, Fig. 3a) and the minimum on 13-Dec 2012 (0.80 m, Fig. 3a). Daily mean (and range) WSEs from July 2011 to April 2013 was 1.91 m (0.40 m) and, from May 2013 until the day before the 9-Feb 2014 breach, was 2.59 m (0.03 m) (Fig. 3a). Water surface elevation data gaps for the 942 day study period from mid July 2011 to the February 2014 breach exist for 7% of the total dataset and occur from 23-Mar 2012 to 19-Apr 2012, 5-Jun 2012 to 11-Jun 2012, and 18-Jan 2013 to 15-Feb 2013. Ten sandbar breaches (and WSE drop) occurred during the period on 11-Nov 2011 (2.22 m), 22-Jan 2012 (1.46 m), 21-Feb 2012 (1.05 m), 3-Mar 2012 (1.02 m), 24-Oct 2012 (0.39 m), 30-Nov 2012 (1.27 m), 26-Feb 2013 (0.73 m), 9-Mar 2013 (0.23 m), 8-Apr 2013 (0.92 m), and 9-Feb 2014 (>1.75 m) (Fig. 3a). Acute and widespread fish kills were associated with the November 2011 and February 2014 breaches. The October 2012 event was a managed breach intended to alleviate harmful water quality conditions for *O. mykiss* (NOAA 2013).

Water temperatures track a sinusoidal seasonal pattern (Fig.3b). The maximum water temperature was recorded on 15- and 16-Jul 2011 (27.4°C) and the minimum on 13-Dec 2013 (-0.5°C). The warmest and coolest mean daily temperatures were recorded on 4-Jul 2013 (23.1°C) and 15-Jan 2013 (4.9°C), respectively. Mean (and standard deviation) temperatures for winter (January-March), spring (April to June), summer (July-September), and fall (October-December) months are 10.7°C (2.0°C), 17.3°C (2.0°C), 17.6°C (2.5°C), and 12.4°C (2.9°C), respectively (Fig. 3b). Overall, mean monthly temperatures for summer and fall months are 3.3°C warmer and 0.7°C cooler, respectively, after the shift towards a predominately sandbar-closed system in May 2013 (Figs. 3a,b). Mean daily water temperature standard deviation is 57% less after the shift for months (January; June-December) when comparisons are possible (Fig. 3b). Daily water temperature data gaps exist for 21% of the total dataset and occur from 1-Sep 2011 to 24-Oct 2011, 9-Dec 2011 to 18-Dec 2011, 10-Feb 2012 to 29-Feb 2012, 17-Mar 2012 to 9-Jun 2012, 3-Oct 2012 to 11-Oct 2012, 22-May 2013 to 23-May 2013, 29-Aug 2013 to 4-Sep 2013, 20-Oct 2013 to 23-Oct 2013, 9-Dec 2013 to 13-Dec 2013, and 1-Feb 2014 to 6-Feb 2014.

Fish Sampling - The total number of *O. mykiss* captured per seine haul (i.e., catch-per-unit-effort, CPUE) for months when at least six seine hauls were performed (July 2011-August 2013) averaged 23.0 *O. mykiss*$\cdot$haul^{-1} but ranged over three orders of magnitude for the 26 month continuous sampling period (Fig. 4). Mean monthly CPUE ranged from a minimum of zero *O. mykiss*$\cdot$haul^{-1} in January 2012 to a maximum of 168.5 *O. mykiss*$\cdot$haul^{-1} in July 2011 (Fig. 4). Like water temperature, standardized catches also followed sinusoidal seasonal pattern; mean CPUE values for winter (January-March), spring (April to June), summer (July-September), and fall (October-December) months were 2.0, 22.1, 51.8, and 6.6 *O. mykiss*$\cdot$haul^{-1}, respectively (Fig. 3b).

Population size - Estimated estuarine *O. mykiss* population sizes (and 95% CIs) for July, August, September, October, and November 2012 are 5135 (3457-8176), 2045 (1107-3818), 306 (140-525), 262 (189-438), and 71 (35-280), respectively. Estimated population sizes (and 95% CIs) in 2013 for May, June, July, and August are 3028 (1491-6118), 2343 (1466-4268), 1787 (1011-2743), and 5485 (2587-11592), respectively. The correlation between mean monthly CPUE and mean monthly estuarine population size estimates is positive and significant and best described by a linear function: population size = 42.14$\cdot$CPUE + 1014.10 ($R^2 = 0.54$, permutation $P < 0.05$) (Fig. 5).

Somatic growth rate measurements - A total of 160 *O. mykiss* were recaptured one month following tagging and mark-recapture growth rate measurements are available for eight total sample months. The maximum number of recaptures (n=32) occurred in October 2012 and July 2013 and the minimum number (n=5) occurred in September 2012. Mean monthly AGRs (and standard deviations) ranged from a minimum of 0.18 mm$\cdot$day^{-1} (0.09 mm$\cdot$day^{-1}) from mid-August to mid-September 2013 and a maximum of 1.06 mm$\cdot$day^{-1} (0.12 mm$\cdot$day^{-1}) from mid-August to mid-September 2012 (Fig. 6a). Likewise, measured mean monthly SGRs (and standard deviations) ranged from a minimum of 0.12%$\cdot$day^{-1} (0.06%$\cdot$day^{-1}) from August-September 2013 and a maximum of 0.49%$\cdot$day^{-1} (0.07%$\cdot$day^{-1}) from August to September 2012 (Fig. 6b). Growth rate differences are partially attributed to population size. The negative linear relationship between estuary population size estimates for month$_t$ and AGRs from month$_{t-1}$ to month$_t$ is significant ($R^2 = 0.60$, permutation $P < 0.05$, Fig. 7a) and is described by:

AGR = $-1.04 \cdot 10^{-4} \cdot$population size + 0.92. For SGRs, the negative linear relationship between population size estimates for month$_t$ and SGRs from month$_{t-1}$ to month$_t$ is nearly significant (R^2 = 0.43, permutation P = 0.10, Fig. 7b) and is described by: SGR = $-2.34 \cdot 10^{-5} \cdot$population size + 0.43.

Scale pattern analysis - A total of 1197 scales and 54418 circuli were measured. The majority of *O. mykiss* scales were collected during mid-month sampling (80.2% of total) followed by fish kill (13.2%) and migrant trap (6.6%) samples. Fork lengths measurements are available for 1161 of the fish sampled for scales and the relationship between scale radius (SR, in μm) and fork length (FL, in mm) is highly significant with nearly all of the variation in body size explained by scale size: FL = 0.1551·SR + 31.35 (R^2 = 0.96, P < 0.001) (Fig. 8). According to mixture analysis of migrant trap samples, three *O. mykiss* groups were detected and defined by total circuli count and standard deviations of circuli count (Fig. 7a). Mean circuli count (and standard deviation) of the smallest group was 21.3 (6.3) circuli, followed by 50.7 (4.3) circuli for the intermediate sized group and 93.8 (2.5) circuli for the largest group (Fig. 9a). Visual assessment of the jitter plot found in Fig. 9b also indicates three groupings size-based groupings from seine and fish kill samples. When pooled across years, the smallest group increased from ca. 25 total circuli in April to ca. 55 circuli twelve months later in March (Fig. 9b). The intermediate size group increased from ca. 60 circuli to ca. 100 circuli for the same time period (Fig. 9b). The largest group increased from ca. 105 circuli in April to ca. 130 total circuli in September, the latest month that this group was observed (Fig. 9b). These values correspond to apparent circuli deposition rates of approximately 0.08 circuli·day^{-1}, 0.11 circuli·day^{-1}, and 0.16 circuli·day^{-1} for the small, intermediate, and large size groups (Fig. 9b), respectively.

Measured values and LOWESS smoothed estimates for circulus spacing and fork length according to circulus number are presented in figures 10a and 10b for all *O. mykiss* size groups. Circulus spacing decreases from circulus number 1 (smoothed spacing = 33.9 μm, Fig. 10a; smoothed FL = 49.0 mm, Fig. 10b) to 9 (smoothed spacing = 17.7 μm, Fig. 10a; smoothed FL = 74.3 mm, Fig. 10b). Spacing then increases from circuli 9 to 43 (overall rate of increase for smoothed values = 0.32 μm·circulus^{-1}, Fig. 10a; smoothed FL at circulus 43 = 204.7 mm, Fig. 10b) with the most rapid increase occurring between circuli 14 and 23 (overall rate of increase for smoothed values = 0.54 μm·circulus^{-1}, Fig. 10a; smoothed FLs at circuli 14 and 23 = 88.5 mm and 118.6 mm, respectively, Fig. 10b). Spacing remains constant from circuli 44-46 (mean smoothed spacing = 28.8 μm, Fig. 10a; mean smoothed FL = 214.0 mm, Fig. 10b) before increasing after circuli 46 and reaching a maximum of 34.1 μm at circuli 133 (overall rate of increase for smoothed values = 0.06 μm·circulus^{-1}, Fig. 10a; smoothed FLs at circuli 46 and 133 = 218.7 mm and 694.2 mm, respectively, Fig. 10b). Beyond circulus number 46, the most rapid spacing increase occurs from circuli 60-67 (overall rate of increase for smoothed values = 0.22 μm·circulus^{-1}, Fig. 10a; smoothed FLs at circuli 60 and 67 = 287.4 mm and 323.7 mm, respectively, Fig. 10b). Mean circuli spacing remains constant from circuli 86 to 133 (mean smoothed spacing = 34.0 μm, Fig. 10a; smoothed FL at circulus 86 = 430.1 mm, Fig. 10b).

Growth rate modeling- A total of 93 recaptured *O. mykiss* were sampled for scales at both tagging and again at first recapture. Of that total, 58 fish were tagged and recaptured within a rearing season (mean tag and recapture dates for 2012 and 2013 when the mark-recapture study was performed are June 28 and August 26, respectively). The remainder of the fish were initially recaptured after an overwintering period (mean tag and recapture dates for

2012 and 2013 are 5-Jul and 8-Feb, respectively). The linear relationships between AGRs (in mm·day^{-1}) and median circulus spacing (MCS, in μm) for the non-overwintering and overwintering groups are both positive and significant and, as expected, the properties differ between the non-overwintering group ($AGR = 4.87 \cdot 10^{-2} \cdot MCS - 0.49$; $R^2 = 0.62$, permutation $P < 0.001$, Fig. 11a) and the overwintering group ($AGR = 2.14 \cdot 10^{-2} \cdot MCS - 0.11$; $R^2 = 0.32$, permutation $P < 0.001$, Fig. 11b).

Growth history reconstruction and validation - According to an analysis of mean monthly water temperatures, the non-overwinter circuli spacing-body growth rate model is assigned to back-calculated dates from 1-May to 31-Oct and the overwinter model is assigned to back-calculated dates from 1-Dec to 31-Mar. For back-calculated days in April and November, the average growth rate estimate from values for both models is used. Occasionally extremely narrow or wide circuli widths were measured which correspond to unrealistic somatic growth and circuli deposition rates. Because of these irregularities, the minimum and maximum growth rates estimated from circuli are capped at $6.51 \cdot 10^{-2}$ mm·day^{-1} and 1.87 mm·day^{-1}, respectively. These values represent the 3rd and 98th percentiles of growth rates estimates by the non-overwintering circulus spacing-somatic growth rate model for all measured circuli and are considered realistic limits based on observed salmonid growth rates in nature (Fisher and Pearcy 1990). Growth trajectories are not made for circuli numbers 1-21 because these growth increments represent the average period of pre-estuarine growth (Fig. 9a) and no upstream water temperature records are available to inform back-calculations. A total of 143 scales sampled from recaptured fish are used to test the accuracy of assigning calendar dates to scale circuli. The minimum and maximum times between tag and recapture are 23 and 215 days, respectively, for this validation analysis. The linear relationship between tagging date (dependent variable) and back-calculated date when back-calculated fork lengths of recaptured fish most closely match measured fork lengths at tagging (independent variable) is strong ($R^2 = 0.93$) and the slope (value = 1.01) is not significantly different from one (95% CI: 0.96-1.05, $P < 0.001$) (Fig. 12).

Discussion

The close correspondence of this field investigation's findings with the laboratory results of Beakes et al. (2014) permits further exploration of the relationships between *O. mykiss* scale properties, somatic growth, and water temperatures in addition to new ecological applications. Traditionally, back-calculations of size-at-time from scales pattern analyses has been limited to annual or seasonal levels based on the assumption that abrupt shifts in circuli banding patterns represent periods of rapid growth change (Panfili et al. 2002). Here I introduce a novel and simple method to date scale circuli based on body size and grow rate estimates derived from scale characteristics which enables reconstruction of juvenile and adult *O. mykiss* growth histories at much finer temporal resolutions than that reported previously. In order to estimate growth trajectories, I relate mark-recapture growth rate measurements to scale growth increments detected by automated image analysis. Previously, reconstruction of fine-scale teleost growth trajectories was limited to the first year of life using otoliths (Pannella 1971, 1974). Since the relationship between growth rate and circuli spacing is independent of fish age (reviewed by Beakes et al. 2014), growth trajectories of individual fish can be generated beyond the first year of life using methods presented in this study for scales.

Similar to Beakes et al. (2014), circulus spacing of field-captured *O. mykiss* is strongly related to somatic growth rates and mediated by temperature. The slope (95% CI) and intercept

(95% CI) of the linear relationship between median circulus spacing (independent variable) and somatic AGR (dependent variable) for non-overwintering fish is $4.87 \cdot 10^{-2}$ $mm \cdot day^{-1} \cdot \mu m^{-1}$ ($3.82 \cdot 10^{-2}$ $mm \cdot day^{-1} \cdot \mu m^{-1}$to $5.71 \cdot 10^{-2}$ $mm \cdot day^{-1} \cdot \mu m^{-1}$) and -0.49 $mm \cdot day^{-1}$ (-0.69 $mm \cdot day^{-1}$ to -0.24 $mm \cdot day^{-1}$), respectively (Fig. 11a). The slope ($5.54 \cdot 10^{-2}$ $mm \cdot day^{-1} \cdot \mu m^{-1}$) and intercept (-0.45 $mm \cdot day^{-1}$) reported by Beakes et al. (2014) for juvenile *O. mykiss* subjected to a hot (20°C) temperature treatment are within the confidence intervals presented here for fish tagged and recaptured within a rearing season. The slope (95% CI) and intercept (95% CI) values for the linear relationship between median circulus spacing and somatic AGR for fish recaptured after an overwintering period are $2.14 \cdot 10^{-2}$ $mm \cdot day^{-1} \cdot \mu m^{-1}$ ($9.66 \cdot 10^{-3}$ $mm \cdot day^{-1} \cdot \mu m^{-1}$ to $3.59 \cdot 10^{-2}$ $mm \cdot day^{-1} \cdot \mu m^{-1}$) and -0.11 $mm \cdot day^{-1}$ (-0.41 $mm \cdot day^{-1}$ to 0.12 $mm \cdot day^{-1}$), respectively (Fig. 11b). The slope ($1.35 \cdot 10^{-2}$ $mm \cdot day^{-1} \cdot \mu m^{-1}$) and intercept ($-1.29 \cdot 10^{-2}$ $mm \cdot day^{-1}$) reported by Beakes et al. (2014) for juvenile *O. mykiss* subjected to the cold (8°C) temperature treatment are within the confidence intervals presented here for fish recaptured after overwintering period. Mean monthly temperatures (and mean tag/recapture period) are 17.9°C (June-August) and 14.5°C (July-February) for the non-overwintering and overwintering groups, respectively. Given these measured temperatures, it is surprising that the circulus spacing-somatic growth rate relationship for overwintering fish did not more closely match the slope ($6.04 \cdot 10^{-2}$ $mm \cdot day^{-1} \cdot \mu m^{-1}$) and intercept (0.72 $mm \cdot day^{-1}$) reported for fish subjected to the warm (14°C) temperature treatment by Beakes et al. (2014). It is possible that scale characteristics for fish in nature are affected by other environmental factors such as increased activity, changing photoperiod, and variable thermal, salinity, and dissolved oxygen regimes.

Scales do not begin forming in unison across the entire body surface of juvenile salmonids (Scarnecchia 1979) and a major limitation of scale pattern analysis likely results from inability to consistently sample the oldest scales containing the most complete growth records. This limitation is likely the primary factor producing the scatter observed in Fig. 12 and highlights the importance of consistently sampling scales from precisely the same body region every time. The median residual value for the relationship between tagging date (dependent variable) and back-calculated dates when back-calculated fork lengths of recaptured fish most closely match measured fork lengths at tagging (independent variable) according to the circuli dating method presented here is -3.4 days and the slope is 1.01 (95% CI: 0.96-1.05, Fig. 12). The residual interquartile range is -23.3 days to 23.3 days and the 5th and 95th percentiles are -79.5 days and 69.6 days, respectively (Fig. 12). As a result of the accurate central tendency but high dispersion (Fig. 12), caution is urged regarding the over-interpretation of back-calculations, particularly at the level of individual fish.

Despite aforementioned limitations, scale pattern analysis can help answer basic ecological questions like, what is the relationship between common growth trajectories and life history properties? Since upstream temperatures in the Pescadero watershed are unavailable, no attempts are made here to identify life history attributes prior to estuarine entry. However, early life histories of Central California Coast *O. mykiss* have already been described in detail (Shapovalov and Taft 1954, Bond et al. 2008, Hayes et al. 2008, 2011, Satterthwaite et al. 2009, 2012). Spawning occurs over an extended period between December and April (Shapovalov and Taft 1954). Juveniles grow slowly in freshwater; Hayes et al. (2008) estimate that age-0 *O. mykiss* in the Scott Creek watershed grow only 0.12 $mm \cdot day^{-1}$, on average, with least growth occurring during summer base flow periods. Likely resulting from protracted emergence periods and low growth performance, 40-60 mm sized fry were observed in natal streams throughout most of the year from late-May to mid-March (Shapovalov and Taft 1954).

Central California Coast *O. mykiss* migrate downstream at all ages but usually after their first winter at age-1 (Shapovalov and Taft 1954, Hayes et al. 2008). Non-linear increases in marine survival occur when *O. mykiss* smolts achieve minimum fork lengths of 150 mm (Bond et al. 2008). Consequently, rapid growth in intermittent lagoonal estuaries prior to ocean entry is critical for survival, similar to the role that inland floodplains provide to juvenile *O. tshawytscha* (Sommer et al. 2001, Jeffres et al. 2008). As the productive capacity of rivers and streams degrade, the importance of these stop-over nursery habitats likely increases.

Variable downstream migration ages and estuary and marine residence periods produced over 30 life history types expressed by Waddell Creek *O. mykiss* (Shapovalov and Taft 1954). Some are much more common than others; Hayes et al. (2008, 2011) describes several juvenile life history pathways typically expressed by Scott Creek *O. mykiss* based on different residence times in the upper watershed and estuary. The "estuary-lagoon rearing pathway" consists of fish recruiting to the estuary after rearing for only a few months upstream (Hayes et al. 2008). Fish following the "combined upper-watershed and estuary-lagoon rearing" pathway remain in the upper watershed for 1-2 years before spending 1-10 months in the estuary prior to ocean entry (Hayes et al. 2008). The "upper-watershed rearing" life history pathway describes two *O. mykiss* types – one that completes their entire life cycle in freshwater and another that migrates rapidly through the estuary to the marine environment after spending one or more years upstream (Hayes et al. 2008). The "smolting twice" life history pathway is comprised of large juvenile fish (>190 mm) that exit the estuary during the late winter and early spring after spending the previous year rearing in the estuary before returning upstream in fall when lagoon water quality conditions deteriorate (Hayes et al. 2011).

Here I use information from marked and recaptured fish in order to estimate growth histories from an additional 919 *O. mykiss* scales sampled shortly before and during severe drought and shifting ecosystem states (Fig. 13). Pescadero *O. mykiss* migrate to the estuary at multiple size classes; according to mixture analysis of fork lengths for *O. mykiss* sampled from 27-Mar to 31-May 2013 at the migrant trap, three size-based cohorts with mean fork lengths of 95 mm, 152 mm, and 222 mm are observed (CEMAR and Alnus Ecological 2013). One typical trajectory during 2011 and 2012 resembles the "combined upper-watershed and estuary-lagoon rearing" life history type described by Hayes et al. (2008); juvenile *O. mykiss* recruit to the estuary at lengths ranging from 100-175 mm FL and double their size by the end of the rearing season in fall or winter (Fig. 13). Another common pathway expressed in 2011 and 2012 resembles the "twice smolting" strategy described by Hayes et al. (2011). Indeed, the presence of this life history type in the Pescadero watershed has been confirmed by otolith microchemical analysis (Rankin 2014). In Pescadero, the double smolts recruit to the estuary at approximately 200 mm FL during March or April and grow rapidly from late spring to fall (ca. 1 $\text{mm}\cdot\text{day}^{-1}$ or faster, Figs. 6a, 13). Pescadero double smolts appear capable of reaching adult sizes after just 6-8 months growing in marine habitats (Fig. 13). The popularity of this life history type during periods of heightened ocean connectivity may result from the production of relatively large juveniles in Pescadero compared to other watersheds in the region (Shapovalov and Taft 1954, Hayes et al. 2008). Given that only 1.4% of the 4981 *O. mykiss* sampled in the estuary between April and August and measured for fork lengths are less than 80 mm, it is likely that the "estuary-lagoon rearing pathway" is either not commonly expressed in the Pescadero watershed or the type is confined to the upper estuary which was not sampled. The anadromous "upper-watershed rearing" life history type (i.e., steelhead) was most likely encountered in July 2011 and July 2012; during those two months, mean *O. mykiss* CPUEs are at least an order of magnitude greater than all other sample months (Fig. 4). It is highly likely that the estuary's carrying capacity was temporarily exceeded during July 2011 and July 2012 (Figs. 4, 5) and many steelhead probably used the estuary purely as a movement corridor instead of a nursery ground. Since scale samples were only obtained from the lowermost 2 km of the watershed in this study, identification of the freshwater resident "upper-watershed rearing" life history type (i.e., rainbow trout) is not possible.

What life history forcing results when the decision to enter the ocean is constrained by disconnection of the marine environment from the estuary? The severe drought which commenced during WY 2011 and continued beyond the end of the study period offers a unique opportunity to answer this interesting ecological question. After nearly 19 months of drought, the Pescadero intermittent estuary shifted from a predominately open estuary to a predominately closed lagoon following closure on 23-Apr 2013 (Fig. 3a). It appears that the double smolts that recruited to the estuary in 2012 were able to exit the system during early spring 2013 but that the 2013 recruits were forced to remain in the lagoon. This prevented the expression anadromous "upper-watershed rearing" life history type in 2013 as a result of the ongoing drought and summer closure (Fig. 13). Instead, these fish likely adopted the "combined upper-watershed and estuary-lagoon rearing" life history type (Fig. 13). Somatic growth for the 2013 land-locked recruits remained elevated for about three months after sandbar formation during late April 2013 (ca. 0.5 $\text{mm}\cdot\text{day}^{-1}$, Fig. 6a; ca. 0.3-0.4 $\%\cdot\text{day}^{-1}$, Fig. 6b) and was probably limited by density-dependent processes (Figs. 7a,b) as more *O. mykiss* recruited to the estuary (Figs. 4, 5) and water quality conditions remained suitable (Huber and Carlson in prep). Measured August-September AGRs and SGRs from mark-recaptured fish in 2013 were six and four times lower, respectively, than the same two month period during the previous year (Figs. 6a,b). Furthermore, the low growth rates appear to persist throughout fall and winter of 2013-2014 (Fig. 13). It is unlikely that density-dependence is a primary cause for the growth crash because recruitment appears to level off by July 2013 (Figs. 4, 5). By September 2013 the estuary converted to a non-salinity stratified fresh/brackish lagoon (Huber and Carlson in prep) and the reduced growth performance may result from a variety of factors related to prolonged closure including a shift of food resources from highly profitable Peracarid crustaceans to less profitable aquatic insects (Robinson 1993, Martin 1995), hypoxia (Brandt et al. 2009, Huber and Carlson 2017), benthic emissions of toxic hydrogen sulfide (Sloan 2006), and less variable thermal regimes (Fig. 3b; Matern et al. 2000).

