# Tradeoffs of juvenile steelhead (*Oncorhynchus mykiss*) rearing in an intermittently closed estuary, northern California USA

William Carson Matsubu

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Reading Committee:

Charles A. Simenstad, Chair

Gregg E. Horton

David A. Beauchamp

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University of Washington

# Abstract

Tradeoffs of juvenile steelhead (*Oncorhynchus mykiss*) rearing in an intermittently closed estuary, northern California USA

William C. Matsubu

Chair of the Supervisory Committee:
Professor Charles A. Simenstad
School of Aquatic and Fishery Sciences

Estuarine environments provide an essential habitat to many aquatic animals and, in some settings, can be susceptible to drastic environmental transformations caused by deviations in connectivity with the ocean. In these intermittently closed estuaries (ICEs), the presence or absence of a barrier beach, naturally controlled by wave action and river flow, determines the mouth state (closed or open). Depending on the frequency and duration of closures and reopenings, ICEs can create a conundrum for inhabitants, especially diadromous fish that must transit between marine and freshwater habitats to reproduce. Changes in connectivity to the ocean not only obstructs migration between the ocean and the river but can also cause deadly conditions, especially for juvenile pacific salmonids (*Oncorhynchus* spp.) that have a narrow range of physiological tolerances for the abiotic variables susceptible to large fluctuations in ICEs. Despite these hurdles, ICEs constitute essential habitats for threatened populations of steelhead (*Oncorhynchus mykiss*). This dissertation utilizes a threatened population of juvenile steelhead in the Russian River estuary, northern California, USA as a case study to examine an

array of relevant topics about the efficacy of a juvenile anadromous fish occupying an ICE. The intersection of a threatened fish with a plastic and complex life history within an understudied system provides many challenges as well as opportunities. In addition to a brief introduction (Chapter 1) and conclusion (Chapter 6), the main chapters of this dissertation (Chapters 2-5) will address knowledge gaps specific to juvenile steelhead in the Russian River estuary.

The second chapter addressed uncertainties regarding what abiotic conditions juvenile steelhead are exposed to and how steelhead may avoid physiologically stressful conditions. Specifically, we answered the following questions: (1) "What are the WQ habitats used by juvenile steelhead during open and closed conditions in an ICE?" and (2) "What behavioural change is evidenced between open and closed conditions that might alter the juvenile steelhead's risk of exposure to stressful WQ?" To answer these questions, we combined thermal sensor encoded acoustic telemetry and coincidental WQ sampling. Chapter two determined that, under open conditions, juvenile steelhead experienced primarily brackish and saline water in the lower and middle reaches and warm freshwater in the upper reach, whereas under closed conditions, they moved greater distances and were found to be aggregating near cool water refugia not used during open mouth conditions. These findings shed light on the abiotic conditions juvenile steelhead are exposed to and emphasize the importance of tributary hydrogeomorphic processes and groundwater linkages in subwatersheds that are sources of cool water refugia in ICEs.

The purpose of the third chapter was to evaluate the vertical response of juvenile steelhead to the physiochemical conditions (i.e., temperature, DO, salinity) in the Russian River estuary. This chapter further explored the acoustic telemetry and simultaneously collected WQ data from chapter two to test the following hypotheses: (i) juvenile steelhead will shift their position in the water column based on prevailing physiochemical conditions; (ii) the degree to which juvenile steelhead adjust their position in the water column will vary with fish size; and (iii) smaller juvenile steelhead will risk potentially stressful conditions to take advantage of prey sources. The results indicated the depth of fish varied in response to the present abiotic conditions and typically reflected the occupation of more energetically and physiologically beneficial habitats, with smaller fish being shallower in the water column when proximate salinities are higher. Results indicated management activities that promote open mouth conditions may create challenges for steelhead that are not acclimated to saline conditions but reveal foraging strategies used by juvenile steelhead that are not yet tolerant of higher salinities.

Macroinvertebrates are fundamental to the food webs, yet their response to management activities that affect connectivity to the ocean is not well understood. The fourth chapter used systematic sampling of the benthic and epibenthic macroinvertebrates to assess factors that affect the diversity and abundance of key food web taxa. Similar to other ICEs, the macroinvertebrate assemblage of the Russian River estuary was primarily composed of taxa that can deal with the variability, either physiologically or behaviourally. Furthermore, the prominent food web taxa were abundant during both open and closed mouth conditions and were found in large aggregations in habitat only inundated during closed mouth conditions. These increased densities in the closure-inundated habitat may reflect more expansive aggregations of key food web taxa that would lead to more efficient foraging for juvenile steelhead.

Although the growth rates of juvenile steelhead in ICEs have been reported near the highest in literature, leading to increased marine survival, the specific factors contributing to this growth have not been specifically evaluated. The fifth chapter incorporated observed growth rates, a diet analysis, and thermal history of juvenile steelhead into a bioenergetics model to explore factors that most influence the growth potential of juvenile steelhead. In this chapter, I confirmed that growth rates of juvenile steelhead in the Russian River estuary rival the highest in literature and are attributed to ample foraging opportunities and the ability of juvenile steelhead to thermo-regulate behaviourally in the heterogeneous abiotic environment. Higher energetic costs due to higher temperatures in the upper reach were possibly buffered by the consumption of more energy dense prey. These results indicated that growth is likely not limiting the recovery of threatened steelhead in the Russian River estuary. With many populations of salmonids imperiled near their southern range, efforts for recovery could benefit from protecting habitats in ICEs and considering the impacts of management activities to the water quality conditions.

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# DEDICATION

I dedicate this dissertation to my family for their inspiring words and actions that allowed me to push myself and pursue my passion. Without the support from my family, I would not have been able to see this PhD through. My parents, Lisa and Paul, have made incredible sacrifices for my siblings and myself, of which I will be eternally grateful. My brother, John, has provided essential support and advice in navigating the challenges of undergraduate and graduate school as a first-generation college student. I would also like to dedicate this to my extended family in Seattle who made my time here much more enjoyable with good company, wine, and kasuzuke black cod, *Anoplopoma fimbria* (Pallas 1814). A special dedication extends to the late Hank Matsubu and Larry Clovis whose generosity and humor always made Seattle feel more like home.

# Chapter 1. INTRODUCTION

Many estuaries are susceptible to drastic environmental transformations caused by deviations in connectivity with the ocean (Whitfield & Elliott, 2011, Moreira et al., 2014). When an estuary is disconnected from the ocean, tidal exchange is eliminated, and if the inflow is greater than evaporation rates, the water elevations increase and inundate supratidal areas (Fig. 1.1; Roshanka & Charith 1998, Behrens et al., 2013). Estuaries that become disconnected from the ocean are common in Mediterranean climates worldwide; 33,286 km (7.6%) of the world's coastlines are included in these classifications, including approximately 18% of the coastlines of North America and Africa and over 10% of the coastlines of Australia, Asia, and South America (Cromwell 1971; Whitfield & Elliott 2011; McSweeney et al. 2017).

The terminology regarding these systems varies around the world and includes "intermittently closed/open lakes and lagoons" (e.g., Dye & Barros 2005; Haines et al., 2006), "temporarily open/closed estuaries" (e.g., Whitfield 1992; Behrens et al., 2013), and "intermittently open/closed estuaries" (McSweeney et al., 2017). Furthermore, "bar-built lagoons", "bar-built estuaries", "coastal lagoons", and "intermittently closed estuaries" are used broadly (Neira & Potter 1992; Ranasinghe et al., 1999; Ranasinghe & Pattiaratchi 2003) and in the U.S. (Moreira et al., 2014; Behrens et al., 2015; Heady et al., 2015; Largier et al., 2019). In this dissertation, I refer to these systems as intermittently closed estuaries (ICEs).

Intermittently closed estuaries are extremely sensitive to human impacts, including climate change, artificial breaching of the estuary mouth, and alterations to inflows. The water mass balance, which determines if and how fast a closed estuary fills, is susceptible to alterations to river inflow (Goodwin 1996; Behrens et al., 2015). For example, if the inflows exceed the volume of water leaving the closed estuary (e.g., through evaporation or seepage), the volume of the estuary increases and inundates low-lying areas, and water will eventually overtop and erode the barrier berm at the river mouth. Furthermore, the low-lying areas inundated during closures are often used by humans and have infrastructure vulnerable to flooding. When inflows are artificially higher than normal, these become flooded unnaturally fast, and action is often initiated to avoid damage to low lying properties. As a result, artificial breaching of barrier berms at the river mouth is prevalent around the world; in New South Wales, Australia, more than half the intermittently closed estuaries are artificially breached to mitigate flooding (Haines et al., 2006).

Regulation of flow, artificial breaching, and construction of infrastructure have changed the timing and duration of river mouth dynamics, triggering alterations to natural ecosystem processes and functions. Some ICEs, including the Bot River in South Africa, are artificially opened to promote the recruitment of species with economic value (Bally 1987). Also, there is much concern for the water quality and pollution concentrations in ICEs near pollution sources, such as the Willis Creek estuary in New South Wells, Australia, proximate to a sewage treatment plant (Hastie & Smith 2005). Although some ICEs in California are breached for management reasons, including flood control and water quality (NMFS 2008), unauthorized artificial breaching is sometimes conducted for recreational purposes (FoCLB 2017). While human activities (i.e., regulated flows and breaching of lagoons) and anticipated effects of climate change (i.e., increased temperatures, changes in freshwater discharge) affect the abiotic conditions in intermittent estuaries (Haines et al., 2006; Saintilan et al., 2016; Largier et al., 2019), alterations to quality of habitat and the response of juvenile salmonids *Oncorhynchus* spp. to the changes in the mouth state remain relatively understudied.

Depending on the frequency and duration of closures and reopenings, ICEs can create a conundrum for inhabitants, especially diadromous fish. Although often considered productive, estuarine closure events not only prevent migration between the ocean and the river but also can cause unfavorable (Robinson 1993, Martin 1995) or deadly conditions (Sloan 2006, Lill et al., 2012, Moreira et al., 2014). With over half the estuaries in California subject to estuary mouth closures (Heady et al., 2014), little is known about the effects of management on inhabitants of California ICEs. The majority of anadromous salmonid populations *Oncorhynchus* spp. in California are in serious decline, with more than half projected to become extirpated in the next five decades (Moyle et al., 2017). With 84% of the populations expected to be negatively impacted by climate change (Moyle et al., 2017), identifying essential habitats and restoring the functions and access to these habitats will allow salmonids to express life history diversity and assist in mediating negative impacts from climate variability (Katz et al., 2013; Moore et al., 2014; Manhard et al., 2017).

Of particular interest are U.S. Endangered Species Act (ESA)-listed Central California Coast steelhead *O. mykiss* that rear in estuaries that can become disconnected from the ocean (NMFS 2008). Interest in maintaining and enhancing suitable habitats for juvenile steelhead in ICEs is understandable, given the estuary composes approximately 5% of the overall watershed, yet 60-90% of the returning adults rear in these estuaries (Shapovalov & Taft 1954; Bond et al., 2008). This increased marine survival is likely a consequence of the extremely high growth rates displayed by juvenile steelhead while rearing in ICEs (Hayes et al., 2008). However, the mechanisms explaining how conditions in ICEs may further enhance the performance of juvenile salmonids and how variations in the duration and timing of estuary mouth closures influence survival and performance remain mostly unknown.

There is a unique opportunity to address these uncertainties in the Russian River estuary (RRE). The seasonal variability inflows, with typical summer artificial flows at 2-4 $m^3\ s^{-1}$ and flashy winter flows often reaching 1000 $m^3\ s^{-1}$, and tidal range (~2.7m) attributes to the intermittency of the RRE ocean connectivity (Behrens et al., 2016). Management of inflows and the practice of artificial breaching have changed the number and duration of closures from a seasonal closure, encompassing the entire dry season, to a more variable frequency, with the typical duration being less than one week on average (Behrens et al., 2013). All populations of salmonids in the Russian River catchment, including Chinook salmon (*O. tshawytscha)*, Coho salmon (*O. kisutch)*, and steelhead, are depressed and listed as either threatened or endangered under the US Endangered Species Act (ESA). Specifically, the Russian River Biological Opinion (RRBO), an analysis of management practices affecting ESA-listed species in the Russian River watershed, states that past actions in the estuary have resulted in “the loss of productive rearing habitat for small juvenile salmonids” (NMFS 2008).

This dissertation enhances the ability to discuss the performance trade-offs of estuary management for juvenile steelhead rearing in the RRE, with an emphasis on issues addressed in the RRBO. In addition to this general introduction (Chapter 1) and the synthesis (Chapter 6), the main chapters (Chapters 2-5) are structured as standalone publications. Chapter two determined the environmental (i.e., temperature, salinity, and dissolved oxygen) exposure of juvenile steelhead in the RRE using temperature sensor encoded acoustic telemetry and simultaneous water quality sampling. Expanding on the acoustic telemetry data, the third chapter evaluated the response (depth) of juvenile steelhead to environmental conditions. The fourth chapter uses data from standardized macroinvertebrate sampling of the benthos and epibenthos to assess factors that affect the diversity and abundance of prey. Using results from the previous chapters, the fifth chapter used a bioenergetics model to explore factors that most influence the potential growth of juvenile steelhead. This dissertation is then concluded with a synthesis that includes a brief summary, implications for estuary management, and recommendations for future research.

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## 1.2 FIGURES

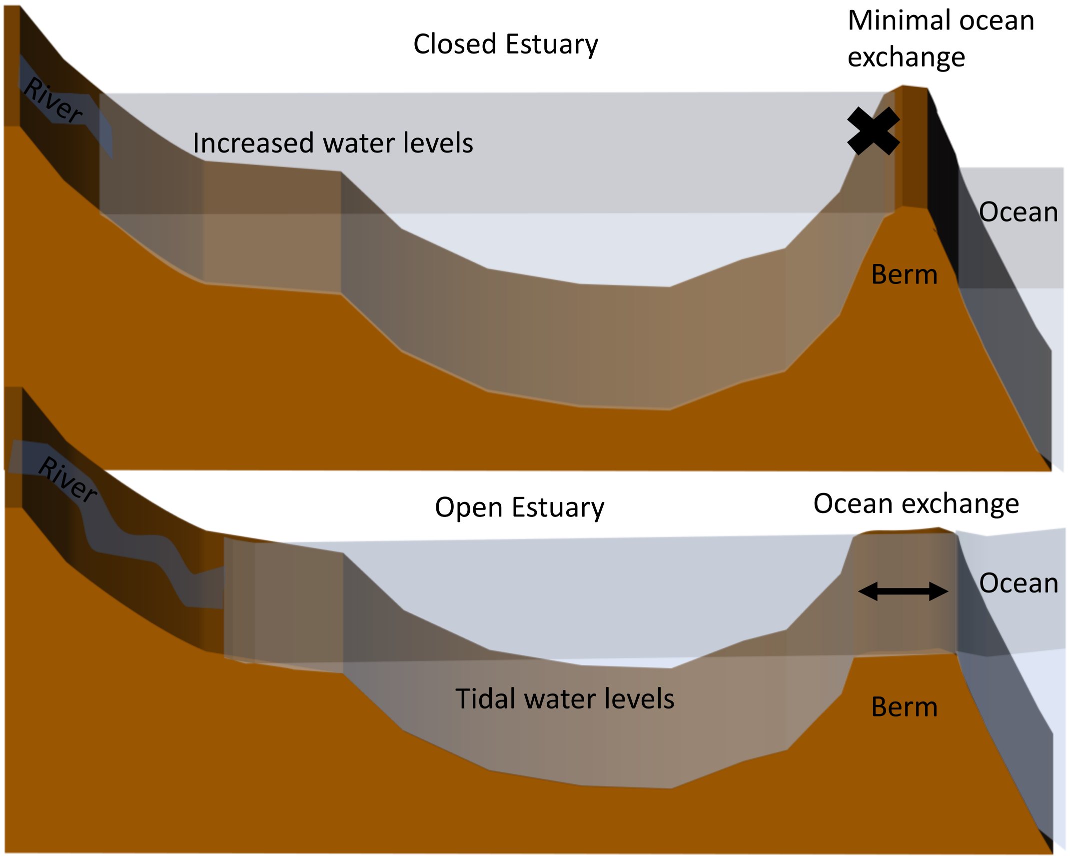

Figure 1.1. Conceptual diagram of an open and closed estuary.

# Chapter 2. Juvenile Steelhead Locate Cold-Water Refugia in an Intermittently Closed Estuary

**Authors**: W. Matsubu, C.A. Simenstad, and G.E. Horton

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## 2.1 ABSTRACT

Many coastal estuaries in Mediterranean climates are susceptible to inlet closures resulting from barrier beach formation. These closures are ecologically important because they eliminate tidal exchange and connectivity of nekton movement to the coastal ocean and, depending on closure duration, can convert a dynamic estuary into a quiescent lagoon. Although closures can create lethal or stressful conditions for nekton and benthic communities, especially obligate diadromous species, under some conditions they can enhance survival of juvenile steelhead *Oncorhynchus mykiss*. However, the mechanisms explaining how closed conditions enhance the growth of juvenile steelhead and how inhabitants avoid physiologically stressful conditions remains unknown. In the present study, recent technological advances in sensor-encoded acoustic telemetry provided the ability to simultaneously locate and determine the temperature of juvenile steelhead as small as 93 mm FL by using mobile and stationary tracking. In the Russian River estuary, an intermittently closed estuary in northern California, we used

acoustic telemetry to infer water quality exposure by linking the temperature of individually tagged fish with water quality profiles collected in close proximity. Under open-inlet conditions, juvenile steelhead experienced primarily brackish and saline water in the lower and middle reaches and warm freshwater in the upper reach, whereas under closed-inlet conditions they experienced warm freshwater in the middle and upper reaches. During closed conditions, juvenile steelhead displayed behavior that suggested the ability to mediate stressful environmental conditions; specifically, they responded to closed conditions by moving greater distances and aggregating near thermal refugia. Our findings show the importance of recognizing these strategies when contemplating changes to estuary management and highlight the significance of tributary hydrogeomorphic processes and groundwater linkages in subwatersheds that are sources of cool water for thermal refugia in intermittently closed estuaries.

## 2.2 INTRODUCTION

Estuarine environments throughout the world are susceptible to both natural and anthropogenic changes caused by deviations in connectivity with the ocean (Whitfield & Elliott 2011; Moreira et al., 2014). For intermittently closed estuaries (ICEs), connectivity to the ocean is determined by the inlet state, the presence or absence of a sand–gravel berm that limits exchange between the river and the ocean, which can be affected by riverine inflow, wind direction and speed, ocean wave action, and mechanical breaching by humans (Whitfield et al., 2012; Behrens et al., 2013). Intermittently closed estuaries, including bar-built, seasonally closed, seasonally tidal, or intermittently open estuaries, are common in Mediterranean climates worldwide, especially in North America, South Africa, and Australia (Whitfield & Elliott 2011). As the interface between freshwater and marine habitats, estuaries are used to some extent by all diadromous fish. The unpredictability of ICEs poses particularly consequential challenges to diadromous species, especially where catchments and their fluvial discharge to estuaries are extensively modified (Elliott et al., 2007). Anadromous salmonids typically use estuaries for acclimation and rearing during presmolt life stages, seaward migration as smolts, and then riverward migration as adults to reproduce in fresh water (Simenstad et al., 1982, Quinn 2005).

Depending on inlet state, water quality (WQ) conditions in ICEs can vary considerably, and changes in connectivity often create stressful conditions for benthic communities and nekton (Saad et al., 2002; Sloan 2006; Lill et al., 2012; Moreira et al., 2014). Open-inlet conditions are tidal, with dynamic marine exchange and longitudinal gradients in salinity and temperature. A closed inlet eliminates or severely reduces tidal exchange and, depending on the duration and inflow, gradually transforms a marine-dominated estuary into a quiescent lagoon. Closed conditions result in increased water levels and amplified vertical stratification after inlet closure (Ranasinghe & Pattiaratchi 1999; Behrens et al., 2015). Increased stratification and decreased mixing cause the dissolved oxygen (DO) in the isolated saline water below the halocline to become hypoxic to anoxic. However, if river inflow is adequate, the freshwater surface layer stays oxygenated, enlarges vertically, and expands onto intertidal and supratidal areas. While the temperature of the freshwater surface layer is largely dependent on local climate, the salinity in the bottom layer absorbs and stores heat, generally surpassing the temperature of the surface layer. This trapped bottom layer experiences a landward propagation or upriver migration, potentially expanding the amount of habitat that is exposed to this layer (Behrens et al., 2016). Reopening of the estuary’s inlet abruptly transforms the lagoon back into a tidally and marine-influenced estuary.

Environmental changes associated with deviations in estuarine connectivity have shaped endemic and transitional biota on evolutionary and proximate scales. On the evolutionary scale, the natural fauna has adapted physiological, metabolic, and/or behavioral mechanisms to survive the natural timing and processes in ICEs (von der Heyden et al., 2015). On the proximate scale, populations must cope with the physiological stress brought on by immediate changes in environ- mental conditions while continuing to forage and minimizing predation risk. Changes in WQ can be so sudden and severe that they cause large-scale mortality (Sloan, 2006; Lill et al., 2012; Netto et al., 2012). Fish kills associated with breaching events during the low-flow season are caused by the sudden outflow of the freshwater lens while the anoxic saline layer remains (Becker et al., 2009). After the transition period, communities reorganize relative to the salinity gradient, but they are often limited by other WQ issues, such as high temperatures and low DO concentrations (Harrison & Whitfield, 2006; Lill et al., 2012; Lanés et al., 2015). Community reorganization includes changes in species richness, which consist of complete losses of species' populations and drastic fluctuations in population densities. The degree and shape of community restructuring typically depend on the needs, tolerances, and mobility of individuals that comprise the community.

Intermittently closed estuaries create a conundrum for diadromous fish. Although often considered productive, estuarine closure events not only prevent migration between the ocean and the river but also can cause unfavorable (Robinson, 1993; Martin, 1995) or deadly conditions (Sloan, 2006; Lill et al., 2012; Moreira et al., 2014). Furthermore, growth rates of juvenile steelhead *Oncorhynchus mykiss* rearing in ICEs have been among the highest reported in the literature for the species and are much higher than those of their upstream counterparts (Bond, 2006; Hayes et al., 2008). Juvenile steelhead rearing in these estuaries disproportionally compose the majority of returning adults even though they constitute a minority of the out-migrants (Bond et al., 2008). However, the mechanisms explaining how conditions in ICEs may further enhance the performance of juvenile salmonids and how variations in the duration and timing of estuary mouth closures influence performance remain largely unknown.

Several possible mechanisms have been proposed to explain how an anadromous fish population could adapt to estuary closure events over both proximate and evolutionary time scales. Although not exhaustive, alternative explanations might include any of the following scenarios, either alone or in combination: (1) fish emigrate out of the estuarine system by moving upstream into freshwater (Hayes et al., 2011); (2) they exploit newly available prey resources without incurring physiological stress (Becker & Laurenson, 2007); (3) they alter their behavior to mediate exposure to stress while maintaining their ability to offset increased energetic costs with foraging efficiency (Webster & Dill, 2006; Webster et al., 2007); and (4) they seek new refugia from stressful WQ conditions (Nielsen et al., 1994; Brewitt & Danner, 2014). Although utilization of newly available habitat in shallow, flooded margins of ICEs has been documented for nonsalmonid fish species (Becker & Laurenson, 2007), there is a dearth of such evidence for anadromous salmonids. Areas that provide shelter from predation or physiological stressors act as refugia and are utilized by a variety of species to increase survival and growth (Nielsen et al., 1994; Dugdale et al., 2013; Brewitt & Danner, 2014).

In this paper, we address the following questions: (1) “What are the WQ habitats that are used by juvenile steelhead during open and closed conditions in an ICE?” and (2) “What behavioral change is evidenced between open and closed conditions that might alter the juvenile steelhead’s risk of exposure to stressful WQ?” To answer these questions, we used a combination of acoustic telemetry and WQ monitoring in the Russian River estuary (RRE) of California. Until recently, no cost-effective method existed to link the simultaneous WQ conditions experienced by small (<120-mm FL) juvenile salmonids to their behavior under ICE conditions. Recent technological advances in sensor-encoded acoustic telemetry, including an on-board temperature sensor, provide the ability to simultaneously track movements and receive and record real-time temperatures that are occupied by fish as small as 93 mm FL. We inferred the WQ experience of individuals by relating the fish's observed temperature (from the acoustic transmitter) to WQ profiles collected in close proximity. Unfortunately, quantifying the abiotic conditions throughout a large, complex, and dynamic environment like the RRE is a time-consuming and expensive endeavor, which prevented us from determining habitat selection. Although these methods did not allow us to quantify the amount of habitat available, the combination of simultaneous WQ profiles, stationary WQ datasondes, previous abiotic mapping (Behrens, 2012), and recent advances in understanding lagoon dynamics (Behrens et al., 2016) provided evidence for a general understanding of the habitats available.

## 2.3 METHODS

### 2.3.1 *Study site*

All fish sampling and operations accompanying acoustic telemetry in the RRE and the lower portions of peripheral tributaries to the estuary were conducted during the late spring and summer of 2014 and 2015. The study was embedded in the Sonoma County Water Agency's (SCWA) estuary WQ and fish monitoring program (Martini-Lamb & Manning, 2015). The 177km Russian River flows from central Mendocino County to the Pacific Ocean in Sonoma County, approximately 90 km northwest of San Francisco Bay. The RRE, including tidal freshwater reaches, extends 12 river kilometers (rkm) upstream from the river inlet to the confluence with Austin Creek (Figure 2.1). Although the general climate of the estuary is coastal, the majority of the 3,846-$km^2$ catchment is characterized as having a warm and dry Mediterranean climate with seasonal rainfall (mean annual rainfall is 76 cm).

### 2.3.2 *Lagoon dynamics and general lagoon WQ conditions*

The RRE was divided into three reaches for effort allocation and analysis due to the varying salinity ranges and to conform with the SCWA's sampling design. During open conditions, the lower (rkm 0.0–1.7) and middle (rkm 1.7–5.0) reaches are primarily saline with a freshwater or brackish layer at the surface, while the upper reach (rkm 5.0–12) is typically tidal freshwater (Figure 2.1). During closed conditions, saline waters become trapped under a thick surface layer and pycnocline in the lower reach, the middle reach, and sometimes parts of the upper reach (Behrens et al., 2016). In addition to increased stratification and elevated water levels during closed conditions, there is an increased intrusion of saline water into the upper reach (Behrens et al., 2016).

The high frequency of inlet closures observed in the RRE is partly attributable to extreme variation in stream discharge (Behrens et al., 2016), which typically ranges from a regulated 2to4$m^3$/s in the summer and often reaches 1,000 $m^3$/s in the winter. Historically, the RRE was closed seasonally for the entire summer, comparable to other small- to mid-sized watersheds along the California coast (Bond et al., 2008; Behrens et al., 2013). However, more recently, closure of the RRE occurs approximately every 43 d, and the inlet stays closed for less than 1 week on average due to human activities (Behrens et al., 2013). Anthropogenic demands, such as water supply, flood prevention, and navigation, have led to infrastructure and management practices that directly or indirectly affect the natural timing and duration of the inlet state in the RRE (NMFS 2008).

We collected our own WQ data in close proximity to fish detections, and a collaborator provided general WQ and water level data. Vertical WQ profile data were collected with a YSI Model 85 hand-held probe (Yellow Springs Instrument Company, Yellow Springs, Ohio) in close proximity to fish detections. In addition to our sampling, the SCWA provided data from stationary WQ datasondes (YSI Series 6600) and from a water level gauge (National Geodetic Vertical Datum of 1929 [NGVD29]) at Jenner, California (Figure 2.1).

### 2.3.3 *Study species*

All populations of salmonids in the Russian River catchment are depressed and listed as either threatened or endangered by the US Endangered Species Act (ESA). Past management actions have resulted in “the loss of productive rearing habitat for small juvenile salmonids at the mouth of the Russian River.” (NMFS 2008 p. xii). More specifically, Central California Coast steelhead are a threatened Distinct Population Segment under the federal Endangered Species Act.

Similar to other Pacific salmon, steelhead are phenotypically variable and encounter a broad range of water quality conditions throughout their life history and distribution (Quinn, 2005). Although the lethal temperature thresholds for juvenile steelhead can be as high as 30.8 °C, growth rates have been found to decline at temperatures above 19 °C (Myrick & Cech, 2000). These thermal thresholds strongly depend on multiple factors, including salinity (Johnsson & Clarke, 1988), DO (Matthews & Berg, 1997), previous thermal exposure (Myrick & Cech, 2000), fish size and diet (Beauchamp, 2009). Similar to other diadromous fish, steelhead must undergo a physiological transformation allowing them to tolerate seawater (Quinn, 2005) and, although some acclimation is possible, younger juvenile steelhead avoid brackish and salt water (Smith, 1990, Zedonis, 1992). In addition to salinity sensitivities, juvenile salmon typically avoid habitat with DO concentrations less than 5 mg/L with mortality occurring below 4 mg/L after prolonged exposure (Carter, 2005). All salmonid populations in the Russian River catchment are depressed and are listed as either threatened or endangered under the U.S. Endangered Species Act (ESA). Past management actions have resulted in "the loss of productive rearing habitat for small juvenile salmonids at the mouth of the Russian River" (NMFS 2008:xii). More specifically, central California coast steelhead are considered a threatened distinct population segment under the ESA.

Similar to other Pacific salmon, steelhead are phenotypically variable and encounter a broad range of WQ conditions throughout their life history and distribution (Quinn, 2005). Although the lethal temperature thresholds for juvenile steelhead can be as high as 30.8°C, growth rates have been found to decline at temperatures above 19°C (Myrick & Cech 2000). These thermal thresholds strongly depend on multiple factors, including salinity (Johnsson & Clarke, 1988), DO (Matthews & Berg, 1997), previous thermal exposure (Myrick & Cech, 2000), fish size, and diet (Beauchamp, 2009). Similar to other diadromous fish, steelhead must undergo a physiological transformation that allows them to tolerate seawater (Quinn, 2005) and, although some acclimation is possible, younger juvenile steelhead avoid brackish water and saltwater (Smith, 1990; Zedonis, 1992). In addition to salinity sensitivities, juvenile salmon typically avoid habitat with DO concentrations less than 5 mg/L, and mortality occurs after prolonged exposure to DO levels below 4 mg/L (Carter, 2005).

### 2.3.4 *Fish tagging*

We captured and tagged 93 juvenile steelhead in the RRE from 5/29/14 to 9/12/14 and 5/21/15 to 7/20/15 (Figure 2.2). We captured 92 individuals with a beach seine (46 m by 4 m with 0.635-cm mesh) and the remaining fish was captured in a downstream migrant trap in Austin Creek, a tributary near the upstream end of the estuary (Figure 2.1).

Acoustic transmitters (MM-412T; 11.0 X 6.6 X 6.1mm [LxWxH], 0.58 g in air, and battery life of 10 days with a 10 second burst) were inserted in juvenile steelhead that met a specific size requirement (weight of $\geq$ 10.0 g) to minimize bias from the tag burden (i.e., size of the transmitter relative to the size of the fish) (Brown et al., 2010). This size range allowed inclusion of larger subyearling steelhead and the older rearing juvenile steelhead in the RRE (Martini-Lamb & Manning, 2011).

Prior to tagging, each juvenile steelhead was placed in a bath of 40 mg/L MS-222 (tricaine methanesulfonate) after which each fish was measured for length (mm FL) and mass (g wet). During surgery, we placed each fish ventral side up on a V-shaped foam lined table with an anesthetic bath of 20 mg/L MS-222 flowing over the gills. The transmitter was inserted into a 6-mm incision on the ventral side of the fish, anterior to the pelvic girdle. The incision was closed with a single size 5-0 absorbable suture (Brown et al., 2013).

After surgery, fish were kept in aerated stream water until fully recovered (10-15 minutes) and then released into the estuary. Initially, we attempted to disperse tagged fish evenly across the three reaches for both inlet states. Unfortunately, low and unpredictable catches and the uncertainty of the inlet state prevented equal distribution of fish releases (supplemental). To compensate for the lack of captures and detections in certain areas, we relocated juvenile steelhead prior to release from areas with high captures to areas where seining efforts were ineffective, or detections were lacking. To evaluate this impact, we conducted analysis comparing movements of relocated and non-relocated individuals. After the recovery period, no fish showed signs of stress and all swam away vigorously.

### 2.3.5 *Acoustic telemetry*

Acoustic receivers were equipped with two submersible hydrophones to detect tagged juvenile steelhead (Map 600 RT transceivers; Lotek Wireless). We used three receivers as stationary receivers and a fourth for mobile tracking. Each transmitter emitted a coded acoustic pulse at a frequency of 200 kHz; when interpreted by the receiver, the coded pulse contained a unique ID and a simultaneous reading from the transmitter's internal temperature sensor. To detect any error in sensor readings, we measured the accuracy of the temperature sensors by documenting acoustic readings at multiple known temperatures prior to implementation. The sensors were within the manufacturer's advertised range of error (±0.8°C).

The three stationary receivers were allocated among five different locations (Figure 2.1). Two of the stationary receivers were always positioned near the upper (Browns Pool) and lower (Jenner) extents of the estuary. The remaining receiver was relocated to one of three sites (Sheephouse, Moscow Bridge, or Bridgehaven) to correspond with the proximity of tagged fish and to maximize detectability of movements (Figure 2.1). We positioned each hydrophone approximately 1 m above the bottom on a 5.08-cm, polyvinyl chloride pipe secured by a concrete umbrella mount.

Mobile tracking was performed from a powerboat propelled with an electric trolling engine or from a manually paddled canoe. The boat's location during each detection was determined by synchronizing the detection time with a daily track log that recorded the location every second on a Garmin eTrex 30 Global Positioning System (GPS) unit. When a fish was detected, a more precise location of the individual was determined using the directional capabilities of the Map 600 RT transceiver and the given signal strength. Field trials to locate hidden transmitters using these techniques found that the error in location was less than 15 m and that the maximum range of this configuration was approximately 90 m.

The allocation of effort for mobile tracking depended on the number and previous location of active deployed transmitters. Mobile tracking surveys started at the inlet of the estuary or just downstream of a stationary receiver. We surveyed upstream until (1) we ended the survey at another stationary receiver, (2) we had located all active transmitters, and/or (3) resources (e.g., propulsion energy source or allocated time) became depleted. Mobile tracking typically occurred daily when active transmitters were present in the estuary. When relocation of an individual was unsuccessful within the expected battery life (10 d), we expanded the next days' survey area to maximize the potential for relocation. Reasons for unsuccessful relocations were unknown, but potential reasons included technological limitations, expiration of transmitter batteries, undetectable location (e.g., behind obstructions), predation, or emigration from the study area.