Despite reduced growth variability and a less diversified *O. mykiss* life history portfolio for year 2013 recruits, the extended sandbar-closed period from May 2013 to February 2014 created abundant aquatic habitat (Fig. 3a) during an extremely dry and stressful period for inland fishes, including federally endangered tidewater goby (*Eucyclogobius newberryi*) (Huber and Carlson in prep). The additional three months of closure during the first one third of WY 2014 may have offset the reduced growth potential in the lagoon during the 2013-2014 rearing season. Measured fork lengths and total circuli counts for November 2011 and February 2014 salvaged fish kill specimens are very similar; median (and interquartile range) of fork lengths for 2011 and 2014 fish kill samples are 236 mm (203-258 mm) and 226 mm (209-245 mm), respectively. Likewise, median (and interquartile range) of total circuli for 2011 and 2014 fish kill samples are 52 circuli (42-58 circuli) and 57 circuli (50-62 circuli), respectively. However, survivors of the November 2011 fish kill would have had three extra months to develop in the high-growth marine environment which could lead to altered maturation schedules (Mangel and Satterthwaite 2008, Satterthwaite et al. 2009, 2010, 2012) in 2012 compared to 2014.

In conclusion, the close agreement between the results of this field study with those from a recently published laboratory investigation permits the development of a new and simple method to reconstruct *O. mykiss* growth and life histories that can benefit both fisheries scientists and conservation managers. The long-term study presented here began shortly before the onset of severe drought which offers a unique opportunity to understand the effects of climate extremes and shifting ecosystem states on California *O. mykiss* estuarine ecology. The "combined upper-watershed and estuary-lagoon rearing" type, anadromous "upper-watershed rearing" type, and "twice smolting" type appear to be important life history pathways for Pescadero *O. mykiss* during periods of estuary-ocean connectivity. Furthermore, fish adopting the "twice smolting" strategy appear capable of achieving adult sizes after a brief period of marine residency. The estuary transitioned to a persistent sandbar-closed phase after just over 1.5 years of drought which reduced the life history portfolio to a single type - the "combined upper-watershed and estuary-lagoon rearing" pathway. These life histories expressed in Pescadero have been described elsewhere for Central California Coast *O. mykiss* (Shapovalov and Taft 1954, Hayes et al. 2008, Hayes et al. 2011) and when different life history patterns are persistent and widespread, they are believed to be locally adaptive and serve as alternative solutions to fitness optimization.

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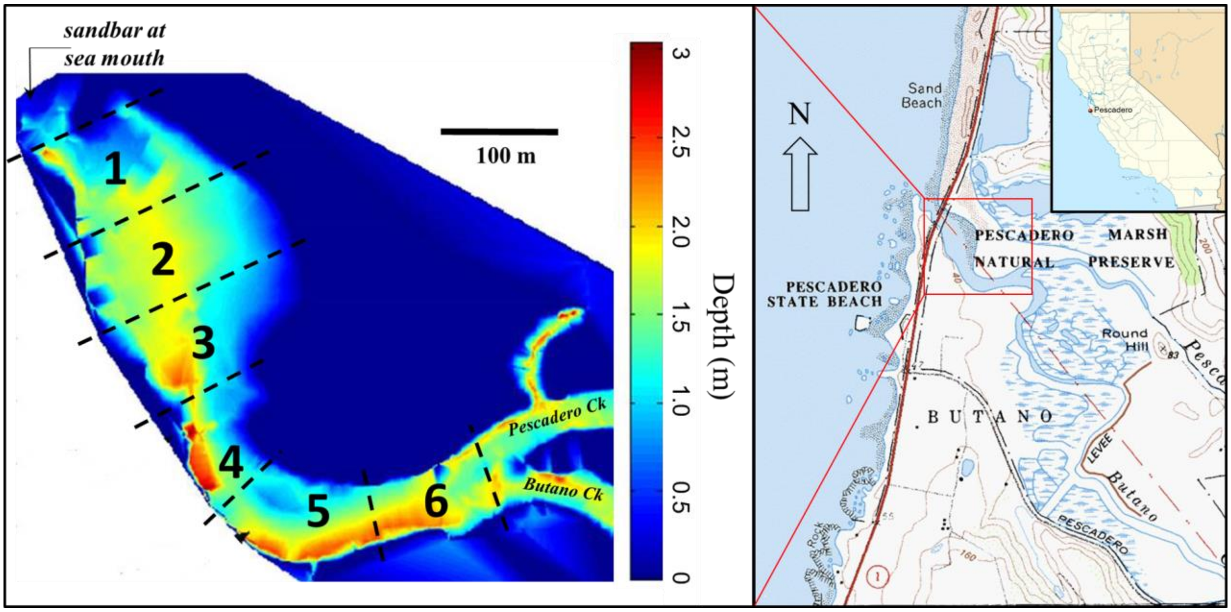


Figure 1. Location of study site and six sampling zones. The Pescadero intermittent estuary is located in Central California, approximately 60 km south of San Francisco. The watershed possesses two major basins that share a confluence in the upper estuary: Pescadero Creek to the north and Butano Creek to the south. The estuary is associated with extensive salt marshes that are periodically flooded during the sandbar-closed ecosystem state.

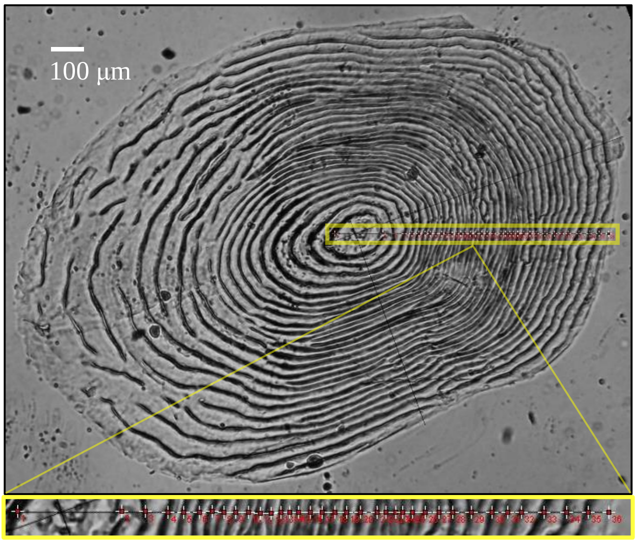
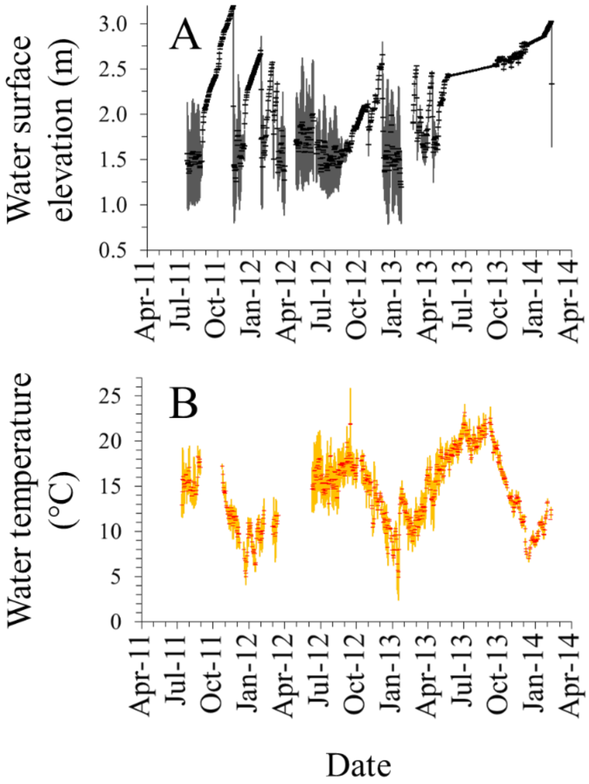


Figure 2. Magnified image of *Oncorhynchus mykiss* scale collected from a 150 mm individual on 20-Jul 2012 showing measurements along the axis that is 20° offset ventrally to the long axis.



Figures 3a,b. Daily mean (black horizontal bars), minimum (grey vertical bars below means), and maximum (grey vertical bars above means) water surface elevations (WSEs) are presented in Fig. 3a. Daily means (horizontal red bars) and standard deviations (orange vertical bars) of water temperature are show in Fig. 3b. Total length of vertical bars in Fig. 3b represents one standard deviation above and below mean daily temperatures. Gaps represent periods when data are missing.

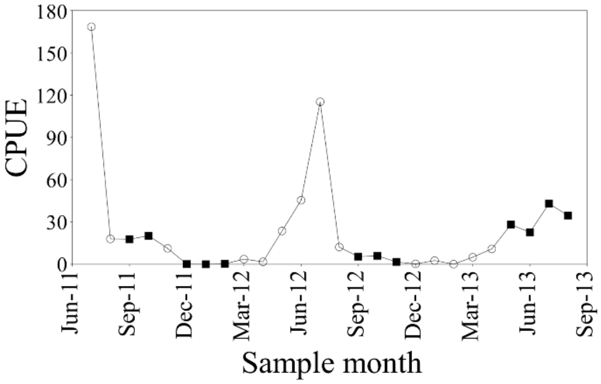


Figure 4. Mean catch-per-unit-effort (CPUE) or number of *Oncorhynchus mykiss* sampled per seine haul for study months when at least six total hauls were performed. Black boxes represent sampling during the sandbar-closed ecosystem state and open circles indicate sampling periods when the estuary is connected to the ocean.

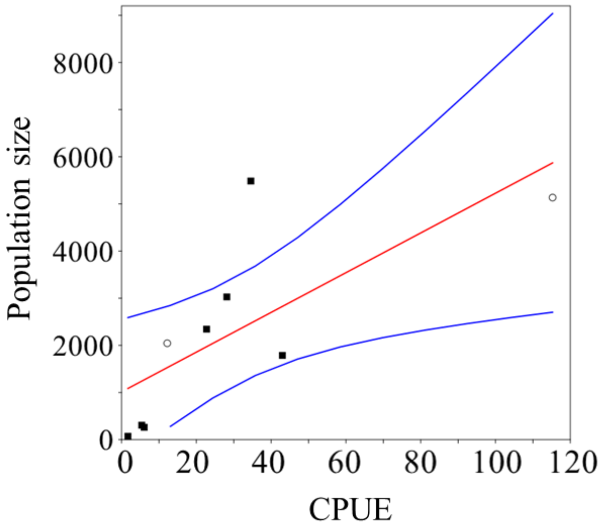
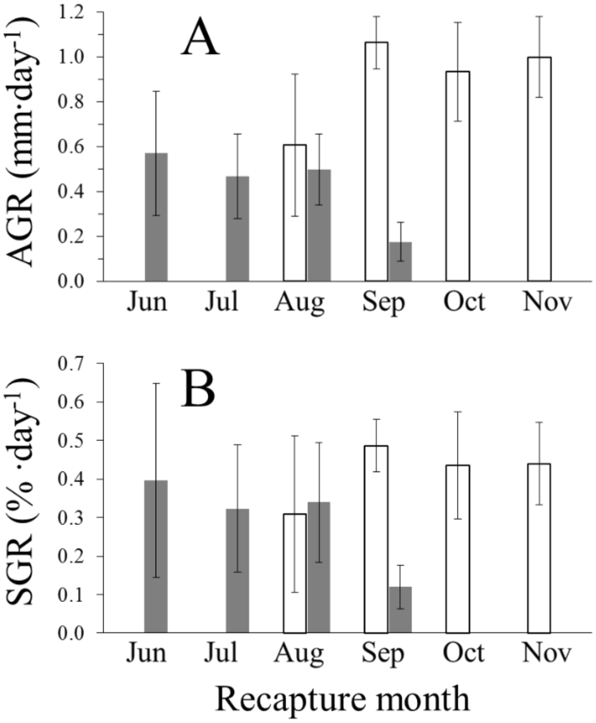
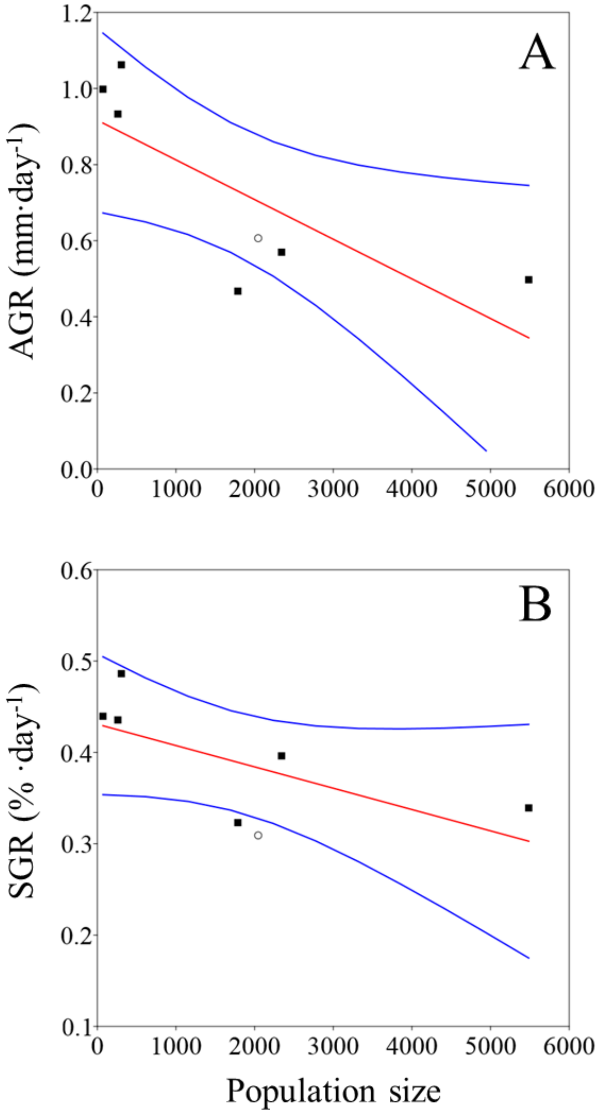


Figure 5. Relationship between *Oncorhynchus mykiss* catch-per-unit effort (CPUE) and estimated estuary population sizes from mark-recapture methods. The linear regression (red line) is positive and significant and described by the following formula: population size = 42.14·CPUE + 1014.10. Black boxes and open circles indicate sampling during the closed and open ecosystem states, respectively, and blue lines represent 95% Working-Hotelling confidence intervals.



Figures 6a,b. *Oncorhynchus mykiss* absolute growth rates (AGRs, Fig. 6a) and specific growth rates (SGRs, Fig. 6b) measured by mark-recapture methods. Open columns represent calendar year 2012 and grey columns represent calendar year 2013. Error bars indicate one standard deviation above and below mean monthly values.



Figures 7a,b. Linear relationships (red lines) for estimated population sizes for month$_t$ versus mean measured absolute growth rates from month$_{t-1}$ to month$_t$ (AGRs, top) and mean measured specific growth rates from month$_{t-1}$ to month$_t$ (SGRs, bottom) from mark-recapture methods. The negative relationship between population size and growth rate is significant for AGR (AGR = $-1.04 \cdot 10^{-4} \cdot$population size + 0.92, $R^2 = 0.60$, permutation $P < 0.05$) but not SGR (SGR = $-2.34 \cdot 10^{-5} \cdot$population size + 0.43, $R^2 = 0.43$, permutation $P = 0.10$). Black boxes and open circles indicate sampling during the closed and open ecosystem states, respectively, and blue lines represent 95% Working-Hotelling confidence intervals.

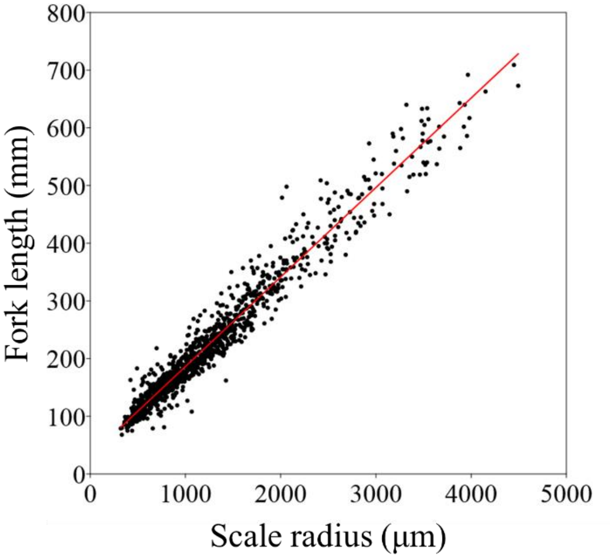
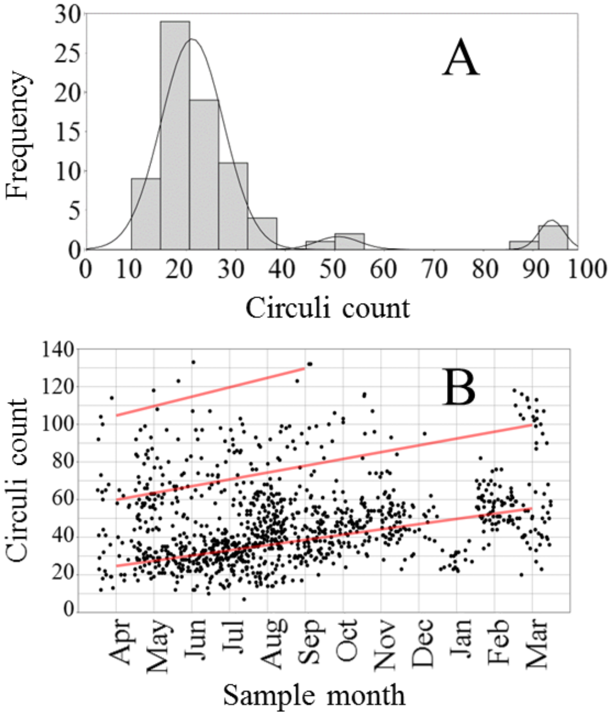
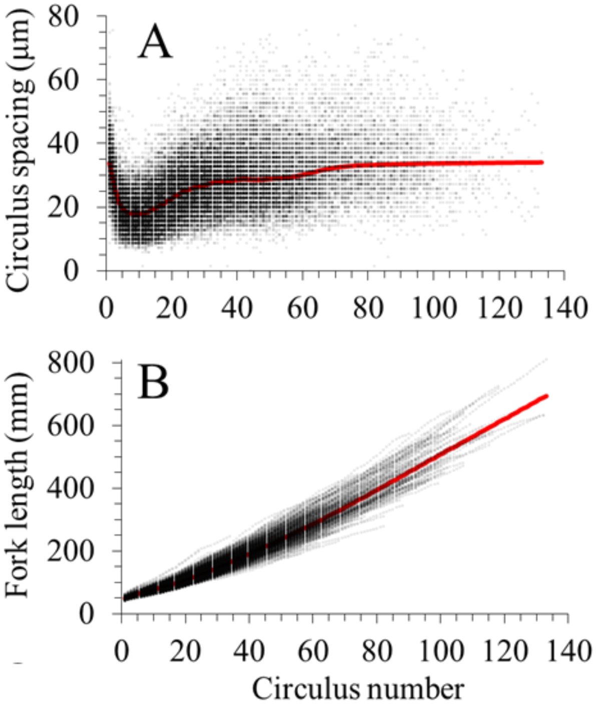


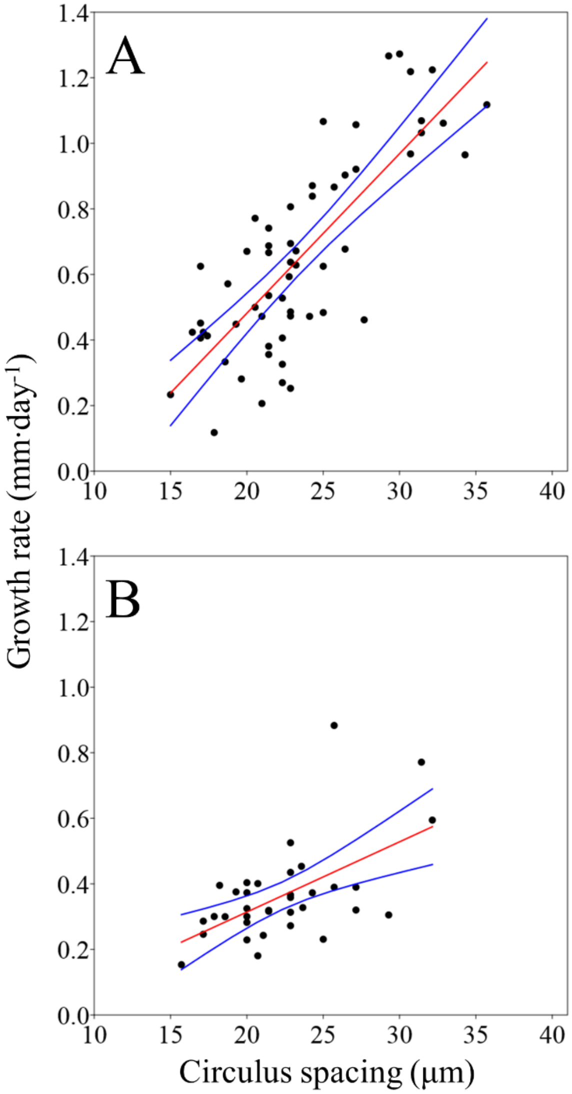
Figure 8. Relationship between scale radius (SR) and fork length (FL) for *Oncorhynchus mykiss* sampled from 2010 to 2014 (FL = 0.1551·SR + 31.35, $R^2 = 0.96$, $P < 0.001$).



Figures 9a,b. Frequency distribution mixture analysis of total circuli counts for *Oncorhynchus mykiss* scales sampled from 26-Apr 2013 to 31-May 2013 at a migrant trap located 2 km upstream of the estuary is shown in Fig. 9a. A jitter plot of total circuli counts for scales sampled from *O. mykiss* by seine hauls or salvaged fish kills is shown in Fig. 9b with visually-approximated trendlines for three size classes.



Figures 10a,b. Measured values (black dots) and LOWESS estimates (red line) of *Oncorhynchus mykiss* circulus spacing (Fig. 10a) and fork lengths (Fig. 10b) according to circulus number. A smoothing factor of 0.1 is used for LOWESS estimates.



Figures 11a,b. Linear regressions (red lines) of absolute growth rates (AGRs) versus median circulus spacing (MCS) and for a group of recaptured *Oncorhynchus mykiss* tagged and recaptured within a rearing season ($AGR = 4.87 \cdot 10^{-2} \cdot MCS - 0.49$, $R^2 = 0.62$, permutation $P < 0.001$, Fig. 11a) and another group of recaptured *O. mykiss* that were re-sampled after an overwintering period ($AGR = 2.14 \cdot 10^{-2} \cdot MCS - 0.11$, $R^2 = 0.32$, permutation $P < 0.001$, Fig. 11b). Blue lines indicate 95% Working-Hotelling confidence intervals.

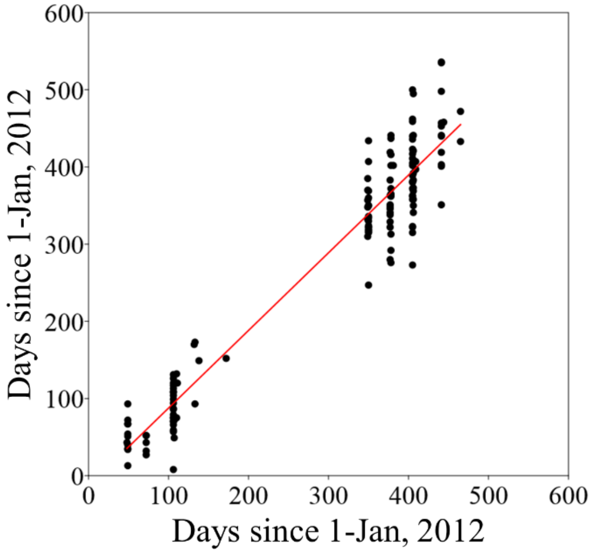


Figure 12. Relationship between the back-calculated date when fork lengths for recaptured fish most closely matched fork length at tagging (x-axis) and tagging date (y-axis). The slope (R^2 = 0.93, $P < 0.001$) of the linear regression is not significantly different from one (value = 1.01, 95% CI: 0.96-1.05) which indicates that the method presented here to assign dates to circuli in this study is valid. Dates are presented as days since 1-Jan, 2012 for ease of visual display.

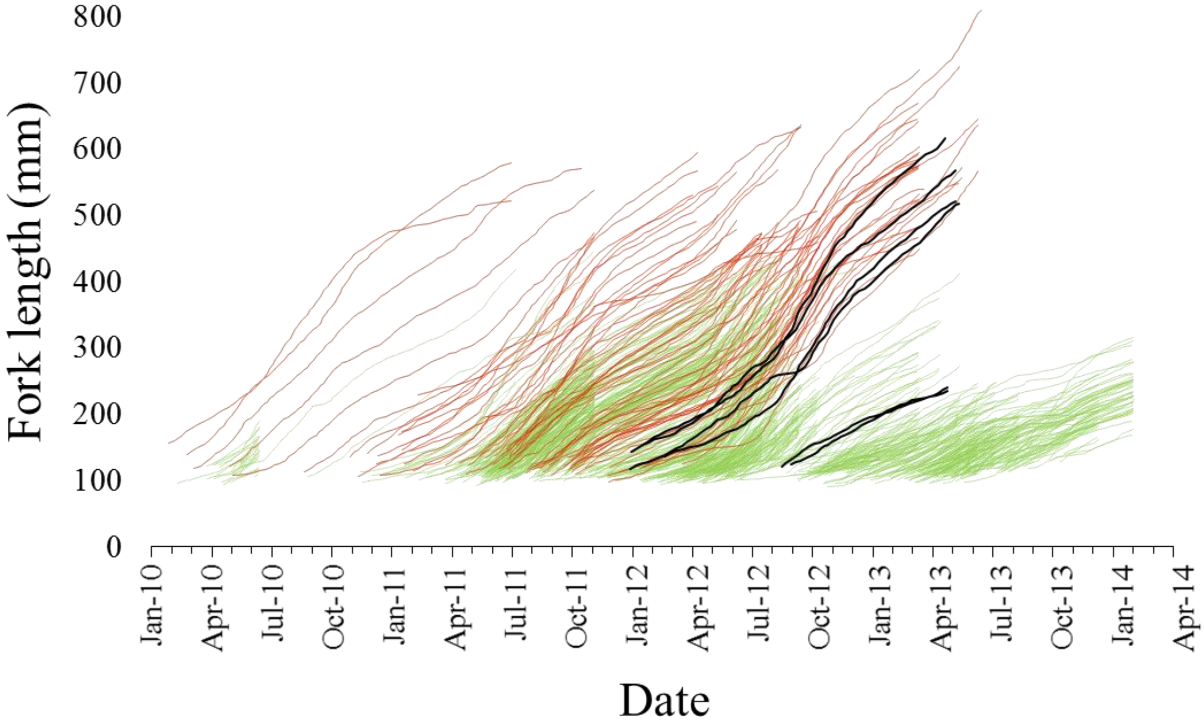


Figure 13. *Oncorhynchus mykiss* growth trajectories reconstructed from scale pattern analyses at sub-weekly to weekly temporal resolution. Green and red lines represent sub-adults (< 450 mm) and adults (≥ 450 mm), respectively, sampled by seine haul or salvaged from fish kills. Black lines represent specimens sampled from the migrant trap.

CHAPTER 5

ENVIRONMENTAL CORRELATES OF FINE-SCALE JUVENILE STEELHEAD TROUT (*Oncorhynchus mykiss*) HABITAT USE AND MOVEMENT IN A SANDBAR-CLOSED CENTRAL CALIFORNIA INTERMITTENT LAGOONAL ESTUARY DURING SEVERE DROUGHT

Environmental correlates of fine-scale juvenile steelhead trout (*Oncorhynchus mykiss*) habitat use and movement in a sandbar-closed Central California intermittent lagoonal estuary during severe drought

Abstract: Intermittent estuaries (IEs) are ubiquitous along California's coast and provide important nursery habitat for iconic and imperiled steelhead (*Oncorhynchus mykiss*) populations. Without proper maintenance and restoration of estuarine habitats, climate change may cause lagoon waters to become too inhospitable for rearing juveniles. Thus, an understanding of steelhead microhabitat preferences in California IEs during environmental extremes can help inform conservation management practices. Here I use sophisticated passive and acoustic telemetry technology to calculate over half a million fish positions for 26 individuals at fine and fine spatial (<1.4 m) and temporal (90 s min interval) scales in a large Central California lagoon after two years of severe drought from late summer through fall 2013. Overall, the fish expressed extremely strong site fidelity and moved very slowly (~0.4 to 0.6 lengths$\cdot$s^{-1}), especially at night when movement rates remained at baseline levels (~40 mm$\cdot$s^{-1}) and core habitat area, defined as the 50% kernel density estimate area (KDE_{50}) contracted by over an order of magnitude ($KDE_{50(day)}$=1185.3 m^2; $KDE_{50(night)}$=113.3 m^2). Rate of movement (ROM) generally tracked solar radiation levels and was moderated by water temperature. Punctuated ROM spikes occurred during crepuscular time periods and maximum hourly ROM (138 mm$\cdot$s^{-1}) was observed during the early study period from 10:00 to 11:00 when water temperatures were optimal (17ºC to 18 ºC). This behavior probably reflects heightened benthic foraging activities when predation risk is minimized or when potential growth rewards are maximized. The fish expressed strong apparent preference for two microhabitat complexes, one located at a point bar along the inside bend of the middle estuary and another closer to the mouth at the upper limit of a flood tide delta. Both zones were shallow (~1.5 m), wind-protected, and possessed cover and sandy substrates that occurred within the fresh or near fresh epilimnion where lagoon water quality was best and benthic prey was likely most abundant. Fish tag transmission detections at upstream receivers outside the triangulation array declined linearly when water temperatures surpassed 18°C and dissolved oxygen concentrations dropped below 7.0 mg$\cdot$L^{-1}. Efforts that limit both vertical and lateral habitat compression caused by degraded water quality occurring at depth and upstream, increase in-stream cover at strategic locations, and prevent sandbar breach-induced fish kills in distressed watersheds until early winter will increase the total amount of functional estuarine habitat available to juvenile *O. mykiss* during extremely dry climatic periods and help populations remain self-sustaining.

Keywords: acoustic telemetry, VEMCO Positioning System (VPS), mobile tracking, microhabitat mapping, habitat compression, diel effects, drought, water quality, climate change, conservation

Introduction

Pacific salmon offer humans immense economic, cultural, and social value and over half of all Evolutionarily Significant Units (ESUs) are listed as threatened or endangered under the Endangered Species Act (ESA) (Ruckelshaus et al. 2002). Abundances of the threatened Central California Coastal (CCC) steelhead (*Oncorhynchus mykiss*) ESU have declined by approximately one order of magnitude over the past 50 years and climate change is considered the primary threat to the viability and persistence of the population complex (Moyle et al. 2017). Extinction of CCC steelhead is possible in the next century without proper management actions, especially those that maintain and restore important estuarine rearing habitats and functions (Moyle et al. 2017).

Of California's 350 estuaries, 86% are considered "intermittent" (Heady et al. 2014). These intermittent estuaries (IEs) are also known regionally as bar-built estuaries, temporarily open/closed estuaries (TOCEs), or intermittently closed and open lakes and lagoons (ICOLLs). They are commonly encountered in small- to medium-sized watersheds with energetic wave climates and wet/dry seasonality like the Mediterranean climate regions of South Africa, Australia, and the Pacific coast of North America (Perissinotto et al. 2010). The ecosystems alternate between open (full tidal exchange), partially open (muted tidal exchange), and closed or lagoonal (no tidal exchange) states depending on the presence or absence of a coastal sandbar at the mouth and the sandbar's size in relation to ocean water surface elevation fluctuations. Ecosystem functioning in IEs is mainly governed by the sandbar regime, freshwater inflows, and mixing levels (Perissinotto et al. 2010). During the closed state, water volume generally increases but water quality usually declines (Perissinotto et al. 2010) and an understanding of the quantity versus quality habitat tradeoffs for rearing juvenile *O. mykiss* in coastal California lagoons is needed to guide conservation management practices.

California IEs are considered "high-risk–high-reward" habitat for juvenile *O. mykiss* (Satterthwaite et al. 2012). During favorable environmental conditions, IEs provide rich growth opportunities during both the closed (Smith 1990, Hayes et al. 2008) and open (Fuller 2011, Huber and Carlson in prep) ecosystem states. Mid- to late-summertime growth rates for CCC steelhead can be 20 to 80 times greater in lagoons than that occurring in freshwater streams (Hayes et al. 2008) because of cooler coastal temperatures and very high abundances of preferred prey items like benthic crustaceans and aquatic insects (Robinson 1993, Martin 1995). Rapid growth during extended estuarine residence enhances marine survival (Bond et al. 2008) and promotes life history diversity (Hayes et al. 2011) which helps CCC steelhead populations remain self-sustaining. However, predation pressures are considered much greater in the estuary compared to upstream habitats (Satterthwaite et al. 2012). Indeed, Osterback et al. (2013) estimated that the median probability of predation by just a single bird species, Western gulls (*Larus occidentalis*), on juvenile steelhead in three Central California Coast watersheds (Waddell, Gazos, and Scott Creeks) is ≥ 0.306 and can range from 0.075 to 0.823 depending on the watershed and year. Also, chronically degraded water quality during drought and extended closure may impair nursery function (Huber and Carlson in prep) or cause it to cease altogether (Jankovitz 2015). Furthermore, animal mass mortality events occasionally occur in IE's from severely degraded water quality (Whitfield 1995), including regular breach-induced fish kills at the study site (Sloan 2006, Largier et al. 2015) caused by widespread anoxia from suspended iron sulfide flocculents (Smith 2009, Richards and Pallud 2016, Richards et al. 2018).

There is concern that reduced precipitation and longer periods of marine disconnection in the future will cause lagoon waters to become too warm and oxygen poor for steelhead growth and survival (Moyle et al. 2017). Therefore, the identification of estuarine habitat features favored by juvenile steelhead, particularly during periods of prolonged drought-induced closure and degraded water quality conditions, will help inform resource management decisions. Unfortunately, determination of fine-scale habitat use patterns for mobile aquatic animals is exceedingly difficult because of the opacity and instability of the underwater environment and limitations of traditional sampling methods. Consequently, minimal or no distinction is made between estuarine microhabitats which limits the conservation implications of scientific research. Recent advances in acoustic telemetry technology, however, have transformed the ability to quantify and relate aquatic animal distributions and movements to habitat parameters over very fine spatiotemporal scales (reviewed by Hussey et al. 2015). My main goal is to use a combination of passive and mobile acoustic telemetry to quantify habitat use and movement patterns for multiple tagged juvenile *O. mykiss* rearing in a Central California IE during severe drought and extended sandbar-closed conditions. Specifically, my objectives are to, 1. extensively monitor physico-chemical conditions throughout the lagoon, 2. determine general attributes and trends of fish habitat use and movement rates at multiple spatial and temporal scales, and 3. explore and describe relationships between habitat use, movement rates, water quality parameters, and physical habitat features. I conclude with a discussion of the conservation implications of my findings.

Methods

Study site - The Pescadero Creek intermittent estuary (IE) is approximately 60 km south of San Francisco (Fig. 1a). The watershed originates in the heavily forested Santa Cruz mountains and is comprised of the Pescadero Creek (150 km^2) and Butano Creek (60 km^2) catchments which share a confluence in the upper estuary (Fig. 1b). Total watershed relief is 732 m and mean annual precipitation ranges from 50 cm near the coast to 130 cm or greater at higher elevations (Bozkurt Frucht et al. 2018). Nearly all precipitation occurs from November to April because of the region's Mediterranean climate. Usually, sandbar formation occurs during the late summer and full breaching during the fall or winter. However, closure periods may persist much longer during drought because of the combined effects of low freshwater inflows and the absence of energetic storm swells. At its fullest when adjacent saltmarshes are flooded, the lagoon’s surface area is approximately $1.00 \cdot 10^6$ m^2, which is one to two orders of magnitude larger than other IEs in the region (Beck et al. 2006).

Environmental data - Physico-chemical parameters were measured throughout the study area both at fixed water depths at multiple locations and at multiple water depths at fixed locations. Depth and salinity sensors (RBR XR-420 CTD) were secured to weighted moorings and positioned approximately 0.25 m above the bed (*SI appendix A*, Fig. A1) at stations 01, 02, 06, 09, 11, and 12 (Fig. 1b). A CTD was also deployed 0.25 m below the water surface at station 06 (Fig. 1b). Lagoon water surface elevation (WSE) data were converted to meters using the NAVD88 vertical datum (GEOID 2009 model). Solar radiation and temperature sensors (HOBO® Pendant Temperature/Light Data Loggers, Onset Computer Corp.) were deployed aerially in the upper estuary (37.260807°N, 122.407951°W) and subaerially at water depths of 0.75 m (stations 02, 03, 06, 08, 12, 13), 1.25 m (stations 02, 06, 08, 12, 13, 14), 1.50 m (station 01), and 1.75 m (stations 08, 12) (Fig. 1b). Additional temperature sensors (HOBO® Pendant Temperature Data Loggers, Onset Computer Corp.) were also deployed (*SI appendix A*, Fig. A2) at 0.25 m (stations 01, 02, 03, 05, 07, 08, 09, 10, 13, 14), 0.75 m (stations 04, 05, 10, 11), 1.25 m (stations 04, 05, 09, 10, 11), and 1.75 m (stations 08, 12) (Fig. 1b). Temperature, salinity, pH, and dissolved oxygen (DO) concentrations were measured by multiparameter water quality sondes (YSI 6600, YSI Inc.) moored to stations 02, 13, and 14 (Fig. 1b) at 1.25 m depth. Water quality sondes (Hydrolab MS5, OTT Hydromet-Hach® Company) were also deployed throughout the water column at 0.60, 1.60, 2.10, and 2.35 m depths at station 08 (Fig. 1b and *SI appendix A*, Fig. A3). Lagoon water quality was also measured every 4 s throughout all navigable waters by kayak using a compact water quality sonde (YSI 600XLM, YSI Inc.) that was slowly bobbed up and down throughout the water column in front of a foot pedal-powered kayak on 25-Sep, 2013 (both pre-noon and post-noon hours) and 21-Nov, 2013 (afternoon only). Geographic coordinates were recorded during water quality cruises using a handheld GPS device (Garmin GPSMAP 78, Garmin Ltd.). All geographic data are presented using the WGS84 datum for coordinates and all times are UTC-8 hours. Data from fixed environmental sensors are analyzed at 15 min intervals except those obtained from the station 08 sondes (30 min pulse rate). Data gaps occur because of instrument unavailability, technical difficulties, or sensor biofouling (*SI appendix A*, Fig. A4).

Fish tagging - Juvenile *O. mykiss* were sampled by beach seine in the middle estuary near station 07 (Fig. 1b) on 9-Sep, 2013. A subset of 35 fish possessing a mean FL of 175 mm and ranging from 139 mm to 206 mm were surgically implanted with uniquely coded acoustic transmitters (VEMCO V5-180 kHz; nominal code transmission delay: 30-90 s range). Fish were anaesthetized with carbon dioxide before tags were inserted into the peritoneal cavity through a 1 cm vertical incision above the ventral midline by a well-trained surgeon. The incision was closed with two absorbable, sterile, and plain gut interrupted surgical sutures (Ethicon Chromic Gut 2–0). Acoustically-tagged fish were also implanted with 12-mm passive integrated transponder (PIT) tags (Oregon RFID, Portland, Oregon). All fish were carefully monitored and released back into the environment after showing visible signs of recovery.

Acoustic telemetry - The fixed array consisted of 14 omnidirectional acoustic receivers (VEMCO VR2W-180 kHz) with partially overlapping detection ranges that were strategically placed according to preliminary range testing (Fig. 1b). All receivers were secured to a line with floats of unequal buoyancies at each end that was threaded through a weighted mooring (*SI appendix A*, Figs. A1, A2) and deployed hydrophone-down in the middle of water column (~0.4 m to 0.7 m water depths). Twelve receivers capable of triangulating fine-scale fish positions comprised the VEMCO Positioning System (VPS) monitoring zone in the middle and lower estuary (Fig. 1b). Eight synchronization transmitters (hereafter 'synctags'; VEMCO V6-180 kHz; nominal code transmission delay: 30-90 s range) were strategically deployed at stations with or without VPS receivers (Fig. 1b). Accurate receiver locations were derived from the observed arrival time differences between synctag signal detections. Fish positions and accompanying unitless horizontal positioning errors (HPEs) were post-processed and provided by VEMCO (Bedford, Nova Scotia). Fixed receivers outside and upstream of the VPS array were placed in the Pescadero and Butano Creek portions of the upper estuary near the confluence (Fig. 1b). Mobile tracking surveys were conducted during the afternoon on 1-Oct, 7-Nov, 21-Nov, and 14-Dec in 2013 throughout all navigable waters using a boat-mounted acoustic receiver (VEMCO VR100) and omnidirectional hydrophone (VEMCO VH165).

Statistical analyses - According to the method described by Smith (2013), I determined absolute estimates of spatial error (HPE_m) via linear regression analysis of the distances between known and calculated synctag locations and associated HPE values. In order to improve the accuracy of fish position measurements, high HPE values, defined as those greater than the 75th percentile in the dataset, were excluded from all analyses. The Spatial Analyst extension in ArcGIS 10.5® (Esri™) was used to calculate two-dimensional kernel density estimations (KDEs; Silverman 1986) from filtered position data for both individually-tagged fish and all tagged fish combined (hereafter 'combined sample'). Kernel density estimation is a popular and useful method to describe probabilistic areas of animal locations because it is nonparametric and, thus, suited for the fact that most organisms are not distributed in well-behaved spatial patterns (Seaman and Powell 1996). Both decile and quartile analyses of KDE values are presented and I consider 0-25%, 0-50%, 50-75%, and 75-100% KDE areas to represent central core, core, activity space, and excursion space steelhead habitat areas, respectively. The Tracking Analyst extension in ArcGIS 10.5® (Esri™) was used to determine distances between positions for individual fish in order to calculate distance traveled per unit time or 'rate of movement' (ROM, sensu Espinoza et al. 2011a). All ROM analyses are restricted to situations when the time interval between successive position measurements is the shortest possible (90 s) in order to minimize error due to deviations from straight path movements. Geographic data are analyzed for both individually-tagged fish and the combined sample using PAST version 3.18 (Hammer et al. 2001). All statistical testing is performed using nonparametric methods and considered significant at the α=0.05 level.

Results

Environmental conditions - The low-lying, flat and wide sandbar permitted frequent sheet-like marine overwash events (*SI appendix A*, Fig. A5a-f) which produced frequent and small daily water surface elevation (WSE) fluctuations (Fig 2). Mean daily WSE was 2.72 m and ranged from a minimum of 2.55 m on 19-Sep to 2.95 m on 14-Dec (Fig. 2). Mean WSE daily range was $4.04 \cdot 10^{-2}$ m and ranged from a minimum of $1.61 \cdot 10^{-2}$ m on 29-Sep to a maximum of 0.11 m on 7-Dec (Fig. 2). Mean daily water surface elevations (and mean daily ranges) increased slightly through the 105 day study period in 2013 (9-Sep to 22-Dec) from 2.63 m ($3.44 \cdot 10^{-2}$ m) to 2.69 m ($3.97 \cdot 10^{-2}$ m) to 2.83 m ($4.74 \cdot 10^{-2}$ m) during the first third (weeks 1-5), middle third (weeks 6-10), and last third (weeks 11-15) of the study, respectively (Fig. 2).

Solar radiation data are only available from 9-Sep to 2-Oct because of extensive biofouling of sensor housing by macroalgae. The relationships between time of day in units of proportion of 24 hours (dependent variable, range: 0.25 to 0.75) and aerial and subaerial lux values (independent variable) are best described by Gaussian functions (Table 1, Fig. 3). Minimum non-zero aerial solar radiation occurred during the morning at 05:30 ($\bar{x}$=1.10 lux) and the evening at 18:45 ($\bar{x}$=0.75 lux) (Fig. 3). Maximum aerial solar radiation occurred at 12:00 ($\bar{x}$=111149.21 lux) (Fig. 3). Pronounced light attenuation-at-depth is observed; according to linear regression analysis of water depth (0.75 m, 1.25 m, 1.50 m, and 1.75 m) versus mean solar radiation-at-depth, daytime darkness occurred at depths ranging from 1.7 m at 06:00 to 2.0 m at 15:45 (Fig. 3).

The depth-averaged mean water temperature (and min to max mean daily values), calculated as the overall mean of mean daily temperatures at 0.25 m, 0.75 m, 1.25 m, and 1.75 m depths at all VEMCO Positioning System (VPS) receiver locations (Fig. 1b), declined steadily from 18.5°C (16.1°C to 21.2°C) to 13.9°C (12.4°C to 16.2°C) to 9.7°C (5.9°C to 13.5°C) during the early (weeks 1-5), middle (weeks 6-10), and latter (weeks 11-15) study period, respectively (Fig. 4). The depth-averaged mean daily temperature range (and min to max daily range) was 1.5°C (0.6°C to 2.4°C), 1.0°C (0.3°C to 1.7°C) and 1.0°C (0.5°C to 1.5°C) during the same three time periods, respectively. The overall mean of mean daily temperatures (and min to max mean daily temperatures) at 0.25 m, 0.75 m, 1.25 m, and 1.75 m water depths at station 08 (Fig. 1b) were 14.0°C (6.0°C to 21.3°C), 13.9°C (5.9°C to 21.2°C), 14.6°C (5.8°C to 21.2°C), 13.8°C (6.0°C to 21.0°C), and 14.9°C (7.9°C to 21.0°C), respectively (Fig. 5a). Overall, water temperatures at 1.25 m water depth in the lower lagoon at station 02 were 0.3°C and 0.7°C cooler than temperatures in the Pescadero Creek (st13) and

Butano Creek (st14) portions of the upper estuary, respectively (Fig. 6a). Mean depth-averaged water temperature during water quality cruises, calculated as the overall mean of mean temperatures during afternoon hours at 0.25 m increments from the surface to 2.75 m depth was 19.3º C on 25-Sep and 13.7º C on 21-Nov (Fig. 7). Water temperature on 21-Sep was 0.5º C cooler overall during the morning compared the afternoon (Fig. 7).