### 2.3.6 *Fish tracking data - environmental experience*

Water quality profiles were collected during mobile tracking at estimated fish locations or when detections were simultaneously being recorded at a stationary array. Profiles consisted of manually recording temperature, DO concentration, and salinity at 0.5-m depth intervals from the surface to the bottom. If time allowed for extended surveying, we repeated this process at least every 30 min at the estimated location of each individual.

Detections were associated with WQ profiles when they met the specific temporal threshold (i.e., within 15 min) and spatial threshold (i.e., within 0.1 km). We used the empirical temperature reading from the sensor on the fish transmitter to infer salinity (psu), DO level (mg/L), and depth (m) from the proximate WQ profile. We determined the minimum, maximum, and mean for each inferred environmental variable within the temperature sensor's error (±0.8°C; Table 1). Vertical stratification was present throughout the study; the severity of vertical stratification was significant enough to infer the exposure with the transmitter's temperature sensor to particular conditions in the water column (Behrens et al., 2016).

### 2.3.7 *Fish tracking data – movement*

Each detection was assigned a rkm and reach. We calculated the overall longitudinal movements by subtracting each individual's minimum detected rkm from its maximum detected rkm. Movement rates (daily longitudinal movement) were estimated by dividing each individual's overall longitudinal movement by its duration of detection (number of days between its release and last detection). Daily longitudinal movements were calculated for individuals that had a detection duration greater than 1 d.

### 2.3.8 *Analysis*

We downloaded the acoustic telemetry data with MapHost (Lotek Wireless) and processed the data with Biomap database management software (Lotek Wireless). The GPS data were downloaded for the mobile tracking detections, WQ profiles, and stationary hydrophones by using DNRGarmin software. All data were eventually compiled into a Microsoft Access database, where extraneous detections were filtered, and temporal data were linked. We examined all spatial correlations and performed all analyses using ArcGIS version 10.3; Microsoft Excel 2013 and RGui version 3.0 were used for calculations, statistical analysis, and plots.

We used a combination of univariate parametric analysis and spatial visualizations for descriptive interpretations. Basic interpretations of tagging, thermal experience, and inferred environmental exposure were based on descriptive statistics. We used two-way ANOVA on $\log_e$ transformed data to determine differences experienced among reaches (inter-reach) and between inlet states. If the model was unbalanced, partial sums of squares (type II) were used to prevent contamination of the sums of squares by other factors in the model (Langsrud, 2003). If the ANOVA suggested a difference, we used Tukey's honestly significant difference (HSD) test ($\alpha = 0.05$) to estimate mean separation. The mean value for each individual in each reach during each inlet state was used in analyses to satisfy the assumption of independence.

## 2.4 RESULTS

### 2.4.1 *Lagoon dynamics and general lagoon WQ conditions*

All of the sampling in 2014 and most of the sampling in 2015 occurred during open conditions (Figure 2.2). When the inlet was open, water levels fluctuated consistently with diurnally mixed tidal cycles, whereas water levels during inlet closure gradually increased until returning to open-inlet conditions. The maximum water elevation (NGVD29) from May 15 to October 15, 2014 and 2015, ranged from less than 1.5 m during open conditions to greater than 2.2 m during closed conditions (Figure 2.2).

Water quality profiles acquired in close proximity to tagged fish during open conditions in the spring and summer of 2014 and 2015 indicated that the lower reach had a mean (±SD) temperature of 15.3 ± 2.9°C, mean salinity of 26.6 ± 7.6 psu, and mean DO concentration of 10.0 ± 2.0 mg/L. The middle was warmer and less saline, with a mean temperature of 17.9 ± 2.7°C, mean salinity of 23.4 ± 9.7 psu, and mean DO of 8.8 ± 1.7 mg/L. The upper reach was characteristically the warmest and freshest, with a mean temperature of 21.5 ± 1.7°C, mean salinity of 7.4 ± 9.2 psu, and mean DO of 8.0 ± 1.5 mg/L. Overall, the mean depth of WQ profiles during open conditions was 2.6 ± 2.6 m.

On May 29, 2015, formation of a sand berm at the inlet of the Russian River disconnected it from the ocean for 16 d until the berm was naturally breached on June 14, 2015. This was the only closure that overlapped with telemetry operations. During the closure, water levels switched from tidal cycles to a steady increase, eventually reaching a maximum of 2.2 m (NGVD29; Figure 2.2). The conditions near fish locations in the middle reach during the closure were warmer and less saline than open-inlet conditions, with a mean (±SD) temperature of 18.9 ± 1.9°C, mean salinity of 7.2 ± 10.1 psu, and mean DO concentration of 7.8 ± 2.4 mg/L. The upper reach was almost completely freshwater, with a mean temperature of 21.3 ± 1.3°C, mean salinity of 0.2 ± 0.7 psu, and mean DO of 7.4 ± 1.8 mg/L. Overall, the mean maximum depth of WQ profiles during closed conditions was 2.3 ± 1.2 m.

Due to a lack of juvenile steelhead catches and detections in the lower reach, we were unable to take WQ profiles in this reach during the closure in 2015. However, WQ data that were independent of fish locations were provided by the SCWA from stationary datasondes, and those data detected a decline in salinity and an increase in temperature for the lower and middle reaches (Figure 3.3). This decrease in salinity was more severe in the middle reach (from 32 to 11 psu) than in the lower reach (from 33 to 19 psu).

### 2.4.2 *Fish tagging*

The mean (±SD) FL and mass of the 93 juvenile steelhead we tagged were 139.3 ± 33.0 mm and 37.8 ± 29.0 g, respectively (Table 2.4). Fish lengths were not significantly different among reaches (ANOVA: $F = 0.301$; df = 2, 90; $P > 0.740$). Across all individual fish, the tag burden was within the recommended tolerance ranges (mean ± SD = 2.44 ± 1.53%). In total, 38 fish were tagged and released in the upper reach, 25 were tagged and released in the middle reach, and 30 were tagged and released in the lower reach (Table 2.4). Overall, fish were detected throughout the length of the estuary (minimum = rkm 0.4; maximum = rkm 12.6; $n$ = 156,110 detections from 85 individuals).

### 2.4.3 *Fish tracking data - environmental experience*

Overall, 401 WQ profiles were obtained in close proximity to detection locations. A portion of detections from 67 individuals (25,655 detections, or 16.4%) met the temporal (within 15 min) and spatial (within 0.1 km) criteria to be associated with a WQ profile. This provided the ability to determine the habitat use of fish in relation to particular WQ conditions across both vertical and horizontal WQ gradients under both open and closed conditions.

When the inlet was open, tagged juvenile steelhead experienced a mean (±SD) temperature of 16.9 ± 2.5°C ($n$ = 147,448 detections from 82 individuals). The fish temperatures differed by reach (ANOVA: $F = 68.18$; df = 2, 86; $P < 0.001$; Figure 2.4). There was a progressive exposure to warmer waters as juvenile steelhead were detected up the estuary: juvenile steelhead in the lower reach experienced the coolest temperatures (mean ± SD = 16.0 ± 2.1°C; Tukey's HSD test: $P < 0.001$), fish in the upper reach experienced the warmest temperatures (20.7 ± 1.7°C; Tukey's HSD test: $P < 0.001$), and fish in the middle reach experienced intermediate temperatures (17.1 ± 1.1°C; Tukey's HSD test: $P < 0.025$).

During open conditions, salinities experienced by juvenile steelhead ranged from 0 to 33.9 psu and generally decreased with increasing distance from the ocean (landward; Figure 2.4). When the estuary was open, tagged steelhead experienced a mean (±SD) salinity of 17.4 ± 13.2 psu ($n$ = 22,155 detections from 64 individuals), and their salinity experience differed among reaches (ANOVA: $F = 86.71$; df = 2, 69: $P < 0.001$). Although we did not detect a difference in mean salinity exposure between the lower reach (25.9 ± 5.4 psu) and middle reach (24.7 ± 7.2 psu; Tukey's HSD test: $P > 0.971$), juvenile steelhead in the upper reach experienced lower salinities (3.6 ± 6.6 psu; Tukey's HSD test: $P < 0.001$).

When the inlet was open, depths experienced were consistent while only nonstressful DO concentrations were occupied. Juvenile steelhead experienced a mean (±SD) depth of 1.4 ± 1.0 m ($n = 22{,}155$ from 64 individuals), with no detectable differences among reaches (ANOVA: $F = 0.13$; df = 2, 69; $P > 0.876$). Mean (±SD) DO experienced was 8.6 ± 1.9 mg/L ($n = 22{,}155$ from 64 individuals). The DO levels experienced differed by reach (ANOVA: $F = 4.83$; df = 2, 69; $P < 0.011$), with fish in the upper reach occupying lower DO concentrations (8.0 ± 0.7 mg/L) than those in the lower reach (9.3 ± 1.2 mg/ L; Tukey's HSD test: $P < 0.009$) but similar to those in the middle reach (8.8 ± 1.8 mg/L; Tukey's HSD test: $P > 0.182$).

During the May–June 2015 closure, we detected 13 individuals in the middle and upper reaches (rkm 2.4–11.6). Overall, the 13 fish experienced a mean (±SD) temperature of 19.9 ± 1.2°C ($n = 8{,}704$ detections). These temperatures did not differ by inlet state (ANOVA: $F = 0.003$; df = 1, 100; $P > 0.960$). The mean temperatures were similar between the middle reach (19.0 ± 1.1°C) and the upper reach (20.2 ± 0.5°C; Tukey's HSD test: $P > 0.893$).

During closed conditions, fish experienced a mean (±SD) salinity of 0.2 ± 0.3 psu ($n = 3{,}507$ detections from 12 individuals). Much lower salinities were experienced in the middle reach during the inlet closure than during open conditions (Tukey's HSD test: $P < 0.001$; Table 2.2). Salinity experience differed by reach, inlet state, and the reach × inlet state interaction (Table 2.2; Figure 2.4). Similar to open conditions, steelhead occupied habitat with nonstressful DO levels during the closure (mean ± SD = 7.7 ± 0.6 mg/L). Even though DO exposure differed among reaches, the vast majority (>99.9%) of DO levels experienced by fish were greater than 4 mg/L. Although juvenile steelhead in the upper reach experienced similar conditions during both inlet states, the fish in the middle reach occupied similar DO levels, shallower depths, and lower salinity water when the inlet was closed (Figure 2.4).

Ordinary kriging among detection temperatures illustrated a general increase in water temperature experienced by fish with upstream distance from the ocean during both open and closed conditions (Figure 2.6), except near the confluences of the tributaries that emptied directly into the estuary: Austin Creek (rkm 11.5) and Willow Creek (rkm 4.1; Figure 2.7). Temperatures near the confluence of Austin Creek were some of the coolest temperatures experienced by fish in the upper reach during the entire study. Although predicted temperatures among inlet states did not appear much different near the confluence of Willow Creek (Figure 2.7), there was a slight decrease in temperature with decreasing proximity to the tributary confluence, which was only observed during the closure.

### 2.4.4 *Fish tracking data-movement*

The largest total movements in the entire study were made by fish released in the middle reach during the closure (Tukey's HSD test: $P < 0.000$; Figure 2.5). Three of these fish moved over 7.8 rkm in 10 d and had the highest daily movement rates when compared to all other tagged fish (Tukey's HSD test: $P < 0.000$; Figure 2.5). In addition to their movements, these were the only fish detected in habitat near the confluences of Austin and Willow creeks. It is important to note that this group of fish was captured in the upper reach and was relocated to the middle reach prior to release.

To evaluate the impact of relocation, we divided the tagged individuals into groups based on the distance (mean ± SD = 3.9 ± 2.7 rkm) and direction of relocation (upstream by 0–4 rkm [$n$ = 21], no relocation [$n$ = 44], downstream by 0–4 rkm [$n$ = 10], and downstream by over 4 rkm [*n* = 18]). Daily movement rates differed by inlet state (ANOVA: $F = 14.26$; df = 1, 88; $P < 0.001$) but not by relocation group ($F = 1.162$; df = 3, 88; $P > 0.331$). The pattern in total movements was similar to daily movement rates, with a difference by inlet state (ANOVA: $F = 96.313$; df = 1, 88; $P < 0.001$) but not by relocation group ($F = 1.681$; df = 3, 88; $P > 0.177$). The fish that were released during the closure had the highest daily movement rates and total movement, even when compared to the relocations of a similar distance during open conditions (Figure 2.5).

## 2.5 DISCUSSION

Our results provide insight into the WQ habitats used by anadromous fish in an ICE and the potential behavioral mechanisms for mediating physiologically stressful conditions caused by closure events. Although movements of adult salmonids and various life stages of other species relative to their environment have been observed (Olson & Quinn, 1992; Childs et al., 2008), including vertical and horizontal movements of salmonids in estuaries (Olson & Quinn, 1992; Plantalech Manel-La et al., 2009; Goetz et al., 2014), there is very little information on real-time responses to changing water conditions after closure of an ICE. This dearth of information extends to diadromous fishes in ICEs around the world. Under open conditions, juvenile steelhead experienced primarily brackish and saline water in the lower and middle reaches and warm freshwater in the upper reach, whereas under closed conditions they moved greater distances, experienced lower salinities and temperatures that were somewhat similar to those occupied during open conditions. Although DO levels were considered nonstressful among all reaches and inlet states, highest DO concentrations were experienced during open conditions in the lower and middle reaches. Narrower ranges of DO were experienced in the upper reach during open conditions and in the middle and upper reaches during closed conditions.

Stressful environmental conditions in ICEs that could prompt a behavioral response can include metabolically demanding temperatures, high salinities, and low DO concentrations. In the RRE, we detected juvenile steelhead in habitat with potentially stressful temperatures and salinities; however, DO concentrations were always adequate. Temperature, a common stressful variable, can increase susceptibility to predation and disease and can lead to decreased growth rates (Coutant, 1973; Myrick & Cech, 2005; Beauchamp et al., 2007). In addition, even with some acclimation, growth of juvenile steelhead decreases as exposure to salinity increases (Morgan, 1991).

When alternate habitats are available, salmonids modify their behavior by seeking less-stressful conditions while avoiding predators. This behavioral response to alternate habitat availability can in turn lead to increases in growth and fitness (Nielsen et al., 1994; Tiffan et al., 2009). The group of juvenile steelhead we released during the May– June 2015 closure appeared to aggregate and occupy less stressful habitats, including lower salinities and temperatures in the middle reach (near the Willow Creek confluence) and lower temperatures in the upper reach (near the Austin Creek confluence). Although at that time of year, the upper reach generally contains more stressful temperatures and similar DO concentrations relative to the other two reaches (Behrens, 2012), all individuals moved into the upper reach within a short period of time (1–4 d).

We suspect that the magnitude of postclosure movements we observed are attributable to the decreased estuary flow resulting from the elimination of tidal cycles, which simplified the environment and (hypothetically) increased the ability of individuals to make intentional horizontal movements (Quinn, 2005). Fish movements are likely hindered in a more complex and dynamic environment, which is often observed in open inlet conditions. Furthermore, the increased stratification from tidal elimination increases the ability of fish to modify their environmental exposure by changing position in the water column (Nielsen et al., 1994). Although evidence suggests that a closed inlet can create conditions that are easier for fish to make volitional movements, we cannot conclude the reasons for these movements. Cues inciting behavioral changes can include site preference (site fidelity), avoidance of stressful physiological conditions and predators, or seeking conditions that promote growth (i.e., temperature or prey resources).

Although reasons for the unprecedented movements are unknown, these fish were the only ones detected in habitats immediately proximate to tributary confluences. In addition, the conditions experienced by fish at those confluences are considered less stressful for juvenile steelhead than the proximate habitats and are especially less stressful when compared to the same locations during open conditions. These instances satisfy the definition of a refuge as a “discrete patch within some larger spatial context” (Torgersen et al., 2012). We hypothesize that these refugia were the product of groundwater and surface water interactions that accumulated due to less mixing during the closure (Torgersen et al., 2012; Kurylyk et al., 2015). Groundwater discharge has been documented as a dominant factor for hydrologic cycles in another ICE (Sadat-Noori et al., 2016); the authors attributed their observation to the highly permeable substrate (i.e., sand and gravel) and low water volume: substrate ratio, which is characteristic of estuarine environments. The importance of these groundwater and surface water interactions has implications for management of the estuary and its inlet dynamics as well as for the benefits provided by tributaries. Our results provide an argument for protecting and/or restoring the groundwater table and hyporheic zone of tributaries, as they not only affect instream rearing habitat but also habitat in the estuarine environment.

Our study design was constrained by several limitations, including the unpredictability of inlet state (open versus closed), low catches of juvenile steelhead of an adequate size for transmitter implantation, and technological bounds. There are restrictions associated with data collected in all acoustic telemetry studies (Klimley et al., 2013; Sandstrom et al., 2013). An important limitation is the tag burden (transmitter weight expressed as a percentage of fish weight), which prevented us from tagging juvenile steelhead weighing less than 10.0 g (53% of the steelhead captured were too small to tag). Moreover, relocating individuals from a site that they were volitionally occupying to a different location may have also altered their behavior. Other studies that have relocated juvenile steelhead to other watersheds have showed no ill effects on the study organisms themselves, but this does not preclude behavioral changes (Moore et al., 2015; Berejikian et al., 2016).

In addition to the limited study design, our interpretations were affected by several uncertainties, including uneven sample sizes, unpredictability of fish movements, and error associated with sampling equipment. Limited battery life of the transmitters (~10 d), episodic tagging events throughout the season, and low catches of juvenile steelhead of an adequate size for transmitter implantation necessitated the use of unbalanced statistical models, which reduced statistical power. Furthermore, we had to incorporate a margin of error associated with the sampling equipment. However, comparisons between entire WQ profile ranges and inferred ranges for WQ variables verified our ability to infer WQ exposure vertically, especially when saline water was present. Overall, the range of possible WQ values for each detection was relatively narrow, especially when considering the physiological tolerances. Despite these uncertainties, our approach allowed us to make spatially explicit comparisons that are valid in a relative sense (i.e., among reaches and between inlet states).

Our results increase the understanding of the environmental conditions experienced by diadromous fish in an ICE. Although extremely productive, estuaries have environmental conditions that at times can be physiologically stressful to their inhabitants, restricting any benefits to those individuals that can successfully mediate the prevailing conditions (Harrison & Whitfield 2012). We hypothesize that anadromous steelhead have persisted through episodic closures because of their ability to modify their behavior and use refugia even when conditions can be physiologically challenging. An important key to species persistence is the phenotypic plasticity exemplified by steelhead in the highly productive but sometimes demanding environment afforded by ICEs in Mediterranean climates, where the combined effects of already warm water temperatures and accelerated climate change are sure to continue (Roessig et al., 2004; Crozier et al., 2008; Crozier and Hutchings 2014). Future research focused on juvenile steelhead in ICEs should include an emphasis on comparing the amounts of habitats available to the amounts of habitats occupied and should examine the utilization of habitats created from increased water levels.

## 2.6 ACKNOWLEDGEMENTS

We are extremely grateful for the assistance provided by the SCWA (Contract Number 13/14-033, Order Number 7339- C5). J. Martini-Lamb's (SCWA) involvement in implementation of the RRE Management Project was crucial to study success. This project would not have been possible without the fieldwork and technical assistance of A. Moratto, D. Favela, E. McDermott, J. Beaton, J. Smith, A. Dockham, A. Iwaki, B. Bei, B. Brawley, and many more. D. Cook's willingness to conduct standardized seining operations around our schedule proved extremely helpful. D. Manning and J. Fuller generously provided valuable input to project design, logistics, and telemetry operations. We greatly appreciate discussions with J. Largier and D. Behrens for their insights into inlet morphology and estuary circulation. We thank D. Beauchamp, J. Hall, G. Marston, T. Quinn, and A. Whitfield for their reviews and helpful comments on the manuscript.

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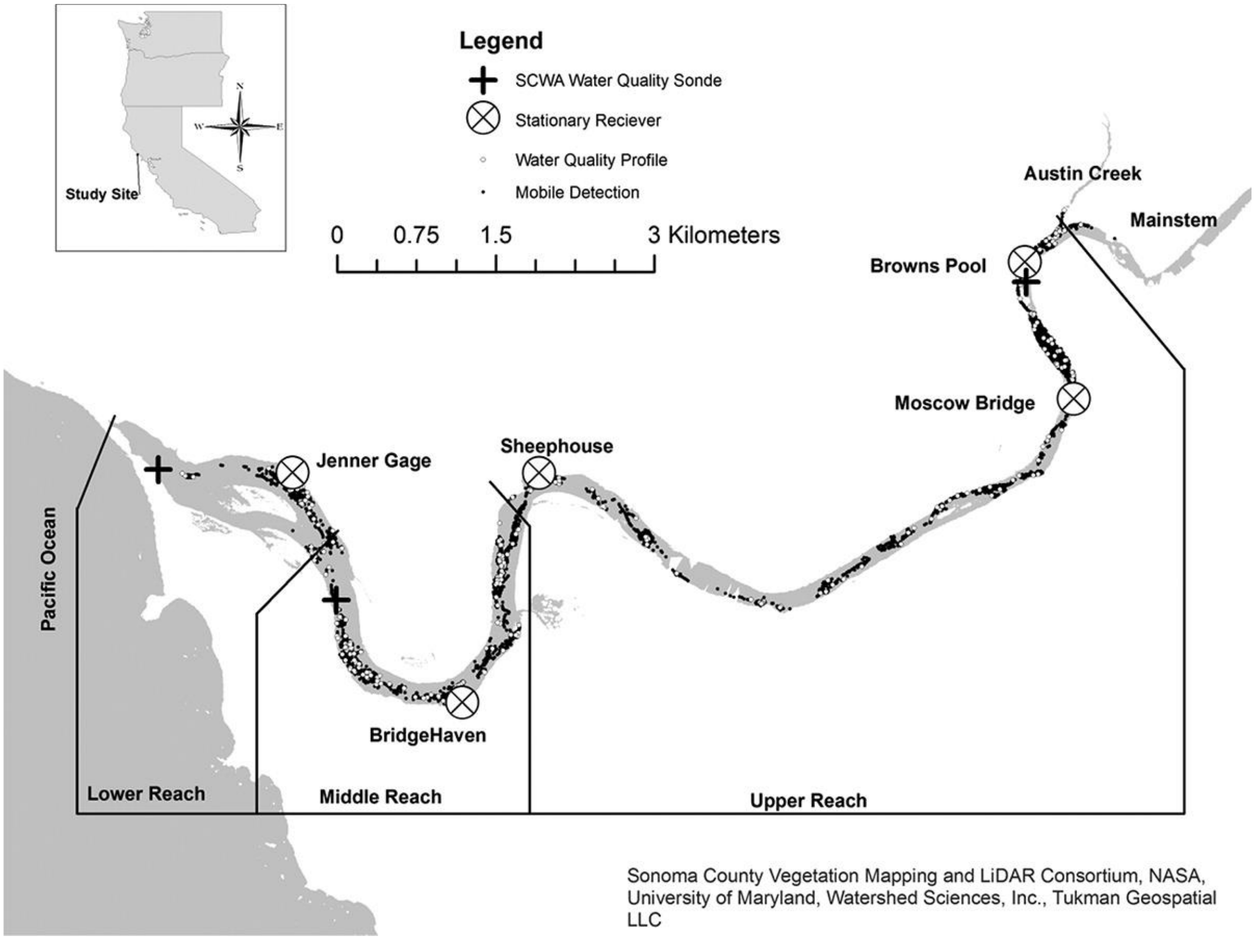
## 2.8 FIGURES



Sonoma County Vegetation Mapping and LiDAR Consortium, NASA, University of Maryland, Watershed Sciences, Inc., Tukman Geospatial LLC

Figure 2.1. Map of acoustic telemetry operations depicting locations of mobile detections, stationary arrays, stationary water quality sondes (SCWA = Sonoma County Water Agency), and water quality profiles obtained during acoustic tracking of juvenile steelhead in three study reaches of the Russian River estuary, 2014–2015.

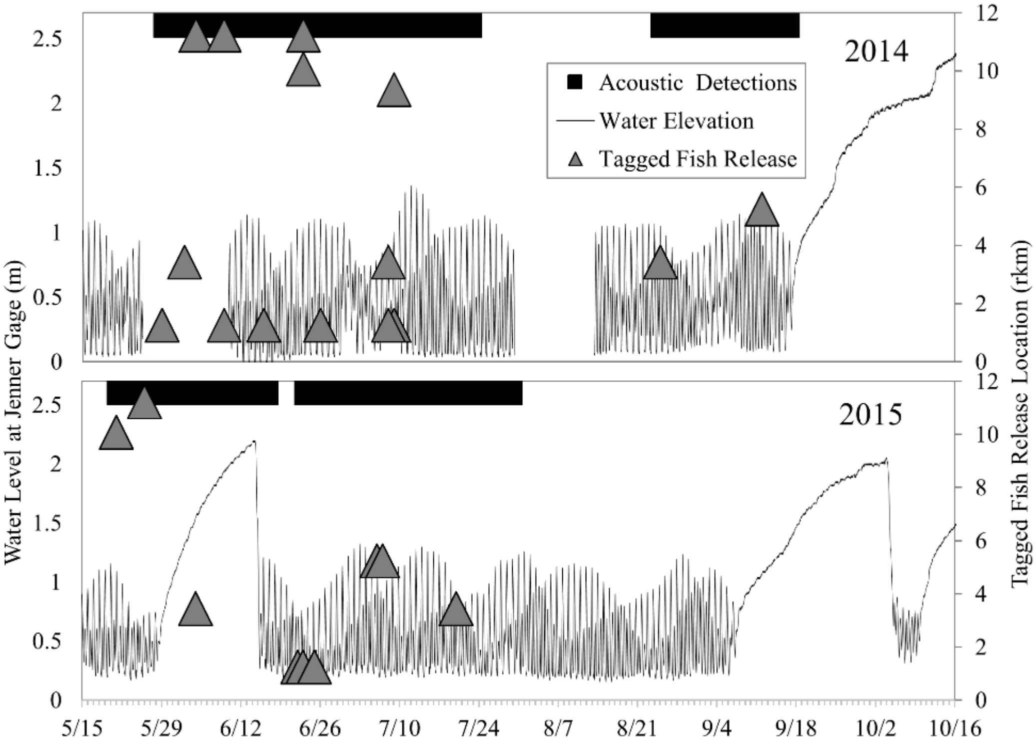


Figure 2.2. Water levels (National Geodetic Vertical Datum of 1929) and acoustic telemetry detections in the Russian River estuarybetween May 15 and October 16 in 2014 (upper panel) and 2015 (lower panel). Missing water level data are attributed to gauge malfunctions; the inlet remained open during all sensor malfunctions.

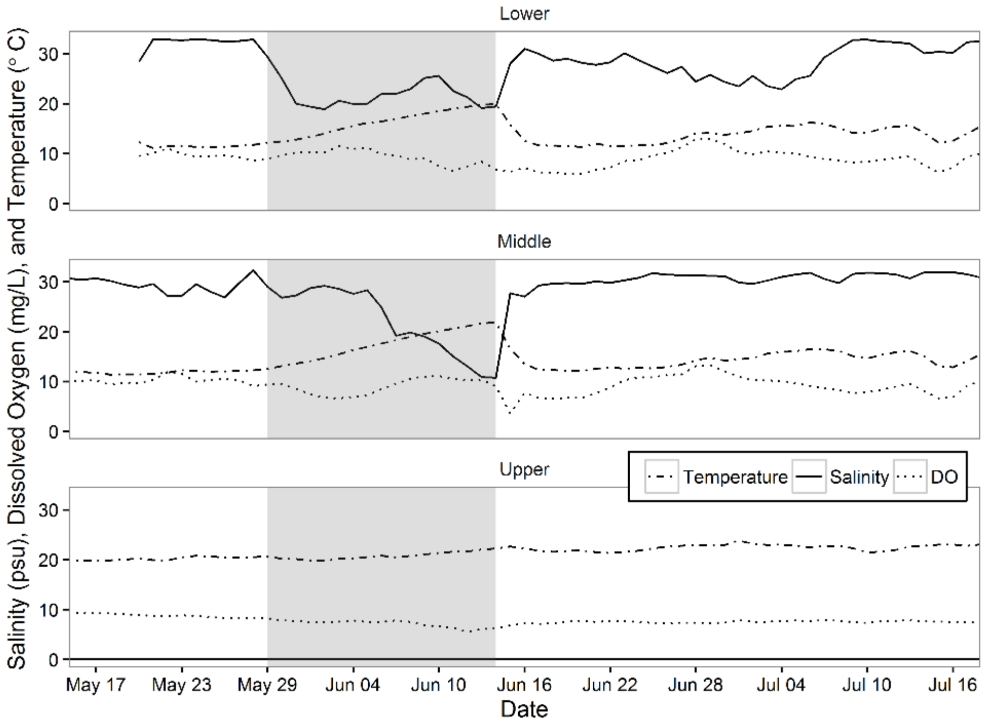

Lower
Middle
Upper
Temperature
Salinity
DO
30
20
10
0
Salinity (psu), Dissolved Oxygen (mg/L), and Temperature (° C)
May 17
May 23
May 29
Jun 04
Jun 10
Jun 16
Jun 22
Jun 28
Jul 04
Jul 10
Jul 16
Date

Figure 2.3. Physiochemical variables in three reaches of the Russian River estuary (lower reach = 0.35 river kilometers [rkm]; middle reach = 2.3 rkm; upper reach = 11.2 rkm), California, from May 15 to July 15, 2015. The gray area encompasses the period of inlet closure that overlapped with acoustic telemetry operations (May 29–June 14). Data are from stationary sondes operated by the Sonoma County Water Agency.

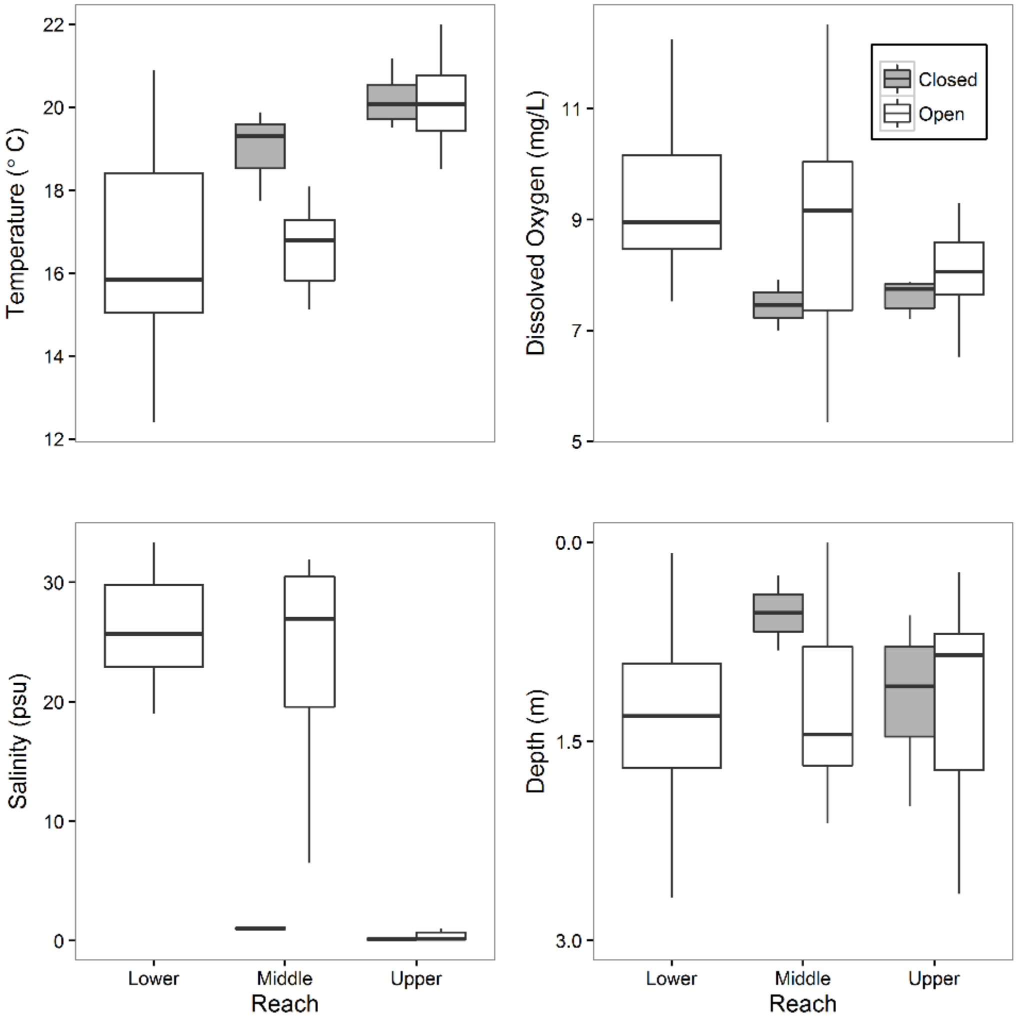


Figure 2.4. Mean temperature, salinity, dissolved oxygen concentration (DO), and depth of all tagged individual steelhead in each reach of the Russian River estuary. Salinity, DO, and depth were inferred by relating the temperature reading from the acoustic transmitter to proximal water quality profiles. The dark-gray boxes represent conditions when the estuary inlet was closed, and open boxes represent conditions when the inlet was open. The box plots show the medians (horizontal line within each box), 25th and 75th percentiles (lower and upper bounds of the box), and 10th and 90th percentiles (lower and upper ends of whiskers).

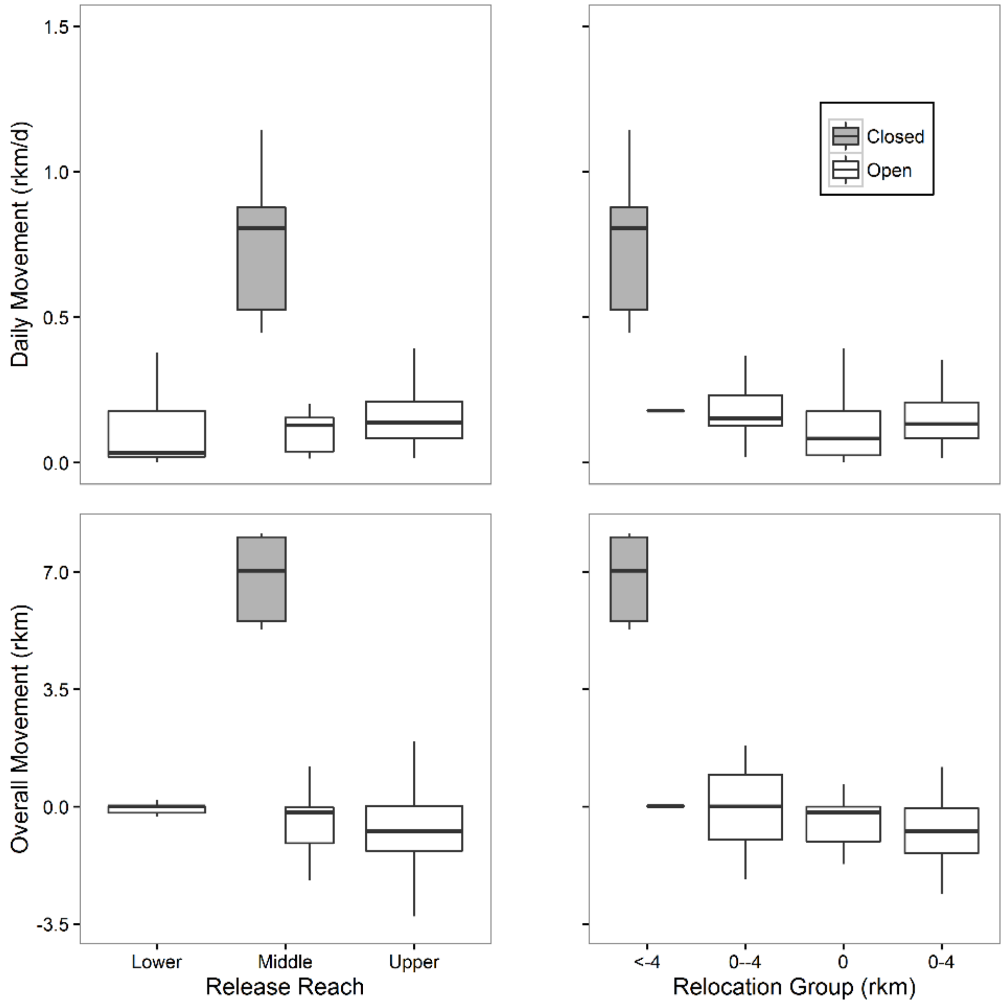


Figure 2.5. Daily movement (upper panels) and overall movement (lower panels) of acoustic-tagged juvenile steelhead from each reach and inlet state in the Russian River estuary during spring and summer of 2014 and 2015. The relocation distances (river kilometers [rkm]) refer to displacements upstream (positive values) versus downstream (negative values). The dark-gray boxes represent conditions when the estuary inlet was closed, and open boxes represent conditions when the inlet was open. There were no detections of fish in the lower reach during the closed-inlet state. The box plots show the medians (horizontal line within each box), 25th and 75th percentiles (lower and upper bounds of the box), and 10th and 90th percentiles (lower and upper ends of whiskers).

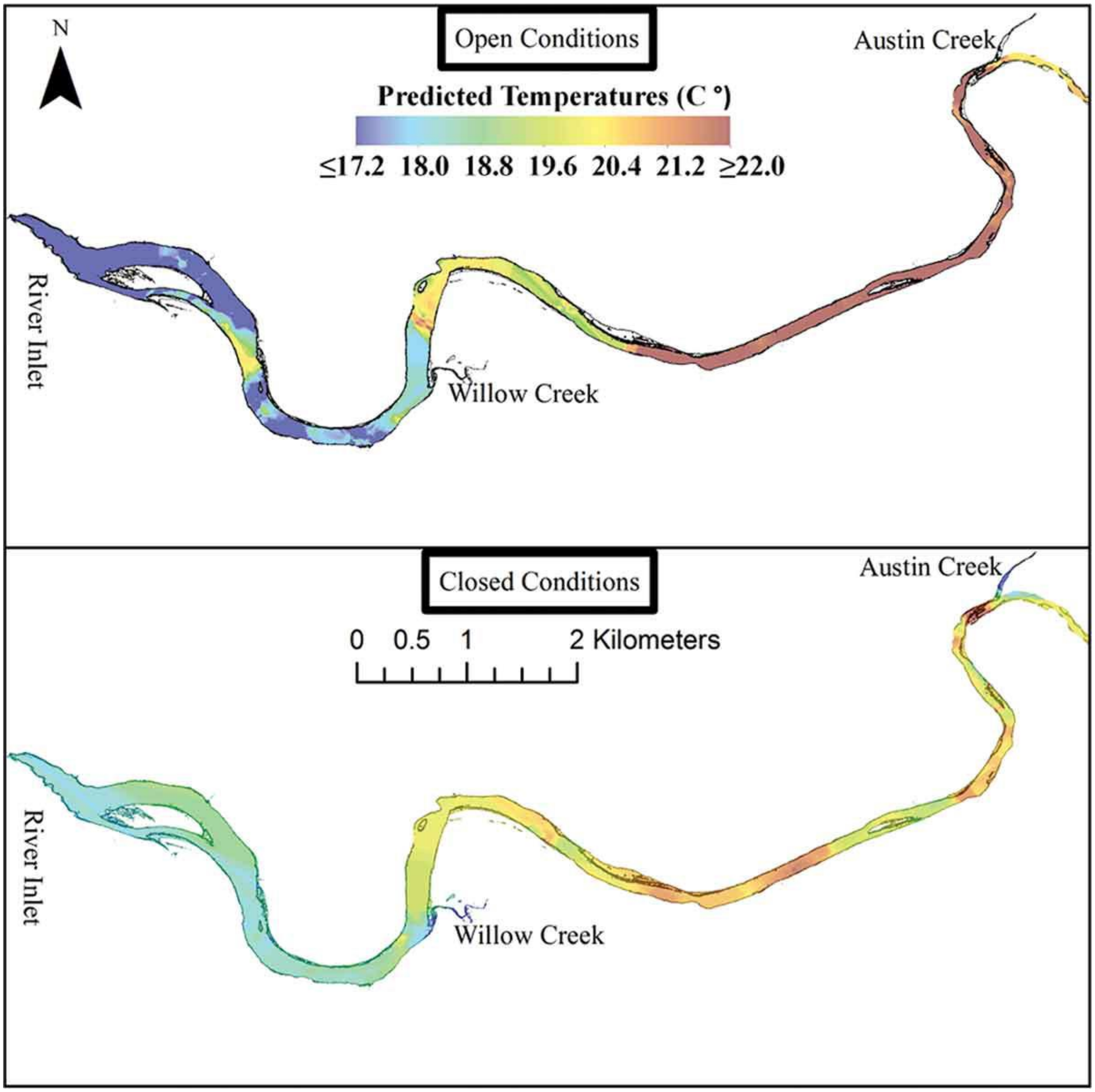


Figure 2.6. Predicted temperatures with maximum available water level for open and closed conditions during the spring and summer of 2014 and 2015 in the Russian River estuary. The heat map reflects the predicted temperature exposure of juvenile steelhead and is created from the ordinary kriging of tagged fish temperatures. Modeled predictions outside of the range of detections are included as a visual example.

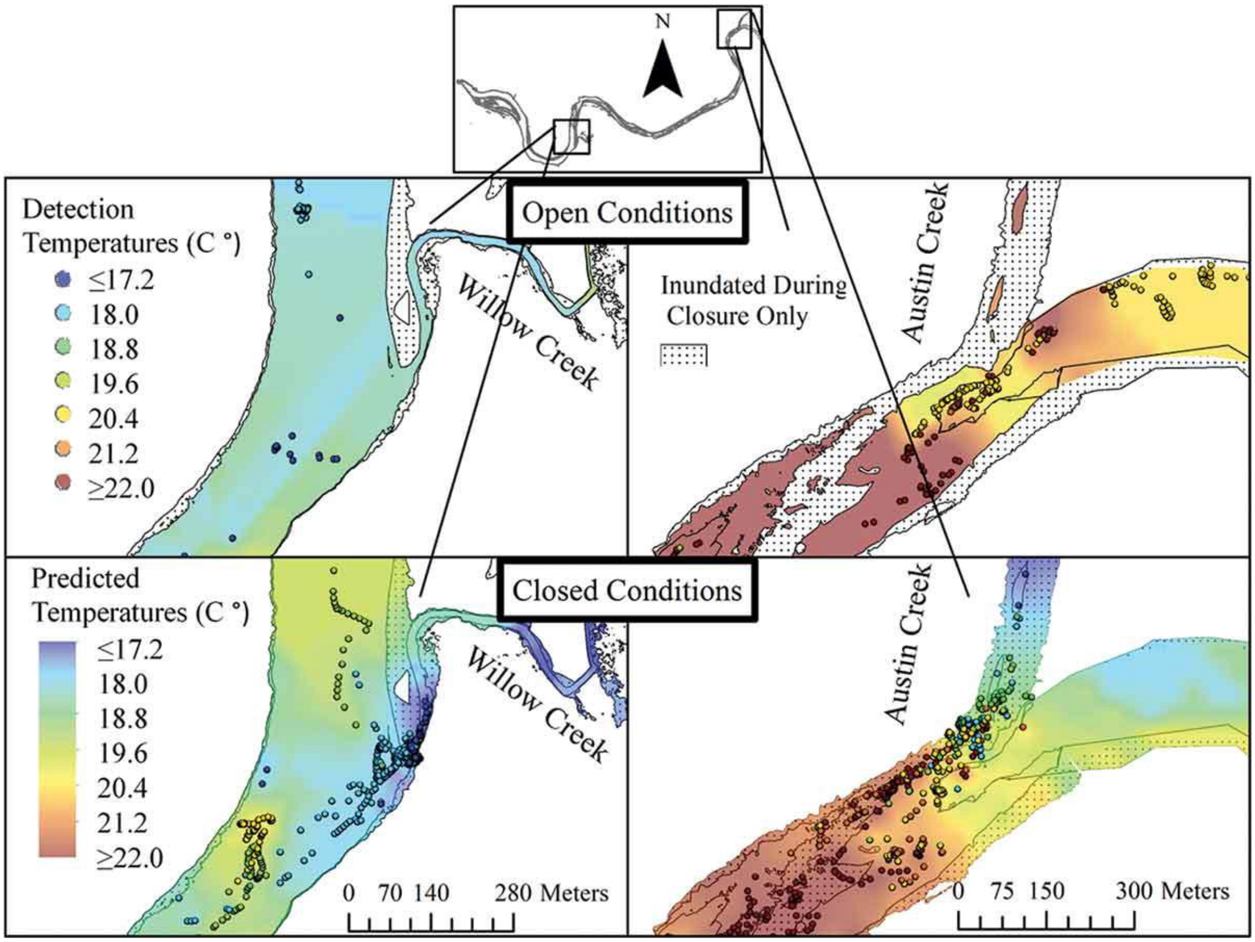


Figure 2.7. Predicted temperatures and location of the surveying vessel at the time of detections during mobile tracking associated with maximum available water level for open-inlet (upper panels) and closed-inlet (lower panels) conditions in the Russian River estuary during spring and summer of 2014 and 2015. The left (rkm 3.6–4.4) and right (rkm 11.3–11.7) panels show contrasts near the confluences of Willow and Austin creeks, respectively. Shading of points indicates the temperature of acoustic-tagged juvenile steelhead. The heat map reflects the predicted temperature exposure of juvenile steelhead and was created from the ordinary kriging of temperatures from tagged fish.

## 2.9 TABLES

Table 2.1. Mean and standard deviation of the range (maximum possible value – minimum possible value) of simultaneous inferred variables (salinity, depth and DO) within the transmitter manufacturer's reported temperature error range (0.8C˚) from vertical water quality profile readings.

| Inlet | Reach | Salinity (psu) | Depth (m) | DO (mg/L) |
|---|---|---|---|---|
| Closed | Middle | 0.13±1.28 | 0.1±0.27 | 0.05±0.15 |
| Closed | Upper | 0.01±0.03 | 0.72±1.18 | 0.37±0.91 |
| Open | Lower | 1.21±2.19 | 0.49±0.62 | 0.48±0.94 |
| Open | Middle | 0.88±2.92 | 0.29±0.54 | 0.29±0.81 |
| Open | Upper | 0.47±1.57 | 0.93±1.32 | 0.39±0.79 |

Table 2.2. Mean values (and SD) of juvenile steelhead exposure to enviromental conditions (Temperature, depth, salinity and DO duing the spring and summer of 2014 and 2015 in each reach of the Russian River estuary. Results include two-way ANOVA tests evaluating the effects of inlet state (closed vs. open), reach (lower, middle, upper) and their interaction. Bold values are significant effects.

| | Open inlet | | | Closed inlet | | Source of variation (*F;P*) | | |
|---|---|---|---|---|---|---|---|---|
| Parameter | Lower | Middle | Upper | Middle | Upper | Inlet | Reach | Inlet X Reach |
| Temperature (°C) | 16.0 (2.1) | 17.1 (1.1) | 20.8 (1.7) | 19.0 (1.1) | 20.1 (0.5) | 0.003;0.960 | 76.22; **0.000** | 4.25; **0.042** |
| Depth (m) | 1.3 (0.7) | 1.3 (0.6) | 1.3 (0.9) | 0.5 (0.4) | 1.4 (1.2) | 0.033;0.857 | 0.10;0.904 | 2.74;0.101 |
| DO (mg/L) | 9.3 (1.2) | 8.8 (1.8) | 8.8 (0.7) | 7.5 (0.7) | 7.7 (6.4) | 1.71;0.194 | 5.0;**0.009** | 0.86;0.357 |
| Salinity (psu) | 26.0 (5.4) | 24.7 (7.2) | 3.6 (6.6) | 1.0 (0.1) | 0.1 (0.1) | 21.94;**0.000** | 99.99;**0.000** | 3.40;0.069 |

Bold values indicate differences at the alpha=0.05 level

## 2.10 SUPPLEMENTAL MATERIALS

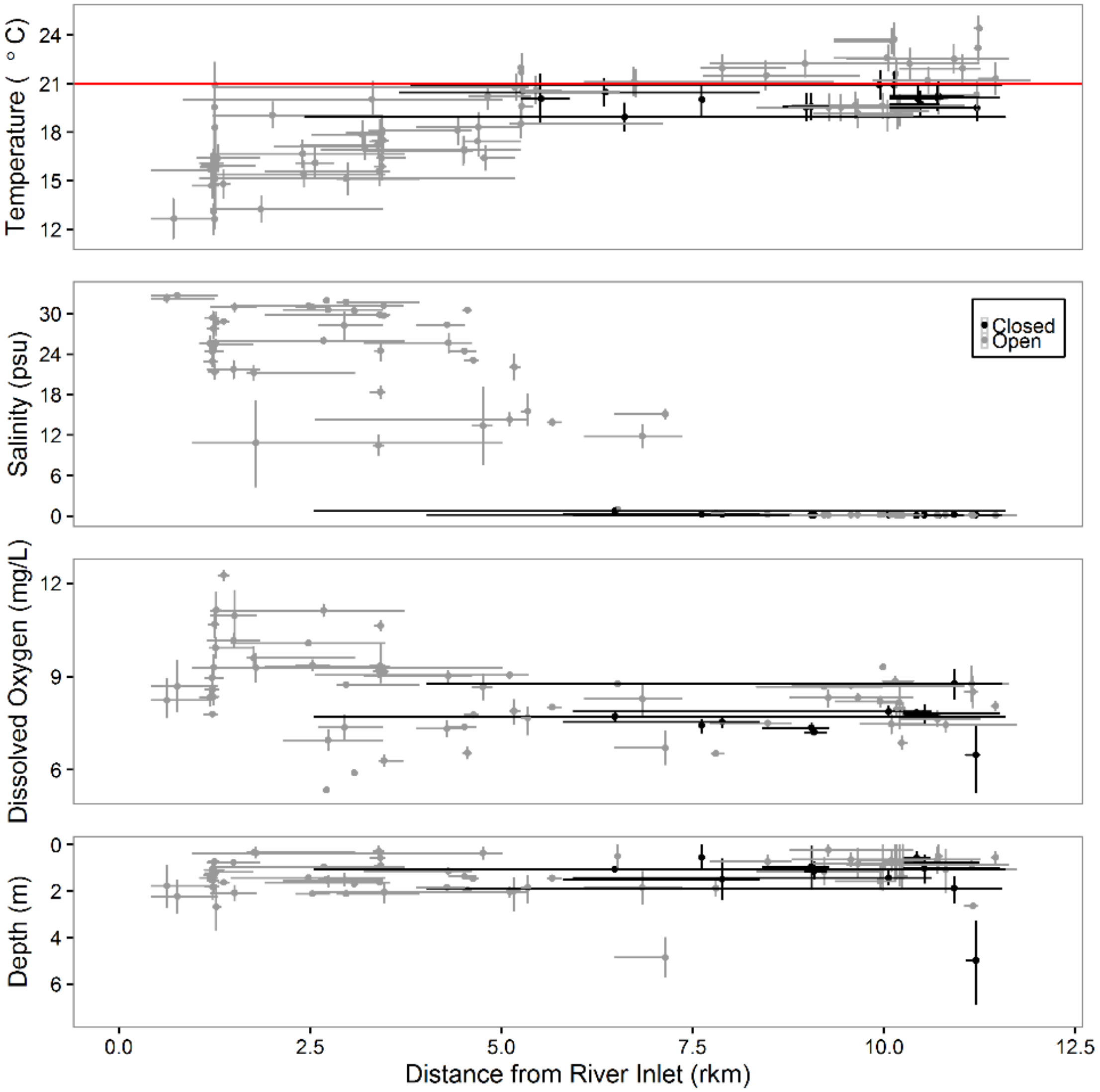


Figure 2.8. The environmental exposure of acoustic tagged juvenile steelhead during the spring and summer of 2014 and 2015 in the Russian River estuary. Black points represent individuals detected during closed inlet conditions and grey points represent individuals detected during open inlet conditions. The x-axis error bars represent the spatial range of detections relative to the river inlet. The y-axis error bars represent the 95% confidence intervals of the extremes caused by the error range (±0.8 °C) of the sensor encoded acoustic transmitters and the proximate water quality profiles. The red horizontal line in the top panel (temperature) corresponds to a temperature where the majority of juvenile steelhead use thermal refuge (Brewitt & Danner 2014).

Table 2.3. Summary of sampling operations. Week, inlet state, number of tagged fish released, number of associated water quality profiles, number of operations in the estuary, and the flow (CFS) at the gage in Guerneville, CA, operated and maintained by USGS.

| Week | Inlet state | Fish Released | Water Quality Profiles | Number of Surveys | Flow (CFS) |
|---|---|---|---|---|---|
| 5/29/2014 - 6/4/2014 | Open | 12 | 18 | 7 | 152 |
| 6/5/2014 - 6/11/2014 | Open | 6 | 28 | 6 | 159 |
| 6/12/2014 - 6/18/2014 | Open | 3 | 20 | 7 | 166 |
| 6/19/2014 - 6/25/2014 | Open | 3 | 6 | 3 | 173 |
| 6/26/2014 - 7/2/2014 | Open | 4 | 22 | 7 | 180 |
| 7/3/2014 - 7/9/2014 | Open | 6 | 4 | 2 | 187 |
| 7/10/2014 - 7/16/2014 | Open | 0 | 14 | 4 | 194 |
| 7/17/2014 - 7/23/2014 | Open | 0 | 8 | 3 | 201 |
| 8/21/2014 - 8/27/2014 | Open | 8 | 5 | 2 | 236 |
| 8/28/2014 - 9/3/2014 | Open | 0 | 16 | 6 | 243 |
| 9/4/2014 - 9/10/2014 | Open | 0 | 9 | 3 | 250 |
| 9/11/2014 - 9/17/2014 | Open | 3 | 5 | 5 | 257 |
| 5/21/2015 - 5/27/2015 | Open | 11 | 13 | 5 | 144 |
| 5/28/2015 - 6/3/2015 | Closed/Open | 0 | 27 | 7 | 151 |
| 6/4/2015 - 6/10/2015 | Closed | 6 | 25 | 6 | 158 |
| 6/11/2015 - 6/17/2015 | Closed/Open | 0 | 18 | 5 | 165 |
| 6/18/2015 - 6/24/2015 | Open | 6 | 5 | 1 | 172 |
| 6/25/2015 - 7/1/2015 | Open | 7 | 21 | 5 | 178 |
| 7/2/2015 - 7/8/2015 | Open | 11 | 22 | 4 | 186 |
| 7/9/2015 - 7/15/2015 | Open | 0 | 29 | 6 | 193 |
| 7/16/2015 - 7/22/2015 | Open | 7 | 28 | 5 | 200 |
| 7/23/2015 - 7/29/2015 | Open | 0 | 33 | 6 | 207 |
| 7/30/2015 - 8/2/2015 | Open | 0 | 22 | 3 | 212 |

Table 2.4. Summary of tagged steelhead. Individual steelhead tagged, release data, size, detections, mean temperature and SD (°C), distance released from river inlet (rkm), minimum rkm, and maximum rkm.

| Tag | Release Date | FL (mm) | Weight (g) | Detections | Temperature | Release rkm | Minimum rkm | Maximum rkm |
|---|---|---|---|---|---|---|---|---|
| 704 | 6/4/2014 | 141 | 33.5 | 116 | 21.3 ± 1.2 | 11.2 | 11.2 | 11.5 |
| 804 | 6/2/2014 | 102 | 13.2 | 1,923 | 18.1 ± 1.4 | 3.4 | 3.3 | 3.5 |
| 904 | 6/9/2014 | 149 | 39.5 | 233 | 23.2 ± 0.4 | 11.2 | 11.2 | 11.3 |
| 1004 | 6/26/2014 | 100 | 11.5 | 2,972 | 16.4 ± 1.7 | 1.3 | 1.0 | 1.9 |
| 1104 | 9/12/2014 | 139 | 30 | 6 | 16.4 ± 0 | 5.2 | 4.7 | 5.2 |
| 1204 | 7/9/2014 | 101 | 12.3 | 3,735 | 15.8 ± 1.8 | 1.3 | 1.1 | 1.3 |
| 1304 | 7/9/2014 | 209 | 116.8 | 16,853 | 15.7 ± 1.7 | 1.3 | 1.1 | 1.3 |
| 1404 | 7/9/2014 | 101 | 11.2 |  |  | 1.3 | 1.3 | 1.3 |
| 1604 | 6/26/2014 | 97 | 10.7 | 522 | 20 ± 3.9 | 1.3 | 0.8 | 5.0 |
| 1704 | 6/2/2014 | 124 | 25.0 | 13,393 | 17.4 ± 2.3 | 3.4 | 3.3 | 3.5 |
| 1804 | 6/4/2014 | 155 | 44.7 | 151 | 22.2 ± 1.0 | 11.2 | 10.2 | 11.3 |
| 1904 | 8/25/2014 | 144 | 37.2 | 755 | 17.9 ± 0.8 | 3.4 | 3.0 | 3.5 |
| 2004 | 9/12/2014 | 134 | 29.0 | 859 | 20.2 ± 0.8 | 5.2 | 4.6 | 5.4 |
| 2104 | 8/25/2014 | 124 | 23.5 | 1,150 | 19 ± 0.7 | 3.4 | 1.2 | 3.5 |
| 2204 | 7/8/2014 | 99 | 10.8 |  |  | 1.3 | 1.3 | 1.3 |
| 2304 | 6/16/2014 | 137 | 29.3 | 81 | 12.7 ± 2.0 | 1.3 | 0.4 | 1.3 |
| 2404 | 6/16/2014 | 166 | 57.1 | 3,357 | 15.6 ± 2.4 | 1.3 | 0.4 | 1.3 |
| 2504 | 5/29/2014 | 151 | 41.8 | 8,284 | 15.9 ± 1.7 | 1.3 | 1.1 | 1.4 |
| 2604 | 5/29/2014 | 141 | 36.9 | 8,375 | 14.7 ± 1.5 | 1.3 | 1.0 | 1.3 |
| 2704 | 6/9/2014 | 138 | 32.5 | 194 | 22.5 ± 0.8 | 11.2 | 9.5 | 11.6 |
| 2804 | 6/23/2014 | 99 | 11.0 | 29 | 23.7 ± 0.7 | 10.1 | 9.4 | 10.2 |
| 2904 | 9/12/2014 | 157 | 47.7 |  |  | 5.2 | 5.2 | 5.2 |
| 3004 | 6/4/2014 | 141 | 40.5 | 2,091 | 21.2 ± 1.0 | 11.2 | 9.9 | 11.9 |
| 3104 | 8/25/2014 | 142 | 34.9 | 635 | 17.2 ± 0.5 | 3.4 | 2.4 | 3.5 |
| 3204 | 6/23/2014 | 97 | 10.7 | 12 | 23.6 ± 0 | 11.2 | 9.4 | 10.2 |
| 3304 | 6/16/2014 | 99 | 11.4 | 1,846 | 16.7 ± 1.8 | 1.3 | 1.2 | 3.7 |
| 3404 | 6/9/2014 | 142 | 34.5 | 563 | 22.2 ± 0.7 | 11.2 | 7.7 | 11.3 |
| 3504 | 6/23/2014 | 123 | 20.7 | 2,862 | 22.6 ± 1.1 | 10.1 | 9.4 | 10.2 |
| 3604 | 6/26/2014 | 111 | 15.1 | 2,692 | 16 ± 2.3 | 1.3 | 1.1 | 1.3 |
| 3704 | 8/25/2014 | 121 | 22.0 | 1,082 | 17.8 ± 1.1 | 3.4 | 2.5 | 3.5 |
| 3904 | 8/25/2014 | 140 | 35.2 | 146 | 18 ± 0.2 | 3.4 | 3.4 | 3.5 |
| 4004 | 6/26/2014 | 178 | 61.4 | 3,872 | 13.2 ± 1.2 | 1.3 | 1.2 | 3.5 |
| 4204 | 8/25/2014 | 149 | 44.5 | 4,578 | 17.1 ± 1.5 | 3.4 | 2.0 | 3.5 |
| 4304 | 6/4/2014 | 132 | 27.9 | 1,180 | 21.9 ± 0.9 | 11.2 | 10.2 | 11.3 |
| 4404 | 5/29/2014 | 117 | 19.2 | 2,484 | 15.9 ± 1.5 | 1.3 | 1.1 | 1.8 |
| 4504 | 6/9/2014 | 139 | 33.6 | 4 | 15.4 ± 0.4 | 1.3 | 1.2 | 1.3 |
| 4604 | 6/9/2014 | 110 | 16.6 | 63 | 24.4 ± 0.0 | 11.2 | 11.2 | 11.3 |
| 4804 | 8/25/2014 | 146 | 36.2 | 80 | 18.1 ± 0.6 | 3.4 | 3.4 | 4.6 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 4904 | 7/9/2014 | 183 | 65.6 | 977 | 21.1 ± 1.8 | 9.4 | 6.1 | 9.4 |
| 5004 | 7/8/2014 | 106 | 15.6 | 21,379 | 17.5 ± 1.5 | 3.4 | 3.3 | 3.5 |
| 5104 | 6/2/2014 | 144 | 37.5 | 1,785 | 15.9 ± 2.4 | 3.4 | 3.3 | 3.5 |
| 5604 | 5/29/2014 | 139 | 30.5 | 3,788 | 15.8 ± 1.3 | 1.3 | 1.1 | 1.3 |
| 5704 | 5/29/2014 | 116 | 18.1 | 8,349 | 16.1 ± 1.7 | 1.3 | 1.1 | 1.4 |
| 5804 | 8/25/2014 | 140 | 37.2 | 7,183 | 16.4 ± 1.1 | 3.4 | 3.4 | 3.8 |
| 5904 | 6/6/2014 | 112 | 14.9 | 715 | 21.6 ± 0.9 | 12.6 | 9.5 | 12.6 |
| 2305 | 7/20/2015 | 219 | 106.4 | 55 | 15.1 ± 0.8 | 3.4 | 2.9 | 3.9 |
| 2405 | 5/26/2015 | 93 | 10.2 | 418 | 20.2 ± 0.7 | 11.2 | 10.1 | 11.3 |
| 2605 | 5/21/2015 | 182 | 66.2 | 248 | 19.5 ± 0.4 | 10.1 | 8.3 | 10.4 |
| 2705 | 6/4/2015 | 109 | 16.0 | 838 | 20.9 ± 0.7 | 3.4 | 5.8 | 11.3 |
| 2805 | 7/20/2015 | 122 | 23.5 | | | 3.4 | | |
| 2905 | 6/4/2015 | 108 | 15.7 | | | 3.4 | | |
| 3005 | 6/25/2015 | 115 | 14.5 | 18 | 20.9 ± 1.3 | 1.3 | 1.3 | 1.3 |
| 3105 | 7/7/2015 | 149 | 41.3 | 108 | 22 ± 0.2 | 5.2 | 5.3 | 5.3 |
| 3205 | 7/7/2015 | 186 | 81.5 | | | 5.2 | | |
| 3305 | 6/23/2015 | 123 | 22.4 | 1 | 18.8 | 1.3 | 1.3 | 1.3 |
| 3405 | 6/25/2015 | 190 | 84.8 | 3 | 12.4 ± 0 | 1.3 | 1.3 | 1.3 |
| 3505 | 6/4/2015 | 148 | 40.3 | 478 | 20.7 ± 1.0 | 3.4 | 3.7 | 8.7 |
| 3605 | 7/20/2015 | 113 | 15.9 | 661 | 15.6 ± 1.5 | 3.4 | 1.9 | 3.6 |
| 3705 | 7/7/2015 | 109 | 15.9 | 852 | 20.5 ± 0.7 | 5.2 | 5.3 | 6.6 |
| 3905 | 5/26/2015 | 168 | 59.5 | 900 | 20 ± 0.6 | 11.2 | 10.1 | 10.8 |
| 4005 | 6/25/2015 | 126 | 24.3 | 12 | 15.7 ± 3.0 | 1.3 | 1.3 | 1.3 |
| 4205 | 7/7/2015 | 98 | 10.8 | 608 | 21 ± 1.1 | 5.2 | 5.3 | 7.2 |
| 4305 | 5/21/2015 | 160 | 48.4 | 138 | 19.7 ± 0.4 | 10.1 | 7.6 | 11.1 |
| 4405 | 6/23/2015 | 141 | 33.2 | 2,674 | 20.8 ± 1.3 | 1.3 | 1.3 | 5.4 |
| 4605 | 7/6/2015 | 198 | 92.9 | 444 | 17.4 ± 1.6 | 5.2 | 4.5 | 5.3 |
| 4805 | 5/21/2015 | 122 | 21.5 | 74 | 19.1 ± 0.6 | 10.1 | 9.1 | 10.4 |
| 4905 | 7/7/2015 | 146 | 36.4 | 22 | 21.7 ± 1.0 | 5.2 | 5.3 | 5.3 |
| 5005 | 5/26/2015 | 168 | 59.7 | 2,181 | 20.1 ± 0.9 | 11.2 | 10.1 | 11.5 |
| 5105 | 7/20/2015 | 161 | 52.9 | 1,607 | 15.4 ± 0.8 | 3.4 | 1.3 | 3.5 |
| 5205 | 5/21/2015 | 131 | 26.9 | 813 | 19.6 ± 0.8 | 10.1 | 9.7 | 10.7 |
| 5305 | 6/4/2015 | 129 | 24.9 | 457 | 20.9 ± 1.1 | 3.4 | 3.4 | 11.6 |
| 5505 | 6/4/2015 | 97 | 11.3 | 51 | 21.3 ± 0.7 | 7.6 | 5.3 | 9.7 |
| 5605 | 6/22/2015 | 210 | 118.0 | 233 | 12.7 ± 1.2 | 1.3 | 1.3 | 1.3 |
| 5705 | 6/25/2015 | 112 | 14.5 | 32 | 19.5 ± 1.3 | 1.3 | 1.3 | 1.3 |
| 5805 | 6/4/2015 | 116 | 17.4 | 1,361 | 18.9 ± 1.7 | 3.4 | 2.4 | 11.6 |
| 5905 | 7/6/2015 | 96 | 10.1 | 1,294 | 19.6 ± 1.3 | 5.2 | 5.3 | 5.4 |
| 6005 | 6/25/2015 | 201 | 107.2 | 2,079 | 15.1 ± 1.7 | 1.3 | 1.1 | 5.2 |
| 6105 | 5/21/2015 | 160 | 44.2 | 369 | 19.5 ± 0.4 | 10.1 | 8.7 | 10.4 |
| 6205 | 7/20/2015 | 136 | 33.9 | 436 | 18.5 ± 1.0 | 3.4 | 5.1 | 7.1 |
| 6305 | 7/7/2015 | 125 | 26.2 | 1 | 22 | 5.2 | 5.3 | 5.3 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 6405 | 6/25/2015 | 111 | 14.4 | 58 | 15.3 ± 2.7 | 1.3 | 1.3 | 1.3 |
| 6505 | 5/26/2015 | 159 | 44.4 | 1,429 | 19.6 ± 0.7 | 11.2 | 10.1 | 11.3 |
| 6605 | 5/21/2015 | 184 | 75.6 | 67 | 19 ± 0.7 | 10.1 | 9.7 | 10.4 |
| 6705 | 6/22/2015 | 210 | 103.7 | | | 1.3 | | |
| 6805 | 6/25/2015 | 112 | 16.3 | 36 | 18.3 ± 2.8 | 1.3 | 1.3 | 1.3 |
| 6905 | 5/21/2015 | 146 | 22.6 | 8 | 19.6 ± 0.0 | 10.1 | 10.0 | 10.0 |
| 7005 | 7/20/2015 | 123 | 24.3 | 502 | 16.8 ± 1.2 | 3.4 | 3.2 | 4.6 |
| 7105 | 6/23/2015 | 108 | 14.1 | 785 | 14.8 ± 1.6 | 1.3 | 1.3 | 1.5 |
| 7305 | 7/20/2015 | 226 | 103.8 | 204 | 16.1 ± 1.0 | 3.4 | 2.3 | 2.8 |
| 7405 | 7/6/2015 | 230 | 144.8 | 438 | 18.3 ± 1.5 | 5.2 | 3.9 | 5.3 |
| 7505 | 7/6/2015 | 102 | 11.4 | 396 | 20.6 ± 1.0 | 5.2 | 5.3 | 5.8 |
| 7605 | 7/6/2015 | 145 | 42.4 | 1,367 | 16.9 ± 1.1 | 5.2 | 2.6 | 5.3 |
| 7905 | 6/22/2015 | 193 | 82.0 | | | 1.3 | | |

# Chapter 3. Juvenile steelhead *Oncorhynchus mykiss* display size related shift of behaviour in an intermittently closed estuary

**Authors**: W. Matsubu, C.A. Simenstad, and G.E. Horton

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## 3.1 ABSTRACT

To understand how the stochastic abiotic conditions in intermittently closed estuaries affect juvenile steelhead *Oncorhynchus mykiss,* we combined thermal-encoded acoustic telemetry with simultaneous water quality sampling in the Russian River estuary (northern California, USA). Our results indicate that the depth of fish varied in response to the present abiotic conditions. Overall, the depth of fish reflected the occupation of more energetically and physiologically ideal habitats. When temperatures were warmer, fish were deeper, but when dissolved oxygen levels were lower, fish were shallower. Higher salinities led to smaller juvenile steelhead occupying shallower depths while larger steelhead were deeper in the water column. Furthermore, we detected smaller fish (99-144 mm FL) readily moving across the halocline and making forays into the deeper saltier conditions and returning into shallower less saline water. While this behaviour increases the foraging opportunities of juvenile steelhead that are not tolerant of high salinities, there are likely tradeoffs with increased vulnerability to avian predation and energetic costs.