Mean salinities (and min to max mean daily values) in the VPS monitoring zone were 2.3 ppt (1.5 ppt to 2.7 ppt), 2.4 ppt (1.5 ppt to 2.8 ppt), 2.5 ppt (1.7 ppt to 3.7 ppt), 2.8 ppt (2.1 ppt to 5.8 ppt), 4.1 ppt (2.6 ppt to 9.1 ppt), and 24.3 ppt (19.2 ppt to 28.5 ppt) within each of the six 0.50 m increments from the water surface to 3.0 m deep, respectively (Figs. 5b, 8). Salinity levels within the top 0.5 m of the water column declined slightly overall from means of 2.6 ppt to 2.7 ppt and 2.0 ppt during the first, middle, and last thirds of the study period, respectively. Mean deep water (2.5 m to 3.0 m depth) salinities also declined from 27.8 ppt to 22.9 ppt to 21.9 ppt for the same three time periods, respectively. Mean salinity at 1.25 m depth at station 02 ($\bar{x}$=2.7 ppt) was similar to that at stations 13 ($\bar{x}$=2.6 ppt) and 14 ($\bar{x}$=2.7 ppt) (Fig. 6b). The halocline was approximately 0.35 m deeper during the mobile survey on 21-Nov compared to 25-Sep (Fig. 7b).

Mean pH levels (and min to max mean daily values) at 0.60 m, 1.60 m, 2.10 m, and 2.35 m water depths at station 08 were 7.9 (7.5 to 8.1), 8.1 (7.9 to 8.4), 7.9 (7.6 to 8.2), and 7.9 (6.8 to 9.3) (Fig. 5c). Mean pH at 1.25 m water depth is similar at stations 02 ($\bar{x}$=8.0), 13 ($\bar{x}$=8.1), and 14 ($\bar{x}$=8.0) (Fig. 6c). Mean daily pH increased by approximately $5.4 \cdot 10^{-3}$ units$\cdot$day^{-1} at station 13 and $4.2 \cdot 10^{-3}$ units$\cdot$day^{-1} at station 14 from 9-Sep to 8-Dec (Fig. 6c). Mean depth-averaged pH, calculated from the overall mean of pH values at 0.25 m increments from the surface to 2.75 m deep, was more alkaline during the water quality cruise on 21-Nov ($\bar{x}$=7.9) compared to 25-Sep ($\bar{x}$=7.3) (Fig. 7c). Overall, pH values from the surface to 1.00 m water depths were greater during the afternoon ($\bar{x}$=7.8) compared to the morning ($\bar{x}$=7.6) on 25-Sep (Fig. 7c). The opposite trend is observed for 1.50 m to 2.75 m water depths; deep-water pH was less during the afternoon ($\bar{x}$=6.9) compared to the morning ($\bar{x}$=7.1) (Fig. 7c).

Mean dissolved oxygen (DO) concentrations (and min to max mean daily values) at 0.60 m, 1.60 m, 2.10 m, and 2.35 m water depths at station 08 were 8.87 mg$\cdot$l^{-1} (6.88 mg$\cdot$l^{-1} to 11.05 mg$\cdot$l^{-1}), 7.16 mg$\cdot$l^{-1} (4.08 mg$\cdot$l^{-1} to 9.80 mg$\cdot$l^{-1}), 4.54 (0.00 mg$\cdot$l^{-1} to 11.01 mg$\cdot$l^{-1}), and 1.86 mg$\cdot$l^{-1} (0.01 mg$\cdot$l^{-1} to 8.61 mg$\cdot$l^{-1}), respectively (Fig. 5d). Mean minimum daily DO concentrations (and min to max minimum daily values) at the same four depths was 7.54 mg$\cdot$l^{-1} (5.85 mg$\cdot$l^{-1} to 10.15 mg$\cdot$l^{-1}), 5.25 mg$\cdot$l^{-1} (1.85 mg$\cdot$l^{-1} to 8.15 mg$\cdot$l^{-1}), 2.61 (0.00 mg$\cdot$l^{-1} to 10.03 mg$\cdot$l^{-1}), and 0.68 mg$\cdot$l^{-1} (0.00 mg$\cdot$l^{-1} to 5.10 mg$\cdot$l^{-1}), respectively (Fig. 5d). Mean DO concentrations (and min to max mean daily values) at 1.25 m water depth was 8.64 mg$\cdot$l^{-1} (6.84 mg$\cdot$l^{-1} to 10.73 mg$\cdot$l^{-1}) at station 02, 6.97 mg$\cdot$l^{-1} (3.87 mg$\cdot$l^{-1} to 10.65 mg$\cdot$l^{-1}) at station 13 and 7.15 mg$\cdot$l^{-1} (5.07 mg$\cdot$l^{-1} to 9.03 mg$\cdot$l^{-1}) at station 14 (Figs. 1b, 6d). Mean minimum daily DO concentrations (and min to max minimum daily values) at stations 02, 13, and 14 were 7.83 mg$\cdot$l^{-1} (5.85 mg$\cdot$l^{-1} to 9.65 mg$\cdot$l^{-1}), 5.34 mg$\cdot$l^{-1} (1.24 mg$\cdot$l^{-1} to 9.70 mg$\cdot$l^{-1}), and 5.23 mg$\cdot$l^{-1} (1.47 mg$\cdot$l^{-1} to 8.37 mg$\cdot$l^{-1}), respectively (Fig. 6d). Mean daily DO increased by approximately 0.28 mg$\cdot$l$^{-1}\cdot$wk^{-1} at station 13 and 0.18 mg$\cdot$l$^{-1}\cdot$wk^{-1} at station 14 from 11-Sep to 8-Dec (Fig. 6d). Mean daytime DO concentrations at stations 13 and 14 were 0.42 mg$\cdot$l^{-1} and 0.21 mg$\cdot$l^{-1} greater, respectively, than mean nighttime DO levels from 11-Sep to 8-Dec (Fig. 6d). Mean daytime DO concentration was 0.06 mg$\cdot$l^{-1} greater than mean nighttime DO concentration at station 02 from 27-Sep to 20-Nov and the difference was 7.4 and 2.7 times less than the diel DO fluxes at stations 13 and 14, respectively, during the same time period (Fig. 6d). Mean depth-averaged

DO concentrations during afternoon hours, calculated as the overall mean of mean DO values at 0.25 m increments from the surface to 2.75 m was 3.9 mg·l^{-1} during the 25-Sep water quality cruise and 6.7 mg·l^{-1} during the 21-Nov cruise (Fig. 7d). The overall mean DO concentration was 17% less during the morning compared to the afternoon on 25-Sep (Fig. 7d). Mean DO was greater than 5.0 mg·l^{-1} only at the surface during the morning and from the surface to approximately 1.0 m depth during the afternoon on 25-Sep (Fig. 7d). Mean DO was greater than 5.0 mg·l^{-1} from the surface to 1.75 m depth on 21-Nov (Fig. 7d). Dissolved oxygen concentrations were lowest in the in the Butano Creek arm of the upper estuary (Fig. 10e).

Passive acoustic telemetry - The 12 receivers in the VPS monitoring zone and two upstream receivers recorded a total of 5906869 fish tag detections during the study period from 9-Sep, 2013 to 22-Dec, 2013. Thirty three unique fish tags were registered by stationary receivers and total detections per fish tag ranged from 162 (T23) to 476175 (T35). A total of 777800 fish positions for 26 tagged individuals (Table 2) and 103229 synctag tag positions were provided by VEMCO. Each fish tag transmission was detected by 3.8 receivers, on average, and at least three receivers detected 69.7% of all fish tag transmissions. Seventy five percent of all fish positions (hereafter 'HPE-filtered') possessed HPE values less than 3.8 which corresponds to an HPE$_m$ value of 1.4 m for this study. Since error potential is greater beyond the bounds of the VPS array (Espinoza et al. 2011b, Smith 2013), many of the filtered positions are located outside the VPS receiver polygon (Fig. 9). Total HPE-filtered positions per tag ranged from 53 (T24) to 55928 (T35). One fish tag (T05) was never detected by passive or active acoustic telemetry and another tag (T31) was detected by mobile tracking only (Table 2). The median number of days between first and last detection by either passive or active telemetry was 94.6 days and ranged from 0.2 (T17) to 102.9 (T33) days (Table 2). The difference between first and last detections by fixed or mobile receivers was less than a week for 12 individuals (Table 2). Nine of the 26 tags producing position data failed to provide more than 2829 HPE-filtered positions and the mean number of HPE-filtered positions for the 17 most data-producing fish tags was 33598 (range: 11692 to 55928). These 'top 17 tags' provided 98.6% of all HPE-filtered fish positions comprising the combined sample.

From 11-Sep to 25-Nov, the mean (and standard deviation, SD) number of individual fish tags detected per day by the VPS was 16.4 (1.3). From 26-Nov, 2013 until 22-Dec, the total number of fish tags detected per day by the VPS declined linearly at a rate of approximately 0.4 tags·day^{-1}. Total daily HPE-filtered positions for all fish combined increased linearly from 11-Sep (806 positions) to 15-Sep (5876 positions) at a rate of approximately 899 positions·day^{-1}. Mean (and SD) number of total daily HPE-filtered fish positions from 17-Sep, 2013 to 8-Nov, 2013 was 5863 (781). Mean daily HPE-filtered fish positions peaked from 9-Nov, 2013 to 19-Nov, 2013 ($\bar{x}$=8277, SD=572). From 20-Nov, 2013 to the end of the study period on 22-Dec, the total number of HPE-filtered daily fish position declined linearly at a rate of approximately 193 positions·day^{-1}. Total number of daily synctag positions increased linearly from 10-Sep (89 positions) to 17-Sep, 2013 (742 positions) at a rate of approximately 89 positions·day^{-1} and remained consistent from then until the end of November ($\bar{x}$=705, SD=36). The total number of synctag positions calculated per day was greatest in December during the study period ($\bar{x}$=858, SD=57).

Receivers outside the VPS monitoring zone in the Pescadero (st13) and Butano (st14) arms of the upper estuary (Fig. 1b) recorded a total of 201404 and 207182 fish tag transmission detections, respectively (Table 2). Stations 13 and 14 detected a total of 30 and 29 unique fish tags, respectively (Table 2). Mean (and SD) number of total detections per day for all tags combined was 1918 (895) at station 13 and 1992 (837) at station 14. Total daily detections ranged from 12 to 4052 at station 13 and 106 to 3585 at station 14. Mean daily detections (and SD) during the first, middle, and last thirds of the study period were 1507 (851), 1940 (347), and 2307 (1129) for station 13, respectively, and 1215 (806), 2743 (376), and 2020 (364) for station 14, respectively. The median number of total detections per tag at station 13 was 898 det·tag^{-1} and ranged from 22 det·tag^{-1} (T01) to 73013 det·tag^{-1} (T24) (Table 2). At station 14, the median value was 299 det·tag^{-1} and ranged from 1 det·tag^{-1} (T28) to 84521 det·tag^{-1} (T31) (Table 2). The mean (and SD) number of unique fish tags detected per day at station 13 was 4.7 (2.5) and ranged from 1 to 21. The mean (and SD) number of unique fish tags detected per day at station 14 was 5.8 (2.7) and ranged from 2 to 13.

Active acoustic telemetry - Mean duration of the four mobile tracking surveys was 150.2 min and ranged from 116.2 min on 14-Dec to 178.1 min on 21-Nov. A total of 493 positions representing 22 unique fish tags were detected during the four mobile tracking surveys (Table 2, Figs 10a-d). Sixteen unique fish tags were detected on 1-Oct and 19 unique tags were detected each on 7-Nov, 21-Nov, and 14-Dec. The minimum number of total positions per tag for all surveys combined was 2 (T31) and the maximum was 45 (T33) (Table 2). Total detections per minute for all tags combined was 1.24, 0.65, 0.70, and 0.77 on 1-Oct, 7-Nov, 21-Nov, and 14-Dec, respectively. The mean (and maximum) number of positions per tag per hour was 3.39 (7.15), 1.77 (4.53), 1.90 (5.05), and 2.11 (5.68) for the same four dates, respectively. On 14-Dec, seven tagged fish were detected in the lower lagoon, two were detected just upstream of the Pescadero-Butano confluence in the lower portions of the upper estuary and 10 were detected in the uppermost portion of the estuary in Pescadero Creek (Fig. 10d). Overall, tagged fish utilized the Pescadero arm of the upper estuary more than the Butano Creek arm (Figs. 10a-d).

Habitat use - The median (and interquartile range) of 25%, 50%, and 75% kernel density estimate (KDE) areas for the 17 top tags (i.e., those that comprise 98.6% of all fish positions) was 114.4 m^2 (48.4 m^2 to 217.4 m^2), 279.8 m^2 (163.4 m^2 to 991.1 m^2), and 1847.6 m^2 (730.7 m^2 to 3924.2 m^2) (Table 2 and *SI appendix B*, Figs. B1 to B17). Minimum and maximum central core, core, and activity space areas ranged from 20.8 m^2 (T07) to 579.2 m^2 (T02), 49.4 m^2 (T07) to 1655.3 m^2 (T02), and 46.0 m^2 (T07) to 3676.4 m^2 (T29), respectively (Table 2 and *SI appendix B*, Figs. B1-B17). The linear regression relationship between size-at-tagging (FL, mm) and core area (C, m^2) is negative and significant and described by C = -14.9*FL + 3205.5 (R^2=0.26; p<0.05; df=16). The linear regression relationship between size-at-tagging (FL, mm) and activity space area (A, m^2) is negative and not significant and described by A = -22.4*FL + 5717.8 (R^2=0.09; p=0.23; df=16).

The 25%, 50% and 75% KDE areas for the combined sample is 184.9 m^2, 1185.3 m^2, and 7290.3 m^2, respectively, during the day (05:00:00 to 18:59:59) and 33.5 m^2, 113.3 m^2, 959.4 m^2, respectively, during the night (19:00:00 to 04:59:59) (Figs. 11, 12a-b). The relationships between KDE decile endpoint (P, %) and the corresponding area for each 10% KDE increment (D, m^2) during both time periods are best described by exponential functions. The diurnal relationship is $D = 0.549\cdot e^{0.110\cdot P} + 452.390$ ($AIC = 2.242\cdot 10^6$) and the nocturnal relationship is $D = 3.205\cdot 10^{-5}\cdot e^{0.211\cdot P} + 72.556$ ($AIC = 4.920\cdot 10^4$) (Fig. 11). Kernel density estimate areas for the combined sample peaked during weeks 5, 10, 11, and 14 when median (and interquartile range) KDE areas were 2827.1 m^2 (525.0 m^2 to 12964.6 m^2), 2278.5 m^2 (300.4 m^2 to 9885.6 m^2), 2883.5 m^2 (312.4 m^2 to 13363.2 m^2), and 1447.4 m^2 (301.1 m^2 to 7804.8 m^2), respectively (Fig. 13). The increased areas during those weeks are associated with increased habitat use in the flood tide delta region of the lower embayment (*SI appendix C*, Figs.C1 to C15).

Movement - The median (and interquartile range) of mean daily rate of movement (ROM) values for the combined sample is 56.9 mm·s^{-1} (49.3 mm·s^{-1}to 76.7 mm·s^{-1}) (Fig. 13). Minimum and maximum mean daily ROM for the combined sample occurred on 11-Sep (35.3 mm·s^{-1}) and 4-Oct (109.1 mm·s^{-1}), respectively (Fig. 13). Above average mean daily ROM ($\bar{x}$=62.1 mm·s^{-1}) occurred from 15-Sep to 18-Oct, 21-Oct, 24 to 25-Oct, and 3 to 4-Nov (Fig. 13). In terms of individual fish, the median (and interquartile range) of mean daily ROM for the top 17 tags is 65.3 mm·s^{-1} (49.2 mm·s^{-1} to 72.3 mm·s^{-1}) and ranges from 43.3 mm·s^{-1} (T07) to 84.5 mm·s^{-1} (T09) (Table 2). The linear regression between FL at tagging (mm) and mean ROM (mm·s^{-1}) for the top 17 tags is negative and not significant (ROM = -0.2·FL + 96.7; R^2=0.08; p=0.28; df=16). The linear regression between ROM (mm·s^{-1}) and core area (C, m^2) is positive and highly significant and described by C = 26.1·ROM - 1010.4 (R^2=0.41; p<0.01; df=16). The linear regression between ROM (mm·s^{-1}) and activity space area (A, m^2) is also positive and significant and described by A = 61.1·ROM - 1933.9 (R^2=0.36; p<0.05; df=16).

Above average ROM values occurred from 06:00:00 to 17:59:59 ($\bar{x}$=76.9 mm·s^{-1}) whereas below average movement rates occurred from 18:00:00 to 05:59:59 ($\bar{x}$=44.4 mm·s^{-1}) (Fig. 14). Minimum and maximum ROM values occurred during the 04:00:00 to 04:59:59 ($\bar{x}$=39.0 mm·s^{-1}) and 06:00:00 to 06:59:59 ($\bar{x}$=93.6 mm·s^{-1}) hourly periods, respectively (Fig. 14). The largest increase in ROM occurred from the 05:00:00 to 05:59:59 and 06:00:00 to 06:59:59 hourly periods (+41.0 mm·s^{-1} change, Fig. 14). The greatest decrease occurred from the 06:00:00 to 06:59:59 and 07:00:00 to 07:59:59 hourly periods (-16.5 mm·s^{-1} change, Fig. 14). During the first third of the study period, mean ROM peaked at mid-day (Fig. 14). From weeks 6 to 15 of the study, mean ROM peaked at dawn and a smaller uptick also occurred during dusk (Fig. 14).

Environmental correlates - Pervasive multicollinearity of physico-chemical variables (Figs. 15a-d) limits statistical testing of individual water quality parameters on habitat use and movement. Water temperatures are negatively correlated to pH values and DO concentrations and positively correlated to salinity levels (Figs. 15a-d). The positive relationship between pH and DO is strong (Fig 15a-d). Both pH and DO are negatively correlated to salinity (Fig. 15a-d). Mean weekly core habitat areas for the combined sample is positively correlated to mean weekly temperature and negatively correlated to mean weekly salinity, pH, and DO but the relationships are tenuous and not significant (Figs. 15a, 16a-d). Similar to the patterns observed for core area, mean daily ROM is positively correlated to mean daily temperature throughout the VPS zone and negatively correlated to mean daily salinity, pH, and DO at 1.60 m water depth at station 08 (Figs. 15b, 16e-h). The positive relationship between mean daily temperature (T) and mean daily ROM for the combined sample (Fig. 15b) is best described by a linear regression below 14.0°C (ROM = 1.1·T + 40.0; R^2=0.10, p<0.05, df=57) and a second-order polynomial function for water temperatures 14.0°C or warmer (ROM = -3.4·T^2 + 120.2·T - 959.2 (R^2=0.62, df=44) (Fig. 16e). At both stations 13 and 14, total daily detections of tagged fish are negatively correlated to water temperature (Figs. 15a, 15b, 16i, 16m) and salinity (Figs. 15a, 15b, 16j, 16n) and positively correlated with pH (Figs. 15c, 15d, 16k, 16o) and DO (Figs. 15c, 15d, 16l, 16p) at 1.25 m water depths.

Fish tag detections at station 13 were 31% higher than the overall daily mean value ($\bar{x}$=1918.1 det·day^{-1}) when mean daily DO concentration was greater than 7.0 mg·L^{-1} and mean daily water temperature was less than 18ºC. Detections at station 13 were 6% less than average when DO was less than 7.0 mg·L^{-1} and temperatures were cooler than 18ºC and 24% lower when DO was less than 7.0 mg·L^{-1} and temperatures were warmer than 18ºC. At station 14, detections were 20% more than the overall mean daily value ($\bar{x}$=1992.1 per day) when mean daily water temperature was less than 18ºC regardless of DO concentrations. When mean daily water temperatures were greater than 18 ºC, fish tag detections were 63% and 60% less than average when mean daily DO concentrations were less than and greater than 7.0 mg·L^{-1}, respectively.

Discussion

Environmental conditions - The severe California drought paradoxically produced more aquatic volume than usual in the Pescadero Creek intermittent estuary (IE) during the late summer and fall because of early sandbar formation on 23-Apr, 2013 and its continued persistence throughout the 105 day investigation beginning on 9-Sep, 2013. While total freshwater runoff during the study period was more than two orders of magnitude less than the long term mean value from 1951 to 2012 (USGS Gauge 11162500), the long infill period commenced more than three months before base inflows occurred and produced fresh or near fresh conditions throughout the lagoon from the water surface to approximately 1.5 m to 2.5 m depths by late summer (Figs. 5b, 6b, 7b, 8). Lagoon water surface elevation (WSE) increased only 40 cm during the study (Fig. 2) and, aside from a moderate salinity spike from the benthos up to ~1.5 m water depth in early and mid-November (Fig. 5b), the frequent sheet-like overwash events over the wide and flat sandbar (Fig. 2 and *SI appendix A*, Figs. A5a-f) did not substantially alter the lagoon's salinity regime (Figs. 5b, 6b, 7b, 8). Saline conditions were restricted to areas deeper than the halocline (Figs. 5b, 7b) such as those found along the thalweg and various deep water pockets (Figs. 12c). Normoxic conditions (≥7.0 mg·L^{-1}) prevailed from the surface to approximately 1.5 to 2.0 m water depths throughout the lower and middle estuary and the lower portion of the upper estuary (Figs. 5d, 6d, 7d, 10e). Water temperatures were highly homogenous in space and variable over time (Figs 4, 5a, 6a, 7a) and, aside from slightly acidic conditions in bottom waters during the afternoon, pH levels were alkaline and at preferred levels for rearing salmonids (Molony 2001; Figs 5c, 6c, 7c). Dark daytime conditions occurred below 1.7 to 2.0 m water depths (Fig. 3), at least during the first three weeks of study period before light sensor biofouling occurred (*SI appendix A*, Fig. A4). The light attenuation-at-depth values observed here are amongst the most extreme ever reported and the "special visual conditions" may have been caused by high levels of light-absorbing chlorophyll molecules, tannins, or both (Guthrie and Muntz 1993; Table 1, Fig. 3 and *SI appendix A*, Fig. A6). Given the environmental conditions encountered during the study period, the strong multicollinearity of physico-chemical variables (Figs. 15a-d), and known physiological tolerances and preferences for *O. mykiss* (Molony 2001) and other juvenile salmonids (Brett 1979, Brett 1995), I focus my analysis on the combined effects of water depth, dissolved oxygen, and temperature on juvenile steelhead habitat use and movement rates.