## 3.2 INTRODUCTION

Throughout much of their range, juvenile salmonids *Oncorhynchus* spp. (Walbaum, 1792) benefit from the use of estuarine habitats (Healey, 1980; Simenstad *et al.,* 1982; Levy & Northcote, 1982; Levings *et al.,* 1986) yet little is known regarding how salmonids react to the heterogeneous, typically dynamic conditions present in estuaries. Juvenile salmonids can spend a year or more rearing in upstream habitat before entering the estuary, but many migrate downstream during their first year and are not always physiologically capable of coping with saline conditions (Cunjak *et al.,* 1989; Hayes *et al*., 2011; Rohtla *et al.,* 2017). Furthermore, while human activities (i.e., regulated flows and breaching of lagoons) and anticipated effects of climate change (i.e., increased temperatures, changes in freshwater discharge) affect the abiotic conditions in estuaries (Haines *et al.,* 2006; Saintilan *et al*., 2016; Largier *et al*., 2019), alterations to habitat and the response of juvenile salmonids to the alterations remains relatively understudied.

Of particular interest are U.S. Endangered Species Act (ESA) listed Central California Coast steelhead *O. mykiss* (Walbaum, 1792*)* that rear in lagoon habitat in estuaries that become disconnected from the ocean, also known as intermittently closed estuaries (NMFS, 2008; McSweeney *et al.,* 2017)**.** Interest in maintaining and enhancing suitable lagoon habitat for juvenile steelhead is understandable given evidence that in systems with lagoon habitat, only about 20% of the downstream migrants rear in the lagoon yet those individuals produce 60-90% of the returning adult population (Shapovalov & Taft, 1954; Bond *et al.,* 2008). This is likely a consequence of the extremely high growth rates displayed by juvenile steelhead rearing in lagoon habitat (Hayes *et al*., 2008). In contrast, body sizes of juvenile steelhead reared in upper-watershed habitat encompass a broader range of sizes when they migrate downstream with an overall smaller mean size (Hayes *et al.*, 2008).

Intermittently closed estuaries are especially sensitive to human-caused disturbances associated with freshwater flow diversion, flow regulation, and manual breaching (Elliott & Whitfield 2011). Such management actions affect the timing of closures and sandbar breaches and how long the estuary will remain in either open or closed states. While much of the ichthyofauna in intermittently closed estuaries are highly tolerant to changes in inlet conditions (Elliott & Whitfield 2011), little is known about how less physiologically-tolerant organisms like juvenile steelhead (Boughton *et al.,* 2017) respond to variable and stochastic estuarine conditions despite evidence that intermittently closed estuaries provides essential habitat to depressed populations of steelhead (Bond *et al.*, 2008; Osterback *et al.*, 2014). Furthermore, access to habitat in intermittently closed estuaries during the open inlet state may be too saline for some juvenile steelhead and too warm or hypoxic under all inlet conditions (NMFS, 2008; Boughton *et al.*, 2017). Juvenile steelhead are known to inhabit littoral and shallow epibenthic estuarine environments (Quiñones & Mulligan 2005; Fuller, 2011), and smaller (<100mm) juvenile steelhead have been found in salinities as high as 30 practical salinity units (PSU) (Matsubu *et al.,* 2017), yet whether specific environmental conditions or other ecological factors (e.g., prey availability) influence the habitats occupied by juvenile steelhead is unknown. The estuary-wide changes to these habitats caused by human disturbances and the high growth potential (Bond *et al.,* 2008; Osterback *et al.,* 2014) may create more risky tradeoffs of juvenile steelhead for various management strategies. For example, it is unknown whether manually breaching the inlet increases the susceptibility of juvenile steelhead to predation or the occupation of environmental conditions that are more physiological costly while juvenile steelhead are trying to take advantage of the high growth potential.

Although studies have evaluated the relationship of juvenile salmonids to the environmental conditions in estuaries, they do not apply to juvenile steelhead in intermittently closed estuaries (Plantalech Mane-la *et al.,* 2009; Mitamura *et al.*, 2017; Smith *et al.,* 2015). For example, these studies were limited to other salmonid species with differing life histories, including Coho salmon O. *kisutch* (Smith *et al*., 2015), Chinook salmon *O. tshawytscha* (Smith *et al*., 2015), and Atlantic salmon *Salmo salar* (Plantalech Mane-la *et al.*, 2009; Mitamura *et al.,* 2017). Furthermore, these studies were limited to fish that were much larger (254 to 430 FL mm) than the size of juvenile steelhead that rear in intermittently closed estuaries (50 to 250 FL mm; Hayes *et al*., 2008). Recent advances in technology, including the decreased size of sensor encoded acoustic transmitters (Lotek Wireless), have allowed the tagging of smaller juvenile salmonids which provides the opportunity to add to the current body of knowledge by looking at smaller, less physiologically developed steelhead while they encounter a heterogeneous and dynamic environment, like an intermittently closed estuary.

Most of the published research on juvenile steelhead volitionally rearing in intermittently closed estuaries is during closed inlet conditions in systems with seasonal river discharge (Bond *et al*., 2008; Hayes *et al*., 2008; Osterback *et al*., 2014) while little is present on how fish will respond under open inlet conditions during the dry season. The purpose of this study was to evaluate the response of juvenile steelhead to the physiochemical conditions (i.e., temperature, DO, salinity) within an intermittently closed estuary. We hypothesize that: (i) juvenile steelhead will shift their position in the water column based on prevailing physiochemical conditions; (ii) the degree to which juvenile steelhead adjust their position in the water column will vary with fish size; and (iii) smaller juvenile steelhead will risk potentially stressful conditions in order to take advantage of prey sources.

## 3.3 MATERIALS AND METHODS

### 3.3.1 *Study area*

We conducted this study within the Russian River estuary (Figure 3.1), Sonoma County, California (38°26'57"N 123°07'13"W). Located along the northern coast of California, the Russian River watershed (3,846 $km^2$) is in a Mediterranean climate and has regulated flows for water supply during the dry season. The Russian River estuary extends 11.7 rkm from the river mouth to Austin Creek and covers approximately 1.62 $km^2$ with typical depths ranging from 2-10 m under open conditions, but the surface area and volume can more than double during an extended closure (Largier & Koohafkan 2016). Due to changes in managed flows and manual breaching, the timing and duration of inlet closures have changed from being historically closed for the entire summer to the present when 0–15 annual closures occur that typically last less than two weeks (Behrens *et al.*, 2013).

For this study, we partitioned the Russian River estuary into two separate hydrogeomorphic sections with contrasting conditions during open inlet conditions. Under open inlet conditions, the lower estuary (0–5.0 river kilometer [rkm]) is typically coastal-ocean dominated with an occasional freshwater lens at the surface, while the upper estuary (5.0–11.7 rkm) is usually freshwater tidal (Behrens *et al*., 2016). Unlike intermittently closed estuaries in more arid areas, inflows exceed the evaporation rate. During closed inlet conditions, water level elevations increase, and the estuary becomes stratified, and the low-lying shorelines near the estuary become inundated (Figure 3.2). Additionally, a saltwater wedge in the lower estuary expands upstream during closed conditions (Behrens *et al.*, 2016).

The Sonoma County Water Agency (SCWA) manually breaches the inlet year-round when water levels start inundating private property, and the SCWA does not anticipate an imminent natural breach. The National Marine Fisheries Service (NMFS) is concerned that breaching activities limit the amount of beneficial habitat for juvenile steelhead, especially young of year fish (NMFS, 2008). To minimize adverse impacts associated with breaching activities and maximize benefits to juvenile steelhead rearing in the Russian River estuary, NMFS recommended that SCWA implement a management plan to minimize exchange with the ocean while still addressing flood risk (NMFS, 2008). This management plan includes delaying breaching events between May 15 and October 15, the season when juvenile steelhead are known to use these environments, and instead attempt to encourage a perched lagoon. During this period, NMFS recommends that SCWA excavate an “outlet channel” to only allow outflow while maximizing habitat accessible to juvenile steelhead. The target average daily water surface elevation from a digital water level gage in the Russian River estuary at Jenner, CA (1.3 rkm) is at least 2.1 m with water levels varying between 1.2 m to 2.7 m (National Geodetic Vertical Datum of 1929, NGVD29).

### 3.3.2 *Study Species*

Many intermittently closed estuaries in northern and central California are used by juvenile steelhead for rearing (Sloan, 2006; Hayes *et al.*, 2008; Fuller, 2011). When rearing in intermittently closed estuaries, juvenile steelhead have varying tolerances and preferences of temperatures and salinities according to their physiological state (Boughton *et al.*, 2017). Furthermore, the metabolism of juvenile steelhead is strongly affected by temperatures in the

Russian River estuary with the modeled potential growth often decreasing at temperatures that are common during the late spring and summer and eventually becoming negative at higher temperatures (Seghesio, 2011). Multiple factors affect the salinity tolerance and preference of juvenile steelhead, including ontogenetic state (Beakes *et al*., 2010) and direct exposure to saltwater (Hayes *et al.*, 2011; Flores & Shrimpton 2012). Juvenile steelhead that have not undergone a physiological transformation to tolerate elevated salinities have elevated stress levels and decreased growth when exposed to higher salinities (Boughton *et al*., 2017). Moreover, low dissolved oxygen (DO) concentrations can prevent somatic growth of juvenile steelhead and eventually lead to mortality (Boughton *et al*., 2017).

### 3.3.3 *Environmental exposure*

We conducted this study in conjunction with a systematic sampling project of the Russian River estuary, conducted by the SCWA, which includes monthly beach seining throughout the estuary, typically with some ancillary seining targeting areas with high catches of steelhead. The catches of steelhead in the estuary are relatively low (<0.2 CPUE), so we were required to tag fish in small batches (typically 3-7 at a time) throughout both sampling seasons (May–August 2014-2015). Furthermore, due to the unpredictable timing and duration of closure events, the number of fish tagged during closed conditions was limited despite efforts to allocate the tags evenly.

In this study, we used environmental exposure data from Matsubu *et al.* (2017), wherein 93 juvenile steelhead were surgically implanted with thermal-encoded acoustic transmitters (Lotek, MM-412-T; 11.0 mm long × 6.6 mm wide × 6.1 mm high; 0.58 g in air; battery life = 10 d with a 10-s burst). Surgical methods conformed to the University of Washington Office of Animal Welfare protocols (Protocol Number 2555-05). We captured steelhead by beach seine and held in aerated stream water until processed. After being anesthetized with buffered 40-mg/L MS-222 (tricaine methanesulfonate), we measured the length (FL mm) and weight (g), of each fish. If the fish weighed more than 10.0 g, we surgically implanted an acoustic tag into the fish. To prevent injury during surgery, we placed each fish ventral side up on a foam lined table with half strength anesthetic (20-mg/L MS-222) continuously flowing over the gills. We made a 6-mm incision on the ventral side of the fish, inserted the transmitter, and closed the incision with an absorbable suture (5-0). After allowing time to recover, the SCWA released the fish.

We tracked fish with both mobile and stationary hydrophones (Map 600 RT transceivers; Lotek Wireless). We positioned stationary receivers on the river bottom at sites where fish where detections were frequent. Mobile tracking employed two hydrophones on each side of a boat or canoe. The power boat was propelled with an electric trolling engine while the canoe was powered by paddling. During mobile tracking, maximum detection power was achieved using the directional capabilities and signal strength of the Map 600 RT-receivers. For more details about methods associated with acoustic telemetry see Matsubu *et al.* (2017).

The depth fish occupied was determined by linking the temperature from sensor encoded acoustic telemetry (i.e., from the transmitter surgically implanted in the fish) with a simultaneously-collected vertical water quality profile (WQP) using a YSI Model 85 hand-held probe (Yellow Springs Instrument Company, Yellow Springs, Ohio). The WQP consisted of temperature, salinity, and DO every 0.5 meters from the surface to the bottom and recording the maximum depth at a location typically within 20 m of fish detection locations (Matsubu *et al.*, 2017). We calculated the depth of each detection as the mean of all WQP depths with temperatures within the error range of the temperature from the sensor encoded acoustic transmitter (±0.8 °C).

### 3.3.4 *Analysis*

To minimize the tagging effects on the behaviour of fish, we only used data collected 24 hours after tagging. Also, we omitted all detections when the stratification of the water column was not strong enough to infer the depth of the fish and omitted all data collected between 7:00 pm to 6:00 am to prevent any effects of diel vertical movements. Due to the lack of detections during August and September, this analysis only focused on fish sampled during May, June, and July. To measure the response of fish to abiotic conditions, we used the relative depth; the distance fish were from the surface as a proportion of the maximum depth, measured while taking the water quality profile (inferred depth/maximum water quality depth).

We used linear mixed effects modeling (LME), with each individually tagged fish as a random effect, to determine if the hourly mean relative fish depth was affected by fish size (FL mm), month (May, June, July), river kilometer (rkm), maximum salinity (PSU), maximum temperature (°C), minimum DO (mg/l) and the interaction of fish size with maximum salinity, maximum temperature and minimum DO (Table 3.1; package 'nlme' in R v.3.1-118; Pinheiro *et al.,* 2014). To focus on the abiotic differences between the upper and lower estuary and to avoid multicollinearity between salinity and temperature, we used a separate model for the lower estuary without temperature as an explanatory variable and separate model for the upper estuary without salinity as an explanatory variable. To conform with the assumption of normally distributed data, we logit transformed the relative depth which was a proportional variable bound between 0 and 1. We implemented a forward stepwise model selection approach comparing Akaike's information criterion corrected for small sample sizes (AICc) from the full model to reduced models (Zuur *et al.*, 2009). To account for autocorrelation of response variables from the lack of independence between detections, we incorporated a correlation structure in the model with the hourly mean detection time and rkm into an exponential correlation structure (Zuur *et al.*, 2009). We accounted for heterogeneity of residuals by incorporating a separate variance structure for each month. Normality was confirmed by evaluating the histograms of residuals from the final models. We performed all data analysis in R (R Development Core Team 2013).

To explore changes in behaviour at a finer scale, we measured the duration of presumable feeding forays for all individuals detected in the lower estuary. A foray was defined as a movement starting from above the halocline moving below the halocline into deeper, saltier water, and then back into the fresher surface layer above the halocline. We defined the halocline as a change of at least 10 PSUs across water layers. If at least 10 PSUs was not observable due to lack of stratification, we did not count it as a foray. We also assessed fine-scale movements and occupation of three individuals over three hours by plotting their depth, salinity, and temperature through time.

## 3.4 RESULTS

### 3.4.1 *General lagoon environmental conditions*

The environmental conditions varied spatially and with the inlet condition. For the entire 2014 and most of the 2015 sampling periods, the Russian River estuary inlet remained open. When the inlet was open, tides controlled the water elevation (range: -0.5–1.2 m NGVD29). During these open inlet conditions, the lower estuary WQPs were primarily composed of moderate to high salinities (23.4 PSU, SD 5.21) with the occasional freshwater or brackish lens at the surface. Exchange with the ocean led to primarily cool (17.1 °C, SD 2.3) temperatures in the lower estuary while the upper estuary was mostly freshwater except for some saline water in the lower extent and deeper holes (Figure 3.2). Much warmer conditions (21.6 °C, SD 1.5) in the upper estuary were frequent due to warm river inflows and minimal marine exchange.

There was one closure during the 2015 study period that lasted from 5/29/2015 to 6/14/2015, during which tidal influence was absent, and water surface elevation gradually increased to greater than two meters (NGVD29). Conditions in the lower estuary gradually changed during this closure as marine inputs decreased, and vertical stratification increased. As water elevations raised and inundated low-lying shorelines, the presence and volume of the freshwater lens at the surface increased and the temperatures gradually increased to 19.4 °C (SD 1.1) while salinities decreased (Figure 3.2).

### 3.4.2 *Factors affecting the depth of juvenile steelhead*

The environmental conditions influenced the depth of juvenile steelhead in the Russian River estuary. Overall, juvenile steelhead typically adjusted their position in the water column in response to conditions that would be considered deleterious (Boughton *et al.*, 2017). For example, DO was an explanatory variable in all the models with ΔAICc<2, with fish occupying shallower depths and avoiding the deeper habitat with low DO concentrations (Tables 3.2 and 3.3).

The primary environmental conditions in the upper estuary that affected fish depth were temperature and DO. In the upper estuary, the best fit model revealed that the fish depth was related to temperature (LME; $F_{1,214}$=2.0, P=0.046), with deeper depths occupied when temperatures were higher (estimate -0.20, SE 0.10). With surface habitats warmer than deeper habitats, juvenile steelhead were moving into the cooler deeper depths when temperatures increased. The relationship between fish depth and DO ($F_{1,214}$=4.2, P<0.001) was similar to temperatures in the upper estuary, with a negative relationship between fish depth and DO concentrations (estimate -2.3, SE 0.05). In contrast to moving to deeper depths to avoid higher temperatures, these results suggest that fish moved to shallower habitats when the deeper habitats had lower DO concentrations.

The position of juvenile steelhead in the water column in the lower estuary was also affected by the abiotic conditions but, unlike the upper estuary, this depended on fish size (Table 3.2). The best-fit model in the lower estuary included month ($F_{2,269}$=16.8, P<0.0001), rkm ($F_{1,269}$=1.7, P<0.0001), DO ($F_{1,269}$=2.2, P=0.1439), and the interaction between fish size and salinity ($F_{1,269}$=3.97, P<0.05) (Table 3.2). The interaction between fish size and salinity possibly reflected differences in the osmoregulatory capabilities for fish of different sizes. For example, when salinities were higher, smaller fish with presumably a lower tolerance to higher salinities were shallower but when salinities were lower, fish of all sizes were relatively deep (Figure 3.3).

### 3.4.3 *Vertical Movement*

Evaluating the vertical movements revealed more size-dependent patterns in the lower estuary. Although fish stayed below the thermohalocline most of the time, fish as small as 99 mm (FL) moved across the thermohalocline and were exposed to a relatively wide range in temperatures and salinities over a short period (i.e., within minutes, Figure 3.4). Out of the 29 fish tracked in the lower estuary, nine fish (99–144 FL mm) were observed making forays from the fresher surface layer into the deeper more saline conditions and then back into the surface layer. These forays ranged from two minutes to 65 minutes with most (65%) lasting less than 20 minutes.

## 3.5 DISCUSSION

Our results indicate that juvenile steelhead rearing in an intermittently closed estuary adjust their position in the water column according to the present physiochemical conditions. We conclude that fish are avoiding habitats with high temperatures or with low DO concentrations to decrease metabolic costs, thereby increasing their growth potential. The evidence from the lower estuary model, as well as the shift in vertical movement behaviour, shows that how fish respond to the dynamic physiochemical conditions presented by intermittently closed estuaries depends on their size. Other studies in the Russian River estuary have shown that physiological conditions and prey abundance are more than sufficient to achieve high growth rates (>0.02 % body weight per day; Seghesio, 2011; Martini-Lamb *et al*., 2015).

In the lower estuary, shallower habitats occupied by smaller fish and vertical movements of smaller individuals were likely a response to higher salinities. We base this on our observation that the water column primarily consisted of DO concentrations and temperatures that were not considered limiting (Figure 3.2; Boughton *et al.*, 2017). Furthermore, we hypothesize that the vertical movements observed were a behavioural response to maximize foraging opportunity (feeding forays into deeper, more saline water) while minimizing physiological stress by moving back into the shallower, less saline water. Webster and Dill (2007) documented similar behavioural patterns in a lab setting where juvenile Chinook salmon made brief forays into stressful conditions for foraging and then returned to more physiologically preferable conditions (Webster & Dill 2006; Webster & Dill 2007). Juvenile Chinook salmon only made these forays across salinity gradients when food availably was high. In the Russian River estuary, such behaviour would allow individuals to access concentrations of typical prey that are mostly epibenthic (Seghesio, 2011; Martini-Lamb *et al*., 2015) in environments that are physiologically costly due to high salinities while having immediate access to less stressful conditions where they could minimize the adverse physiological effects of high salinity for extended durations. Although we found smaller individuals in environments with high salinities, the physiological effects of short, intermittent exposures are unknown but we contend that this behaviour may present tradeoffs between elevated avian predation risk in shallow water (Collis *et al.*, 2001; Osterback *et al.*, 2013; Pink & Abrahams, 2018) and opportunities for high estuarine growth (Smith, 1990; Hayes *et al.*, 2008).

The primary lines of evidence that intermittently closed estuaries provide vital habitat to juvenile steelhead are high growth rates and increased size at ocean entry which, in turn, increases marine survival (Bond *et al.*, 2008; Osterback *et al.*, 2014). These studies suggest a dramatic (60x) increase in marine survival for juvenile steelhead that reach 160 mm (FL) before ocean entry as compared to the smallest individuals. Individuals that do not reach 160 mm before ocean entry would be selected against which could lead to more risk-taking behaviour. The published 160 mm size threshold is somewhat similar to fish size in the present study in which individuals were observed making vertical forays in the lower estuary (maximum size 144 mm FL).

Management of intermittently closed estuaries can be challenging, especially when balancing anthropogenic impacts and environmental needs. Our results indicate that management activities that promote open inlet conditions may create challenges for steelhead that are not acclimated to saline conditions but reveal foraging strategies by juvenile steelhead that are not yet tolerant of higher salinities. Due to human activities, the Russian River estuary is now open more often during the dry season (Behrens *et al.*, 2013) meaning that smaller individuals may exhibit risky behaviour during a season when, historically, such behaviour would be unnecessary. During an extended closure or in the upper estuary during open conditions, saline conditions are less prominent and would not require smaller juvenile steelhead to modify their behaviour unless high temperatures or anoxic conditions were present. Although sub-optimal conditions can be avoided by seeking cooler water at tributary confluences or upstream movements into cooler riverine/stream habitat, Matsubu *et al.* (2017) found that longitudinal movements large enough to change exposure and selection of cold water refugia near tributary inlets only occurred during closed conditions.

While the present study identifies abiotic conditions that alter the behaviour of juvenile steelhead, the mechanisms leading to those conditions, as well as biotic factors and their interactions warrant further exploration. Information on causal factors influencing changes in prey distribution and potential increased productivity during a prolonged closure, coupled with changes in fish depths relative to the physiochemical conditions presented here would allow insights into biotic mechanisms that interact with abiotic mechanisms to influence juvenile steelhead demographics and body size structure in intermittently closed estuaries. The ability to evaluate changes in behaviour during transitions between open and closed conditions is essential to fully understand how fish will respond proximally to changing physiochemical and biological conditions associated with management activities. For example, fish response and therefore the desirability of a given outcome from either natural- or management-related actions (e.g., breaching) will depend on the timing of these events relative to the water quality tolerance of individuals, particularly salinity. With such short closures and variable timing, this has been quite challenging to quantify, and further research is necessary to reveal impacts caused by human disturbances. Future advancements in water quality instrumentation and models, and fish location technology (e.g., ability to tag smaller fish, longer tag life) will provide opportunities to address these uncertainties.

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## 3.8 FIGURES

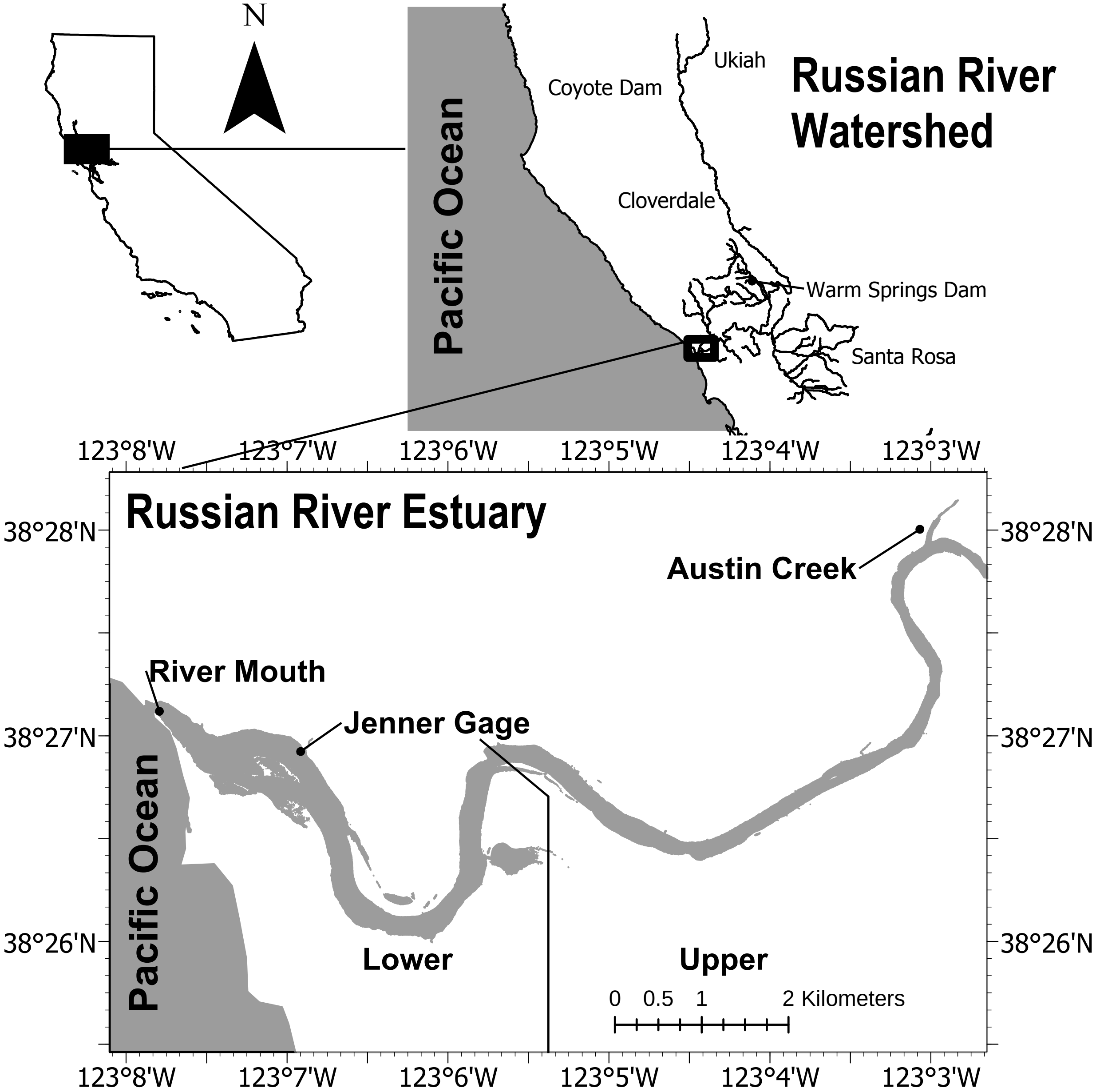

Figure 3.1. Map of the lower and upper Russian River estuary, California.

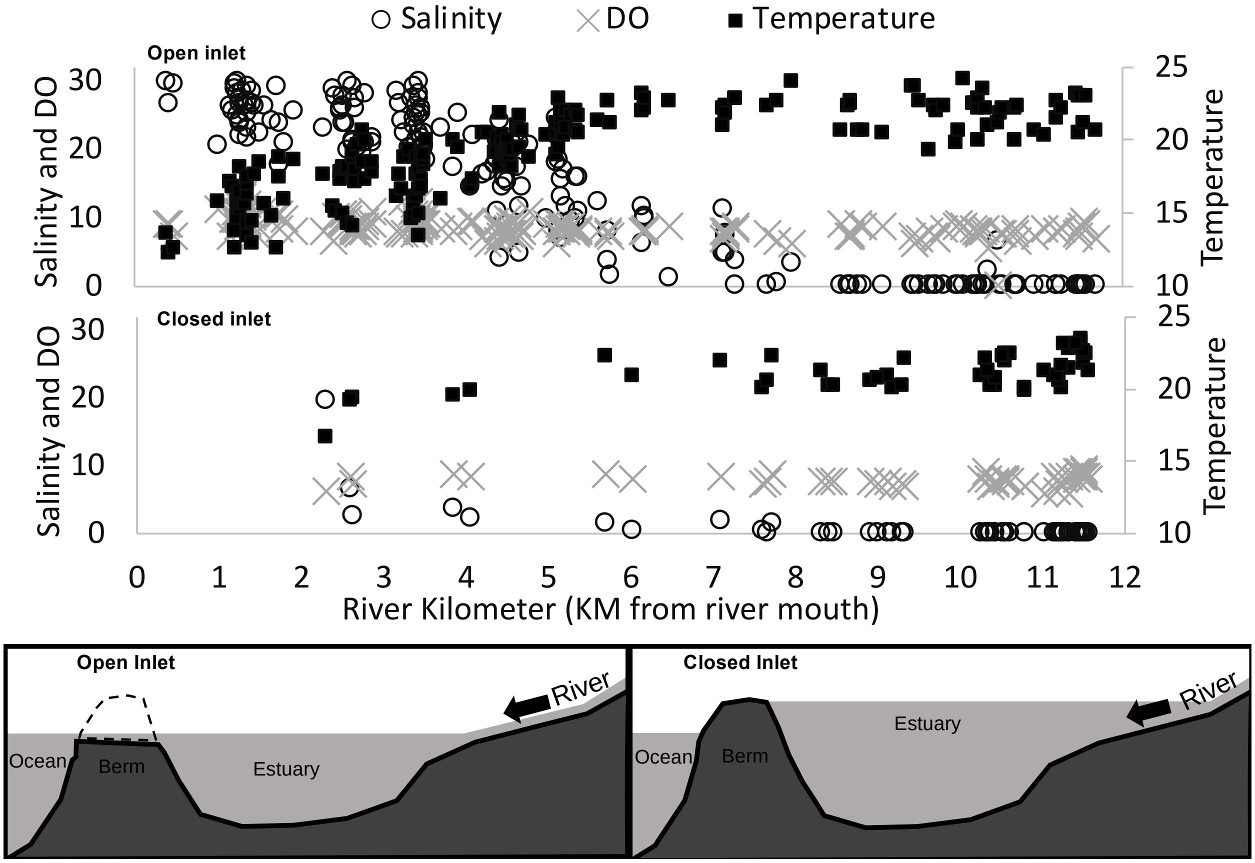

Figure 3.2. Water quality conditions and conceptual diagram of open and closed contrasts. Top panels: The mean temperature, salinity, and DO from water quality profiles taken while simultaneously tracking tagged juvenile steelhead during 2014 and 2015 from May - July. Data in the top panel were collected during open conditions and the data in the middle panel were collected during closed conditions. Bottom panel: conceptual diagrams of open (left) and closed (right) inlet conditions reflecting increased water levels inundating habitat.

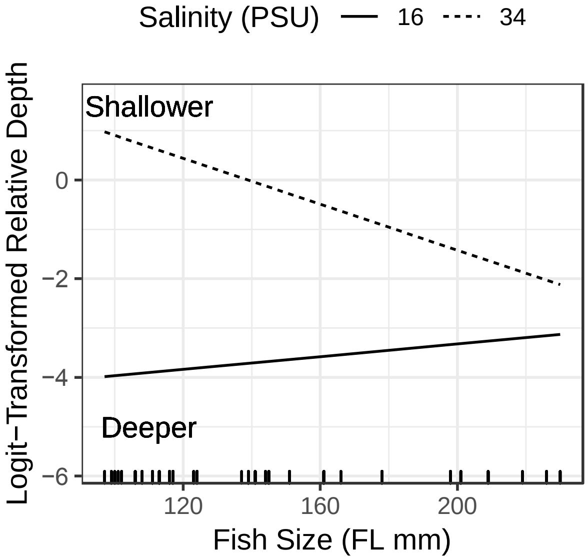

Figure 3.3. Predicted depth of juvenile *Oncorhynchus mykiss* in the lower estuary in response to the maximum salinity of 16 PSU (solid) and 34 PSU (dotted). Estimates are calculated from averaging all other variables. Shading indicates 95% confidence intervals. Rug along the x-axis indicates the sizes of tagged Oncorhynchus mykiss.

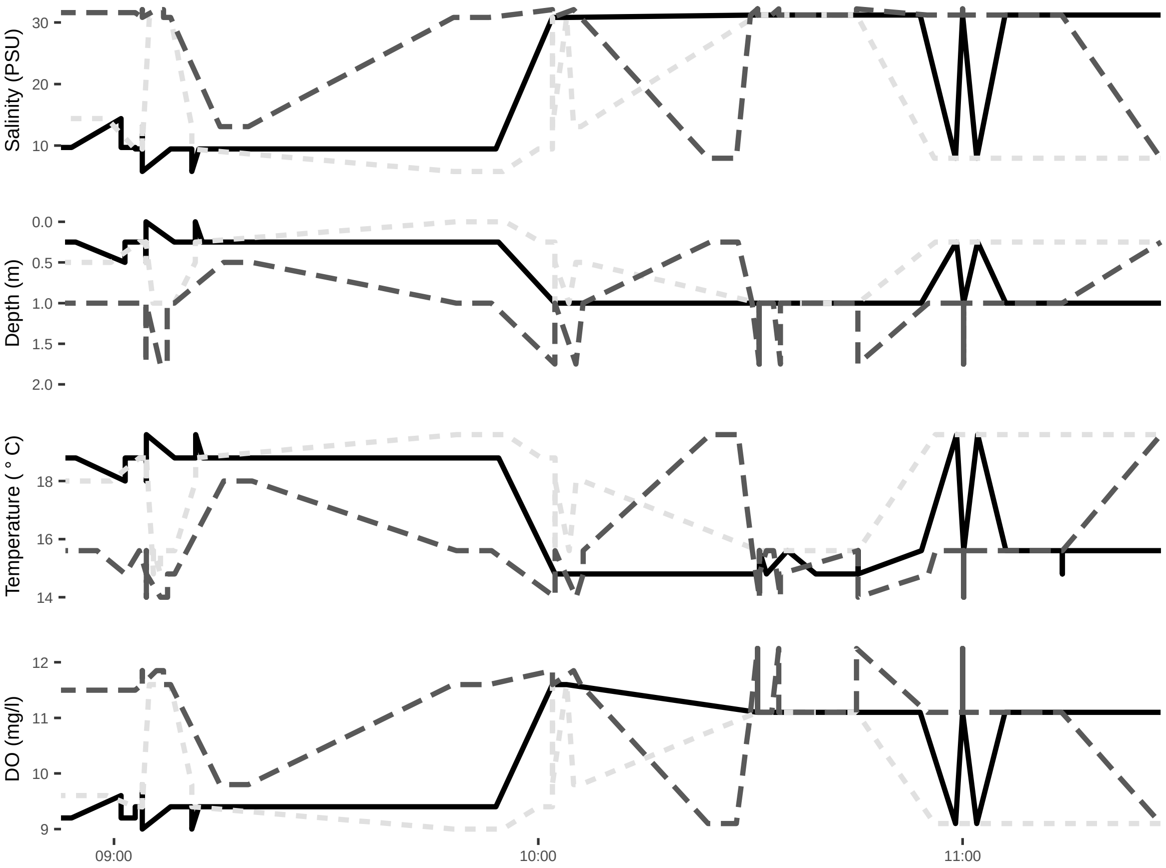

Figure 3.4. Vertical movements and exposure of juvenile steelhead The four panels include the salinity, depth and temperature and dissolved oxygen (DO) of three tagged juvenile *Oncorhynchus mykiss* (dark grey and long dash = 102 FL mm, black and solid line = 124 FL mm, and light grey and dotted = 144 FL mm), June 5, 2014.