Habitat use - The exponential diurnal and nocturnal relationships between kernel density estimate (KDE) decile endpoint and corresponding areas for each 10% KDE increment (Fig. 11) indicate that *O. mykiss* mainly used a very small portion of the overall wetted habitat, especially at night. According to the relationships presented in Fig. 11, there was a 90% chance of fish position occurring in only 10% (night) to 33% (day) of the overall area in the VEMCO Positioning System (VPS) monitoring zone which was located in the most heavily used region of the lagoon by tagged steelhead (Figs. 9, 10a-d). While a conservative estimate of fish swimming speed, mean rate of movement (ROM) was approximately 0.4 to 0.6 fish lengths$\cdot$s^{-1} when corrected for the relatively slow (~0.25 mm$\cdot$day^{-1}) and uniform somatic growth rates occurring during the study period (Huber and Carlson in prep). At these speeds swimming is sustained and juvenile salmonids engage in routine behaviors like foraging and station holding (Beamish 1978). Thus, alternating periods of station holding in central core habitats at night while resting and feeding forays outside of central core habitats during the day most likely produce the observed habitat use and movement patterns (Figs. 12 a-b, 14 and *SI Appendices B and C*, Figs B1-B17, C1-C15). Territoriality, or the tendency for fish to remain in an isolated and restricted area, is expressed by juvenile salmonids rearing in freshwater streams (Quinn 2005) and the general non-overlapping spacing and small sizes of central core areas for the top 17 tags (*SI appendix B,* Figs. B1-B17), suggest that Pescadero *O. mykiss* behaved territorially in the estuary, at least during the day. Nocturnal core areas for all fish combined was more than ten times smaller than diurnal core areas (Figs. 11, 12a-b) and the remarkable habitat use shift suggests that fish adopted more schooling behaviors at night, particularly amongst complex large woody debris (LWD) structure along the lagoon's wetted margin (Figs. 12b and *SI appendix A*, Fig. A7) in a possible effort to reduce vulnerability to terrestrial predators occurring along the shore.

Juvenile *O. mykiss* heavily favored two distinct microhabitat complexes in the Pescadero IE. One was located at the point bar along the inside bend of the middle estuary another at the flood-tide delta region of the lower embayment (Figs. 12a-b and *SI appendix A*, Figs. A8a-c, A9a-c). Within each complex, fish occupied more peripheral zones closer to the shore at night (Figs. 12a-b). Both microhabitats were shallow (<1.5 m water depth, Figs. 12a-c) and sheltered from Pacific winds (*SI appendix A*, Fig. A10) which are strong in the region (Williams 2014). The expansion of core and activity space areas during weeks 5, 10, 11, and 14 (Fig. 13) coincided with increased ROM and utilization of the downstream complex (Fig. 13 and *SI appendix C*, Figs. C1-C15) which suggests that the upper complex was most preferred. The upper microhabitat possessed extensive LWD structure and the marginal woody material that was recruited by rising water levels (*SI appendix A*, Figs. A7, Aa-c) appear heavily favored at night by steelhead (Fig. 12b). The lower microhabitat was largely devoid of LWD but occurred adjacent to a cliff face that is 12 m tall (*SI appendix A*, Figs. A9a-c, A10). Quiñones and Mulligan (2005) observed that juvenile *O. mykiss* preferred marginal estuarine habitats, especially those associated with overhanging riparian vegetation in a similarly sized northern California IE (Smith River estuary) also devoid of abundant in-stream cover. The northeastern-facing rocky cliffs provided daytime shade and possible protection for steelhead occupying the lower complex (*SI appendix A*, Figs. A9a-c, A10). The apparent preference for calmer water in both microhabitat complexes may result from an aversion to displacement by hydraulic forces which would presumably incur energetic costs and may make fish more vulnerable to terrestrial predators, especially at night while resting (Fig. 14).

Interestingly, juvenile *O. mykiss* expressed distinct avoidance of the thalweg area (Figs. 9, 12c) despite the existence of favorable water quality conditions existing there and elsewhere in the surface water layer (Figs. 5a-d, 6a-d). Consequently, *O. mykiss* appear to strictly prefer microhabitats where the benthic substrate occurs within the oxygenated and lighted freshwater epilimnion. Indeed, abundances of preferred benthic macroinvertebrate prey for Pescadero juvenile *O. mykiss* are more than four times greater at water depths of 0.65 m or less than at depths of 0.75 m or greater and abundances are particularly low below the halocline where hypoxic and anoxic conditions prevail (Robinson 1993, Martin 1995). My findings are similar to those of Eby and Crowder (2002) who observed that fishes occupied all depths when the Neuse River estuary was fully oxygenated but were restricted to shallow oxygenated zones during times of deep water hypoxia.

In addition to the vertical habitat compression occurring in the water column, lateral habitat compression resulting from worsened water quality occurring upstream (Figs. 6a-d, 10e) is evident. Of all the physico-chemical parameters measured, dissolved oxygen (DO) concentrations were most variable and regularly exceeded stressful (≤5.0 mg·L^{-1}) and lethal (≤2.0 mg·L^{-1}) limits for juvenile *O. mykiss* both at depth and upstream (Molony 2001; Figs. 5d, 6d, 7d, 10e). Minimum daily DO at 1.25 m depth was greater than 5.0 mg·l^{-1} for all study days at the station closest to the mouth (st02) and hypoxic (≤ 5.0 mg·l^{-1}) for 35 days (st13) and 41 days (st14) in the upper lagoon (Figs. 1b, 6d). Fish tag transmission detections at the uppermost receivers declined linearly when mean daily water temperatures in the Pescadero and Butano arms of the upper estuary warmed above 18°C and mean daily DO concentrations declined below 7.0 mg·L^{-1} (Figs. 1b, 16i,l,m,p). The avoidance behavior likely results from a combination of diminished growth rewards and heightened predation risks in subnormoxic environments. Pedersen (1987) reports that juvenile *O. mykiss* require DO concentrations of approximately 7.0 mg·L^{-1} for proper growth and food conversion efficiency and food consumption declines below 6.0 mg·L^{-1}. Maximum swimming speeds for juvenile salmonids are reduced by 30% to 43% at DO concentrations between 5.7 mg·L^{-1} to 5.9 mg·L^{-1} (Jones 1971) and there is little capacity for anaerobic metabolism below 5.1 mg·L^{-1} (Kutty 1968) which is required for burst swimming (Drummond and Black 1960) and, thus, predatory escape. Not surprisingly, zero tagged *O. mykiss* were detected by mobile tracking surveys in the Butano Creek arm of upper estuary beyond ~150 m of the confluence (Figs. 10a-d) where lagoon DO levels were most harmful to aquatic life (Fig. 10e). The unused estuarine habitat is also the region where nearly all *O. mykiss* mortalities were observed following a breach-induced fish kill that occurred 54 days after this study when the lagoon drained after being closed for 291 days (Jankovitz 2015, Fig. 10f). One tagged individual (T03) was amongst the 263 accounted steelhead mortalities.

Movement - Aside from a major peak at dawn and a minor peak at dusk, fish movement rates closely tracked daily changes in light intensity (Fig. 14). Approximately 45% less movement occurred at night compared to day when fish moved at consistently low baseline levels (~40 mm·s^{-1}; Fig. 14). Some movement while resting may have been required to replenish oxygen across the gill boundary layer. Mean ROM from 06:00:00 to 06:59:59 ($\bar{x}$=94 mm·s^{-1}), when surface light intensities increased over three orders of magnitude, was more than twice as fast as mean ROM during the previous 12 hours ($\bar{x}$=44 mm·s^{-1}) (Fig. 14). The appetites of many fish species either peaks at dawn or dusk or is spread more evenly throughout the day (Boujard and Leatherland 1992). The crepuscular ROM spikes (Fig. 14) indicate that fish increased foraging activities at times when predation risks were most minimized during the visual feeding time window. The larger and more consistent peak at dawn indicate that fish may take more foraging risks when hungry after a nighttime fasting period.

Water temperature moderated the effects of time-of-day on movement rates. According to the polynomial relationship between mean daily ROM for the combined sample and mean daily temperature, maximum ROM (89 mm·s^{-1}) is predicted to occur at 17.4°C and approximately 39% and 49% less movement is predicted to occur when water temperatures are

13°C and 21°C, respectively. The temperature-ROM relationship observed here (Fig. 16e) closely resembles the thermal relationships for juvenile salmonid food consumption, food conversion efficiency, and growth rate (Brett 1979, 1995). Levels for all processes increase to a maximum as water temperature warms to an optimum value near 17ºC to 18 ºC before declining at higher temperatures (Brett 1979, 1995; Fig. 16e). Cold temperatures and slow digestion rates limit fish feeding activity regardless of food abundance (Brett 1979, 1995) and juvenile salmonid appetites and activity levels decline at hot temperatures. Near the optimum ROM temperature, ration size, scope for activity, and growth potential are maximized for juvenile salmonids (Brett 1979, 1995). Maximum ROM occurred at dawn when temperatures throughout the lagoon were suboptimal and during the late morning when temperatures were optimal (Figs. 4, 14) and these observations suggests that juvenile *O. mykiss* are most willing to engage in risky foraging activities when potential growth rewards are maximized.

The degree to which fishes in California IEs utilize sandbar overwash events to move into the marine environment is not currently known. Of the 12 fish retained in the passive array for less than a week, two (T11 and T25) were last recorded by the downstream VPS receivers (stations 01-12) and 10 were last recorded by non-VPS receivers in the Pescadero (st13; n=5) and Butano (st14; n=5) arms of the upper estuary (Fig. 1b, Table 2). Two additional fish tags (T02 and T19) that were undetected after November were last recorded by VPS receivers (Table 2). The daily WSE ranges for the dates of final detection for the four fish last detected by downstream receivers were 23 mm (15-Sep), 21 mm (16-Sep), 46 mm (19-Nov), and 59 mm (27-Nov). Seaward movement on those dates was unlikely given the fish sizes and relatively small WSE fluctuations (Fig. 2). Predation rates in Central California IEs are considered high (Satterthwaite et al. 2012, Osterback et al. 2013) and it is more likely that the fish were removed from the system by predators. Indeed, multiple predatorial avian species were observed at the lagoon during the study period, including Western gulls (*L. occidentalis*), Brandt's cormorants (*Phalacrocorax penicillatus*), and brown pelicans (*Pelecanus occidentalis*) (*SI appendix A*, Figs. A11a-d) and PIT-tagged juvenile Pescadero steelhead juveniles from a previous study were amongst the mortalities detected at the nearby Año Nuevo Island Western gull colony site (A. Osterback, pers. comm., 8-Oct, 2014). It is also possible that some fish moved rapidly upstream and evaded subsequent detection by fixed or mobile receivers. Technical issues like premature fish tag battery failure cannot also be ruled out. Given the potential confounding factors, no formal analysis of survival is presented here using telemetry data.

The mobile tracking data indicate that the steady decline in the number of unique fish tags detected per day and total number of detections per day for all tags combined beginning during the third week of November by fixed receivers can be attributed to upstream movement by a large portion of the rearing cohort. More than half of all remaining tagged fish were detected in the Pescadero arm of the far upper estuary on 14-Dec after not being observed there during the first three mobile surveys (Figs. 10a-d). The individuals located far upstream may have been in the early stage of a "twice smolting" life history path that is a unique and popular CCC *O. mykiss* strategy (Shapovalov and Taft 1954, Hayes et al. 2011, Huber and Carlson in prep). Hayes et al. (2011) suggest that declining lagoon water quality at the end of rearing period causes upstream movement of juvenile *O. mykiss*. Given that DO conditions improved over time as temperatures declined (Figs. 5a,d, 6a,d, 7a,d), it appears that the upstream movement was possibly triggered by declining fall day lengths, low temperatures (Figs. 4, 5a, 6a, 7a), or a combination of both factors. The 10 fish located farthest upstream in mid-

December were smaller-at-tagging overall ($\bar{x}$=173 mm FL, range: 139 mm FL to 201 mm FL) than the seven located closest to the mouth ($\bar{x}$=182 mm FL, range: 139 mm FL to 206 mm FL) and the two fish centrally located near the confluence ($\bar{x}$=174 mm FL) (Fig. 10d). Production of Na^+,K^+-ATPase, while less than the spring peak, occurs during fall and winter for some CCC *O. mykiss* and larger individuals are generally more salt-tolerant but exceptions are common (Hayes et al. 2011). Consequently, the larger fish remaining near the mouth in December may have been more osmotically prepared for marine life than the upstream fish and did not respond to any environmental triggers for upstream movement (Fig. 10d). Marine survival for *O. mykiss* asymptotes at large smolt body sizes (Ward and Slaney 1988 as cited in Mangel and Satterthwaite 2008) and it is also possible that the *O. mykiss* individuals detected far upstream had not attained threshold sizes during a potential late fall life history decision window. Interestingly, three of the fish detected far upstream on 14-Dec (T06, T30, T33) subsequently returned to the VPS array which suggests that upstream movement is not entirely unidirectional for all fish or that some fish may have changed life history decisions. If these interpretations are correct, smaller arrival size, slower growth, later estuarine arrival, or a combination of these factors may promote twice smolting life history expression for CCC steelhead.

Management relevance - The findings of this investigation in addition to earlier and follow-up studies by university and state government scientists indicate the critical importance of providing a sizeable fresh or near-fresh oxygenated surface water layer for rearing steelhead during sandbar-closed conditions (Smith 1990, Jankovitz 2015). The severe California drought persisted until water year 2016 and Jankovitz (2015) reports that poor water quality during summer 2015 "terminated all *O. mykiss* production and probably survival throughout the lagoon." In 2015, sandbar formation occurred in late July during base freshwater inflows. Initially a shallow brackish water epilimnion formed but was lost by late summer when saline conditions, hot water temperatures, and very low DO concentrations prevailed throughout the water column (Jankovitz 2015). While quasi-annual acute breach-induced fish kills have been observed at Pescadero since the mid-1990s (Sloan 2006, Smith 2009, Largier et a. 2014), the situation in 2015 represents the first documented case of a potential kill caused by chronic degradation of water quality during the closed state. Such events may occur more frequently in the future without proper management actions guided by sound scientific principles. Besides promoting freshwater infill, other actions that alleviate hypoxia and anoxia at depth and upstream would benefit steelhead and other estuarine fishes. Habitat quality in the cover-poor lagoon could be improved immediately by additions of LWD structure, particularly in locales that are easily accessed from preferred feeding grounds (Grand and Dill 1997). Lastly, efforts should be made to prevent breach-induced fish kills from occurring until at least late fall when "twice smolting" fish have moved upstream and mortality risk for the population is more spread in space.

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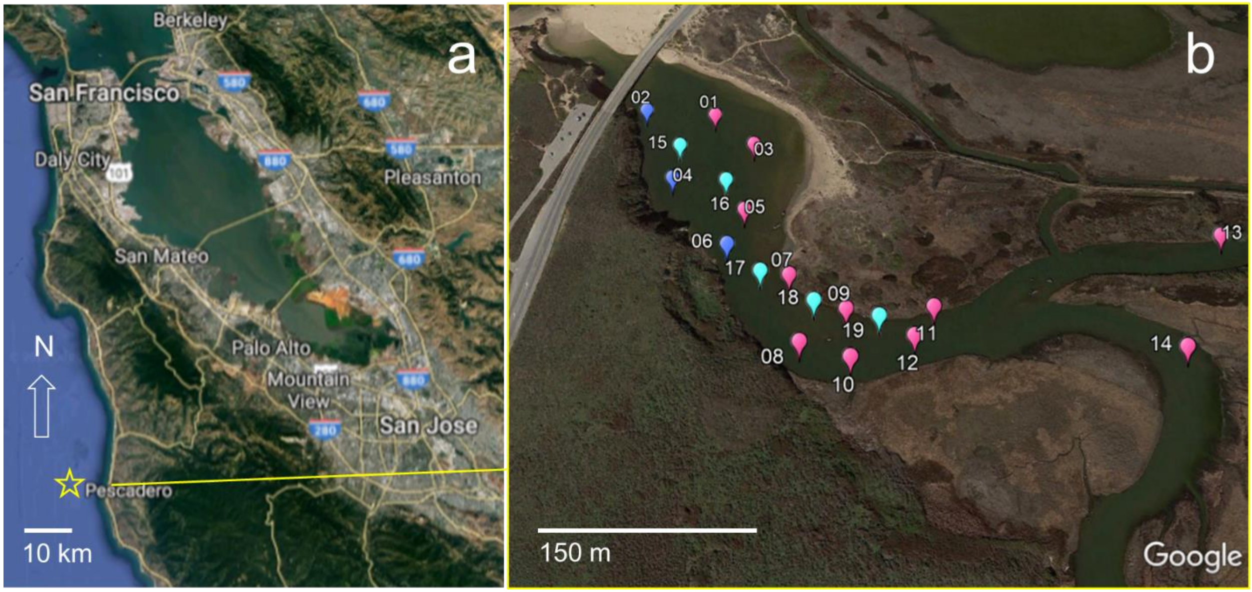
Table 1. Gaussian equation parameters and Akaike information criteria (AIC) for relationships between mean aerial and sub-aerial solar radiation values at multiple water depths (lux, dependent variable) and time-of-day (proportion of 24 hours, independent variable) from 0.25 to 0.75 (06:00 to 18:00).

Depth (m)	a	b	c	AIC
aerial	$1.13 \cdot 10^5$	0.499	0.103	$1.076 \cdot 10^9$
0.75	12116.00	0.501	0.094	$3.961 \cdot 10^6$
1.25	5654.30	0.514	0.010	$2.630 \cdot 10^6$
1.50	3540.80	0.498	0.010	$7.715 \cdot 10^5$
1.75	2111.30	0.505	0.100	$1.731 \cdot 10^5$

Table 2. Passive and active acoustic telemetry information for individually tagged juvenile *O. mykiss*. Fork length (FL) at tagging, kernel density estimates (25%, 50%, and 75% KDE), rate of movement (ROM), and ROM standard error (SE) are also shown. Estimates of ROM are presented for all fish providing HPE-filtered position data and KDE estimates are restricted to the 17 fish providing nearly all of all HPE-filtered position data (see text for details).

Tag ID	FL (mm)	Total VPS pos.	Tot st13 detections	Tot st14 detections	Total mob. pos.	First VPS detection	Last VPS detection	First st13 detection	Last st13 detection	First st14 detection	Last st14 detection	First mob. detection	Last mob. detection	KDE_{25} (m^2)	KDE_{50} (m^2)	KDE_{75} (m^2)	Mean ROM ($mm \cdot s^{-1}$)	SE ROM ($mm \cdot s^{-1}$)
T01	139		22	2	3			9/10/13 20:54	9/10/13 15:05	9/10/13 17:24	9/10/13 17:25	10/1/13	12/14/13					
T02	140	30569	1618	548	23	9/11/13 6:39	11/19/13 19:37	9/10/13 12:47	11/12/13 15:49	9/13/13 1:48	11/16/13 17:23	10/1/13	11/7/13	579.2	1655.3	4997.0	76.9	1.4
T03	206	36923	645	628	18	9/23/13 13:15	12/19/13 8:03	9/26/13 10:30	12/6/13 4:47	9/12/13 4:41	11/13/13 16:07	11/7/13	12/14/13	114.4	279.8	1847.6	54.3	0.4
T04		492	2661	309		9/11/13 6:43	9/12/13 19:00	9/10/13 17:20	9/16/13 6:56	9/13/13 3:26	9/14/13 8:20						23.1	1.9
T05	152																	
T06	185	25844	29361	1414	22	9/12/13 20:26	12/20/13 22:25	9/10/13 10:24	12/22/13 3:44	9/10/13 10:50	12/5/13 12:17	10/1/13	12/14/13	61.7	220.7	1500.1	47.9	0.5
T07	168	42293			23	9/12/13 0:17	12/22/13 22:07					11/7/13	12/14/13	20.8	49.4	95.4	43.3	0.5
T08	182	59073	2019	167	20	9/11/13 17:05	12/15/13 2:37	12/14/13 8:22	12/20/13 23:46	9/18/13 14:57	12/15/13 20:51	10/1/13	12/14/13	43.0	118.9	262.0	49.7	0.5
T09	177	57383	1035	370	30	9/11/13 15:23	12/9/13 3:51	9/12/13 5:45	12/19/13 17:54	9/11/13 3:07	12/6/13 1:45	10/1/13	12/14/13	185.7	741.4	3416.6	84.5	0.5
T10	172	37811	3563	28072	22	9/11/13 7:55	12/21/13 15:59	9/14/13 6:39	12/16/13 7:02	9/14/13 8:29	12/22/13 1:43	10/1/13	11/21/13	217.4	1135.1	4427.8	72.9	0.5
T11	189	1092	1408	11		9/11/13 14:26	9/15/13 15:47	9/10/13 17:02	9/12/13 15:37	9/11/13 20:04	9/12/13 16:57						22.1	2.1
T12	179	54500	2942	200	30	9/11/13 16:55	12/8/13 1:53	11/4/13 12:09	12/22/13 14:33	9/26/13 15:29	12/20/13 5:32	10/1/13	12/14/13	65.6	163.4	960.0	65.3	0.8
T13	188	57681	6229	702	35	9/17/13 16:01	12/22/13 14:10	9/11/13 4:59	9/17/13 9:23	9/11/13 7:30	10/4/13 23:40	10/1/13	12/14/13	264.3	991.1	4610.2	49.2	0.5
T14	172		62	461				9/11/13 18:43	9/16/13 3:07	9/11/13 9:56	9/15/13 16:20							
T15	188		295	141				9/10/13 9:52	9/10/13 19:25	9/11/13 10:41	9/11/13 13:55							
T16	170	32170	761	2269	19	9/11/13 7:43	12/6/13 1:40	9/10/13 11:08	12/6/13 4:30	9/10/13 5:16	12/6/13 11:49	11/7/13	12/14/13	105.3	243.0	1364.1	65.9	0.7
T17	170		112					9/11/13 2:02	9/10/13 20:36									
T18	173	20247	7477	99	4	9/19/13 6:17	12/1/13 2:16	10/21/13 1:28	12/9/13 2:50	9/23/13 14:28	12/1/13 13:05	12/14/13	12/14/13	48.4	213.6	730.7	47.6	0.6
T19	195	3194	1086	45124	25	9/11/13 7:42	11/27/13 16:37	9/10/13 10:40	11/20/13 18:05	9/10/13 8:47	11/26/13 13:05	10/1/13	11/21/13				69.1	2.0
T20	189		296	37				9/10/13 3:36	9/10/13 17:51	9/9/13 23:35	9/10/13 18:54							
T21	170		29					9/11/13 4:00	9/10/13 20:37									
T22	172	62306	556	22271	30	9/11/13 8:15	12/22/13 13:13	9/28/13 3:40	11/6/13 1:43	9/25/13 16:11	11/7/13 0:22	10/1/13	12/14/13	35.5	81.0	201.9	43.4	0.4
T23	195		97	178				9/10/13 11:07	9/10/13 23:04	9/11/13 1:11	9/11/13 5:25							
T24	162	60	73013	289	14	10/2/13 4:00	10/2/13 5:59	9/10/13 14:24	12/22/13 0:17	9/10/13 7:44	10/3/13 0:58	11/7/13	12/14/13				104.5	31.1
T25	172	1134				9/11/13 7:43	9/16/13 6:35										41.2	6.8
T26	189	158	414	70		9/12/13 21:20	9/13/13 6:41	9/10/13 12:48	9/15/13 1:28	9/10/13 11:50	9/15/13 9:25						26.8	3.7
T27	159	250	118	36		9/11/13 12:49	9/13/13 7:23	9/10/13 17:25	9/13/13 7:47	9/11/13 14:40	9/12/13 17:48						76.9	32.0
T28	150	1358	238	1		9/11/13 17:18	9/15/13 10:44	9/10/13 20:03	9/10/13 18:29	9/15/13 21:12	9/15/13 21:12						25.1	3.0
T29	139	32511	512	314	25	9/11/13 17:19	12/21/13 2:02	9/10/13 13:50	12/15/13 18:58	9/11/13 2:27	12/16/13 3:11	10/1/13	12/14/13	138.7	1477.8	5154.3	72.3	1.0
T30	172	13643	23956	18423	20	9/14/13 20:46	12/19/13 22:29	9/10/13 10:36	12/22/13 4:26	9/12/13 12:42	11/30/13 10:48	10/1/13	12/14/13	126.5	477.6	2890.7	53.5	0.9
T31	166			84521	2					9/11/13 11:14	12/21/13 15:31	11/21/13	12/14/13					
T32	201	3749	30592	50	21	9/18/13 9:25	12/5/13 18:00	9/10/13 8:09	12/16/13 19:57	9/11/13 4:19	12/4/13 11:46	10/1/13	12/14/13				114.3	4.0
T33	168	65074	9825	442	45	9/12/13 19:45	12/22/13 12:00	9/10/13 13:38	12/18/13 22:50	9/11/13 3:25	12/21/13 13:31	10/1/13	12/14/13	248.0	841.2	3123.6	72.4	0.6
T34	200	67057	462		33	9/11/13 15:30	12/18/13 17:27	9/19/13 14:43	12/10/13 7:09			10/1/13	12/14/13	267.6	1084.0	3924.2	69.3	0.6
T35	200	71228		32	29	9/11/13 6:57	12/14/13 15:50			9/12/13 2:38	11/26/13 6:18	10/1/13	12/14/13	23.3	70.5	573.7	65.5	0.4



Figures 1a-b. (a) The Pescadero Creek intermittent estuary is located along California's Central Coast approximately 60 km south of San Francisco; (b) Passive telemetry station locations including those with receivers (purple), synchronization transmitters (light blue), and both receivers and synchronization transmitters (dark blue).