## 3.9 TABLES

Table 3.1. Summary of variables used in the mixed effects model of the lower reach with sample sizes, means (SD), and ranges.

| Variable | Description | Type | Encoding | Summary |
|---|---|---|---|---|
| **Lower Model** | | | | |
| Relative Depth | Distance from the surface as a proportion of the maximum depth from the WQ profile (0-1) | Response variable | Numeric | 0.61 (SD 0.4) |
| Fish Size | Size of tagged fish (FL mm) | Fixed effect | Numeric | 139 mm (97-230) |
| Month | Month fish was detected (May, June, July) | Fixed effect | Factor | N = 3 |
| Maximum Salinity | Maximum salinity from vertical water quality profile | Fixed effect | Numeric | 30.8 (SD 3.2) |
| Minimum DO | Minimum DO (mg/l) from vertical water quality profile | Fixed effect | Numeric | 8.3 (SD 1.2) |
| Tag | The unique tag serial number of each tagged fish | Random effect | Factor | N=29 |
| RKM | Distance from river mouth (km) | Correlation structure and fixed effect | Spatial | N=306 |
| Date Hour | Mean time of detections grouped by hour | Correlation structure | Time | N=306 |
| **Upper Model** | | | | |
| Relative Depth | Distance from the surface as a proportion of the maximum depth from the WQ profile (0-1) | Response variable | Numeric | 0.7 (SD 0.3) |
| Fish Size | Size of tagged fish (FL mm) | Fixed effect | Numeric | 137 mm, (93-184 mm) |
| Month | Month fish was detected (May, June, July) | Fixed effect | Factor | N = 3 |
| Inlet condition | Status of the inlet (open vs closed) | Fixed effect | Factor | N = 2 |
| Maximum Temperature | Maximum temperature from vertical water quality profile | Fixed effect | Numeric | 22.0 (SD 1.3) |
| Minimum DO | Minimum DO (mg/l) from vertical water quality profile | Fixed effect | Numeric | 7.7 (SD 1.7) |
| Tag | The unique tag serial number of each tagged fish | Random effect | Factor | N= 30 |
| RKM | Distance from river mouth (km) | Correlation structure and fixed effect | Spatial | N=248 |
| Date Hour | Mean time of detections grouped by hour | Correlation structure | Time | N=248 |

Table 3.2. Mixed effects models with ΔAICc <2 for predicting the depth of *Oncorhynchus mykiss* in the lower and upper estuary.

| Estuary Location | Model | d.f. | logLik | AICc | ΔAICc | wAICc |
|---|---|---|---|---|---|---|
| Lower | **FL * S + Month + RKM + DO** | 13 | -540.95 | 1109.2 | 0 | 0.212 |
| | FL * S + Month + DO | 12 | -542.18 | 1109.4 | 0.27 | 0.185 |
| | FL + S + Month + DO | 11 | -543.47 | 1109.8 | 0.68 | 0.151 |
| | FL + S + Month + RKM + DO | 12 | -542.67 | 1110.4 | 1.25 | 0.113 |
| Upper | **Month + T + DO** | 10 | -465.98 | 952.9 | 0 | 0.239 |
| | Month + Inlet + T +DO | 11 | -464.99 | 953.1 | 0.23 | 0.212 |
| | Month + DO | 9 | -467.91 | 954.6 | 1.7 | 0.102 |

Footnotes: d.f.: Degrees of freedom; ΔAICc: change in AICc with respect to the top-ranked model; logLik: Model maximum log-likelihood; wAICc, AICc weights. These models are those with the lowest AICc from mixed effects models that evaluated the influence of fish length (FL), Salinity (S), Temperature (T), Dissolved Oxygen (DO), Month, distance from River Mouth (RKM), and the river inlet (Inlet). The parameter estimates for the top-ranked models (bold) models are shown in Table 3.3.

Table 3.3. Parameter estimates for the top ranked mixed effects models (Table 3.2) to evaluate the influence of fork length (FL), Salinity, Temperature, dissolved oxygen (DO), month, distance from River Mouth (rkm). Reference Month is May.

| Location | Effect | Estimate | Std.Error | T-value | p-value |
|---|---|---|---|---|---|
| Lower | (Intercept) | -7.93 | 4.32 | -1.84 | 0.07 |
| | FL | 0.03 | 0.03 | 1.21 | 0.24 |
| | Salinity | 0.44 | 0.14 | 3.16 | 0.00 |
| | June | -1.39 | 0.33 | -4.21 | 0.00 |
| | July | -2.25 | 0.43 | -5.22 | 0.00 |
| | RKM | -0.21 | 0.13 | -1.60 | 0.11 |
| | DO | -0.18 | 0.07 | -2.48 | 0.01 |
| | FL:Salinity | 0.00 | 0.00 | -1.97 | 0.05 |
| | | | | | |
| Upper | (Intercept) | 6.62 | 2.24 | 2.95 | 0.004 |
| | Temperature | -0.20 | 0.10 | -2.00 | 0.046 |
| | DO | -0.24 | 0.06 | -4.22 | 0.000 |
| | June | -1.86 | 0.37 | -4.96 | 0.000 |
| | July | -1.65 | 0.52 | -3.11 | 0.002 |

# Chapter 4. Influence of mouth state on the assemblage composition and abundance of macroinvertebrates important to the food web in an intermittently closed estuary, northern California USA

**Authors**: W. Matsubu, C.A. Simenstad, and E. Seghesio

## 4.1 ABSTRACT

Only certain animals can tolerate the diverse and dynamic physiochemical conditions in estuaries; tolerating these conditions allow them to exploit the inherent high productivity of these estuaries. Access to this productivity is particularly uncertain in intermittently closed estuaries—those with an intermittent ocean connection. Usually, many of these estuaries are managed to mediate water quality degradation and to avoid flooding of low-lying properties and infrastructure. The effects of managing (e.g., breaching, regulated inflows) these systems are relatively understudied, yet intermittently closed estuaries compose essential rearing habitat and foraging opportunities to at risk species. More specifically, macroinvertebrates uniquely adapted to intermittently closed estuaries are often fundamental components of constrained food webs, yet the response of macroinvertebrate communities to management activities that affect connectivity to the ocean is not well understood. To assess impacts of management activities on the food web variability, this study of epibenthic and benthic invertebrates of the main channel and margin habitats in the Russian River estuary, California, USA was conducted from 2009 to

2018 to assess the assemblage composition and abundance of macroinvertebrates in that intermittently closed estuary. We found that the abundance and compositions of macroinvertebrates varied between open and closed mouth states. Furthermore, we found expansive aggregations of mobile epibenthic and less mobile benthic macroinvertebrates in habitats only inundated when the mouth was closed. Most taxa appear adapted to the changing conditions in the Russian River estuary. As a result, key food web macroinvertebrates are likely to be resilient to management activities in the Russian River estuary.

## 4.2 INTRODUCTION

Estuaries are among the most productive ecosystems in the world (Teal, 1962; Mitsch and Gosselink, 2000; Day et al., 2013), but due to wide-ranging environmental conditions, only some animals can take advantage of this high productivity (Elliott and Whitfield, 2011). This potential exclusion is especially the case for fauna in intermittently closed estuaries—those that have an intermittent connection to the ocean and, depending on the timing and duration of connection or disconnection to the ocean, experience estuary-wide physiochemical changes (Whitfield et al., 2012; McSweeney et al., 2017). Similar to all inhabitants of intermittently closed estuaries, benthic infauna and more mobile epibenthic macroinvertebrates must cope, physiologically or behaviourally, with the typically stochastic and highly variable estuary-wide physiochemical changes (Robinson, 1993; Lill et al., 2012). While these macroinvertebrates often compose an essential extensive base of the estuary's food web, little is known regarding whether or how management actions that change the timing and duration of connectivity to the ocean affect the macroinvertebrate communities (Hughes et al., 2014).

Environmental conditions vary considerably and often dynamically in intermittently closed estuaries. Rapid transition from an open mouth to a closed mouth (closure) or closed mouth to open mouth (breach) can have similarly rapid changes on the water quality and quantity (Largier and Talhaard, 1991; Behrens et al., 2015), and is often responsible for dramatic shifts in habitat for motile organisms such as fishes and some of their prey. An open mouth allows the free outflow of nutrients, undergoes tidal fluctuations, and usually has a longitudinal salinity and thermal gradient that is somewhat predictable (Chuwen et al., 2009). In contrast, when intermittently closed estuaries are disconnected from the ocean, they have less dynamic circulation, and a decreased longitudinal salinity gradient. When associated with adequate inflows, the volume of motile macroinvertebrate and fish habitat increases when the mouth is closed (Whitfield et al., 2012). Due to the absence of flushing, a closed intermittently closed estuaries is especially vulnerable to water quality degradation (Ranasinghe and Pattiaratchi, 1998) and pollution (Hastie and Smith, 2005) - which is often remedied by artificially breaching the mouth (Haines et al., 2006).

Management of intermittently closed estuaries is common around the world and often has uncertain implications for inhabitants. Due to the estuary-wide changes associated with transitioning between open and closed states, intermittently closed estuaries are sensitive to human manipulations that affect the scale and frequency of connectivity to the ocean. For example, when the mouth is closed and inflows are artificially higher than outflows (e.g., evaporation, seepage), the water elevations increase faster than under the naturally lower flows, causing water to eventually overtop and erode the closed mouth (Goodwin, 1996; Behrens et al., 2015). Furthermore, humans often build infrastructure in the low-lying areas that become flooded when the mouth is closed. Because of this, actions to artificially manage estuary outflow (e.g., mechanical breaching) are taken to avoid property and infrastructure damage. As a result, artificial breaching of intermittently closed estuaries is common around the world (Haines et al., 2006; Behrens et al., 2013). Consequences of these actions strongly influence the abiotic conditions, and as a result, affect the biota (Whitfield et al., 2012; Lill et al., 2012) with sometimes uncertain consequences to the food web.

The goal of this study is to investigate the influence of mouth state (open mouth vs. closed mouth) to ecologically important macroinvertebrates. More specifically, this study aims to study the effects of mouth state on the assemblage composition, and abundance of epibenthic and benthic macroinvertebrates that are prominent in the food web of the Russian River estuary (RRE), northern California, USA. After identifying the prominent taxa in the RRE benthic and epibenthic communities, we test two hypotheses related to the mouth dynamics. First, we will test the hypothesis that there is no change in taxa composition between open and closed mouth states. Secondly, we will test the hypothesis that the mouth state (open mouth vs. closed mouth) does not affect the relative availability of macroinvertebrates that are a key component of the food web. Because of the applied management drivers, we specifically focus on macroinvertebrates that are essential components of the food webs in California’s estuaries. Intermittently closed estuaries in California are used by commercially and culturally important fishes, including flatfishes (Pleuronectidae), Pacific herring (*Clupea pallasii*), rockfish (Scorpaenidae) and Pacific salmonids (*Oncorhynchus* spp.) (Bond et al., 2008; Hughes et al., 2014). Although these species consume macroinvertebrates common in the region’s intermittently closed estuaries (Needham, 1940; Shapovalov and Taft, 1954; Hughes et al., 2014), the general patterns and effects of management decisions on this essential prey base is not well understood even though over half of the estuaries in California are subject to mouth closures (Heady et al,. 2014).

## 4.3 METHODS

To improve the understanding of human disturbances to macroinvertebrates in intermittently closed estuaries the Sonoma County Water Agency (SCWA) sampled macroinvertebrates at four sites distributed throughout the RRE (Fig. 4.1) during the dry season (May 15 – October 15) from 2009-2018. At each site, epibenthic and benthic macroinvertebrate communities were sampled along the thalweg and at the margins of the shoreline. In addition to describing the macroinvertebrate communities, we compared the epibenthic and benthic macroinvertebrate assemblages between open and closed mouth states.

### 4.3.1 *Study Site*

We used the RRE in northern California (38°26'57.2"N 123°07'13.0"W) as our study site. The Russian River watershed (3,846 $km^2$) is in a Mediterranean climate (Fig. 4.1), and typical minimum flows during the summer of between approximately 2 to 4 $m^3sec^{-1}$. When the mouth is open, the RRE is tidal with a surface area of approximately 1.62 $km^2$, but when the mouth is closed, the surface area can more than double. The upstream extent of tidal and brackish conditions is approximately 12 river kilometers (rkm), yet the increased elevation of water levels during a mouth closure can extend to up to 20 rkm. Compared to the spectrum of intermittently closed estuaries with varying durations of closures, the RRE has frequent and short closures. Under management regimes in recent years, the estuary has undergone 0-15 closures a year that typically last less than two weeks. However, historically, the estuary mouth would remain closed for the entire summer (Behrens et al., 2013). Human actions aimed at breaching the sandbar at the mouth are a primary cause for these changes; for example, after the 1960s, about four out of every five breaches have been artificially induced (Behrens et al., 2013).

We sampled four sites in the RRE: River Mouth (rkm 0.2), Penny Point (rkm 1.4), Willow Creek (rkm 4.5), and Freezeout Bar (rkm 9.6) (Fig. 4.1). These sites were chosen to represent the characteristic positions along the salinity gradient and the spectrum of habitats available in the RRE. The River Mouth and Penny Point sites are relatively proximate to the mouth and are typically marine dominated during when the mouth is open. The Willow Creek site is just upstream from the confluence of Willow Creek and has mixed physiochemical conditions when the mouth is open, often including a freshwater lens above the denser marine layer (Robart and Largier, 2017). Freezeout Bar, the most upstream site, is typically freshwater dominated, but with tidal fluctuations when the mouth is open. Closure from sand piling up in the mouth stops the tidal intrusion of salt water, resulting in the greatest physiochemical changes occurring at the River Mouth and Penny Point, especially if the closure lasts for an extended period. When the mouth is closed, the water level elevation can increase to as high as 3.0 m (NGVD29), which inundates low lying shorelines and previously disconnected tributaries. When the mouth is closed, stratification also increases, which results in a freshwater lens developing above trapped salt water and an upstream propagation of saline waters (Behrens et al., 2014).

### 4.3.2 *Physical measurements*

A water gage located in the estuary at Jenner, California, 1.2 rkm from the mouth of the estuary, measured the elevation of the water level (National Geodetic Vertical Datum of 1929 [NGVD29]). We inferred the mouth state from the change of water level from a tidal pattern (open) to a steady increasing (closed) pattern and the rapid decline back to the dynamic, base level tidal elevation (open) (Fig. 4.2). We designated the date of closure as the first observed change in water level pattern from tidal to the steady increase in elevations, and the date of reopening as the first transition back to tidal fluctuations. We collected water quality profile data at each site during each sampling event using a YSI Model 85 hand-held probe (Yellow Springs Instrument Company, Yellow Springs, Ohio). These profiles measured the salinity (PSU), temperature (°C), and DO (mg $l^{-1}$) every 0.5 m from the surface to the bottom at the deepest location within the sampling site.

### 4.3.3 *Macroinvertebrate sampling*

In this study, epibenthic and benthic macroinvertebrates were assessed over ten years (2009 to 2018) from May to October as part of standardized sampling suggested by the National Marine Fisheries Service (NMFS 2008). We sampled the benthos with a 0.0024-$m^2$ PVC benthic core sampler to a depth of 0.1 m and capped with a removable suction cup. We sampled epibenthic organisms at the sediment-water interface in two habitats using two different sampling designs: (1) the shoreline margin; and (2) main channel (Fig. 4.3). We sampled the shoreline margin with an epibenthic net equipped with rectangular mesh (0.5-m x 0.25-m with 106-µm mesh) that was deployed 10 m from shore and then pulled along the bottom perpendicular back to shore. We also sampled the main channel with a weighted epibenthic sled (0.5-m x 0.25-m opening with 500-µm mesh) towed behind a boat for 10 m against the current along and aligned with the thalweg (Fig. 4.3).

This sampling design was conducted perpendicular to the thalweg along three transects at each estuary site (Fig. 4.3). Each transect consisted of three epibenthic sled and benthic core samples in the main channel (a total of nine each per site) spread out evenly across the transect and one epibenthic net and benthic core at the shoreline margin (Fig. 4.3). We also deployed epibenthic net samples that occurred between each of the three transects (one in each transect and a total of five per site). After 2014 and only when the mouth was closed, we added one additional epibenthic sled main channel sample along the shoreward margin of each transect, exclusively in habitats inundated during closures (four in each transect and a total of 12 each site: Fig. 4.3). Benthic core samples (four in each transect and a total of 12 each site) were distributed between the location of every main channel and margin sample within a transect (Fig. 4.3) except for the added main channel samples taken during closures after 2014.

We preserved all captured macroinvertebrates in 10% buffered formalin for laboratory analysis. In the lab, we rinsed each sample through a106-µm sieve. Processing included identification and enumeration of macroinvertebrates focused primarily on invertebrates from the phylum Arthropoda. After 2015, the focus transitioned to a emphasis on taxa essential to California estuary food webs, herein named food web taxa, including *Americorophium* spp. (*A. spinicorne, A. stimpsoni*), *Gnorimosphaeroma insulare, Eogammarus confervicolus,* Chironomidae (dipteran flies), Ephemeroptera (Mayflies), Corixidae (water boatmen), Hydrobiidae (snails), *Neomysis mercedis*, and Polychaeta. Due to these changes in the identification focus, we used the data from 2009 to 2015 to identify the prominent taxa and data from all years (2009-2018) to measure impacts to the food web taxa. We standardized invertebrate data to density per area ($m^{-2}$) for the benthic core sampling and volume ($m^{-3}$) for the epibenthic net and sled sampling (margin and main channel).

### 4.3.4 *Statistical analysis*

To investigate differences between open and closed mouth states, we analyzed the relative abundance and taxonomic composition with univariate and multivariate statistics. To identify the prominent taxa at all sites, we described the taxa that composed the highest densities of macroinvertebrates found at each site before 2016. The average density of each food web taxa per site on each sampling event was used in multivariate analyses to evaluate assemblage composition using with the R 3.1.1 Vegan package (Oksanen et al. 2011). Prior to analysis, we converted density data to be proportional 0-1 and then used an arcsine square root transformation. We used permutational multivariate analysis of variance (PERMANOVA) to determine significantly different assemblages between open and closed mouth states. Factors included: site (River Mouth, Penny Point, Willow Creek, and Freezeout Bar); mouth (open, closed); and season (before or after August 1st). We used non-metric multidimensional scaling (NMDS) to visualize differences among the sites and mouth state using the Vegan package (Oksanen et al. 2011). Both the PERMANOVA and the NMDS were employed on a Bray-Curtis dissimilarity matrix.

Furthermore, we also compared the densities of food web taxa in the main channel to the additional main channel samples taken exclusively in the closure-inundated habitat (Fig. 4.3). Although season was incorporated into the analysis, we only present statistics for the effects of the mouth, and site. All analysis and figures were made in Rgui (R Development Core Team 2012) and ArcGIS (ESRI 2018).

## 4.4 RESULTS

### 4.4.1 *Environmental conditions*

Sampling occurred during both closed and open mouth states from 2009 to 2018 (Fig. 4.2). Among the periods of mouth closures, our data drew from 13 sampling events with a mean closure duration of 10.1 days ([± 1 SD = 5.9) and a maximum closure duration of 22 days. When the mouth is open, the estuary water levels varied tidally (range = -0.2 - 1.2 m); when the mouth is closed, the estuary had no tidal fluctuation, and the water level increased to as high as 2.7 m. River discharge reached 900 $m^3s^{-1}$ in the winter and spring, typically decreased to 2.8 $m^3s^{-1}$ by

June or July, and stayed below 4.25 $m^3s^{-1}$ through October, except for a few temporary exceptions where flows increased to 7.0 $m^3s^{-1}$ (Roettger et al. 2017).

The estuary was naturally mixed with a longitudinal salinity gradient under both open and closed states (Fig. 4.4). Salinities observed in the vertically averaged water qualify profiles were highest when the mouth was open at River Mouth (mean ± SD, 26.7 PSU ± 5.0), Penny Point (25.0 PSU ± 4.6), and Willow Creek (17.7 PSU ± 5.6) and low at Freezeout Bar (0.2 PSU ± 0.4) (Fig. 4.4). When the mouth was closed, over the ten years of sampling, the estuary never converted entirely to a freshwater lagoon, but the salinities were generally lower at the River Mouth, Penny Point, and Willow Creek sites, and slightly higher at Freezeout Bar.

The mean temperatures of the water column was warmest furthest upstream and coolest closer to the mouth (Fig. 4.4). Temperature at the furthest upstream site (Freezeout Bar) was warmest and had similar temperatures during open (21.5 °C ± 2.1) and closed states (21.8 °C ± 1.1). Temperatures at River Mouth were lowest when the mouth was open (14.5 °C ± 2.0) and increased to a mean of 18.2 °C (± 1.5) when the mouth was closed. Penny Point temperatures were also higher when the mouth was closed (open 15.5 °C ± 2.1; closed 18.6 °C ± 1.5). Differences in temperatures at Willow Creek was least extreme between open (18.34 °C ± 2.0) and closed (20.0 °C ± 1.6) states (Fig. 4.4).

The mean DO levels of the water column were similar between the open and closed mouth states at all sites except at Freezeout Bar, which had lower DO levels when the mouth was closed (Fig. 4.4). Throughout this study, hypoxic (<2.0 mg $l^{-1}$) conditions were found in 13% of the water quality profiles but were never anoxic (0.0 mg $l^{-1}$). The hypoxic conditions were limited to the deeper depths (5.1 ±1.8 m; >80% of the max depth) and detected during both open and closed states.

### 4.4.2 *Prominent macroinvertebrates*

Overall, we identified epibenthic and benthic macroinvertebrate taxa from 16 phyla, 27 classes, 63 orders, and 167 families. Higher resolution identification found 109 unique genera and 70 unique species. Over 95% of the macroinvertebrates captured were from the phyla Arthropoda, Mollusca, Nematoda, Annelida, and Platyhelminthes (Table 4.1). Due to a priority on key food web taxa, many diverse taxa found in the samples were not identified to a high taxonomic resolution, including Harpacticoida, Nematoda, Ostracoda, and Turbellaria. We found that the diversity of samples was rarely affected by mouth state or site (Supplemental: Table 4.1).

The prominent macroinvertebrates (>95% numerical composition) was composed of few taxa and varied by sampling type and site (Fig. 4.5; Supplemental Tables 4.2, 4.3, and 4.4). Overall, Nematoda was the most abundant taxa at the lower sites in the benthos (>30%), and main channel samples (>20%) while Ostracoda (35%) and Hydrobiidae (23.1%) dominated the margin samples (Fig. 4.5). In the benthic samples, the distribution of dominant taxa became more equally distributed further upstream, with decreased proportional contributions of Nematoda and increased contributions of *Americorophium* spp. and *G. insulare* at the upstream sites (Fig. 4.5). Except for at the River Mouth, the margin samples were dominated by very few taxa (2-4), especially Ostracoda, Hydrobiidae, and *G. insulare* at the middle sites (Penny Point and Willow Creek) and Corixidae at Freezeout Bar. Furthermore, the prominent taxa in the main channel samples varied the most by site with the relative contributions of taxa unique at each site and no observable longitudinal pattern as observed in the benthic or margin samples (Fig. 4.5).

Comparisons between open and closed mouth states across epibenthic sampling types revealed shifts in the proportional distribution of taxa (Fig. 4.5). For example, the proportion of *G. insulare* at Willow Creek increased in the margin samples when the mouth was closed but decreased in the main channel samples. Similarly, at Freezeout Bar, proportions of Corixidae in the margin habitat increased when the mouth was closed and decreased in the main channel. Inverse to the pattern of *G. insulare* and Corixidae, at Willow Creek the proportional contribution of Hydrobiidae snails decreased in the margin samples when the mouth was closed but increased in the main channel samples (Fig. 4.5; Supplemental Tables 4.2, 4.3, and 4.4).

### 4.4.3 *Influence of site and mouth state on the assemblage structure of food web taxa*

We found that the assemblages varied by reach, which reflected differences across the longitudinal salinity gradient (Figs. 4.6; Supplemental Table 4.5). For example, the assemblage at the most upstream site, Freezeout Bar, was different from all other sites for all sampling types (Fig. 4.6; Pairwise PERMANOVA: $P<0.001$). Furthermore, the assemblages in the middle two sites, Penny Point and Willow Creek, were not different for any sampling type (Pairwise PERMANOVA: $P>0.05$). The assemblage at the site with the most saline influence, River Mouth, was different from all other sites for all sampling types (Pairwise PERMANOVA: $P>0.05$) except for Penny Point in the margin (Pairwise PERMANOVA: $P<0.001$) and benthos (Pairwise PERMANOVA: $P<0.007$) (Fig. 4.6).

The overall assemblages for all sampling types varied by mouth state (Fig. 4.6) but pairwise comparisons revealed that the effects were site- and type-specific (Supplemental Table 4.5). For example, the assemblage at Freezeout Bar and Penny Point were not affected by the mouth state for any sampling type (Supplemental Table 4.5). The assemblage at the River Mouth was affected by the mouth in the benthos and margin sampling types while the Willow Creek assemblage was only influenced by the mouth in the margin samples (Supplemental Table 4.5).

### 4.4.4 *Abundance of key food web taxa*

Macroinvertebrates that are essential to the food web were relatively abundant in the RRE (Figs 4.7, 4.8 and 4.9). The abundance of specific food web taxa varied across the sites, but differences in the total abundance of taxa were less dramatic due to averaging across the individual taxa. The differences in abundance across sites reflected the tolerance of individual taxa to salinity, with less euryhaline species, including Corixidae, Ephemeroptera, and Chironomidae most abundant at Freezeout Bar which was the site with the lowest salinity (Figs 4.7, 4.8 and 4.9).

The additional sampling of the closure-inundated habitats detected large aggregations of food web taxa that were previously missed with the other sampling methods. When compared with the main channel samples, the total densities of the key food web taxa were higher in the closure-inundated, shallow littoral habitat at the Penny Point, Willow Creek, and Freezeout Bar (Fig 4.10). The most substantial changes were attributed to higher densities of Hydrobiidae snails (up to 100x) and *Americorophium* spp. (up to 20X) at Penny Point and Willow Creek, and Corixidae (30x) at Freezeout Bar (Fig 4.10). Furthermore, higher densities of *N. mercedis* were found in the closure-inundated habitat at Willow Creek (4x). Total densities were similar at River Mouth, but the closure-inundated samples were dominated by Hydrobiidae snails (84% of total) while Hydrobiidae snails composed only ~5% main channel total when the mouth was open and ~30% in the main channel when the mouth was closed (Fig 4.10).

## 4.5 DISCUSSION

We found that the community of macroinvertebrates in the RRE is primarily composed of taxa that can deal with the abiotic variability in intermittently closed estuaries either through physiological adaptations or behaviourally. As a result, changes in the mouth state had limited impacts on the assemblages and abundance of macroinvertebrates. Similar to permanently open systems, taxa were distributed relatively consistently along the salinity gradient under open and closed states, with the least euryhaline taxa most common in the tidal freshwater sites. For example, Corixidae, Chironomidae, and Ephemeroptera were most abundant at Freezeout Bar, but were rarely found in the sites with higher salinities. In contrast, other taxa such as Nematoda, Turbellaria, and *E. confervicolus* are more common in the lower estuary.

Overall, the primary macroinvertebrate taxa found in the RRE were able to deal with the varying conditions because these species are euryhaline or mobile. The combination of euryhaline and freshwater taxa important to the food web suggest that the assemblage is adapted for either mouth state, whether it be saline/brackish when the mouth is open or primarily freshwater. Furthermore, some taxa, including tuberous *Americorophium* spp., have life history characteristics and behaviours that may mediate unpredictable environmental disturbances. These amphipods are euryhaline and have unique life history and ecological characteristics including dwelling in a “U” shaped tubes in the substrate (Eriksen, 1968; Thiel and Watling, 2015) that may provide a refuge from deleterious conditions but would likely dry out after an abrupt opening. The Hydrobiidae snails found in the RRE have an operculum that can seal off the snail from changes in physical conditions although they are not very mobile. Other key food web taxa, including *G. insulare*, *E. confervicolus*, and *N. mercedis*, are all very motile and euryhaline and can not only avoid deleterious conditions, but can also take advantage of increased resources, including detritus in newly inundated habitat. (Stimpson, 1856; Heuback, 1969; Bousfield, 1979; Tomika et al., 2006)

Our study primarily focused on differences between of open and closed mouth states throughout the entire tidal length of the estuary. The logistical constraints of systematic sampling, unpredictability in timing of mouth closures and breaches, and regulatory permitting restrictions prevented our ability to examine more immediate impacts that were observed in other studies that had the flexibility to impose open and closed mouth states into a Before-After-Control-Impact framework (e.g., Lill et al., 2011). Despite sampling for ten years in the RRE, we were not able to sample the estuary after conversion to a full freshwater lagoon as seen in other California intermittently open estuaries (Smith, 1990). However, information from those other systems derives from much longer closures. Regardless, this study reflects current, long-term conditions in the RRE that are characterized by many (0-15) short (mean duration seven days) closures per year, predominantly during the dry season (Behrens et al., 2009).

### 4.5.1 *Studies in other California intermittently closed estuaries*

Although the majority of estuaries in California are susceptible to mouth closures (Heady et al. 2014), the effects of mouth dynamics on macroinvertebrate assemblages of intermittently closed estuaries in California are understudied and are limited to unpublished literature (e.g., Robinson 1993). Robinson (1993) evaluated the macroinvertebrate assemblage before and during a closure in Pescadero Lagoon (Central California). Initially, after the closure, stratification of the Pescadero Lagoon increased, and deeper saline waters became anoxic resulting in decreases or loss of marine and euryhaline species; however, the euryhaline and freshwater species distribution and abundance eventually increased as water quality conditions improved.

Comparisons between the RRE and Pescadero Lagoon are limited due to differences in mouth closure timing and duration, total estuary sizes, depths, and inflow. For example, the Pescadero Lagoon typically closes for the entire dry season (Largier et al. 2015), while the RRE undergoes an unpredictable number of short closures (0-20 a year; duration <2 weeks), especially under the more recent direct management of the mouth closures (Behrens et al. 2013). Also, the study in Pescadero Lagoon was limited to 0.65 rkm, relatively the same distance between the lower two sampling locations in RRE (River Mouth = 0.2 rkm and Penny Point = 1.2 rkm). Furthermore, most of our water quality profiles indicated that the depths at which hypoxia was observed in the RRE (>5.0 m) were twice the maximum depth in the Pescadero lagoon sites (1.5-2.5 m; Robinson 1993). In other words, DO levels in the RRE remained above hypoxic levels throughout the depth range sampled in the Pescadero Lagoon. We cannot confidently preclude any impacts of more deleterious effects due to the rare occurrences and confined presence of hypoxic conditions in the RRE.

### 4.5.2 *Global comparisons*

Much of the peer-reviewed literature regarding macroinvertebrates in intermittently closed estuaries are from studies conducted in other parts of the world (Hirst 2004; Dye and Barros 2005; Hastie and Smith 2006, Lill et al., 2011). Most intermittently closed estuaries are somewhat parallel in their underlying physical processes, and their interactions with ecological functions, but broad differences in hydrogeomorphology, climate patterns, and sampling designs prevent direct comparison of the results. Given the stochastic timing of mouth closure and reopening of intermittent estuaries, whether it be controlled or naturally, comparisons both between different estuaries and within the same estuary is typically challenging but inherently insightful about the evolution of macroinvertebrate assemblages, reproductive strategies, and adaptability (Whitfield et al., 2012, Lill et al., 2011).

Many estuaries in South America are intermittently closed, yet literature regarding the influence of mouth state on macroinvertebrates is sparse, with most examples limited to southern

Brazil, including the Camacho Lagoon (Netto et al., 2012). The Camacho Lagoon rainfall (1,260 mm $yr^{-1}$) has no seasonal pattern, and the lagoon only breaches naturally, without human intervention, during extreme river discharge events (Vieira da Silva et al., 2011) and can stay closed for multiple years. Netto et al. (2012) observed decreases in the biomass (90%) and density of macroinvertebrates in the Camacho Lagoon near the mouth after breaching but detected less of an impact further upstream. One of the mechanisms of decreased macroinvertebrate populations in the Camacho Lagoon is a loss due to scouring during a breaching event, likely not an issue in the RRE due to the overall size (Largier et al., 2019).

Over two-thirds of the estuaries in South Africa have an intermittent connection to the ocean, but most of the literature is limited to comparisons among estuaries or the study of breaches during the wet season when flows are high (e.g., Teske and Wooldridge 2001, Whitfield et al., 2012). Generally, mouth breaching events in South Africa are associated with declines of macroinvertebrate abundance, but an increase in diversity (Whitfield et al., 2012). These studies contrast with the RRE because the estuaries studied can remain disconnected from the ocean for years and mostly include natural breaches during the wet season which are associated with different hydrologically dynamics (Oretega-Cisneros and Scharler 2014). In contrast, most concerns in intermittently closed estuaries in California are with artificial breaching during the dry season, and they tend only to be closed during the dry season.

Intermittently closed estuaries in Australia and New Zealand are some of the more studied, but there is still uncertainty regarding the effects of intermittent closures due to natural variation, scale of temporal sampling, and the size of the estuary. For example, Gladstone et al. (2006) evaluated the effects of breaching on macroinvertebrate communities in four intermittent estuaries in New South Wales, Australia by sampling the benthos near the mouth (five meters from center). They found that the macroinvertebrate communities varied after breaching, but these differences could not be distinguished from natural variation (e.g., taxa generation time and seasonal variation) in unchanged estuaries. Hastie and Smith (2006) compared the benthic macrofaunal communities of intermittently closed estuaries and permanently open estuaries, finding that although there were differences in the macrofaunal communities among the contrasting estuary types, the catchment size, had a greater influence on the invertebrate assemblages than the connection to the ocean. Also, Lill et al. (2012) found a significant impact from mouth breaching on the assemblage of epibenthic macroinvertebrates, but no increase in taxa diversity per sample. They detected changes in the assemblage composition with daily sampling, but these changes were almost undetectable when analyzed across weekly sampling. Lill et al. (2012) also found higher densities of macroinvertebrates after breaching events due to concentrating the population into a smaller area but concluded that a net expulsion of individuals out to the ocean led to a decrease in the overall population in the estuary.

### 4.5.3 *Conclusions*

The previously used fixed sampling with large temporal intervals between each sampling event is incapable of fully capturing distributional changes to the assemblage. For example, Lill et al. (2012) found that breaching the mouth affected the assemblage composition with daily sampling, but these changes were almost imperceptible when analyzed across weekly sampling. We propose increased temporal and spatial resolution at one “intensive” study site as the water level increases directly after a closure and just before and after a breach. Furthermore, keeping fixed locations of benthic cores near the water’s edge and adding additional cores as water levels rise and then resampling all sites after a mouth breach will provide the ability to measure the colonization rate of tube-dwelling *Americorophium* spp. and quantify the number of individuals killed after a breach.

There are multiple sources of productivity in estuarine ecosystems, and there are high rates of nutrient recycling (Nixon et al. 1986; Maher et al. 2019), so identifying the source of nutrients and changes to the production of higher trophic levels is challenging. With the confined sampling design and short mouth closure durations in this study, we were unable to determine if changes in densities were associated with changes in productivity or the community redistributing with increasing water levels. In order to better understand how productivity changes with closure duration, future research should focus on (1) if inundation of vegetated shallows (with closure) promotes detritus cycling and availability; and (2) if aquatic plant growth increases with closure duration.

In conclusion, our investigations of macroinvertebrates found that the key food web taxa commonly found in the RRE 2009-2018 were abundant during both open and closed mouth states and the mouth only affected the assemblage structure for some site- and type-specific comparisons. Furthermore, taxa were distributed along the salinity gradient with the least euryhaline taxa most common in the tidal freshwater site, Freezeout Bar. This site had a unique assemblage from the other sites and was not affected by mouth state for any sampling type. In order to make informed decisions regarding the management of intermittently closed estuaries, research and management activities should focus on the physiological tolerances, including salinity and DO, and the mobility of key food web taxa and avoid actions that would create unavoidable deleterious conditions.

## 4.6 ACKNOWLEDGEMENTS

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## 4.8 FIGURES

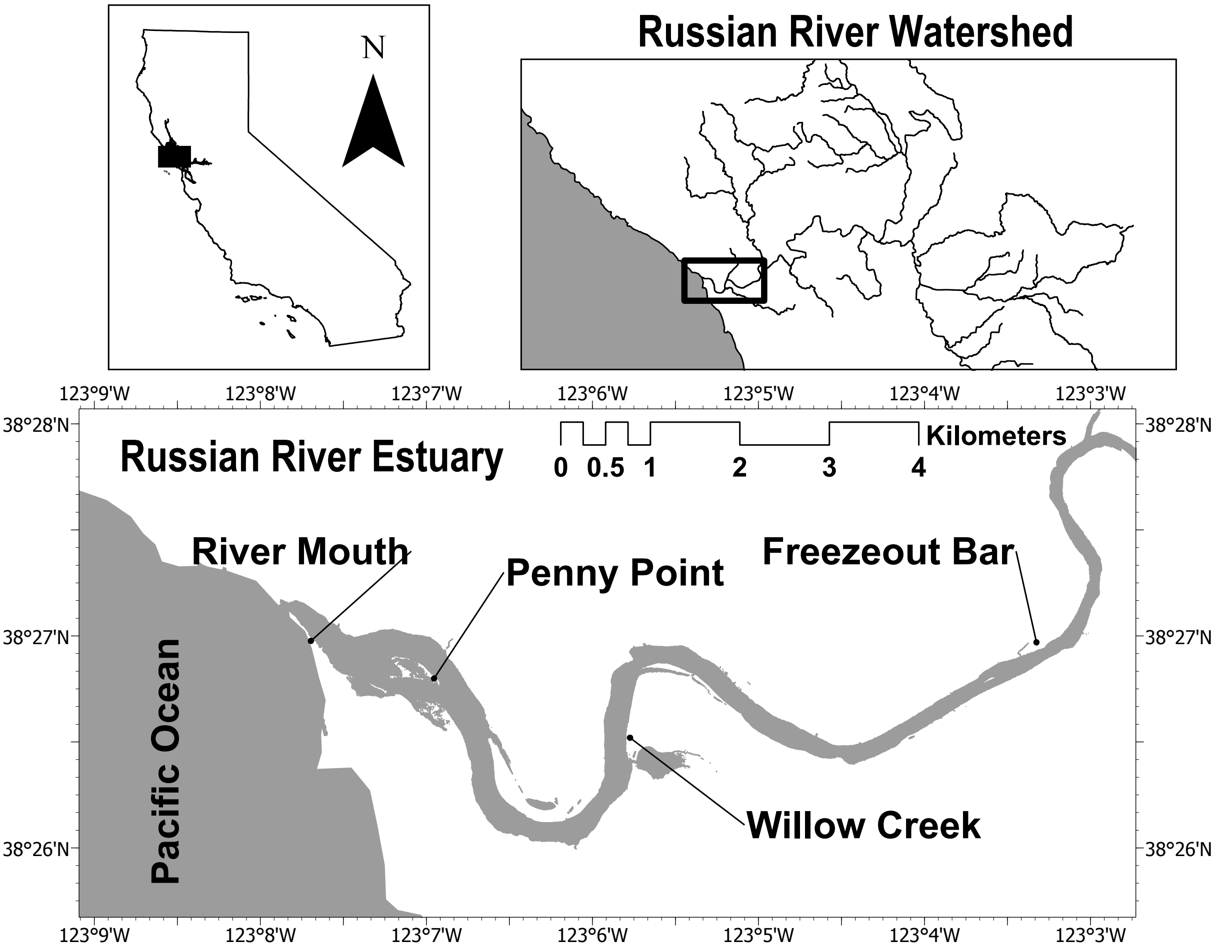

Figure 4.1. Location of the four sampling sites distributed along the Russian River estuary, Northern California USA: River Mouth, Penny Point, Willow Creek, and Freezeout Bar.

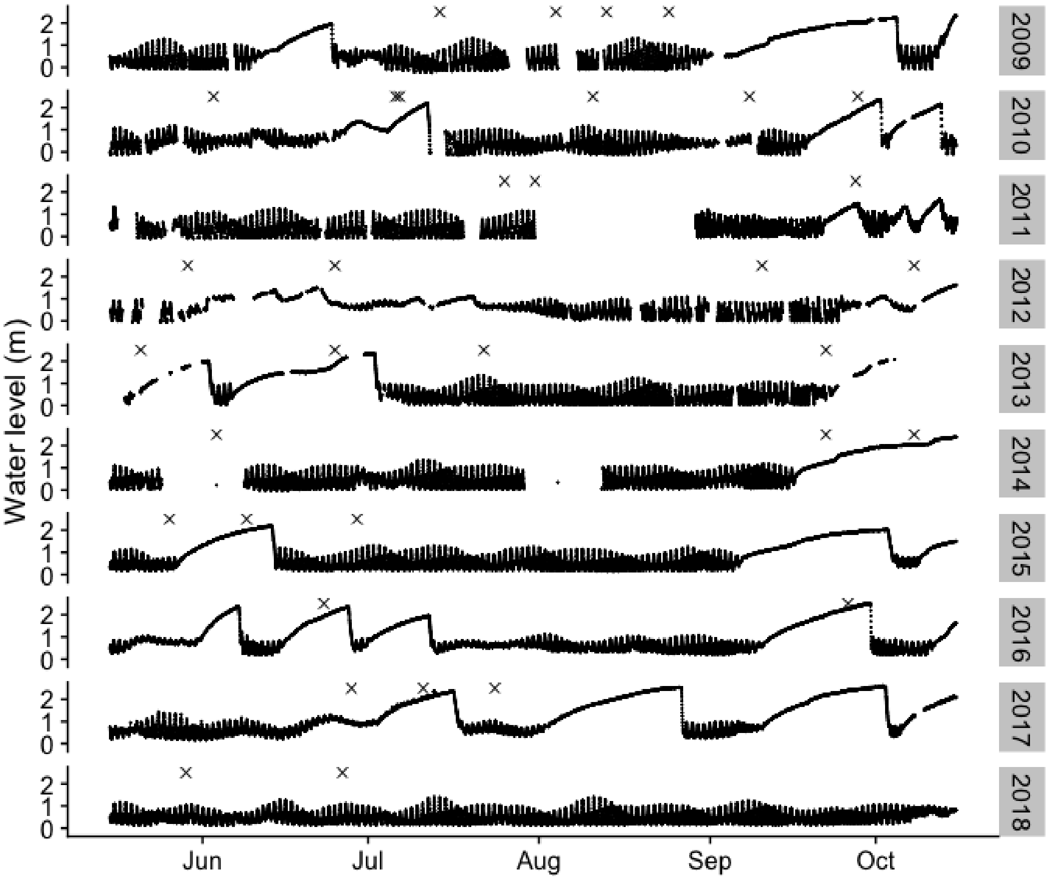

Figure 4.2 Water level of the Russian River estuary from mid-May to mid-October and dates of macroinvertebrate sampling (x). Breaks in the water level indicate when the gage was malfunctioning.

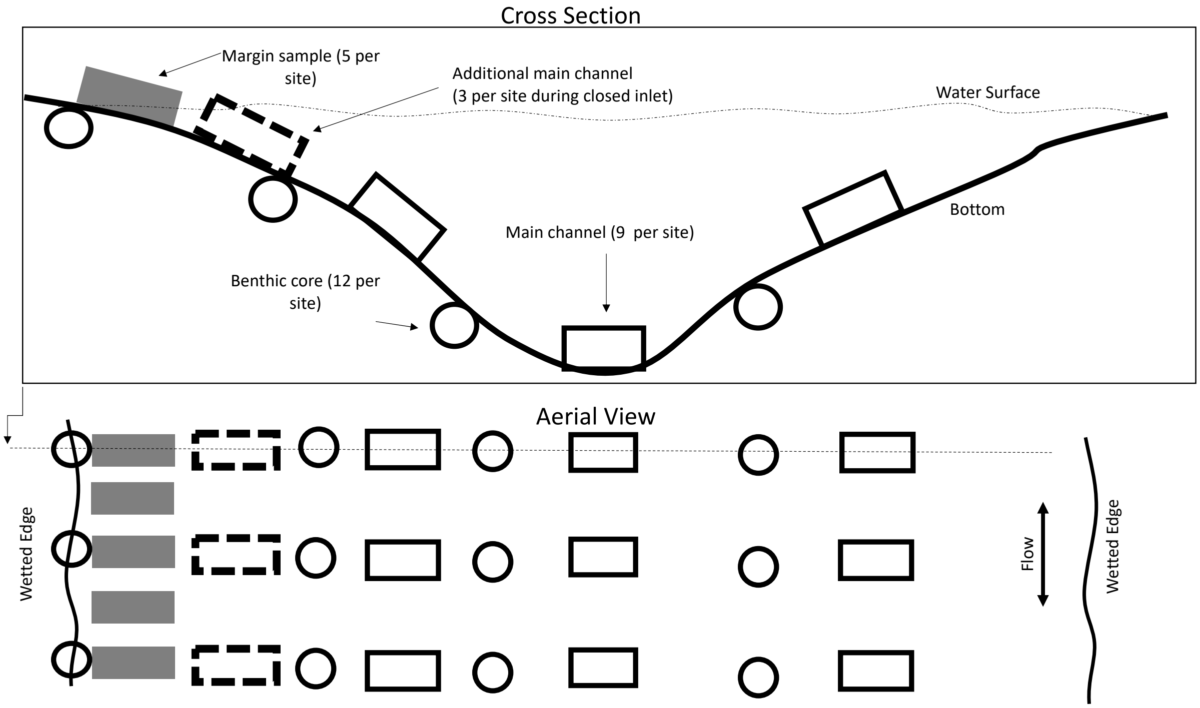

Figure 4.3 The macroinvertebrate sampling design in the Russian River estuary, 2009-2018. The top panel represents a horizontal cross section of one transect in the sampling design. The bottom panel is an aerial view of the sampling design at a single site. Open rectangles with solid outline = main channel sampled with epibenthic sled; black circles = benthic core samples; gray rectangles = margin sampled with the epibenthic net; the hollow rectangles with dashed outline indicate epibenthic sled taken exclusively in habitat inundated when the mouth was closed.

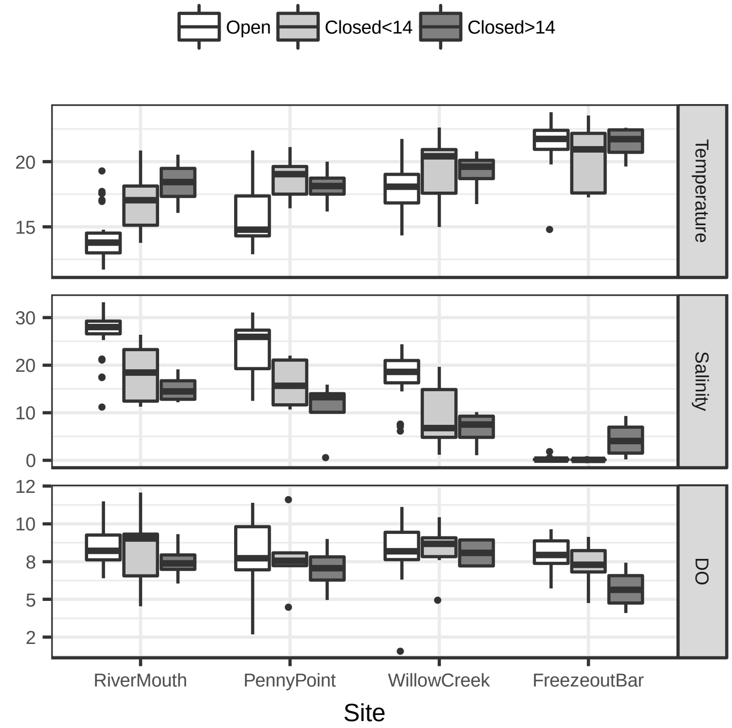

Figure 4.4 Boxplot of the temperature, salinity, and DO at each site for open and closed (<14 days and > 14 days) mouth states.

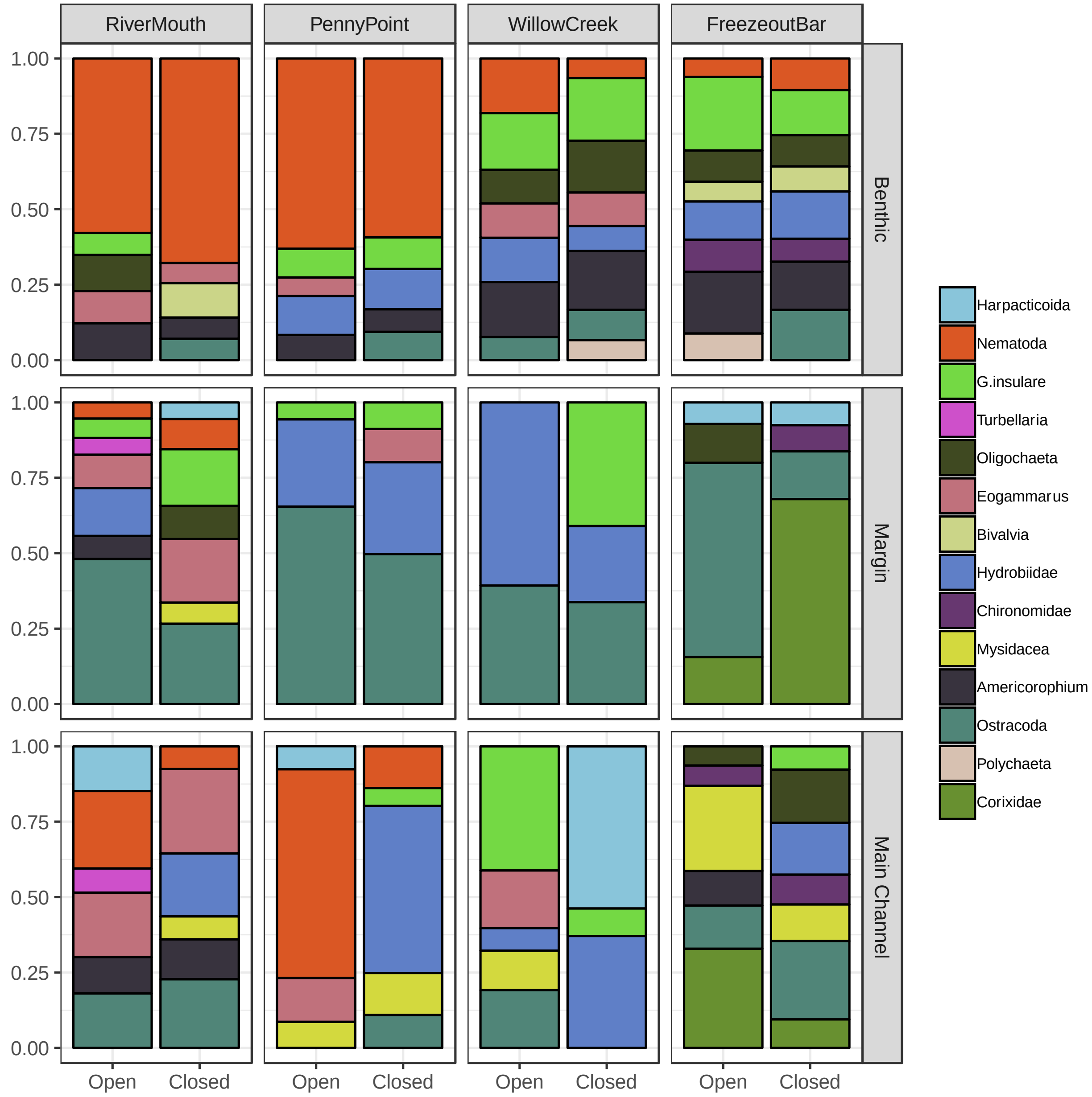

Figure 4.5. The contribution of the most abundant taxa (95% of overall density) for each sampling type for site under open and closed mouth states.

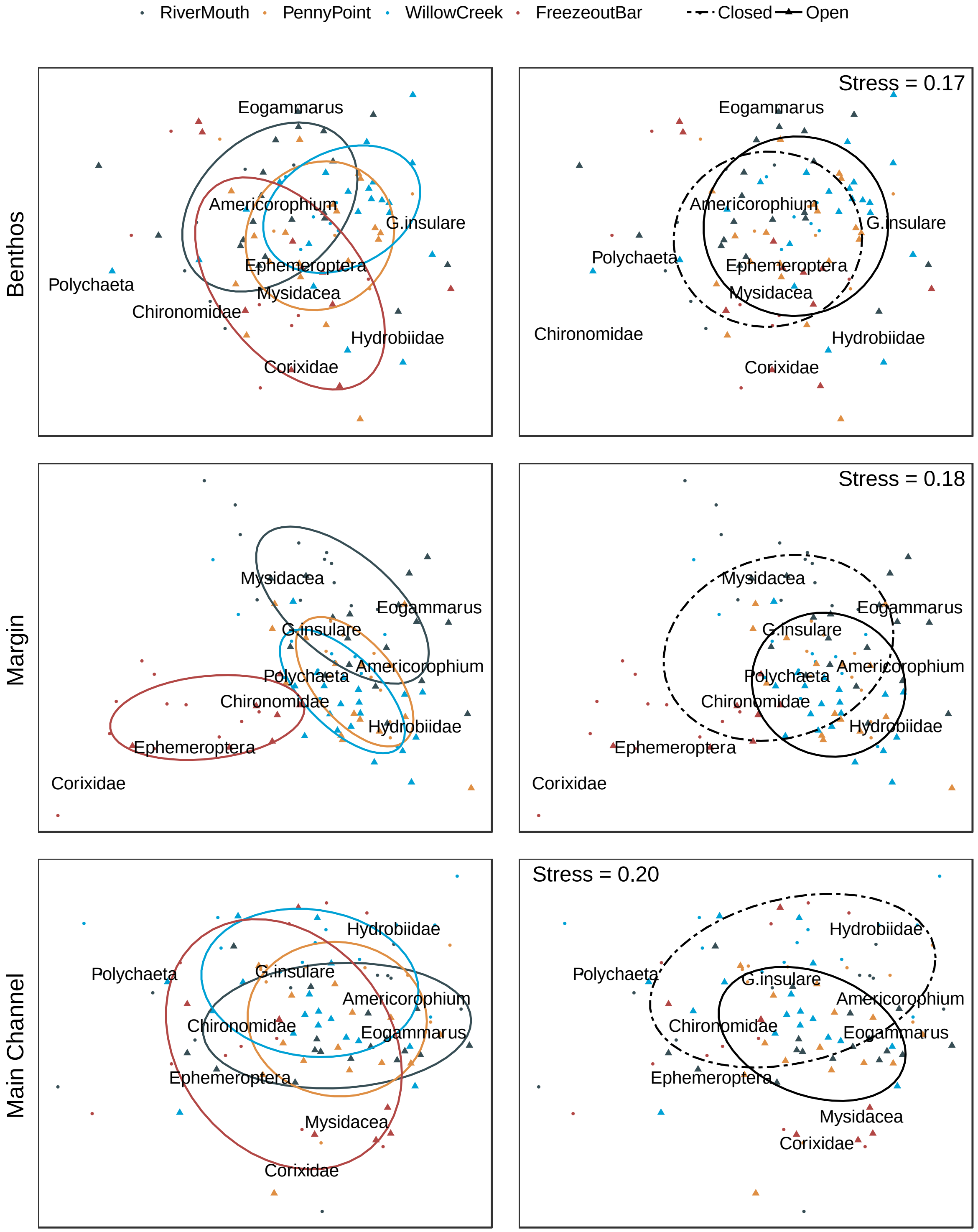

Figure 4.6. Nonmetric multidimensional scaling ordination (organism densities based on Bray–Curtis similarity) of species assemblage structures in the benthos (top panels), margin (middle panels), and main channel (bottom panels) comparing sites (left panels) and mouth state (right panels). Ellipses show 1 SD of two-dimensional point spread around the mean.

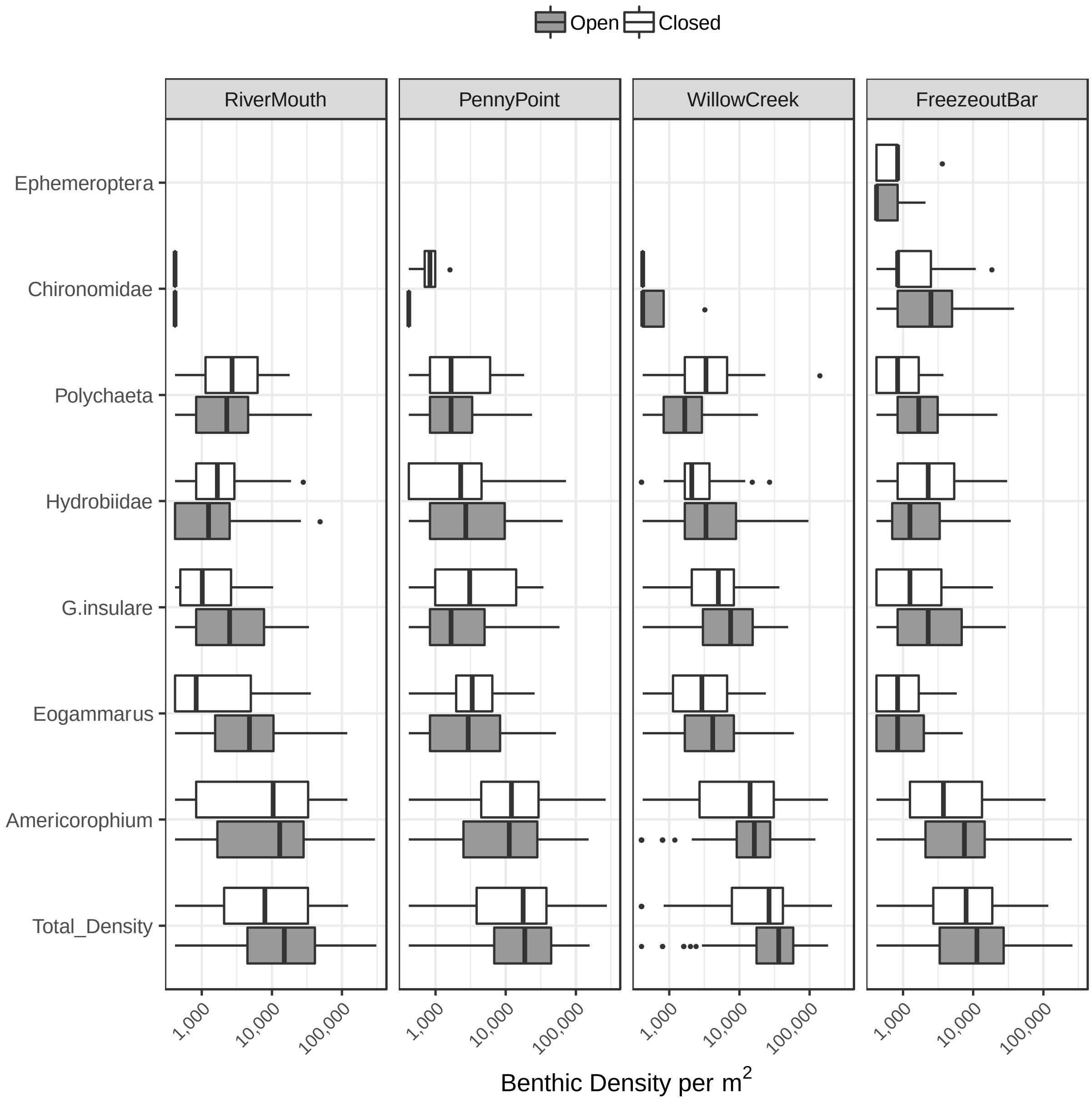

Figure 4.7. Densities of macroinvertebrates important to the food web found in the benthos across four sites during open (gray) and closed (white) mouth states.

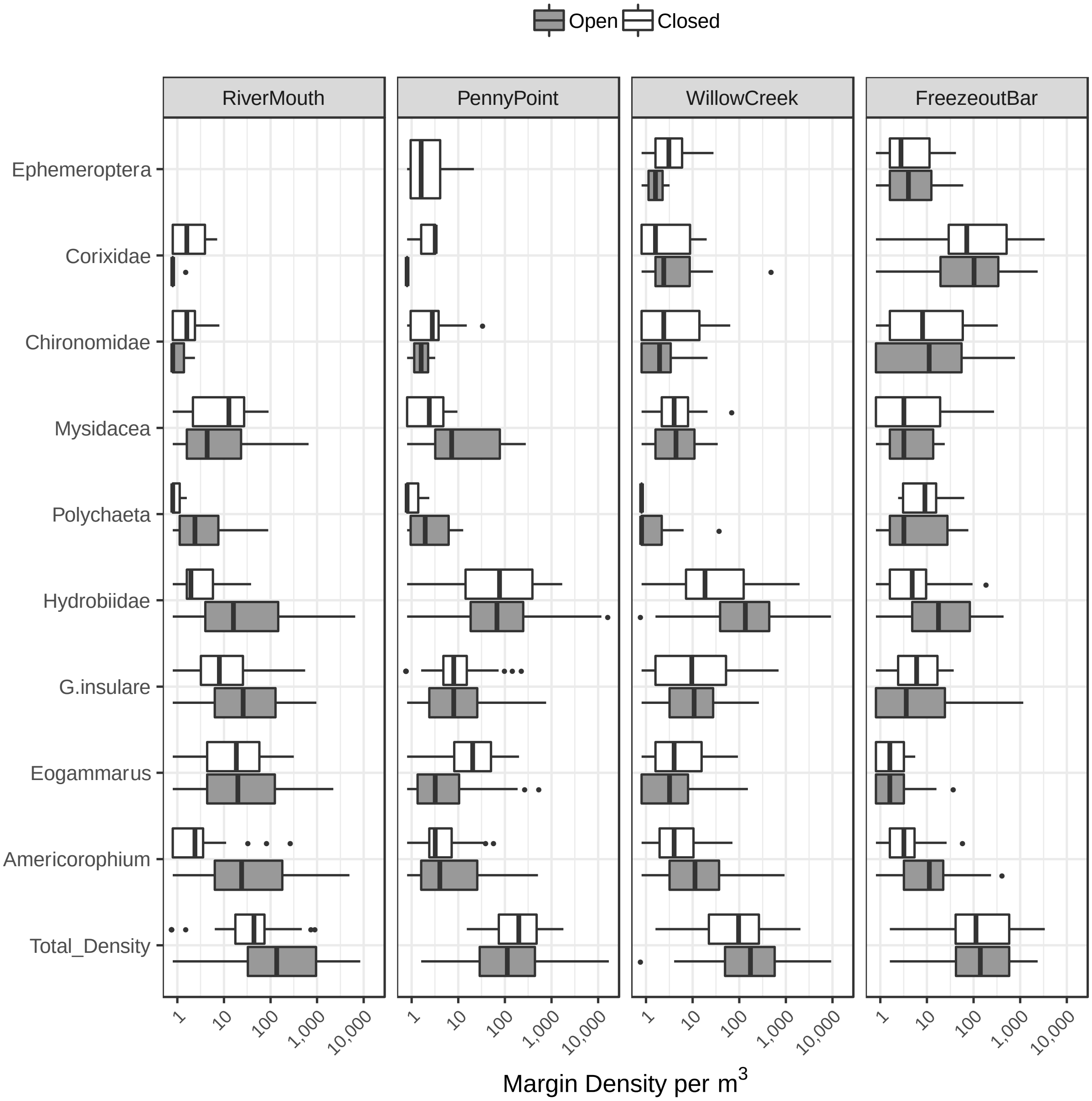

Figure 4.8. Densities of macroinvertebrates important to the food web found in the margin habitat across four sites during open (gray) and closed (white) mouth states.

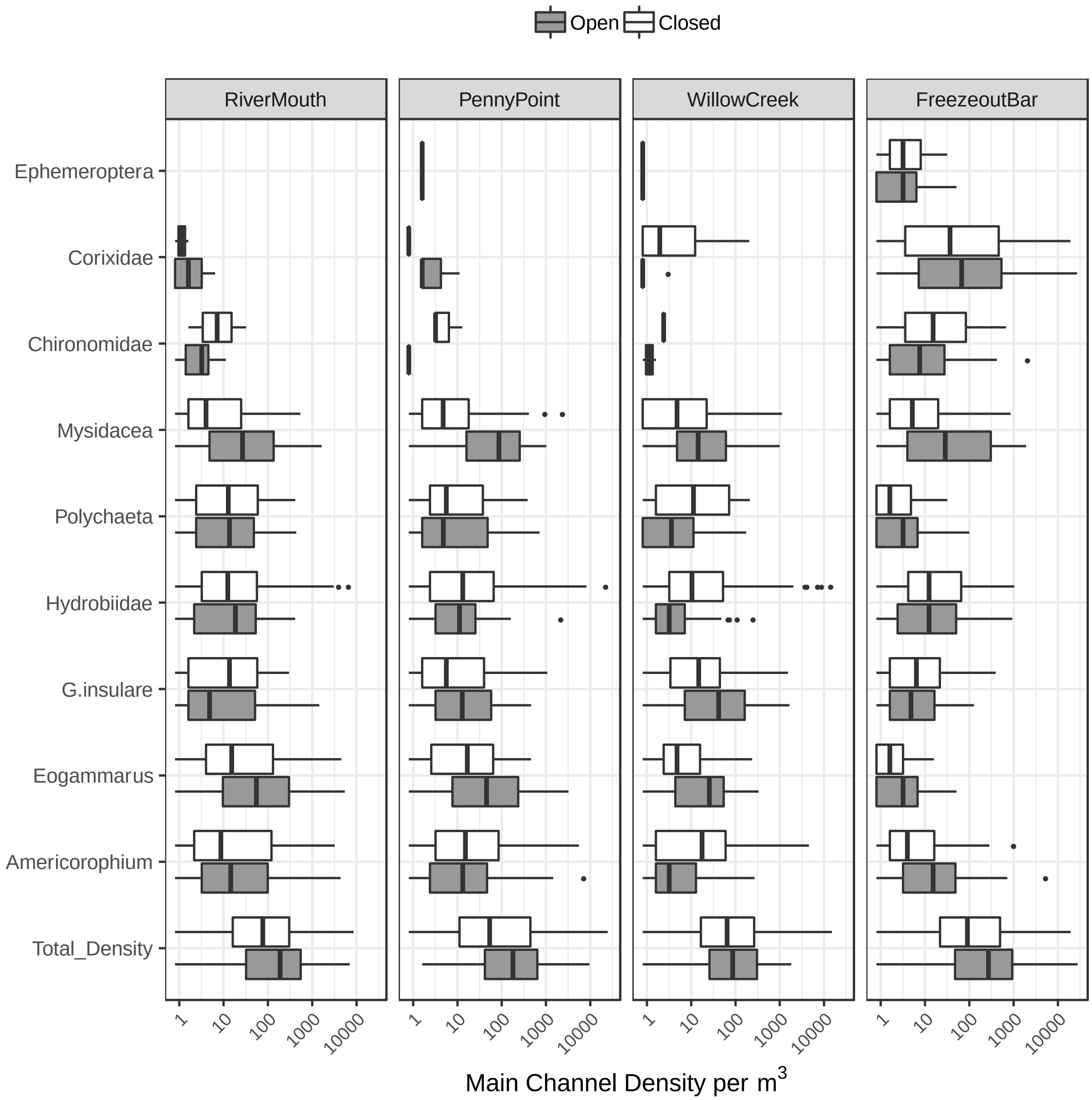

Figure 4.9. Densities of macroinvertebrates important to the food web found in the main channel across four sites during open (gray) and closed (white) mouth states.