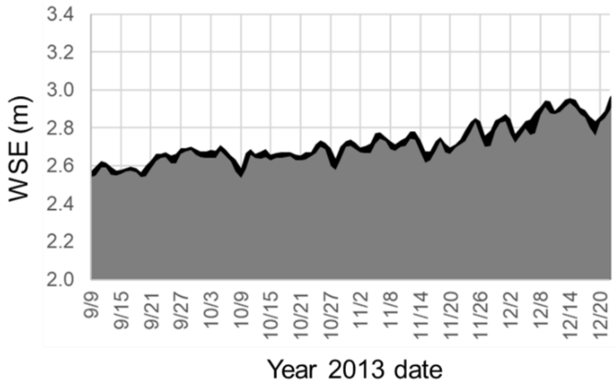


Figure 2. Maximum (black) and minimum (grey) water surface elevations (WSEs) during the study period from 9-Sep, 2013 to 22-Dec, 2013. The irregular pattern was due to small-scale sediment aggradation and erosion of the coastal sandbar by frequent sheet-like marine overwash events over the broad flat sandbar (see *SI Appendix A*, Fig. A5a-f).

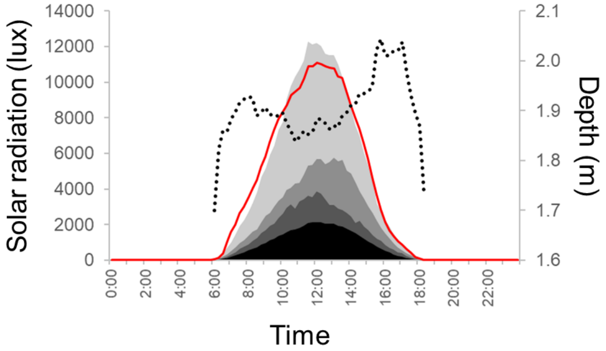


Figure 3. Mean areal (red line) and sub-aerial solar radiation at 0.75 m (light grey area), 1.25 m (grey area), 1.50 m (dark grey area), and 1.75 m (black area) water depths (primary y-axis) according to time-of-day. The aerial values are divided by 10 for ease of visual display. Dotted black line represents estimated depth of zero solar radiation (secondary y-axis).

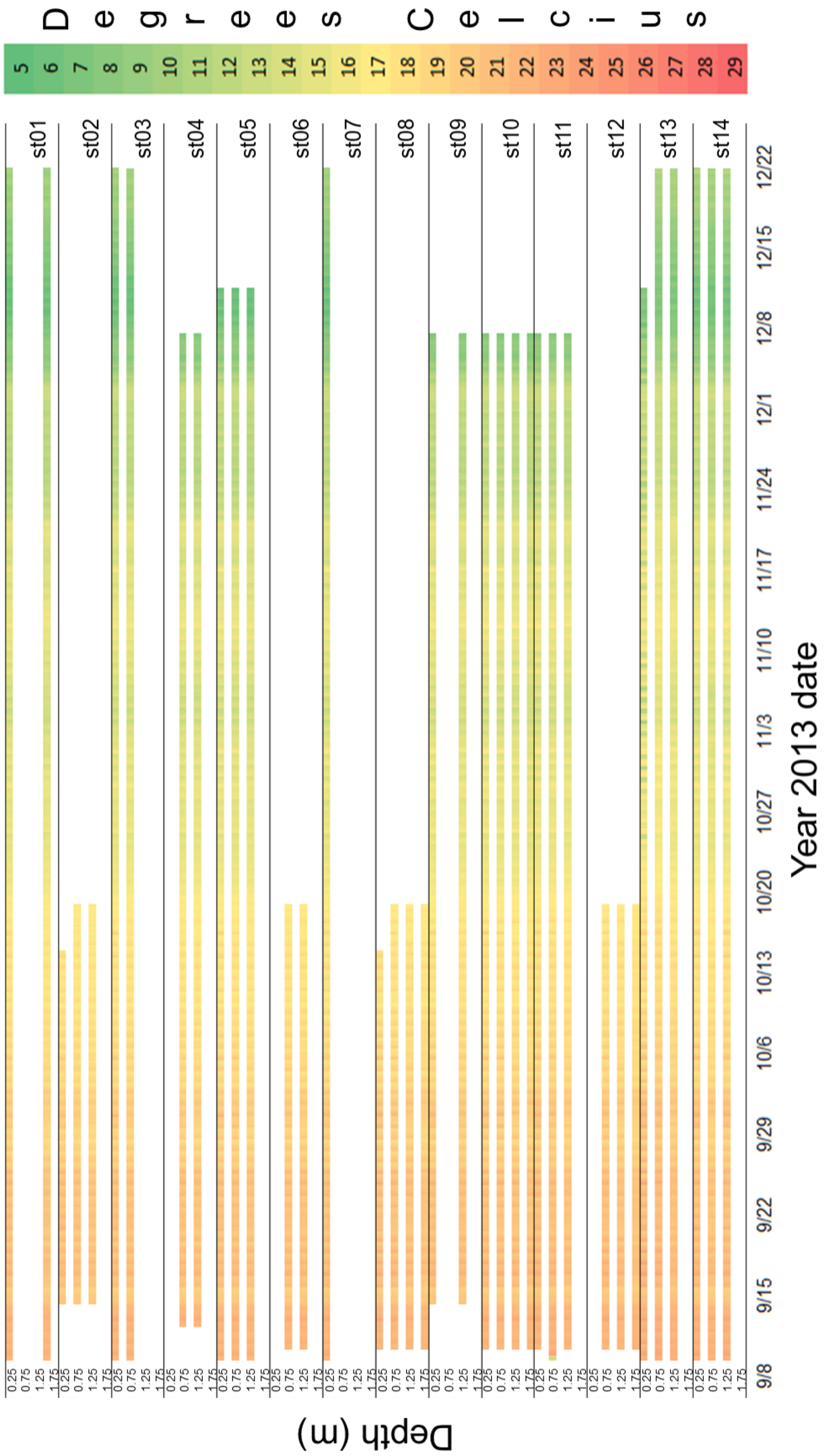
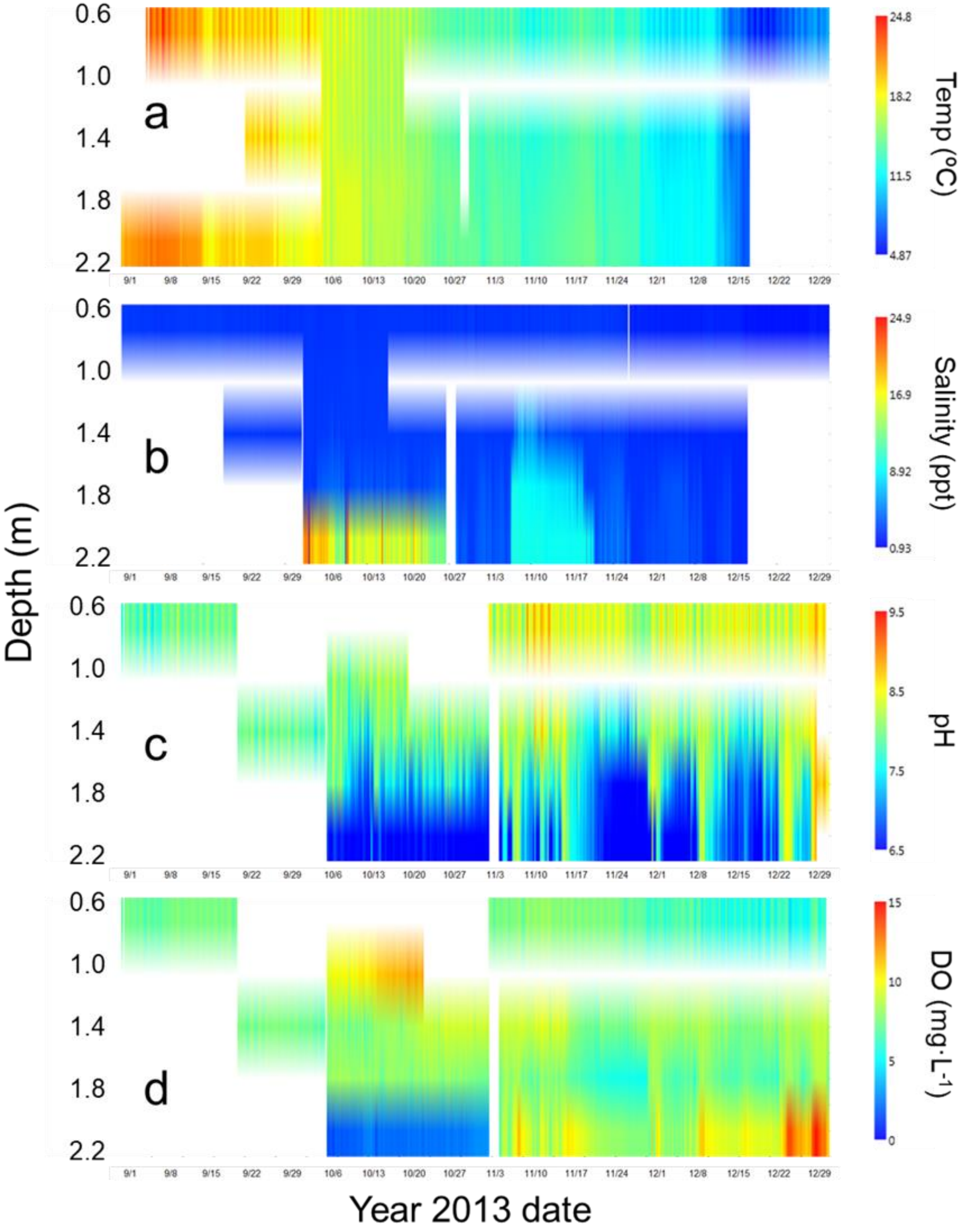
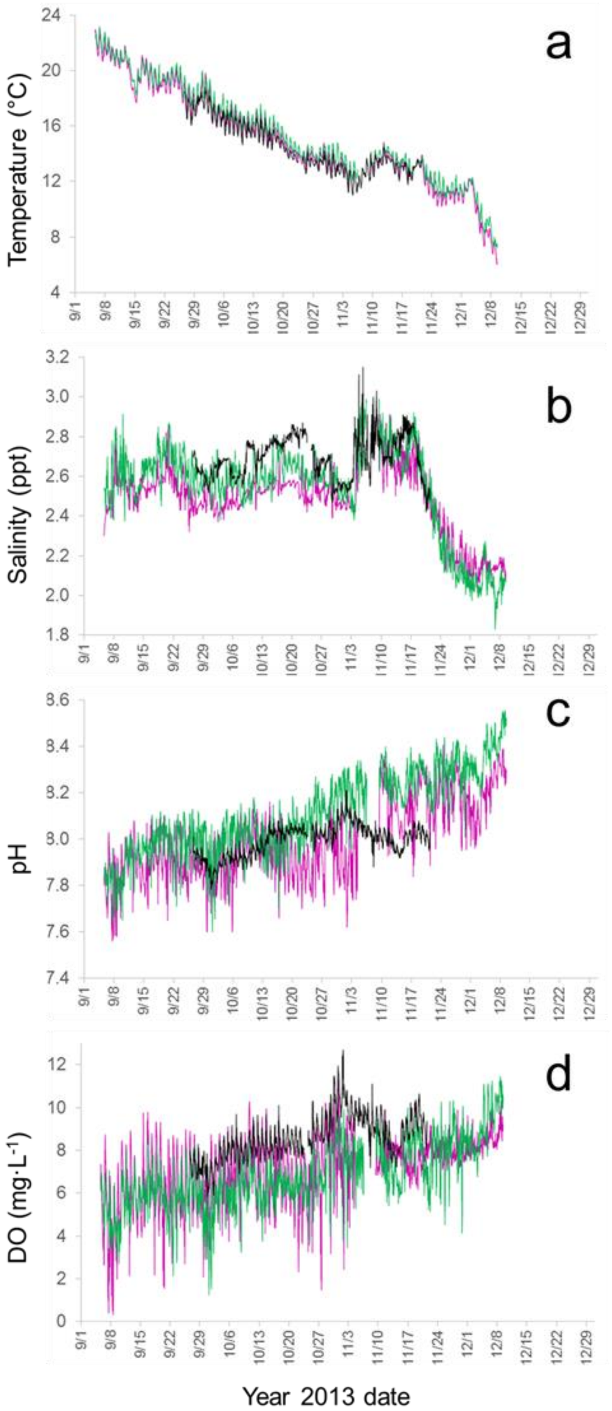


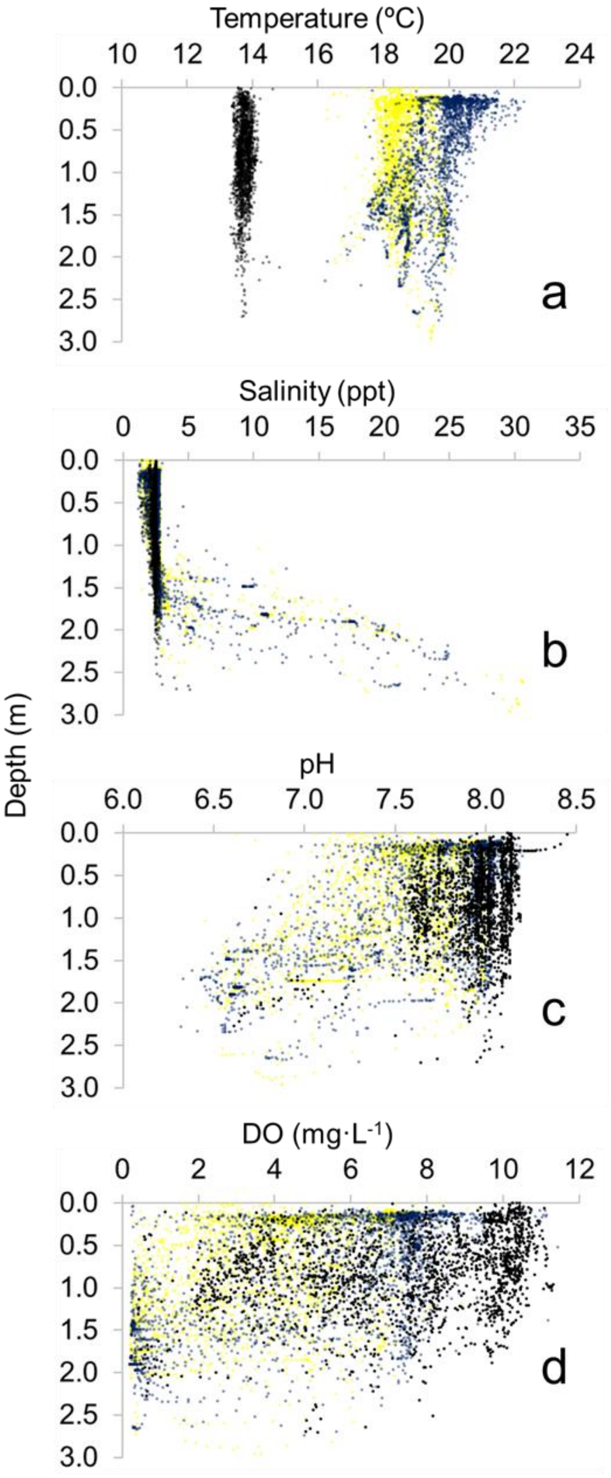
Figure 4. Thermal profiles from 0.25 m to 1.75 m water depths at all stations possessing acoustic receivers (see Fig. 1b).



Figures 5a-d. Water column profiles of (a) temperature, (b) salinity, (c) pH, and (d) dissolved oxygen in the middle of the study reach at station 08.



Figures 6a-d. Measurements of (a) temperature, (b) salinity, (c) pH, and (d) dissolved oxygen at 1.25 m water depth at stations 02 (black), 13 (purple), and 14 (green).



Figures 7a-d. Measurements of (a) temperature, (b) salinity, (c) pH, and (d) dissolved oxygen during afternoon water quality cruises on 25-Sep, 2013 (blue) and 21-Nov, 2013 (black) and a morning cruise on 25-Sep, 2013 (yellow). Water quality generally declined at depth and upstream (see Fig. 10e).

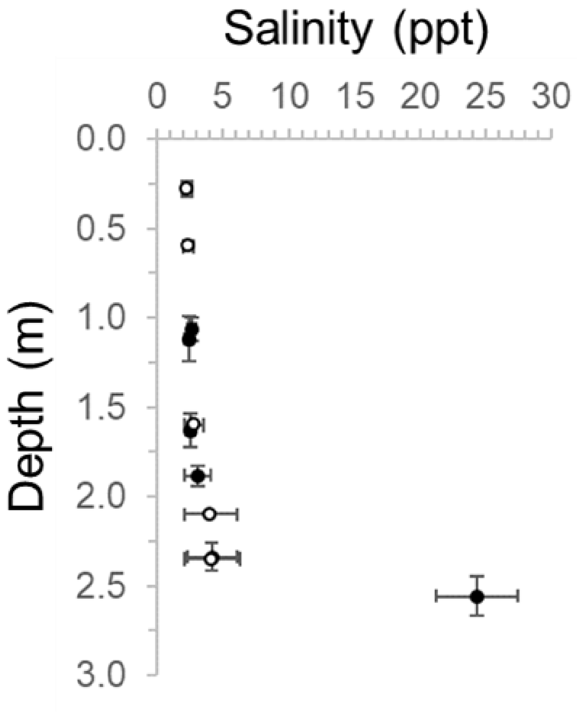


Figure 8. Salinity measurements at multiple water depths in the VPS monitoring zone from a combination of sensors at fixed distances from the water surface (white circles) or benthic substrate (black circles). Total error bars lengths represent two standard deviations.

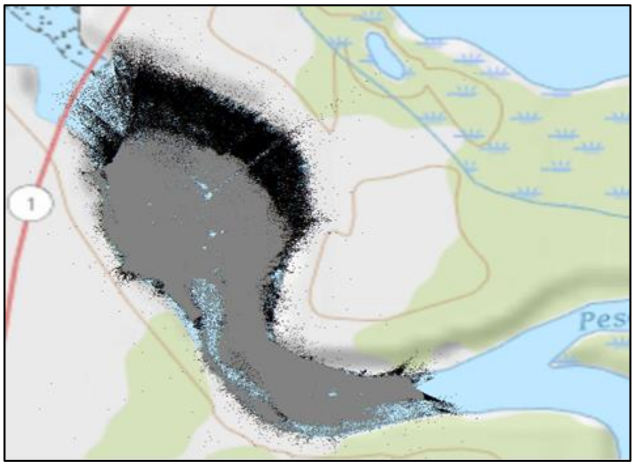
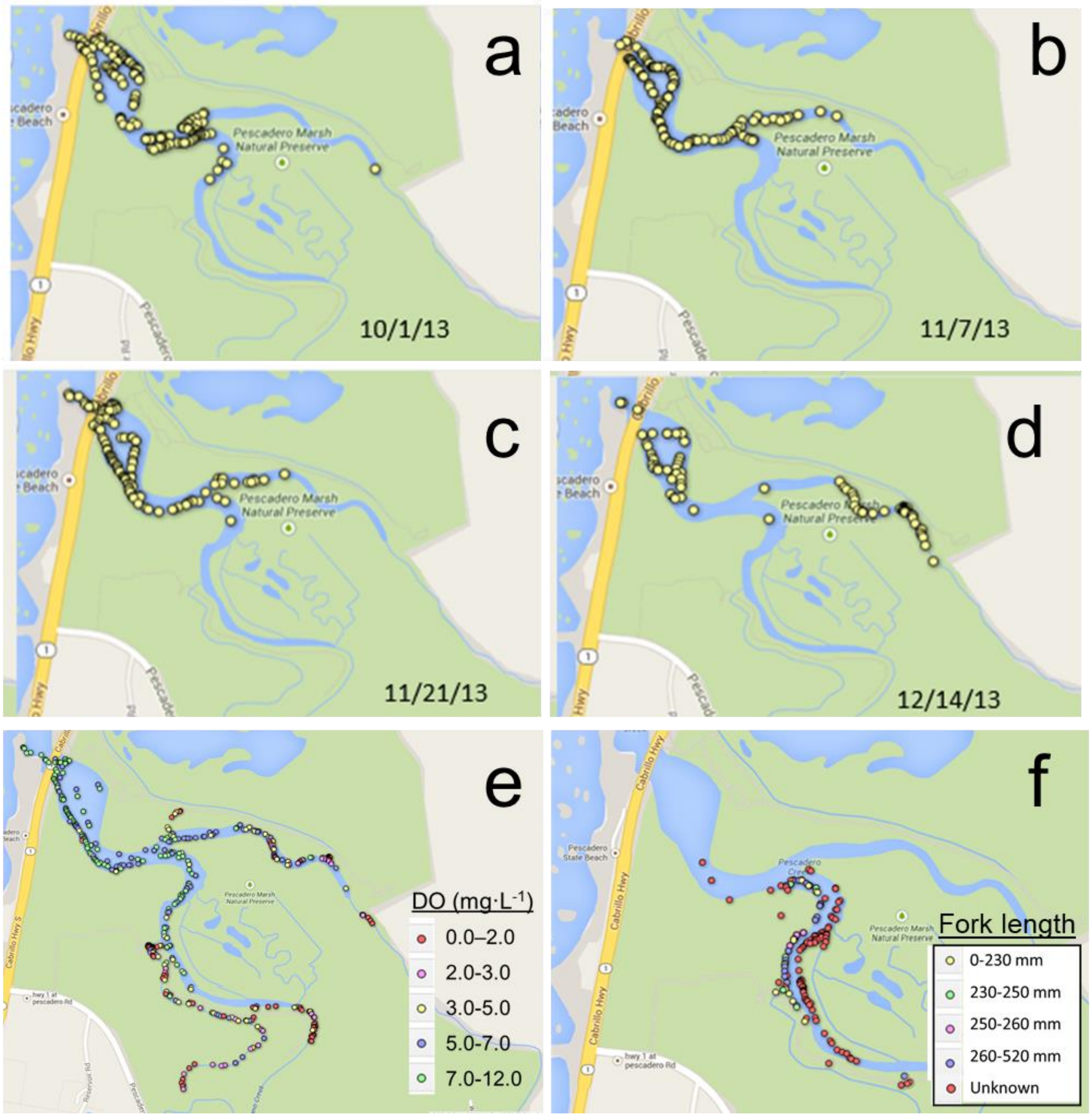


Figure 9. All (black) and HPE-filtered (grey) triangulated fish positions provided by the VEMCO Positioning System (VPS) (see text for details).