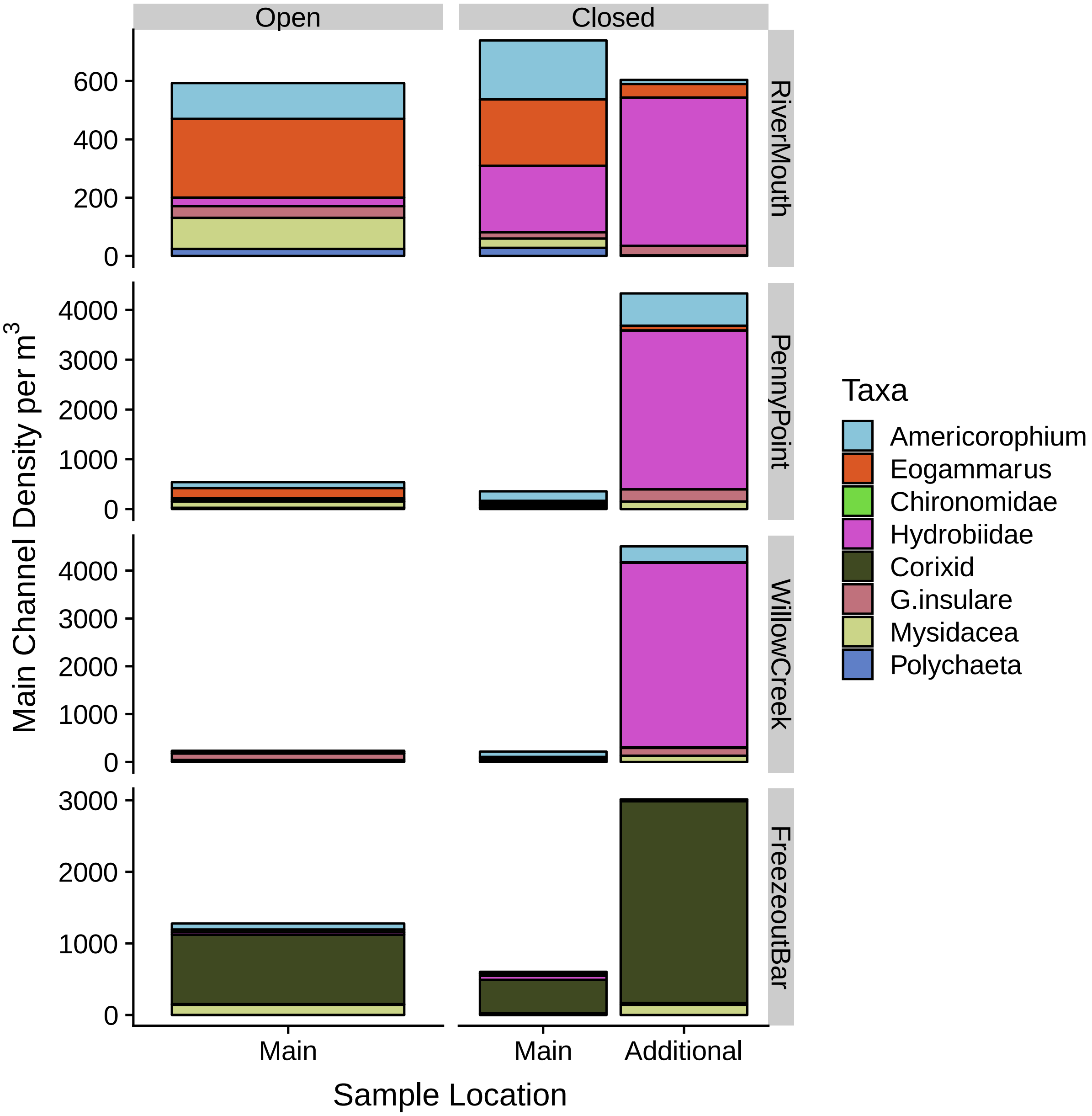

Figure 4.10. Mean density of the food web taxa in the main channel during open and closed mouth states and additional samples taken in the habitat that is inundated during closed mouth conditions.

## 4.9 TABLES

Table 4.1. The most abundant phyla and subphyla in the Russian River Estuary from 2009 -2015.

| **Phyla** | **Benthos** | **Margin** | **Main channel** |
|---|---|---|---|
| Arthropoda (subphylum Crustacea) | 38.7% | 60.1% | 51.7% |
| Mollusca | 9.1% | 23.6% | 11.4% |
| Nematoda | 30.6% | 2.4% | 22.6% |
| Arthropoda (subphylum Hexapoda) | 0.8% | 8.3% | 6.4% |
| Annelida | 15.4% | 3.5% | 4.8% |
| Platyhelminthes | 0.5% | 1.6% | 2.2% |

Table 4.2. The most abundant taxa (composing more than 95% of overall density) in the benthic core samples.

| **Taxa** | **River Mouth** | **Penny Point** | **Willow Creek** | **Freezeout Bar** | **Total** |
|---|---|---|---|---|---|
| Nematoda | 38.0% | 49.0% | 9.3% | 3.0% | 31.2% |
| *Americorophium spinicorne* | 4.6% | 5.9% | 17.2% | 21.9% | 9.7% |
| Oligochaete | 10.0% | 4.2% | 14.5% | 10.5% | 9.4% |
| *Americorophium* spp. | 5.7% | 4.1% | 10.5% | 10.4% | 6.8% |
| Hydrobiidae | 2.0% | 5.9% | 10.9% | 11.4% | 6.3% |
| *Gnorimosphaeroma insulare* | 2.2% | 4.7% | 11.0% | 13.7% | 6.2% |
| *Eogammarus confervicolus* | 4.2% | 6.0% | 7.9% | 1.0% | 5.5% |
| *Americorophium stimpsoni* | 5.5% | 7.1% | 3.5% | 1.7% | 5.1% |
| Ostracoda | 4.2% | 4.6% | 5.6% | 2.7% | 4.6% |
| Foraminifera | 10.4% | 2.2% | 0.7% | 0.1% | 4.6% |
| Bivalvia | 4.6% | 1.1% | 0.6% | 3.9% | 2.4% |
| Capitellidae | 0.8% | 0.8% | 2.4% | 0.7% | 1.2% |
| Nereididae | 1.1% | 0.5% | 1.0% | 4.1% | 1.1% |
| *Armandia brevis* | 1.6% | 0.9% | 0.4% | 0.0% | 0.9% |
| Chironomidae | 0.0% | 0.0% | 0.1% | 8.4% | 0.7% |

Table 4.3. The most abundant taxa (composing more than 95% of overall density) in the epibenthic main channel samples.

| **Taxa** | **River Mouth** | **Penny Point** | **Willow Creek** | **Freezeout Bar** | **Total** |
|---|---:|---:|---:|---:|---:|
| Nematoda | 20.8% | 47.1% | 1.6% | 0.4% | 22.6% |
| Harpacticoida | 18.8% | 6.5% | 44.4% | 0.1% | 14.5% |
| Hydrobiidae | 6.0% | 14.5% | 18.1% | 5.6% | 10.3% |
| *Eogammarus confervicolus* | 15.4% | 10.3% | 5.4% | 0.1% | 9.3% |
| Ostracoda | 12.3% | 4.8% | 1.2% | 14.8% | 8.8% |
| *Neomysis mercedis* | 3.2% | 4.9% | 2.3% | 19.6% | 6.9% |
| *Corixidae* | 0.0% | 0.0% | 0.0% | 26.3% | 5.3% |
| *Americorophium spp.* | 6.0% | 1.5% | 4.1% | 5.5% | 4.2% |
| *Gnorimosphaeroma insulare* | 0.8% | 1.9% | 13.9% | 1.5% | 3.1% |
| Turbellaria | 5.5% | 0.7% | 0.3% | 0.2% | 2.2% |
| Nereididae | 2.3% | 2.8% | 1.9% | 0.1% | 2.0% |
| *Americorophium spinicorne* | 1.9% | 0.7% | 0.9% | 3.1% | 1.6% |
| Oligochaeta | 1.1% | 1.0% | 0.3% | 4.0% | 1.6% |
| Diplostraca (suborder Cladocera) | 0.0% | 0.0% | 0.0% | 7.0% | 1.4% |
| Chironomidae | 0.0% | 0.0% | 0.0% | 5.3% | 1.1% |

Table 4.4. The most abundant taxa (composing more than 97% of overall density) in the margin samples.

| **Taxa** | **River Mouth** | **Penny Point** | **Willow Creek** | **Freezeout Bar** | **Total** |
|---|---:|---:|---:|---:|---:|
| Ostracoda | 38.8% | 65.5% | 22.2% | 27.4% | 35.5% |
| Hydrobiidae | 14.0% | 15.7% | 60.8% | 3.6% | 23.1% |
| Corixidae | 0.0% | 0.0% | 0.7% | 25.8% | 6.8% |
| *Americorophium* spp. | 13.4% | 1.1% | 3.1% | 0.7% | 5.9% |
| *Gnorimosphaeroma insulare* | 6.0% | 5.7% | 5.9% | 0.7% | 4.6% |
| *Eogammarus confervicolus* | 9.7% | 4.4% | 0.8% | 0.1% | 4.3% |
| Diplostraca (suborder Cladocera) | 0.0% | 0.1% | 0.0% | 14.4% | 3.7% |
| Oligochaeta | 1.5% | 0.4% | 0.6% | 9.5% | 3.2% |
| Harpacticoida | 2.0% | 3.4% | 2.3% | 5.4% | 3.1% |
| Nematoda | 5.0% | 1.6% | 1.1% | 0.5% | 2.4% |
| Turbellaria | 4.3% | 0.2% | 0.1% | 0.1% | 1.6% |
| Chironomidae | 0.0% | 0.1% | 0.2% | 4.2% | 1.2% |
| *Americorophium spinicorne* | 1.5% | 0.1% | 0.5% | 0.7% | 0.9% |
| *Neomysis mercedis* | 1.3% | 0.1% | 0.6% | 0.5% | 0.7% |

Table 4.5. Summary statistics of PERMANOVAs comparing invertebrate assemblage composition among sites, season, and mouth condition for the different sampling types.

| Type | Site | Factor | DF | SS | MS | F | $R^2$ | p |
|---|---|---|---|---|---|---|---|---|
| Margin | All | Site | 3 | 5.72 | 1.91 | 13.60 | 0.28 | 0.00 |
| | | Mouth | 1 | 1.20 | 1.20 | 8.56 | 0.06 | 0.00 |
| | | Season | 1 | 0.08 | 0.08 | 0.59 | 0.00 | 0.74 |
| | | Residuals | 97 | 13.59 | 0.14 | | 0.66 | |
| | | Total | 102 | 20.59 | | | 1.00 | |
| | River Mouth | Mouth | 1 | 1.19 | 1.19 | 8.09 | 0.23 | 0.00 |
| | | Season | 1 | 0.07 | 0.07 | 0.49 | 0.01 | 0.80 |
| | | Residuals | 27 | 3.99 | 0.15 | | 0.76 | |
| | | Total | 29 | 5.26 | | | 1.00 | |
| | Penny Point | Mouth | 1 | 0.28 | 0.28 | 2.13 | 0.09 | 0.06 |
| | | Season | 1 | 0.05 | 0.05 | 0.38 | 0.02 | 0.90 |
| | | Residuals | 21 | 2.78 | 0.13 | | 0.89 | |
| | | Total | 23 | 3.11 | | | 1.00 | |
| | Willow Creek | Mouth | 1 | 0.40 | 0.40 | 3.17 | 0.10 | 0.01 |
| | | Season | 1 | 0.04 | 0.04 | 0.28 | 0.01 | 0.93 |
| | | Residuals | 28 | 3.54 | 0.13 | | 0.89 | |
| | | Total | 30 | 3.97 | | | 1.00 | |
| | Freezeout Bar | Mouth | 1 | 0.38 | 0.38 | 3.30 | 0.15 | 0.02 |
| | | Season | 1 | 0.41 | 0.41 | 3.50 | 0.16 | 0.02 |
| | | Residuals | 15 | 1.75 | 0.12 | | 0.69 | |
| | | Total | 17 | 2.54 | | | 1.00 | |
| Benthos | All | Site | 3 | 2.91 | 0.97 | 6.54 | 0.16 | 0.00 |
| | | Mouth | 1 | 0.92 | 0.92 | 6.20 | 0.05 | 0.00 |
| | | Season | 1 | 0.93 | 0.92 | 6.22 | 0.05 | 0.00 |
| | | Residuals | 93 | 13.83 | 0.15 | | 0.74 | |
| | | Total | 98 | 18.59 | | | 1.00 | |
| | River Mouth | Mouth | 1 | 0.60 | 0.60 | 3.22 | 0.10 | 0.01 |
| | | Season | 1 | 0.24 | 0.24 | 1.28 | 0.04 | 0.25 |
| | | Residuals | 28 | 5.19 | 0.19 | | 0.86 | |
| | | Total | 30 | 6.03 | | | 1.00 | |
| | Penny Point | Mouth | 1 | 0.08 | 0.08 | 0.68 | 0.03 | 0.63 |
| | | Season | 1 | 0.06 | 0.06 | 0.55 | 0.03 | 0.76 |
| | | Residuals | 20 | 2.35 | 0.12 | | 0.94 | |
| | | Total | 22 | 2.50 | | | 1.00 | |
| | Willow Creek | Mouth | 1 | 0.26 | 0.26 | 1.47 | 0.05 | 0.20 |
| | | Season | 1 | 0.13 | 0.13 | 0.73 | 0.03 | 0.61 |
| | | Residuals | 25 | 4.43 | 0.18 | | 0.92 | |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Total | 27 | 4.82 | | | 1.00 | |
| | Freezeout Bar | Mouth | 1 | 0.27 | 0.27 | 1.19 | 0.04 | 0.28 |
| | | Season | 1 | 0.32 | 0.32 | 1.42 | 0.05 | 0.16 |
| | | Residuals | 28 | 6.30 | 0.22 | | 0.91 | |
| | | Total | 30 | 6.89 | | | 1.00 | |
| Main Channel | All | Site | 3 | 1.32 | 0.44 | 3.98 | 0.10 | 0.01 |
| | | Mouth | 1 | 0.38 | 0.38 | 3.45 | 0.03 | 0.00 |
| | | Season | 1 | 0.40 | 0.40 | 3.61 | 0.03 | 0.00 |
| | | Residuals | 105 | 11.63 | 0.11 | | 0.85 | |
| | | Total | 110 | 13.74 | | | 1.00 | |
| | River Mouth | Mouth | 1 | 0.07 | 0.07 | 0.68 | 0.03 | 0.66 |
| | | Season | 1 | 0.09 | 0.09 | 0.88 | 0.03 | 0.49 |
| | | Residuals | 25 | 2.42 | 0.10 | | 0.94 | |
| | | Total | 27 | 2.58 | | | 1.00 | |
| | Penny Point | Mouth | 1 | 0.07 | 0.07 | 0.68 | 0.03 | 0.67 |
| | | Season | 1 | 0.09 | 0.09 | 0.88 | 0.03 | 0.51 |
| | | Residuals | 25 | 2.42 | 0.10 | | 0.94 | |
| | | Total | 27 | 2.58 | | | 1.00 | |
| | Willow Creek | Mouth | 1 | 0.22 | 0.22 | 2.01 | 0.07 | 0.08 |
| | | Season | 1 | 0.03 | 0.03 | 0.26 | 0.01 | 0.95 |
| | | Residuals | 27 | 2.99 | 0.11 | | 0.92 | |
| | | Total | 29 | 3.24 | | | 1.00 | |
| | Freezeout Bar | Mouth | 1 | 0.06 | 0.06 | 0.55 | 0.03 | 0.80 |
| | | Season | 1 | 0.32 | 0.32 | 3.04 | 0.15 | 0.01 |
| | | Residuals | 17 | 1.77 | 0.10 | | 0.83 | |
| | | Total | 19 | 2.15 | | | 1.00 | |

Table 4.6. The mean density and standard error of the prey taxa in the main channel and closure inundated main channel samples.

| | | Open | Closed | |
|---|---|---|---|---|
| Site | Taxa | Main | Main | Closure-inundated |
| River Mouth | *Americorophium* spp. | 122.6 (38.8) | 202.4 (62.1) | 14 (12.4) |
| | Chironomidae | 0.2 (0.1) | 0.4 (0.3) | 0 (0) |
| | Corixidae | 0.1 (0.1) | 0 (0) | 0 (0) |
| | *E. confervicolus* | 269.9 (54.3) | 227.6 (71.3) | 46.8 (16.8) |
| | Hydrobiidae | 29 (5.9) | 227.5 (89.2) | 508 (461.7) |
| | *G. insulare* | 40.4 (13.5) | 21.6 (5.8) | 33.2 (7.9) |
| | *N. mercedis* | 106.5 (21.2) | 32.4 (10.9) | 2.2 (0.8) |
| | Polychaeta | 24.6 (5.9) | 27.9 (6.7) | 0 (0) |
| | Total | 593.4 (93.8) | 739.7 (172.9) | 604.1 (473.1) |
| Penny Point | *Americorophium* spp. | 121.1 (69.1) | 191 (97.5) | 649.8 (432.7) |
| | Chironomidae | 0 (0) | 0.1 (0.1) | 1.1 (1.1) |
| | Corixidae | 0.1 (0.1) | 0 (0) | 0 (0) |
| | *E. confervicolus* | 198.4 (45.5) | 45.6 (12.4) | 93.3 (40) |
| | Hydrobiidae | 34.3 (20.6) | 23.3 (6.6) | 3191.7 (1953.5) |
| | *G. insulare* | 35.3 (6.8) | 24.9 (11.5) | 246.8 (101.3) |
| | *N. mercedis* | 127.5 (19.3) | 43.1 (34.9) | 150.3 (85) |
| | Polychaeta | 23.9 (8.9) | 28.1 (9) | 0 (0) |
| | Total | 540.6 (107.5) | 356 (120.8) | 4332.9 (2006.5) |
| Willow Creek | *Americorophium* spp. | 13.8 (3.2) | 110.6 (53.5) | 331.5 (263.3) |
| | Chironomidae | 0 (0) | 0 (0) | 0.2 (0.2) |
| | Corixidae | 0.1 (0) | 0.1 (0.1) | 17.1 (12.1) |
| | *E. confervicolus* | 37.1 (4.7) | 14.6 (3.5) | 10.5 (8.4) |
| | Hydrobiidae | 6.7 (2.2) | 21.4 (7.4) | 3850.8 (1327.7) |
| | *G. insulare* | 135.4 (21.4) | 46.8 (14.1) | 163 (125.6) |
| | *N. mercedis* | 37.8 (8.6) | 8 (4) | 131.8 (92.8) |
| | Polychaeta | 4 (1.8) | 14 (4.3) | 0 (0) |
| | Total | 234.8 (29.4) | 215.5 (63.3) | 4504.9 (1277.4) |
| Freezeout Bar | *Americorophium* spp. | 83.1 (42.3) | 24.1 (11.9) | 2.1 (1.1) |
| | Chironomidae | 34.3 (17.1) | 30.4 (9.6) | 6.6 (4.9) |
| | Corixidae | 968.8 (294.1) | 467.8 (207.5) | 2816.7 (1558.8) |
| | *E. confervicolus* | 1.9 (0.6) | 1 (0.3) | 0.7 (0.5) |
| | Hydrobiidae | 36.4 (9.1) | 54.3 (16.1) | 17.5 (9.3) |
| | *G. insulare* | 8.6 (1.7) | 16.2 (5.2) | 24.7 (14.6) |

| | | | |
|---|---|---|---|
| *N. mercedis* | 142.1 (28.5) | 7.9 (2.6) | 143.3 (75.6) |
| Polychaeta | 1.2 (0.8) | 0.6 (0.4) | 0 (0) |
| Total | 1279 (304.9) | 602.1 (209.9) | 3011.7 (1574.9) |

## 4.10 SUPPLEMENTAL

To assess the influence of site and mouth on the diversity we calculated diversity indices (Shannon-Wiener's diversity [*H*], taxa richness [*S*], and evenness [*E*]). We calculated *S* by enumerating the number of unique taxa per site. We calculated the *H* and *E* as follows:

$$\text{Shannon-Wiener's Index: } H = \Sigma p_i * \log p_i$$

$$\text{Evenness: } E = \frac{H}{\log(S)}$$

where *p* is the proportion of each taxon (*i*) density divided by the total density.

We analyzed the diversity metrics using two-way Analysis of Variance (ANOVA) tests, with mouth state (open and closed) and site (Freezeout Bar, Willow Creek, Penny Point, and River Mouth) on the log-transformed *S* and square transformed *E* and *H*.

#### 4.10.1.1 Diversity – influence of mouth state on the benthos

Overall, the benthos was composed of relatively few taxa *(S:* 8.6 ± 3.9; *H*: 1.9 ± 0.5*)* that were evenly distributed (*E: 0.9 ± 0.1)*. The mouth affected the benthos taxa richness (ANOVA: $F_{1,101}$=,11.8, *P*<0.001), the Shannon's Index (ANOVA: $F_{1,101}$=,11.8, *P*=0.007), but not Evenness (ANOVA: $F_{1,101}$= 1.7, P=0.19). The taxa richness (Tukey's HSD: P<0.002) and Shannon's Index (Tukey's HSD: P=0.007) were lower during closed conditions.

#### 4.10.1.2 Diversity – influence of mouth state on the main channel

In comparison to the benthic samples, taxa richness in the epibenthic main channel habitat was higher (*S:* 10.3 ± 7.8), but the Shannon's Index (*H*: 1.45 ± 0.8) and Evenness (E: 0.6 ± 0.25) were lower. The condition of the mouth did not affect the taxa richness (ANOVA: $F_{1,75}$=

0.02, P=0.65), Shannon’s Index (ANOVA: $F_{1,75}$= 0.16, P=0.68) or Evenness (ANOVA: $F_{1,75}$= 0.54, P=0.46).

#### 4.10.1.3 Diversity – influence of mouth state on the margin

The taxa richness (*S:* 10.1 ± 5.7), Shannon’s Index (*H*: 1.59 ± 0.7*)* and Evenness (*E*: margin 0.7 ± 0.2) in the epibenthic margin samples were similar to the epibenthic main channel samples. Although no differences were detected in the taxa richness (ANOVA: $F_{1,76} = 3.7,$ P>0.05) or Shannon’s Index (ANOVA: $F_{1,76} = 3.7,$ P=0.06), the Evenness decreased during closed conditions (ANOVA: $F_{1,76} = 6.9,$ P=0.01; Tukey's HSD: P<0.05).

Figure 4.11 Supplemental Summary table of the diversity indices. Mean taxa richness, evenness, and Shannon’s index (±1 SD) in samples collected in the benthos, margin, and main channel during open and closed inlet states.

| Type | Mouth | Site | Taxa Richness | Evenness | Shannon’s Index |
|---|---|---|---|---|---|
| Benthic | Open | River Mouth | 9.80 (4.19) | 0.92 (0.05) | 2.02 (0.47) |
| Benthic | Open | Penny Point | 9.16 (3.56) | 0.93 (0.05) | 1.99 (0.44) |
| Benthic | Open | Willow Creek | 9.88 (3.39) | 0.92 (0.05) | 2.05 (0.42) |
| Benthic | Open | Freezeout Bar | 6.83 (3.10) | 0.93 (0.06) | 1.68 (0.5) |
| Benthic | Closed | River Mouth | 7.85 (4.24) | 0.91 (0.09) | 1.73 (0.62) |
| Benthic | Closed | Penny Point | 8.52 (3.75) | 0.93 (0.04) | 1.90 (0.49) |
| Benthic | Closed | Willow Creek | 8.39 (4.46) | 0.92 (0.11) | 1.80 (0.66) |
| Benthic | Closed | Freezeout Bar | 6.00 (3.22) | 0.91 (0.12) | 1.51 (0.60) |
| Main | Open | River Mouth | 14.53 (11.88) | 0.73 (0.21) | 1.78 (0.87) |
| Main | Open | Penny Point | 12.63 (7.87) | 0.73 (0.25) | 1.74 (0.82) |
| Main | Open | Willow Creek | 6.04 (2.80) | 0.63 (0.25) | 1.11 (0.57) |
| Main | Open | Freezeout Bar | 8.13 (5.07) | 0.63 (0.28) | 1.30 (0.75) |
| Main | Closed | River Mouth | 12.33 (7.33) | 0.65 (0.23) | 1.60 (0.80) |
| Main | Closed | Penny Point | 11.49 (6.37) | 0.67 (0.24) | 1.59 (0.74) |
| Main | Closed | Willow Creek | 8.20 (5.64) | 0.63 (0.28) | 1.26 (0.76) |
| Main | Closed | Freezeout Bar | 10.92 (7.93) | 0.66 (0.27) | 1.43 (0.82) |
| Margin | Open | River Mouth | 11.28 (6.01) | 0.78 (0.17) | 1.83 (0.66) |
| Margin | Open | Penny Point | 10.33 (2.87) | 0.73 (0.12) | 1.70 (0.43) |
| Margin | Open | Willow Creek | 8.44 (3.92) | 0.75 (0.19) | 1.52 (0.53) |
| Margin | Open | Freezeout Bar | 11.76 (6.93) | 0.73 (0.23) | 1.69 (0.69) |
| Margin | Closed | River Mouth | 7.58 (4.42) | 0.69 (0.24) | 1.30 (0.64) |
| Margin | Closed | Penny Point | 11.75 (3.21) | 0.75 (0.08) | 1.82 (0.35) |
| Margin | Closed | Willow Creek | 8.24 (4.85) | 0.66 (0.21) | 1.31 (0.62) |
| Margin | Closed | Freezeout Bar | 12.34 (8.48) | 0.68 (0.25) | 1.59 (0.88) |

# Chapter 5. Rapid growth in a dynamic environment: factors affecting the growth of juvenile steelhead (*Oncorhynchus mykiss*) in an intermittently closed estuary, northern California, USA

**Authors**: W. Matsubu, C.A. Simenstad, D.A. Beauchamp, D.G. Cook and G.E. Horton

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## 5.1 ABSTRACT

Estuaries that become disconnected from the ocean are complex environments that play a pivotal role in the growth and marine survival of threatened steelhead (*Oncorhynchus mykiss*). We used bioenergetics modeling to investigate the biotic and abiotic conditions that influence the growth potential of juvenile steelhead in the Russian River estuary, an intermittently closed estuary in northern California, USA. We found that empirical growth rates of juvenile steelhead from a mark recapture study during their transitional residence in the Russian River estuary rival the highest in literature. To achieve these growth rates, consumption rates (proportion of maximum daily consumption; $P_{cmax}$) were relatively high ($0.54 \pm 0.13$ $P_{cmax}$), and in habitats with elevated temperatures, diets were 24.1% more energy dense than in the cooler habitats. Simulations of growth rate potential across different temperatures found that juvenile steelhead have no or negative growth at temperatures greater than 22.9 °C. These results indicate that

growth is likely not limiting the recovery of threatened steelhead in the Russian River estuary. With many populations of salmonids imperiled near their southern range, efforts for recovery could benefit by protecting habitat in intermittently closed estuaries and considering the impacts of management activities to the water quality conditions.

## 5.2 INTRODUCTION

The size that fish reach early in life affects survival during later stages in life (Sogard, 1997). This size-selective survival is the case for anadromous Pacific salmonids *Oncorhynchus* spp., with marine survival strongly dependent to the size achieved prior to out-migration (Ward et al., 1989; Nislow et al., 2000; Beamish & Mahnken 2001; Melnychuck et al., 2007; Thompson & Beauchamp, 2014). The size achieved prior to out-migration is particularly important for threatened populations of juvenile steelhead *Oncorhynchus mykiss* in watersheds with estuaries that become disconnected from the ocean, known as intermittently closed estuaries (ICEs) (Hayes et al., 2008). Despite the often-stochastic estuarine circumstances, juvenile steelhead that rear in ICEs have been found to have an accelerated growth rate and much higher marine survival (up to 6000% increase) than individuals that rear in upstream habitat exclusively (Bond et al., 2008; Hayes et al., 2008; Osterback et al., 2014).

Intermittently closed estuaries are common in temperate climates around the world (McSweeney et al., 2017) and comprise the majority of estuaries in California (Heady et al., 2014). The temporary connection to the ocean in ICEs is the defining difference from permanently open estuaries. An ICE becomes disconnected from the ocean by the building of a sand berm across the river mouth and is affected by river inflow, tidal flow, and wave action; a natural reconnection of the estuary to the ocean occurs when water elevations overtop and erode the sand berm at the river mouth (Ranasinghe & Pattiaratchi, 1998; Behrens et al., 2013). Similar to permanently open estuaries, an ICE with a free connection to the ocean is tidal with saline or brackish conditions in the lower estuary. In contrast, an ICE not connected to the ocean has no tidal exchange and becomes salt-stratified with freshwater inflows ponding over the denser saline layer if freshwater inputs exceed evaporation (Chuwen et al., 2009). This freshwater layer expands in volume and inundates low lying areas. Human activities have changed the timing and duration of closures through altered flows and manually breaching the mouth (Haines et al., 2006; Behrens et al., 2013; Slinger et al., 2017; Largier et al., 2019).

Similar to other estuary types, ICEs are used by many animals, including ecologically and commercially important fishes, but are limited by the high abiotic variability (Harrison and Whitfield, 2005; Elliott et al., 2007; Whitfield et al., 2012 ; Hughes et al., 2014). Fish in ICEs benefit from the high productivity (Bond et al., 2008; Osterback et al., 2014), refuge from piscivorous predators (Becker and Laurenson, 2007, Becker et al., 2011), but also experience high rates of avian predation (Frechette et al., 2013; Osterback et al., 2013) and fish kills from the physiochemical variability (Becker et al., 2009). Due to this high-risk, high-reward scenario, many fishes with various types of life-history strategies use ICEs, but the use of a specific ICEs depends on the physiological tolerances of individuals and the timing of mouth state dynamics (open vs closed) (Elliott et al., 2007). In addition to the physiochemical variability, the physical disconnection from the ocean creates inherent challenges for diadromous fishes. The behavioural adaptability of anadromous steelhead and seasonal timing of mouth state dynamics of California ICEs has led to the use of ICEs by juvenile steelhead (Bond et al., 2008; Hayes et al., 2008; Osterback et al., 2014; Osterback et al., 2018).

Many of the populations of anadromous Pacific salmonids in California are at risk of extirpation due to climate change and human disturbances (Wenger et al., 2011; Katz et al., 2013; Moyle et al., 2019). To avoid losing these evolutionary distinct populations, it is imperative to identify essential habitats and understand the vulnerability of habitat quality to the anticipated changes. The same factors that affect connectivity to the ocean in ICEs, including hydrological drought, habitat modification, and other sources of altered freshwater flows, affect the quality of upstream habitat (Lake, 2011; Woelfle-Erskine et al., 2017; Obedzinski et al., 2018). While steelhead in California streams and tributaries often have low growth and survival during the summer (Hayes et al., 2008; McCarthy et al., 2009; Sogard et al., 2009, Grantham et al., 2012), growth rates are often rapid when rearing in ICEs (Hayes et al., 2008; Osterback et al., 2014). The source of the high growth in ICEs and impact of climate variability to the growth potential in ICEs has not been evaluated in published literature. Understanding the benefits of unique habitats upstream and in ICEs, and potential consequences (e.g., climate change and human disturbances) to those habitats is an essential challenge in anadromous fish recovery efforts.

Changes to the mouth of ICEs affect factors influencing the growth of juvenile salmonids, including changes to temperature (Behrens et al., 2015; Largier et al., 2019) and accessibility to prey (Lill et al., 2012.; Netto et al., 2012). For example, when the mouth closes during the summer or fall, the water temperatures initially increase, but this increase can be followed by cooling (Largier et al., 2019). Increased temperatures speed up the metabolism rates of fish, which incurs increased energy costs (Jobling, 1994; Beauchamp et al., 2007; McCullough et al., 2009; Mantua et al., 2010). Some of the increased energetic costs of high temperatures can be offset by increased consumption rates or transitioning to more energy dense diet, but increased temperatures eventually incur energetic costs that prevent any growth from occurring (Beauchamp, 2009). Inherently, the growth of steelhead strongly depends on the amount and energetic value of ingested prey (Filbert & Hawkins, 1995; Jenkins & Keeley, 2010; Jonsson et al., 2013), yet changes to the mouth have mixed consequences to prey abundance (Robinson, 1993; Teske & Wooldridge, 2003; Lill et al., 2012; Netto et al., 2012; Whitfield et al., 2012).

Bioenergetics models are useful tools for evaluating the relative importance of temperature, prey availability, prey energy density, and body size (Hanson et al., 1997). We will combine realized growth rates, the sampling of diets, and measurements of the thermal experience as inputs into a bioenergetics model to assess what affects the growth rates and identify potentially limiting factors for potential growth. First, we will use the energy density of diets and the thermal experience in bioenergetics modeling to determine what consumption rates are required for observed growth rates. These calculated consumption rates will then be used to conduct sensitivity analyses to determine the growth rate potential for different fish sizes, temperatures, and diet compositions. In order to understand how ICEs benefit juvenile steelhead and anticipate future impacts from climate change we have the following objectives: 1) to characterize the growth rates of juvenile steelhead rearing in the Russian River estuary (RRE); 2) quantify the influence of mouth state and reach on the diet composition and energy density of estuary rearing juvenile steelhead; 3) to identify how the abiotic and biotic factors influence the growth rate potential of juvenile steelhead; 4) determine how the growth rate of juvenile steelhead in the RRE will be affected by various climate change and management sceneries.

## 5.3 METHODS

### 5.3.1 *Study system*

The Russian River drains a moderate-sized (drainage 3,846 $\mathrm{km}^2$) northern California coast watershed located approximately 100 km north of San Francisco in Mendocino and Sonoma counties, California, USA. The catchment is in a Mediterranean climate with two dams on major tributaries that regulate flows for water supply and flood control. The steep topography, absence of snowmelt, and seasonal rain pattern leads to seasonal flows; flashy high flows occur during the winter (can exceed 1000 $\mathrm{m}^3\mathrm{s}^{-1}$) and low flows are common during in the summer (2-4 $\mathrm{m}^3\mathrm{s}^{-1}$). The flows during the dry season and tidal prism (0-2 x 10 $^6$m $^3$) are inadequate to prevent closure of the estuarine entrance caused by longshore drift and wave action piling sand across the mouth (Behrens et al., 2009, 2013). When the mouth is closed, the water level elevations increase and inundate low lying shorelines and properties which is alleviated by artificially breaching the mouth. Closures of the estuary's mouth typically last approximately two weeks and are ended by regulatory mandated manual breaching during the dry season but can also end by natural breaching resulting from overtopping which leads to erosion of the barrier berm at the mouth (Behrens et al., 2013).

The tidal extent of the RRE extends approximately 12 river kilometers (rkm) upstream, near the confluence of Austin Creek (Fig. 5.1). Abiotic conditions and structure vary spatially with estuary connectivity to the ocean. During open conditions, the lower reach (0-1.7 rkm) is dominated by marine and brackish waters while the middle reach (1.7-5.0 rkm) is mixed brackish and freshwater, and the upper reach (5.0-12.0 rkm) is characteristically tidal freshwater. After the mouth closes and exchange with the ocean is eliminated, water stratification increases, and saltwater intrudes further upstream (Behrens et al., 2016). The short duration of closures under the current management regime usually prevents the RRE from transforming into a freshwater lagoon with saline conditions still prevalent in the lower portions of the estuary.

### 5.3.2 *Fish capture*

We captured juvenile steelhead with a beach seine (46 m long, 4 m tall, 5 mm mesh) in the estuary and with a downstream migrant trap (DSMT) in Austin Creek (Cook, 2004; Manning & Martini-Lamb, 2014; Martini-Lamb & Manning 2015). Beach seining occurred throughout the estuary from May 15 to October 15. We operated the Austin Creek DSMT usually from mid-April until the creek became disconnected from the river due to decreased flows (June to July). Due to the high variability of spring flows in Austin Creek, the DSMT consisted of a rotary screw trap (1.53 m diameter) when flows were high, and a funnel net trap (plastic weir panels [5 mm mesh], funnel net [3 mm mesh], and a wooden live box) when decreased flows rendered the rotary screw trap ineffective.