Figures 10a-f. Fish positions during all four mobile tracking surveys (a-d), dissolved oxygen (DO) concentrations at 1.0 to 2.0 m water depths on 25-Sep, 2013 and 21-Nov, 2013 (e), and locations and sizes of *O. mykiss* mortalities from the 9-Feb, 2014 breach-induced fish kill (f). The uppermost extent of navigable waters is indicated in 'e'. An acoustically tagged fish was amongst the mortalities shown in 'f'.

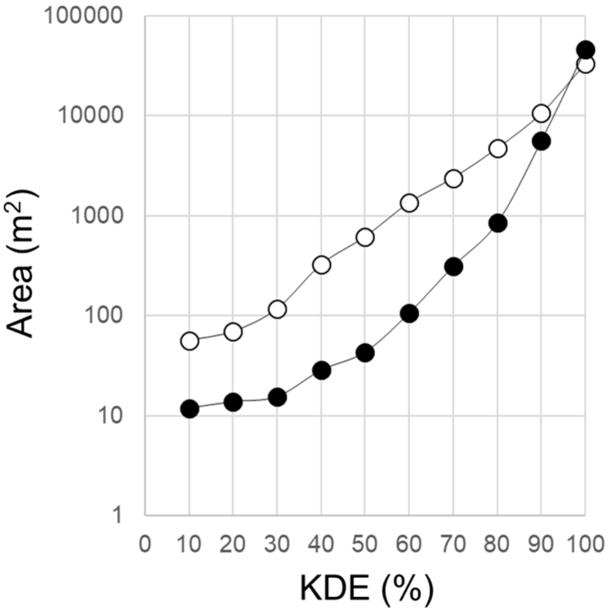
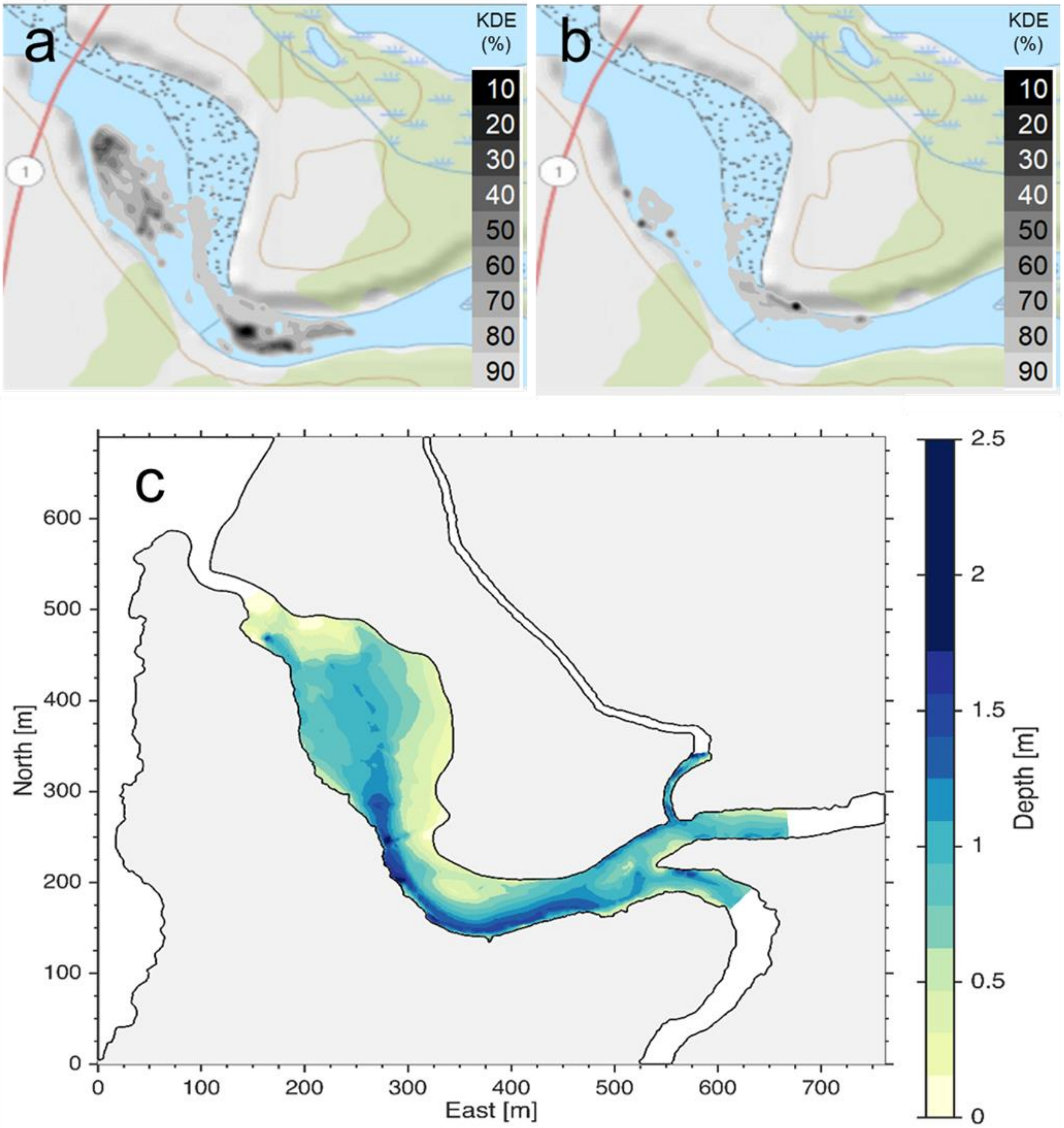


Figure 11. Exponential relationships between KDE decile endpoint and corresponding area for each 10% KDE increment during the day (05:00:00 to 18:59:59, open circles) and night (19:00:00 to 04:59:59, black circles).



Figures 12a-c. (a) Bathymetry map of study site. Map of (b) diurnal (05:00:00 to 18:59:59) and (c) nocturnal (19:00:00 to 04:59:59) KDE decile areas. The bathymetry map is redrawn from Williams (2014) and data were obtained in November 2010 when the lagoon water surface elevations were approximately 0.25 m lower than November 2013.

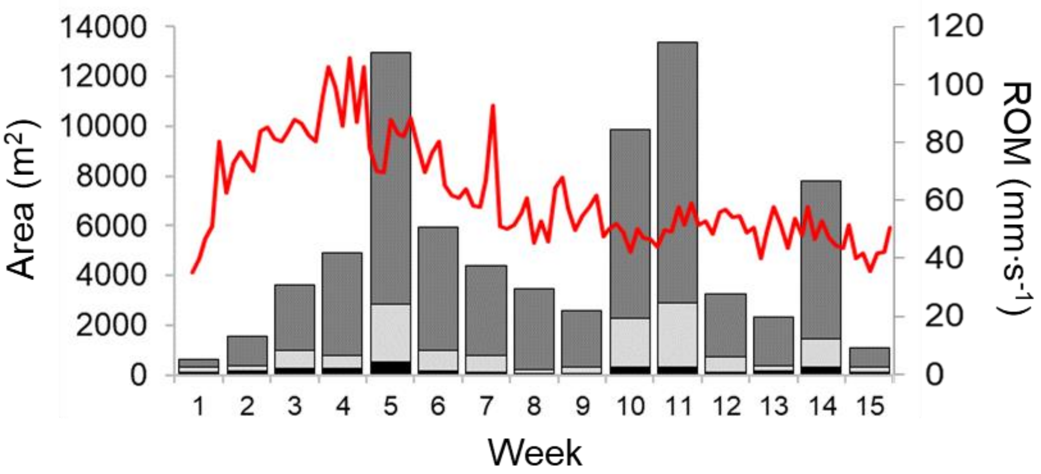


Figure 13. Mean weekly central core (0-25% KDE, black bar), core (0-50% KDE, black and light grey bar), and activity space (50-75% KDE, grey) areas for all acoustically tagged fish combined. Mean daily rate of movement (ROM, red line) for the combined sample is also presented.

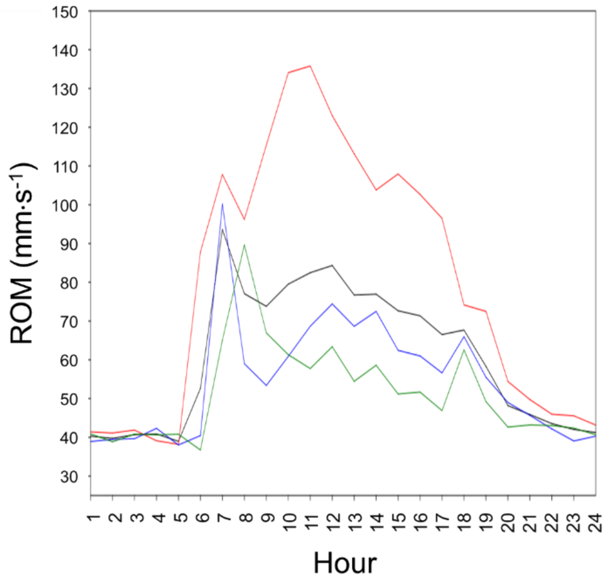
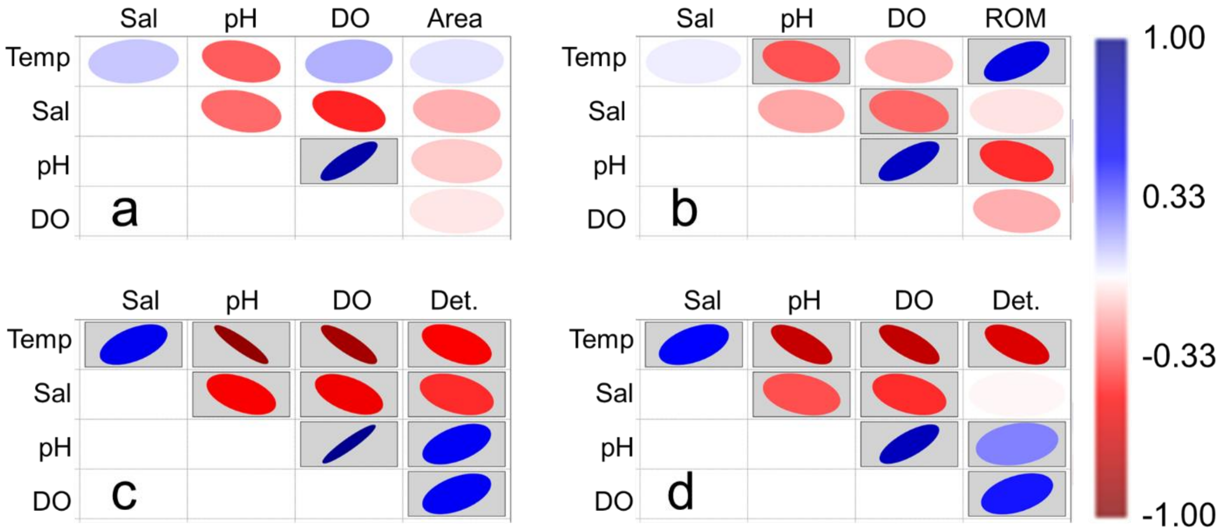
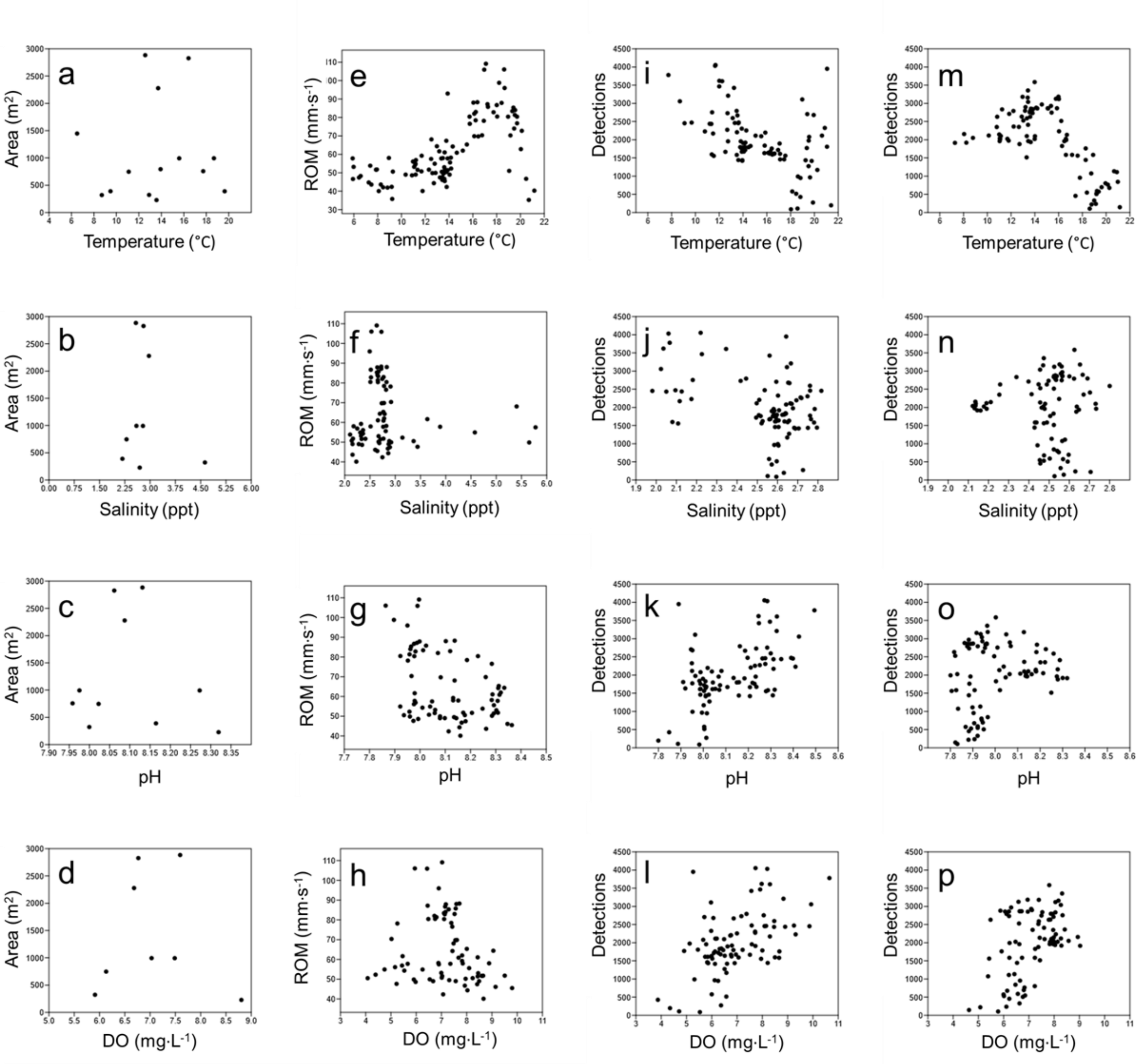


Figure 14. Mean hourly rate of movement (ROM) during the first third (study weeks 1-5, red), middle third (weeks 6-10, blue), last third (weeks 11-15, green), and entire (weeks 1-15, black) study periods.



Figures 15a-d. Pearson r correlation matrices for (a) mean weekly physico-chemical measurements and mean weekly core areas (50% KDE) for all fish combined, (b) mean daily physico-chemical measurements and mean daily ROM values for all fish combined, and mean daily physico-chemical measurements and total daily fish tag detections at stations 13 (c) and 14 (d). Blue upward and red downward sloping ellipses indicate positive and negative associations, respectively. Narrower and darker ellipses represent stronger associations and significant relationships are boxed. Scatterplots of the relationships between core areas in (a), ROM values in (b), and detections in (c) and (d) and water quality parameters are presented in Figs. 16a-p.



Figures 16a-p. Relationships between physico-chemical parameters and (a) mean weekly core areas for all tagged fish combined, (b) mean daily rate of movement (ROM), (c) total daily detections at station 13, and (d) total daily detections at station 14. Water temperatures for a-h represent depth-averaged daily mean values from 0.25 m, 0.75 m, 1.25 m, and 1.75 m water depths at all VPS receiver locations. Salinity, pH, and DO data for a-h are from station 08 (1.60 m depth). Water quality data for i-p are from their respective stations at 1.25 m water depths.

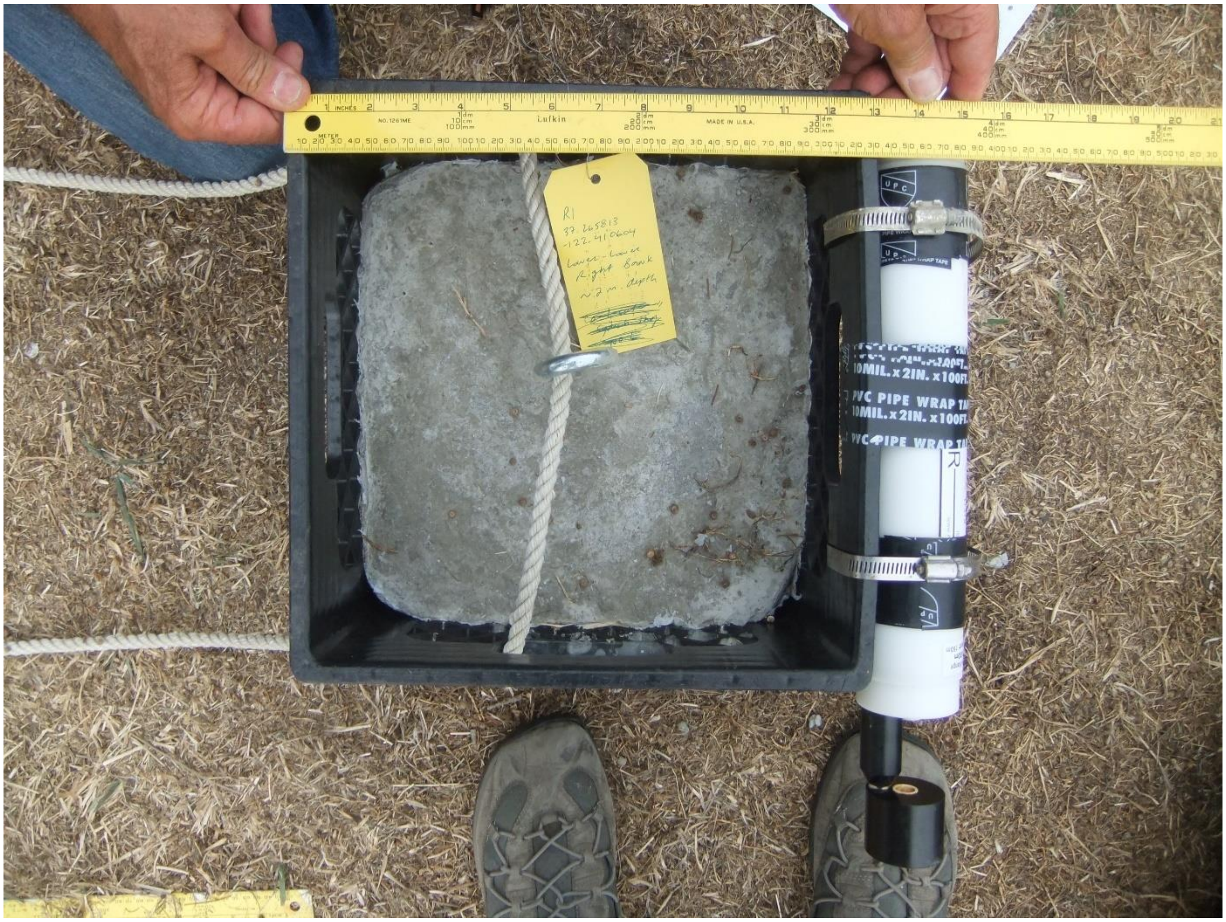


Figure A1. Mooring with central eye bolt and attached CTD.

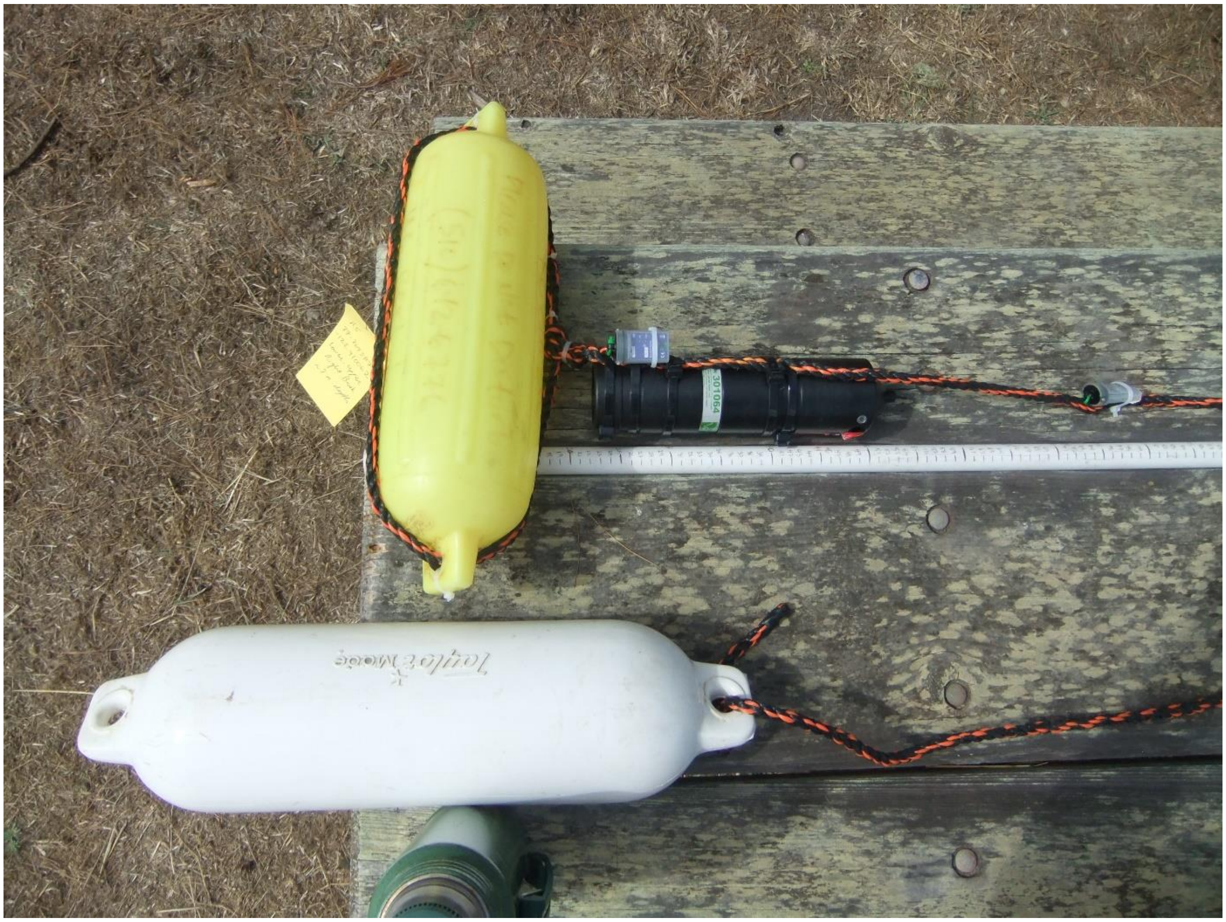
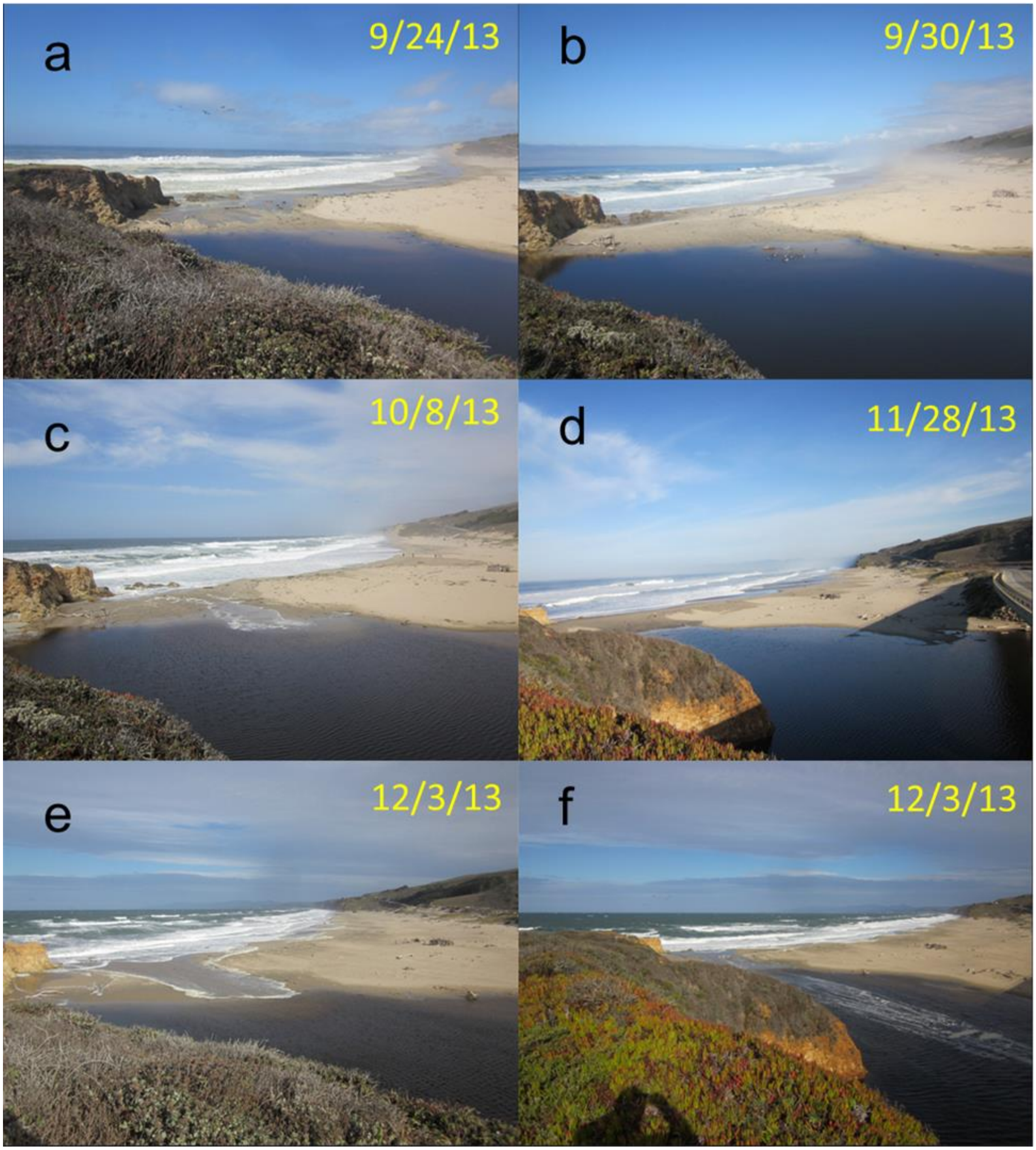


Figure A2. Dual floats and line that was threaded through then mooring eye bolt. Thermal sensors were attached to the line at fixed distances.

Figure A3. Arrangement of sondes that provided water quality data at multiple depths at station 08. The data are presented in Figs. 5a-d.

Figure A4. Equipment biofouling by macroalgae.



Figures A5a-f. Mouth condition during the early (c) and latter (d-f) investigation period. Sheet-like marine overwash over the wide and flat sandbar commonly occurred throughout the acoustic telemetry study.

Figure A6. The lagoon water possessed a dark brown-green hue during the telemetry study. The light attenuation-at-depth levels were amongst the most extreme ever reported and created special visual conditions for fish. The photograph shows the lagoon just upstream of the coastal sandbar and is facing north.

Figure A7. Large woody debris complex present at the lagoon margin in the vicinity of station 09 that was recruited by rising water levels and heavily favored by juvenile steelhead at night (see Fig. 12b).

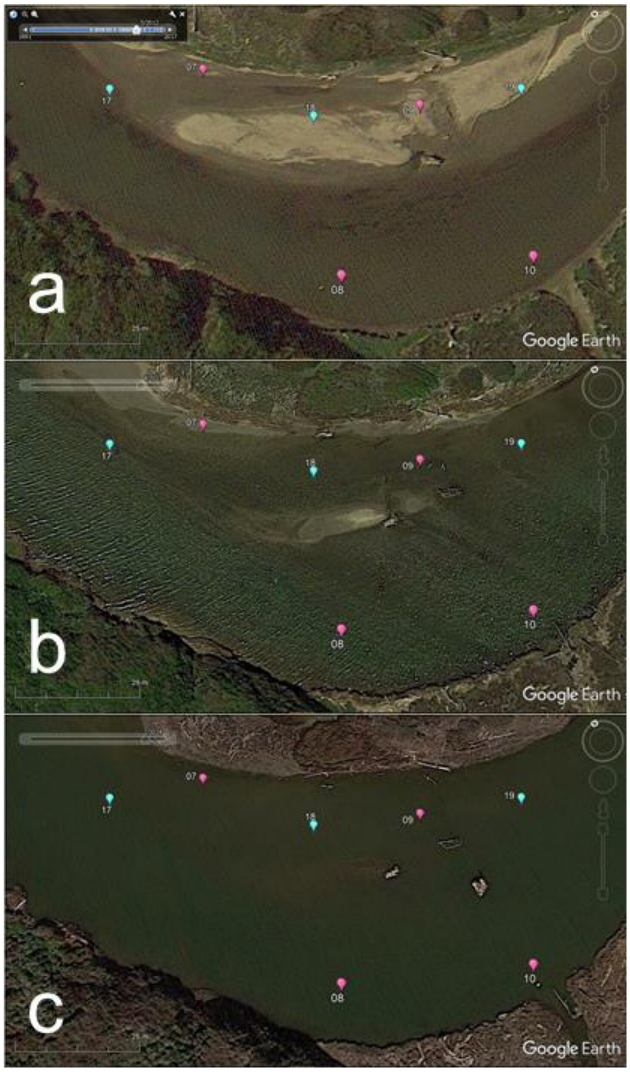


Figure A9a-c. Satellite images containing the preferred microhabitat complex at the sandy point bar along the inside bend of the middle estuary (see Figs. 5a-c). Images are from May 2012 (a), April 2013 (b), and February 2014 (c) during multiple estuarine states and infill levels. Note how the favored LWD complex from the bar's surface to the northern bank and is recruited into the aquatic ecosystem by rising water levels.

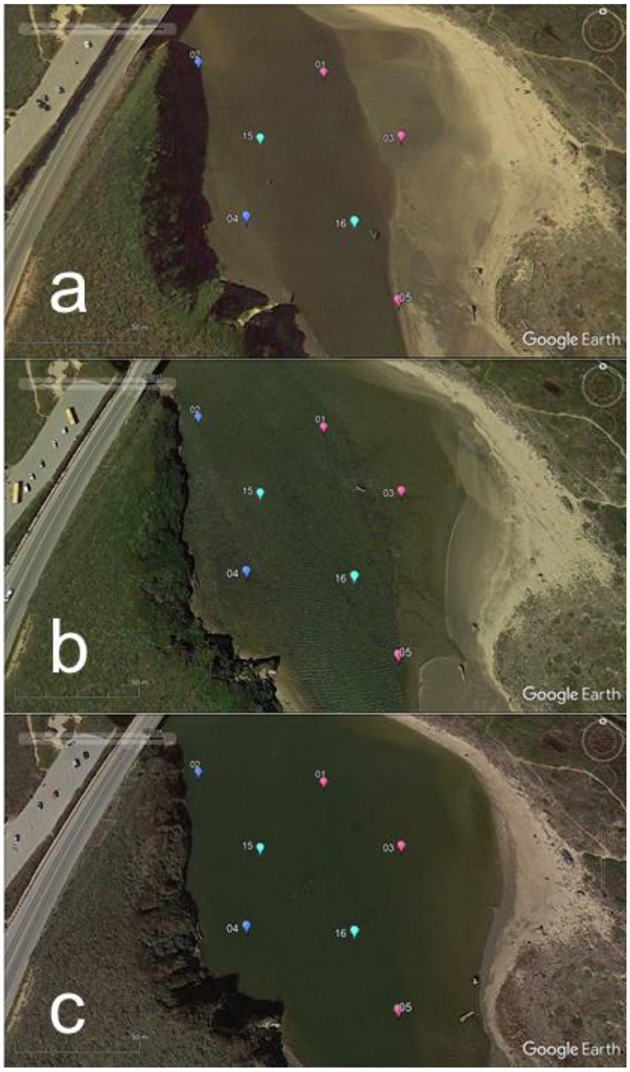


Figure A9a-c. Satellite images containing the preferred microhabitat complex in the lower lagoon that was located at the upper end of the sandy flood-tide delta and adjacent to rocky cliffs (see Figs. 5a-c). Images are from May 2012 (a), April 2013 (b), and February 2014 (c) during multiple estuarine states and infill levels. Note the rocky cliff face along the southwestern edge of the lagoon.

Figure A10. Lower estuary embayment during the telemetry study. Note that the preferred nocturnal microhabitats in this area (see Fig. 5b) are sheltered from strong Pacific winds and adjacent to rocky cliffs. The photograph was obtained near the northern terminus of the Highway 1 bridge and is facing southeast.

Figure A11a-d. Avian predators photographed at the study site during the investigation period. Species include (a and b) Western gulls (*Larus occidentalis*), (c) Brandt's cormorants (*Phalacrocorax penicillatus*), and (d) brown pelicans (*Pelecanus occidentalis*). Nancy Frost provided the image for 'a' (https://www.flickr.com/photos/34620405@N04/).

Figure B1. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for fish tag T02.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure B2. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for fish tag T03.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure B3. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for fish tag T06.

Figure B4. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for fish tag T07.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure B5. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for fish tag T08.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure B6. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for fish tag T09.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure B7. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for fish tag T10.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure B8. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for fish tag T12.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure B9. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for fish tag T13.

Figure B10. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for fish tag T16.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure B11. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for fish tag T18.

Figure B12. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for fish tag T22.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure B13. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for fish tag T29.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure B14. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for fish tag T30.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure B15. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for fish tag T33.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure B16. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for fish tag T34.

Figure B17. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for fish tag T35.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure C1. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for the combined sample during week 1 of the study.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure C2. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for the combined sample during week 2 of the study.

Figure C3. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for the combined sample during week 3 of the study.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure C4. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for the combined sample during week 4 of the study.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure C5. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for the combined sample during week 5 of the study.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure C6. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for the combined sample during week 6 of the study.

Figure C7. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for the combined sample during week 7 of the study.

Figure C8. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for the combined sample during week 8 of the study.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure C9. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for the combined sample during week 9 of the study.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure C10. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for the combined sample during week 10 of the study.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure C11. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for the combined sample during week 11 of the study.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure C12. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for the combined sample during week 12 of the study.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure C13. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for the combined sample during week 13 of the study.

Figure C14. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for the combined sample during week 14 of the study.

USGS The National Map: National Boundaries Dataset, National Elevation Dataset, Geographic Names Information System, National Hydrography Dataset, National Land Cover Database, National Structures Dataset, and National Transportation Dataset; U.S. Census Bureau - TIGER/Line; HERE Road Data

Figure C15. Central core (black), core (black and dark grey), activity space (grey), and excursion space (light grey) habitat areas for the combined sample during week 15 of the study.

CHAPTER 6

EPILOGUE

Epilogue

In this dissertation I explore the direct and indirect impacts of watershed disconnection on estuarine-dependent native California fishes, including iconic and imperiled salmonid populations from the Great Central Valley and Central Coast. The timing of my doctoral research coincided with a severe and historic drought that occurred from water years 2012 to 2016 followed by one of the wettest years on record in 2017. Here I reflect on lessons learned from my research during the early drought period and follow-up studies and current event information provided by government scientists.

Artificially propagated fall run Chinook salmon (*Oncorhynchus tshawytscha*) from five Central Valley hatcheries currently comprise the majority of salmon harvested by the California and Southern Oregon commercial ocean fishery and California recreational fishery (Kormos et al. 2012, Palmer-Zwahlen and Kormos 2013; 2015). Over two billion juvenile Central Valley fall run Chinook salmon (CVFRCS) have been planted throughout fresh and brackish water habitats upstream of the Golden Gate from 1946-2012 (Huber and Carlson 2015). Offsite releases of CVFRCS directly into the San Francisco Estuary (SFE) have increased since the 1980s and there has been a dramatic shift towards releasing fish in large batches and at similar times, sizes, and locations since the turn of the 21st century (Huber and Carlson 2015).

Soon after near record high escapement levels were observed in 2000, the CVFRCS population complex declined by more than one order of magnitude. The population was in an official state of collapse from 2006-2009 and the commercial and recreational fisheries were completely closed in 2008 and 2009 for the first time in their approximate 90 year histories (McEvoy 1990, Lindley 2009). The closures required provision of 170 million dollars in federal disaster relief aid from 2008-2010 (Upton 2013). The seismic event sent ripple effects throughout the state's economy and approximately 500 million to two billion dollars and 5,000 to 23,000 jobs were lost (Schwarzenegger 2008; 2009). Since 2009 substantial fishing season curtailments have regularly occurred and, since 2013, commercial landings have declined. In 2017 only 37% of the total permitted vessels participated in the ocean harvest and more than half of the catch was caught by 20% of participating boats according of California Department of Fish and Wildlife (CDFW) records (The Santa Rosa Press Democrat, 1-March, 2018). Besides the direct effects of lost investment returns to fishers, indirect effects of the diminished fisheries have also negatively impacted Native American tribes, the food industry, the hotel industry, charter boat operators, boat repair shops, equipment manufacturers, and other economic sectors.

Population recovery for CVFRCS has been hampered by extremely poor freshwater and marine habitat conditions during the recent drought. In response to the hostile inland habitat conditions, the Coleman National Fish Hatchery (CNFH) adopted the popular contemporary state hatchery practice of releasing fish directly into the SFE and this activity homogenized the biological portfolio for all hatcheries combined even further. Unfortunately, the estuary-planted fish are currently straying at alarmingly high rates because of impaired navigational abilities from trucking operations. This is an ecological dilemma because hatchery fish are invading new habitats en masse and may interbreed and compete with wild fish directly and indirectly. It is also an economic conundrum because hatcheries are unable to meet broodstock and egg production goals. In 2017, for instance, the CNFH produced only half of their intended amount of fertilized eggs because of very low pre-spawning adult returns to the hatchery.

Many CNFH fish strayed to the Nimbus hatchery and 23% of the egg quota shortfall was filled by transfers back to the CNFH (The Sacramento Bee, 2-March, 2018). Recently the Oroville dam spillway failure presents a near literal example of the dangers of "putting too many eggs in one basket" and relying too heavily on hatchery production for fishery sustainability. Massive debris loading by operation of the auxiliary spillway caused the emergency engineering of a makeshift filtration system in order to save millions of Feather River hatchery salmon and steelhead eggs and juveniles (The Mercury News, 21-March, 2017). While gallant efforts by hatchery personnel prevented widespread mortality of the young fish and eggs, the stranding of wild-origin salmon downstream of the dam during main spillway reconstruction is a concern to advocacy groups who claim that massive amounts of juvenile mortality may harm future fisheries.

The California Hatchery Scientific Review Group (HSRG) was formed in 2010 with the federal disaster relief aid funds in order to synthesize information about hatchery operations. One of the group's major conclusions is the need for more coordinated hatchery management practices (California HSRG 2012). My co-author, Dr. Stephanie Carlson, and I readily provide the release database to the public as a supplement to the journal-published version of chapter two (Huber and Carlson 2015). I hope that the hatchery data not previously accessible to scientists and other interested parties facilitates consensus building and helps solve challenging and pressing ecological and economic issues in the future. The publication appears to be well received; as of 24-April, 2018, the article has received 870 hits, been downloaded 271 times, and been cited nine times in the peer-reviewed literature according to escholarship.org and Google Scholar. The research was featured in the Delta Science Panel Lead Scientist Report in July 2015 and in February 2016 the findings were presented to a U.S. House of Representatives Subcommittee on Water, Power and Oceans hearing about strategies to improve salmon populations in Central Valley rivers. Furthermore, the release database is integral to a follow-up study by scientists from the Carlson Laboratory at UC Berkeley and the National Oceanic and Atmospheric Administration (Sturrock et al. in prep).

Approximately 91% of California's coastal wetland habitats have been destroyed since 1850 (Larson 2001) and Pescadero provides the most extensive saltmarsh habitat remaining between Elkhorn Slough approximately 90 km to the south and San Francisco Bay approximately 35 km to the north. Indeed, the California Coastal Commission considers Pescadero to be one of the two "most critical estuarine and wetland resources in the Central Coast region". The beach-estuary-saltmarsh ecosystem complex provides critical stop-over habitat for migrating birds and serves as a hotspot for native California biodiversity. In addition to threatened steelhead (*O. mykiss*), Pescadero also supports conservation-listed tidewater goby (*Eucyclogobius newberryi*), California red-legged frog (*Rana draytonii*), San Francisco garter snake (*Thamnophis sirtalis tetrataenia*), western pond turtle (*Actinemys marmorata*), and snowy plover (*Charadrius alexandrinus*).

Coastal lagoons are considered "high-risk-high-reward" habitat for juvenile *O. mykiss* (Satterthwaite et al. 2012) and my findings suggest that rewards and risks are especially high at the Pescadero intermittent estuary (IE). During favorable rearing conditions, extremely rapid somatic growth rates for extended time periods produces the largest steelhead smolts observed in the region and possibly the State. The "twice smolting" life history type (Hayes et al. 2011) is apparently a popular and successful life history strategy for Pescadero steelhead and the most rapidly growing smolts probably require little or no marine residence in order to achieve adult sizes. The cool coastal summertime microclimate coupled with Pescadero's large size and association with highly productive saltmarsh habitat likely enables Pescadero steelhead to experience marine-like growth rates without being exposed to marine predators. While body growth rates slowed after the first year of drought, the lagoon nevertheless provided abundant aquatic habitat during an extremely dry period. Prolonged sandbar-closed conditions extended the rearing period for the slow growing 2013 cohort which enabled members to achieve sizes approaching that observed during non-drought or early drought years.

While the Pescadero IE provides critical ecosystem services most of the time, a recent history of regular breach-induced fish kills since the mid-1990s indicates that temporary and complete losses of ecosystem functions can occur (Jankovitz 2014; 2015; 2016a,b, Largier et al. 2015). Unfortunately the situation appears to be worsening over time. In 2016 two breach-induced mortality events were documented to occur during the same season for the first time (Jankovitz 2016a,b). The kill on 1-November, 2016 was more severe than the kill on 10-December, 2016 and produced the most steelhead mortalities ever observed (Jankovitz 2016a). The disappearance of steelhead in July 2015 represents the first documented case of a potential widespread kill caused by chronically degraded water quality during the closed state (Jankovitz 2015). The occurrence confirmed the concerns of experts who claim that climate change will cause California IE waters to become too stagnant, warm, and oxygen poor to support rearing steelhead (Moyle et al. 2017).

The importance of the Pescadero estuary-marsh ecosystem complex to California's biodiversity and signs of growing distress merits high restoration priority. My findings and the results of earlier (Smith 1990) and follow-up (Jankovitz 2015) studies indicate the *supreme importance of maintaining and promoting a sufficiently sized fresh and oxygenated surface water layer for proper ecosystem functioning during prolonged drought-induced sandbar closure*. During negative water balance conditions this may not be possible and efforts that promote marine connectivity during extremely dry periods should help improve estuarine water quality and prevent complete loss of system functions. Other efforts that reduce anoxia and hypoxia at depth and upstream, such as re-establishing surface water connectivity in Butano Creek and reducing potential sources of nutrient pollution, should increase the total amount of functional habitat available to steelhead and other fishes in the estuary. Strategic additions of complex large woody debris in close proximity to preferred point bar and reverse flood tide delta habitats would immediately improve habitat conditions for steelhead. Lastly, efforts that prevent breach-induced fish kills from occurring until at least early winter will improve the resiliency of steelhead populations to stochastic environmental events.

This dissertation complements recent graduate student research about Pescadero IE geochemistry (Sloan 2006, Smith 2009, Richards 2016), hydrodynamics (Williams 2014), and groundwater hydrology (Volpi 2014). It also builds on earlier fish and macroinvertebrate studies conducted during the 1980s and 1990s (Smith 1990, Robinson 1993, Martin 1995) before Highway 1 bridge reconstruction, the marsh restoration project, and quasi-annual fish kills occurred. The situation in Pescadero has improved since I began my field work in July 2011 (Wall Street Journal, San Francisco Bay Area edition, 12-January, 2012). The Pescadero Lagoon Science Panel was assembled in 2013 and produced a final report in 2015 that helps pave a path forward for scientists and managers (Largier et al. 2015). Recently, preemptive managed breaches by federal and state agencies have improved water quality conditions and prevented large-scale fish kills from occurring (NOAA 2013, Jon Jankovitz, pers. comm., 16-November, 2017). The San Francisco Regional Water Quality Control Board (SFRWQCB) recently released a draft report of the Sediment Total Maximum Daily Load (TMDL) for the

Pescadero-Butano watershed (Bozkurt Frucht et al. 2018). The SFRWQCB is currently considering listing the Pescadero Marsh as impaired for low dissolved oxygen according to water quality data that I gathered during my dissertation research, much of it unpublished (Kevin Lunde, pers. comm., 4-May, 2018). University scientists are currently using repeat photography to monitor coastal sandbar dynamics at Pescadero. Floodplains in the upper watershed have been restored and plans to alleviate fish passage and water quality problems caused by sediment aggradation in the upper estuary/lower Butano Creek mainstem should soon move forward. The severe drought during the 1970s eliminated coho salmon (*O. kisutch*) from Pescadero and Butano creeks and there is renewed interest to reintroduce salmon to the basins once passage issues in Butano Creek are remedied. Local, state, and federal governments have recently pledged up to $6.4 million to make the habitat improvements (San Mateo Daily Journal, 14-July, 2017).

In summary, the direct and indirect effects of river discontinua from hydropower dams and coastal sandbars cause pronounced changes to rearing conditions and patterns of habitat use for two iconic California salmonid populations, especially during drought. The discontinuities contribute to ecological shocks in the form of a collapsed lucrative salmon fishery and recurring animal mass mortality events at one of California's most important coastal wetland ecosystems. Resources management solutions in both systems are hampered by a lack of access to basic scientific information. In this dissertation I synthesize, analyze, and interpret abundant pre-existing and field-gathered empirical datasets and my findings can help inform management decisions during the 21st century. Given the rapid pace of habitat destruction during the Anthropocene and the expected consequences of climate change, the need for more informed environmental stewardship is urgent.

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