All handling of fish conformed to the University of Washington's Office of Animal Welfare protocols (Protocol Number 2555-05) and the SCWA National Marine Fisheries Service Section 10 research permit. Captured steelhead were held in aerated buckets. Processing started with each fish anesthetized in buffered MS-222 at a dose of 40mg/l or Alka-Seltzer ®. After adequate anesthesia was ensured, we scanned each fish for or inserted a passive integrated transponder (PIT), and measured the length (mm FL) and weight (g wet). Fish were allowed to recover before released at the point of capture. If temperatures exceeded 21.1°C, salmonids were identified and released to avoid unnecessary harm.

### 5.3.3 *Diet Composition*

After capture, stomach contents of juvenile steelhead were obtained by gastric lavage, a non-lethal method of emptying the stomach contents without injuring fish (Hartleb & Moring, 1995). The sieved stomach contents were preserved in 10% formalin in the field. In the laboratory, we identified prey taxa to class, family, or order (depending on the physical state of the organism) under a dissecting microscope and recorded the wet weight. We obtained the total wet weight of stomach contents from each fish by adding the total weight of all prey taxa to the weight of the unidentified material. We assigned energy density values (kJ/g wet weight) to functional groups of prey based on literature values from similar systems (Table 5.1).

To determine whether the diet composition differed among reaches or mouth condition, we analyzed the diet composition with analysis of similarity (ANOSIM). We used the percentage of composition of each prey taxon on a Bray-Curtis dissimilarity matrix. After omitting any prey taxon found in less than 2.5% of the diets, we tested for differences among reaches by mouth state with ANOSIM of the arcsine-square-root-transformed proportional data. We conducted the multivariate analysis with the "vegan" package (Oksanen et al., 2011) in R version 3.4.2 (R Core Development Team 2013).

The mean energy density (kJ/g) of each diet was estimated from the proportional gravimetric contribution of each prey taxon ($p_i$) and the energy density of each prey taxon ($ED_i$):

$$ED_{prey} = \sum p_i ED_i \tag{5.1}$$

We used two-way analysis of variance (ANOVA) to compare the mean energy density of diets between reaches and by mouth state. Post hoc analysis was conducted using Tukey's HSD (Zar, 1984).

### 5.3.4 *Fish Growth*

We calculated the empirical growth rates of juvenile steelhead from recaptures of previously PIT-tagged fish. To avoid error associated with sampling, we only included specific growth rates from juvenile steelhead that had been at large for more than seven days between capture events. No fish were captured and recaptured exclusively during closed mouth conditions, so no comparisons between mouth conditions were possible.

To facilitate comparisons with other studies and to compensate for size-dependent growth rates of salmonids (Elliott et al., 1995; Sigourney et al., 2008; Sogard et al., 2009), we calculated a standardized mass-specific growth rate (SMSGR) (Ostrovsky, 1995):

$$SMSGR = \frac{w_2^b - w_1^b}{b \text{ x } t} \tag{5.2}$$

where $b$ is an allometric growth rate exponent (Ostrovsky, 1995), $t$ is the time (days) between capture events, and $W_1$ and $W_2$ are the fish weights (g) at the initial capture and recapture, respectively. We used a value of 0.31 for $b$, which is similar or a replacement to what has been calculated for other salmonids species (Elliott et al., 1995; Elliott & Hurley 1995, 1997; Sigourney et al., 2008; Vøllestad et al., 2004; Grade & Letcher, 2006) including juvenile steelhead (Heady, 2012). We also included the SMSGR from studies that determined the maximum growth of juvenile steelhead across different temperatures under controlled conditions. This included populations of juvenile steelhead from the American River, CA (Myrick & Cech, 2005), Battle Creek, CA (Heady, 2012), San Lorenzo River, CA (Heady, 2012), and Scott Creek, CA (Heady, 2012). Unless the SMSGR was already calculated (Heady, 2012), we used the mean starting mass and ending mass (Myrick & Cech, 2005) and only included studies that reported *ad libitum* feeding multiple times a day.

### 5.3.5 *Thermal exposure*

We used temperatures for the bioenergetics model inputs from two sources, water quality profiles taken during beach seining activities and with sensor encoded acoustic telemetry. Vertical water quality profiles were recorded with a YSI Model 85 handheld probe and consisted of measuring the dissolved oxygen, salinity, and temperature every 0.5 m from the surface to the bottom.

We surgically implanted temperature encoded acoustic transmitters into juvenile steelhead to document their thermal history in the RRE (Matsubu et al., 2017). We tagged 93 individual steelhead with sensor encoded acoustic transmitters (MM-412-T; 11.0 mm long × 6.6 mm wide × 6.1 mm high; 0.58 g in air; battery life = 10 d with a 10-s burst) between the spring and summer of 2014 and 2015. To prevent the spread of disease or pathogens, we soaked all transmitters and surgical equipment in a 10% povidone-iodine (Betadine) for 24 hours followed by a rinse in a sterile saline solution before the surgery. To ensure maximum control and minimal impact to the fish, we placed the fish ventral side up on a foam lined table with an anesthetic bath (MS-222) flowing over the gills. After wiping the incision site with a sterile saline solution, we inserted the transmitter into a 6-mm incision on the ventral side of the body cavity. We sutured the incision with a size 5-0 absorbable suture. After surgery, the fish were held in aerated water until fully recovered from the anesthetic (approximately 10 minutes) and then released into the wild.

To determine the thermal exposure and movements of juvenile steelhead, we detected tagged juvenile steelhead with mobile tracking and stationary receivers. The frequency, duration, and allocation of effort for mobile tracking depended on the number of active tags deployed and the last relocation of each tag. Mobile tracking surveys started either at the mouth or just downstream of a stationary receiver. We then tracked upstream until ending the survey at another stationary receiver; we located all active transmitters, or ran out of the allotted time. After the initial detection, we tracked tagged juvenile steelhead for at least 30 minutes. Mobile tracking typically occurred every day until we could no longer relocate any juvenile steelhead. For more details on the tagging procedures and tracking see Matsubu et al. (2017).

### 5.3.6 *Fish Performance*

We calculated the percent of maximum consumption ($P_{cmax}$), total consumption (g), and the growth potential of juvenile steelhead with Fish Bioenergetics 4.0 for R (Deslauriers et al., 2017), which is based on the Wisconsin Bioenergetics Model (Hanson et al., 1997). Parameters of the model specific to steelhead were included from Rand et al. (1993). We used literature values for the energy density (kJ/g) of the predator (4.0 kJ/g; Lowery & Beauchamp, 2015) and prey (Supplemental Table 5.1). For thermal inputs into Fish Bioenergetics 4.0 (Deslauriers et al., 2017), we used mean temperature of all detections weighted by hour for each fish. We acknowledge that the Wisconsin bioenergetics model assumes a daily time step, but the variable distribution of temperature detections and extended duration between recaptures prevents us from adopting this scale. We assumed the thermal conditions associated with detections represented time-weighted estimates of average daily thermal experience. Water quality profiles were averaged and interpolated across sampling dates for the thermal exposure outside of the battery life of the acoustically tagged individuals and for non-acoustically tagged fish.

The Wisconsin Bioenergetics Model (Hanson et al., 1997) is based on an energy balance equation where the consumption $C$ of prey biomass equals metabolic demands $M$, waste $W$, and any loss or gain in growth $G$. If the body mass, thermal experience, and diet are known, the model estimates the daily energy consumption required to achieve a particular final weight over the prescribed simulation period. Alternatively, if we know the consumption rate, thermal experience, and energy density of the prey, then the model can estimate a daily growth rate (Hanson et al., 1997). The simplified version of this model is as follows:

$$C = M + W + G \tag{5.3}$$

A typical application to determine factors limiting growth calculates $C$ as a proportion of the calculated maximum daily consumption rate $C_{max}$ (Beauchamp, 2009). The $P_{cmax}$ is calculated by determining the proportion of $C_{max}$ required to achieve overall consumption rate $C$.

$$C = p \, * C_{max} \tag{5.4}$$

### 5.3.7 *Sensitivity analysis*

To determine the sensitivity of growth to varying feeding rates and temperatures, we conducted simulations for two size classes of fish, juvenile steelhead entering the RRE during their first year of life (2.4 g), and individuals entering the RRE during their second year (10.0 g; Bond et al. 2008; Osterback et al., 2014; Martini-Lamb & Manning, 2011). Inputs used to simulate temperature-dependent growth rates include $P_{cmax}$, $ED_{prey}$, temperature, and body mass (Hanson et al., 1997; Beauchamp 2009).

To determine which combinations of $P_{cmax}$, $ED_{prey}$, and temperature are needed to reach the size for increased marine survival, we conducted additional simulations of growth predicting fish weight through time. Separate simulations were conducted for temperatures near the upper limit of temperatures observed (18-22 °C), representative $ED_{prey}$, and for size specific $P_{cmax}$ (± SD) of 2.4g and 10 g fish. We ran these simulations from the first day a fish entered the estuary through the end of the rearing season (day 150).

## 5.4 RESULTS

### 5.4.1 *Water Temperature*

The water temperatures varied among the RRE sample sites, through time, and among years (Fig. 5.2). There was more variation, both within and among years, at the lower sites than the upper sites. Temperatures at the freshwater-dominated sites were generally higher (approximately 3-5 °C) than the lower sites and increased early in the season to more than 20 °C between day 175 to 250, then gradually decreased as the season progressed. Temperatures at the lower two sites, Bridgehaven and Jenner Gulch, did not show a seasonal trend, rarely exceeded 20 °C, and were typically around 13 °C to 17.5 °C (Fig. 5.2).

### 5.4.2 *Diet*

Overall, the diet of juvenile steelhead was primarily composed of few taxa and varied spatially. The diet composition did not differ between the middle and lower reach (ANOSIM: R = 0.06, $P = 0.212$), but the upper reach was significantly different from the other two, lower reaches (ANOSIM: R = 0.2, $P = 0.001$). The diets in the lower and middle RRE were mainly composed of epibenthic crustaceans—the gammarid amphipods *Eogammarus confervicolus* and *Americorophium* spp., and the isopod *Gnorimosphaeroma insulare.* In addition to these epibenthic crustaceans observed in the diets from the lower estuary, the upper reach was more diverse with adult and aquatic life stages of insects including Chironomidae, Ephemeroptera, and Corixidae (Fig. 5.3).

The change in diet composition was reflected in the $ED_{prey}$ (mean [± SD] = 3.29 kJ/g ± 1.01). There was no difference between the $ED_{prey}$ between the lower (2.92 kJ/g ± 0.5), and middle (2.95 kJ/g ± 0.7) reaches or between open and closed mouth conditions (Tukey's HSD test: $P>0.05$). The increased consumption of adult insects in the upper reach led to higher $ED_{prey}$ (3.65 kJ/g ± 1.3) than the other two reaches (Tukey's HSD test: P<0.001).

### 5.4.3 *Growth and consumption rate*

We calculated the individual growth rates of 83 juvenile steelhead in the RRE from recaptured PIT- and acoustic- tagged fish. Of these, 15 individuals were initially tagged at the Austin Creek DSMT and recaptured throughout the estuary (Fig 5.4). Early in the season, there were two size classes observed for the recaptured fish; the smaller size class was composed of fish with an average weight of 2.4 grams and the larger size class of fish that weighed about 10.0 g (Fig. 5.4). Although most of the smaller fish were initially tagged at the upstream sites, fish that weighed less than 3.0 grams were both initially tagged and recaptured in the lower estuary (Fig. 5.4). Both size classes appear to be able to reach the 60.0g threshold for increased marine survival (Osterback et al., 2014), though some of the fish in the smaller initial size class did not reach the 60.0 g threshold by the latest sampling date (Fig 5.4). Juvenile steelhead rearing in the

RRE for several months their first year of life reach the same size as juvenile steelhead that spend multiple years in upstream tributaries (Hayes et al., 2008; McCarthy et al., 2009; Thompson & Beauchamp, 2016).

Juvenile steelhead in the RRE had relatively high growth and consumption rates. The SMSGR (6.13% ± 2.53) in the RRE was similar to, or higher than studies that fed juvenile steelhead *ad libitum* under controlled conditions at similar temperatures (Fig. 5.5; Heady, 2012; Myrick & Cech, 2004). Bioenergetics modeling revealed that juvenile steelhead foraged at approximately 54% (± 13%) of the maximum consumption rate. There was a positive relationship between steelhead size and $P_{cmax}$ (regression, $F_{1,83}$=12.03, p<0.01, $R^2$ =0.13), with smaller juvenile steelhead (< 30 g) foraging at a slightly lower rate ($P_{cmax}$ 0.49 ± 0.10).

### 5.4.4 *Growth Sensitivity Analysis*

The modeled growth rate potential for juvenile steelhead varied with fish size, reach, and temperature exposure. Similar to other studies (Beauchamp et al., 2009; McCarthy et al., 2009; McCullough et al., 2009; Thompson & Beauchamp, 2016), the temperature-dependent growth curve simulations show an eventual decrease at higher temperatures (Fig. 5.6). This decrease is more severe for the larger fish, with growth rates becoming negative (-0.01 g $g^{-1}$ $day^{-1}$) at the upper range of fish exposure temperatures for all modeled scenarios (23.0 °C). The growth potential of larger fish was up to 33.2% less than the smaller fish at the lower temperatures fish experienced. Foraging on the more energy dense diet in the upper estuary increased the growth rate potential and dampened some effects of higher temperatures (Fig. 5.6). There were no modeled scenarios with positive growth at temperatures greater than 23.1°C.

Steelhead consuming the more energy dense prey in the upper reach (3.65 kJ/g) had a higher growth rate potential (Fig 5.6). During open conditions, temperatures experienced in the upper reach (range = 18.1–23.0 °C) spanned a wide range of potential growth rates (2.4g; range = 0.10 – 0.00 g $g^{-1}$ $day^{-1}$, 10g; range = 0.07 – -0.01 g $g^{-1}$ $day^{-1}$). The maximum growth potential decreased during closed conditions (2.4g; range = 0.09 – 0.063 g $g^{-1}$ $day^{-1}$, 10 g range = 0.06 – 0.03 g $g^{-1}$ $day^{-1}$), but the minimum growth potential remained relatively high due to the lower maximum temperatures fish occupied (range = 19.6–21.6 °C) (Fig. 5.6.).

Modeled growth potential decreased in the lower and middle reaches due to foraging on a lower energy dense diet (2.93 kJ/g). Across the range of temperatures experienced by juvenile steelhead in these reaches (open; range = 15.0-19.1 °C, closed; range = 18.1-19.7 °C), the minimum growth potential remained relatively higher for both 2.4 g steelhead (open; range = 0.09 – 0.07 g $g^{-1}$ $day^{-1}$, closed; range = 0.08 – 0.07 g $g^{-1}$ $day^{-1}$) and 10.0 g steelhead (open; range = 0.06 – 0.04 g $g^{-1}$ $day^{-1}$, closed; range = 0.05 – 0.04 g $g^{-1}$ $day^{-1}$).

The simulations of growth through time demonstrated the increased ability for fish to reach the threshold for increased marine survival if they foraged on the more energy-dense diet under 22°C in the upper reach (Fig. 5.7). Furthermore, fish that foraged at the upper range of consumption rates would be able to reach the threshold faster and at higher temperatures. If fish fed on lower energy dense diets, they were not able to reach the threshold at temperatures greater than 20 °C, even if they increased their foraging rate. No feeding rate or diet composition was able to reach the threshold for increased marine survival (60 g; Bond et al., 2008; Osterback et al., 2014) at temperatures greater than 22 °C.

## 5.5 DISCUSSION

Empirical growth rates and modeled growth potential of juvenile steelhead in the RRE are not only similar or higher than those in productive coastal estuaries (Osterback et al., 2014) but rival the highest observed rates in the comparable literature (Heady, 2012; Myrick & Cech, 2005). Furthermore, when considering the influence of temperature on varying sizes of juvenile steelhead, this study confirms previous work regarding the increase in sensitivity with fish size (Beauchamp, 2009). The observed $P_{cmax}$ from this study exceeds or even doubles what has been observed for juvenile steelhead in tributaries (Goby et al., 2007; McCarthy et al., 2009; Thompson & Beauchamp, 2016). We conclude that the heterogeneous abiotic conditions and ample supply of prey contribute to the high growth rates of juvenile steelhead rearing in ICEs. For example, the higher energy dense prey ($ED_{prey}$ = 3.65 kJ/g ± 1.3) consumed in the warmer upper estuary compensated for some of the increased metabolic costs of increased temperatures (up to 23°C).

We did not expect juvenile steelhead in the RRE to have growth rates similar to juvenile steelhead fed *ad libitum* under controlled conditions, especially considering steelhead under controlled conditions were fed unnaturally high energy dense pellets (Myrick & Cech, 2005; Heady, 2012). One reason for the exceptionally high growth in the RRE may be attributed to the ability of juvenile steelhead to forage throughout the day while steelhead in the other studies were only fed specific times throughout the day. Furthermore, the juvenile steelhead under the controlled conditions were held at a few specific temperatures (Heady, 2012 [14°C, 20°C, and 24 °C]; Myrick & Cech, 2005 [11 °C, 15 °C, and 19 °C]) while juvenile steelhead in the RRE were exposed to a variety of temperatures which allowed steelhead to behaviourally thermoregulate (Matsubu et al., 2017; Chapter 3). Another consideration is a potential difference in the allocation of energy into either lipids or somatic growth (Brett & Groves, 1979; Post & Parkinson, 2001). The allocation of energy to somatic growth increases with predation risks (Post & Parkinson, 2001; Hurst & Conover, 2003; Biro et al., 2005). We hypothesize that the increased predation risks in the RRE has led to more energy being allocated to somatic growth while the fish in the artificial settings have lower predation risks allowing the allocating of more energy to lipids.

Most of the literature regarding the fast growth of juvenile steelhead in ICEs is derived from Scott Creek Lagoon, California (Bond et al., 2008; Hayes et al., 2008, Osterback et al., 2014). We hypothesize that the same conditions led to the fast growth rates of steelhead that rear in the Scott Creek Lagoon (Hayes et al., 2008, Osterback et al., 2014) but comparisons between the two systems must be limited due some notable contrasts between Scott Creek and the Russian River. A pronounced difference is a disparity in scale, with the Russian River watershed (3,846 $km^2$), considerably larger than the Scott Creek watershed (78 $km^2$). Furthermore, the timing of mouth closures is much different, with the Scott Creek mouth typically closing once during the dry season for longer periods (mean duration of water year 2002-2004 = 241 days; Osterback et al., 2018) and the RRE undergoing many (0-15) closures that typically last less than 14 days (Behrens et al., 2013). A major factor contributing to the differences of mouth dynamics are the inflows during the dry season, where typical Russian River flows are 2-4 $m^3s^{-1}$ while the Scott Creek has much lower flows (0.1 $m^3s^{-1}$). In addition, water just upstream of the Scott Creek estuary is approximately 2.5 °C cooler than the temperatures within the Scott Creek estuary, while temperatures in most of the river above the RRE are similar to the upper estuary (Martini-Lamb & Manning, 2014; Fullerton et al., 2018; Osterback et al., 2018). In the Russian River, the only potential cooler water sources are likely from groundwater and tributaries that typically become fully disconnected and inaccessible during the dry season in open mouth conditions. In contrast, tributaries connecting to the RRE become re-joined when water elevations increase during closed mouth conditions. Juvenile steelhead have been observed taking advantage of cooler temperatures (approximately 2.5 – 4.0 °C) in and around tributaries only during closed mouth conditions (Matsubu et al., 2017).

Due to the sporadic and often brief timing of mouth closures in the RRE, we were not able to empirically compare the growth of juvenile steelhead between open and closed mouth conditions. However, the growth simulations do allow feasible comparisons between mouth conditions. When considering the growth simulations from this study, and documented movements and use of thermal refugia during closed mouth conditions (Matsubu et al., 2017), we conclude that fish can grow fast enough to reach the size for increased marine survival as seen in other studies (approximately 60g; Bond et al., 2008; Osterback et al., 2014) during open and closed conditions as long as fish can find habitat below 22 °C. Habitat occupied by juvenile steelhead was above 22 °C in the upper estuary after fish have been able to rear for a few weeks early in their outmigration. This warming period early in the season was potentially beneficial as it provided the opportunity for fish to move into the lower reaches and possibly acclimate to the saline conditions while in the cooler temperatures of the lower estuary. Evidence to support this is the lack of recaptures in the upper estuary during the warmest time of year. Although temperatures can rise above 22 °C during closed mouth conditions, changes in estuarine hydrology during closed conditions can provide compensation. For example, the increased stratification and reconnection to intermittent tributaries (Matsubu et al., 2017) provides juvenile steelhead increased opportunities to behaviourally mediate the high temperatures when less stressful temperatures are available (Berman & Quinn, 1991; Tiffan et al., 2009; Armstrong et al., 2013).

We hypothesize that the importance of ICE habitats to juvenile salmonids will increase with the anticipated adverse effects to upstream habitats from climate change and human population growth (Wenger et al., 2011; Moyle et al., 2019). The survival of juvenile salmonids in intermittent streams, common in Mediterranean climates where intermittent estuaries occur, is directly linked to flow (Grantham et al., 2012; Woelfle-Erkine et al., 2017; Obedzinski et al., 2018). Water extraction is expected to increase with population growth (Koniecski & Heilman, 2004; Grantham et al., 2010), and the changes to projected summer stream flows due to climate change (Mannion, 1995; Karl et al., 2009) will negatively impact juvenile salmon rearing habitat upstream, especially in intermittent streams (Grantham et al., 2012; NMFS 2012). The low flows associated with lower survival of juvenile salmonids in intermittent streams allow ICE mouths to close and remain closed for extended periods. While elevated water levels in a closed ICE increase the amount of habitat in the estuary, it also reconnects tributaries that empty directly into the estuary. A naturally functioning ICE may buffer some of the negative consequences to upstream habitats, but there remains uncertainty regarding water quality conditions (e.g., hypoxia) in absence of the artificially high freshwater inflows (Becker et al., 2009; Whitfield et al., 2012), and the ability for other anadromous salmonids to migrate to and from the ocean.

A diversity of life history strategies that use different habitats allows populations of salmonids to buffer major disturbances to a single habitat, including ocean conditions, estuarine conditions, or upstream habitats (Katz et al., 2013; Moyle et al., 2013; Moore et al., 2014; Manhard et al., 2017). We contend that only using growth as a metric to evaluate conditions overlooks complex and important ecological processes, including estuarine contributions to life history complexity and survival. Although it's counterintuitive, accelerated growth for juvenile salmonids prior to outmigration can alter the life history trajectories that can decrease the overall population productivity (Lew, 2003; Tillotson & Quinn, 2016). Tillotson and Quinn (2016) found that faster growth of juvenile Sockeye salmon (*O. nerka*) led to an increased rate of age-1 smolts when, historically, that population was mostly age-2 smolts. These age-1 smolts were smaller than the age-2 smolts and, due to size-selective marine survival, the smaller age-1 smolts had approximately twice the ocean mortality of age-2 smolts. The changing thermal regime, due to climate change and the high discrepancy between growth in upstream and estuarine habitats, likely impacts the life history diversity of steelhead in the Russian River which warrants further research.

The effects of climate change and management will continue to alter the geomorphology and hydrology of ICEs (Anthony et al., 2009; Brito et al., 2012; Chapman, 2012) and can change the connectivity of different estuary types which would create new challenges for diadromous fishes (Haines and Thom, 2007; Gillanders et al., 2011). These results have implications for the recovery of anadromous salmonids that use ICEs. The fast growth rates of juvenile steelhead rearing in ICEs with the bioenergetics modeling corroborates similar growth rates as seen in other systems and has identified that the combination of ample foraging opportunities and heterogenous thermal conditions allow juvenile steelhead to maximize their growth potential. With the degradation of estuarine habitats and the decline of salmonids throughout California (Moyle et al., 2017), this research has not only reiterated the unique importance of ICEs for steelhead but has identified that increased growth potential will only occur when adequate temperatures and prey are available. We cannot confidently conclude that conditions during an extended closure would benefit steelhead due to the uncertainty regarding water quality conditions and prey resources of an extended closure. An improved understanding of ICE hydrology and prey resources would provide a better understanding of the tradeoffs for managing these systems in the face of climate change.

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## 5.8 FIGURES

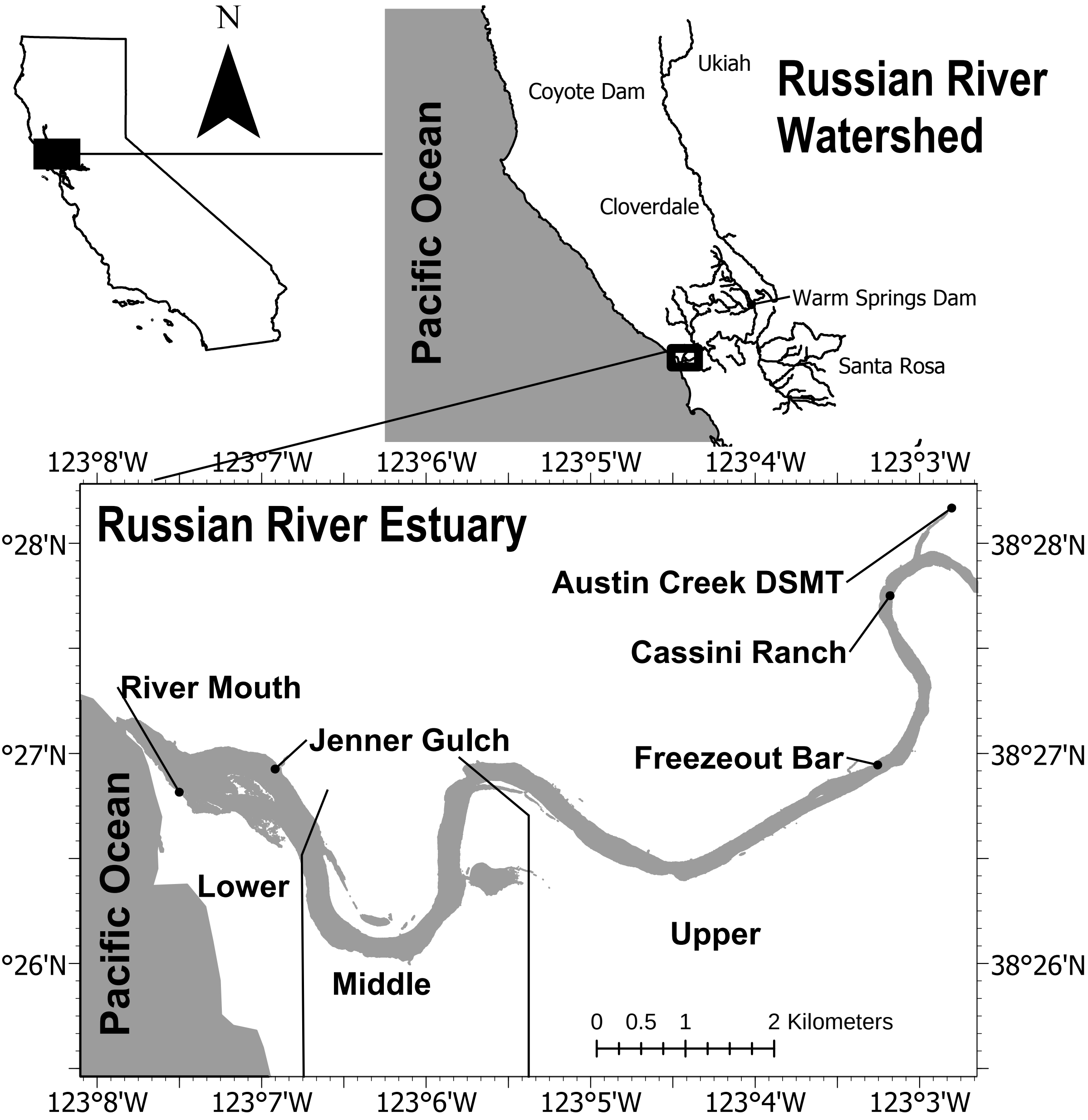

Figure 5.1. Map of the sampling sites and reaches in the Russian River estuary.

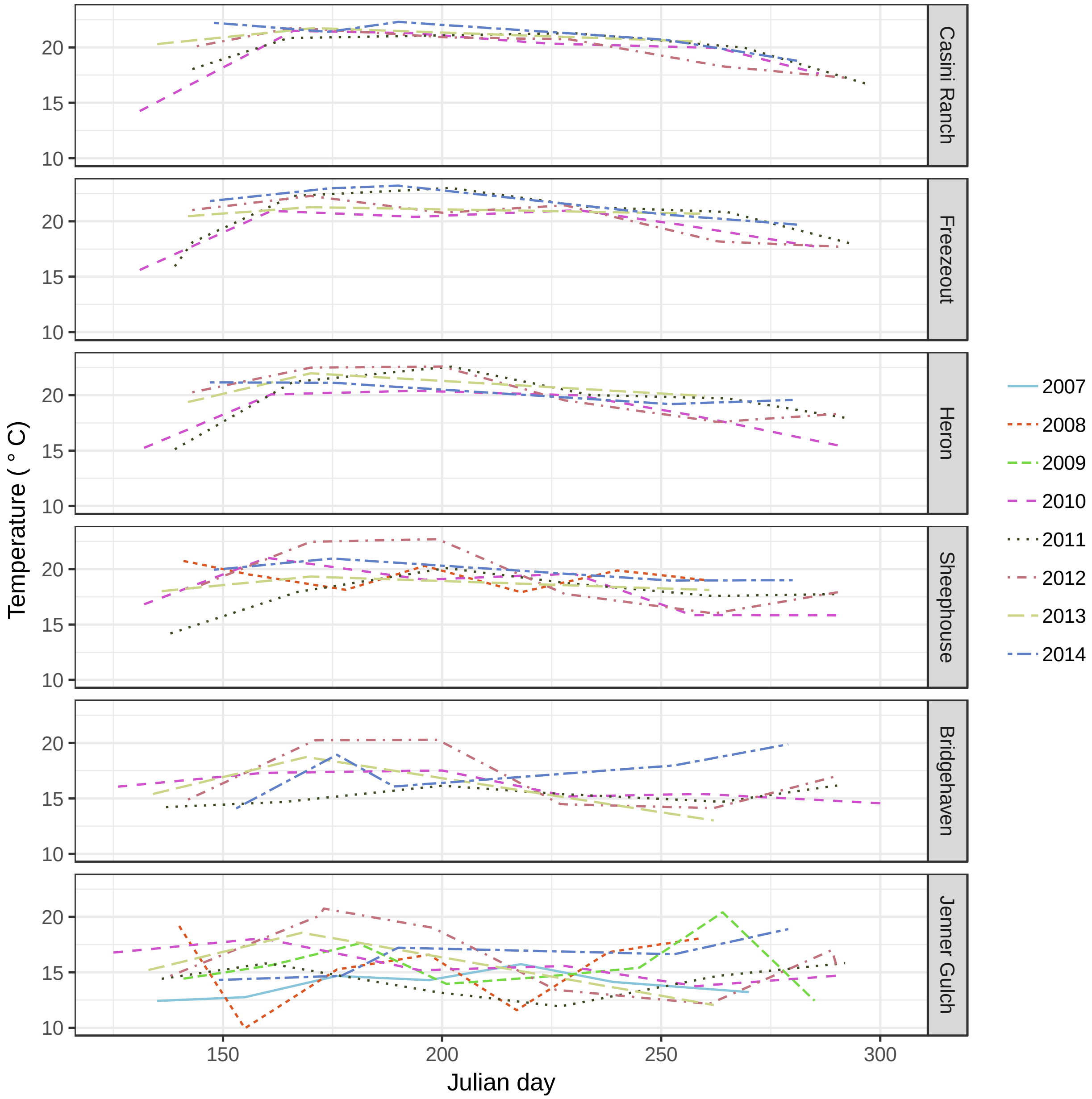

Figure 5.2. The mean temperatures from the water quality profiles at all of the sites juvenile steelhead were recaptured. These were used as inputs into the bioenergetics model for the recaptured fish that were not tagged with sensor encoded acoustic telemetry. Shaded range represents the zone where growth is within 10% of the maximum potential growth.

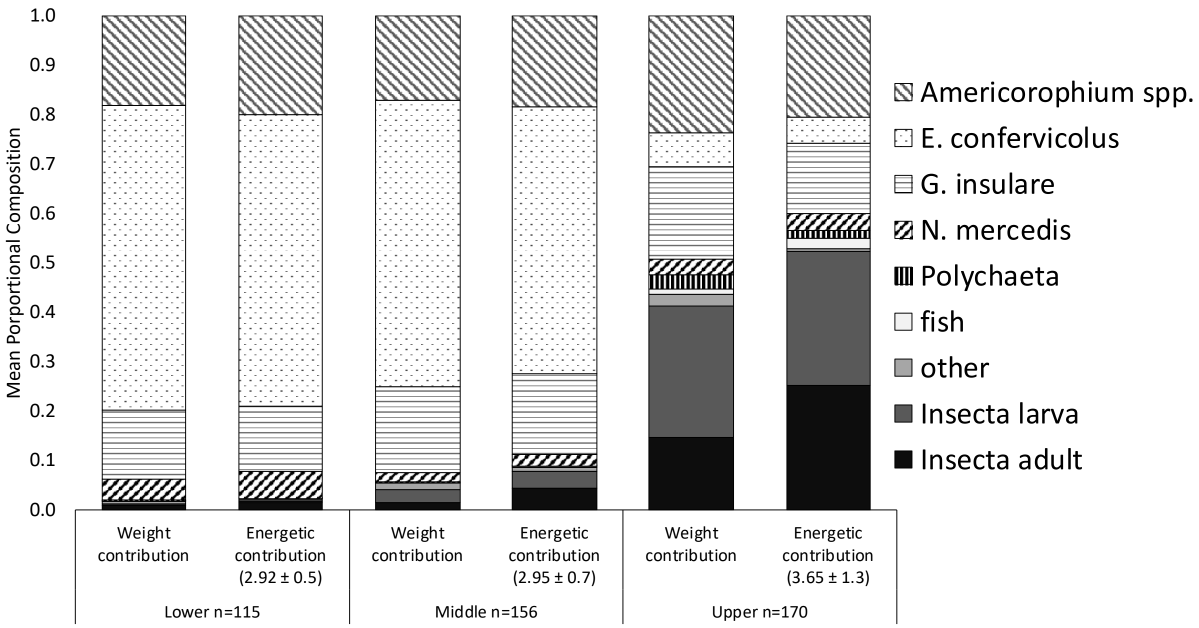

Figure 5.3. The mean proportional gravimetric composition and energetic composition (kJ/g) of juvenile steelhead diet in the Russian River estuary by reach.

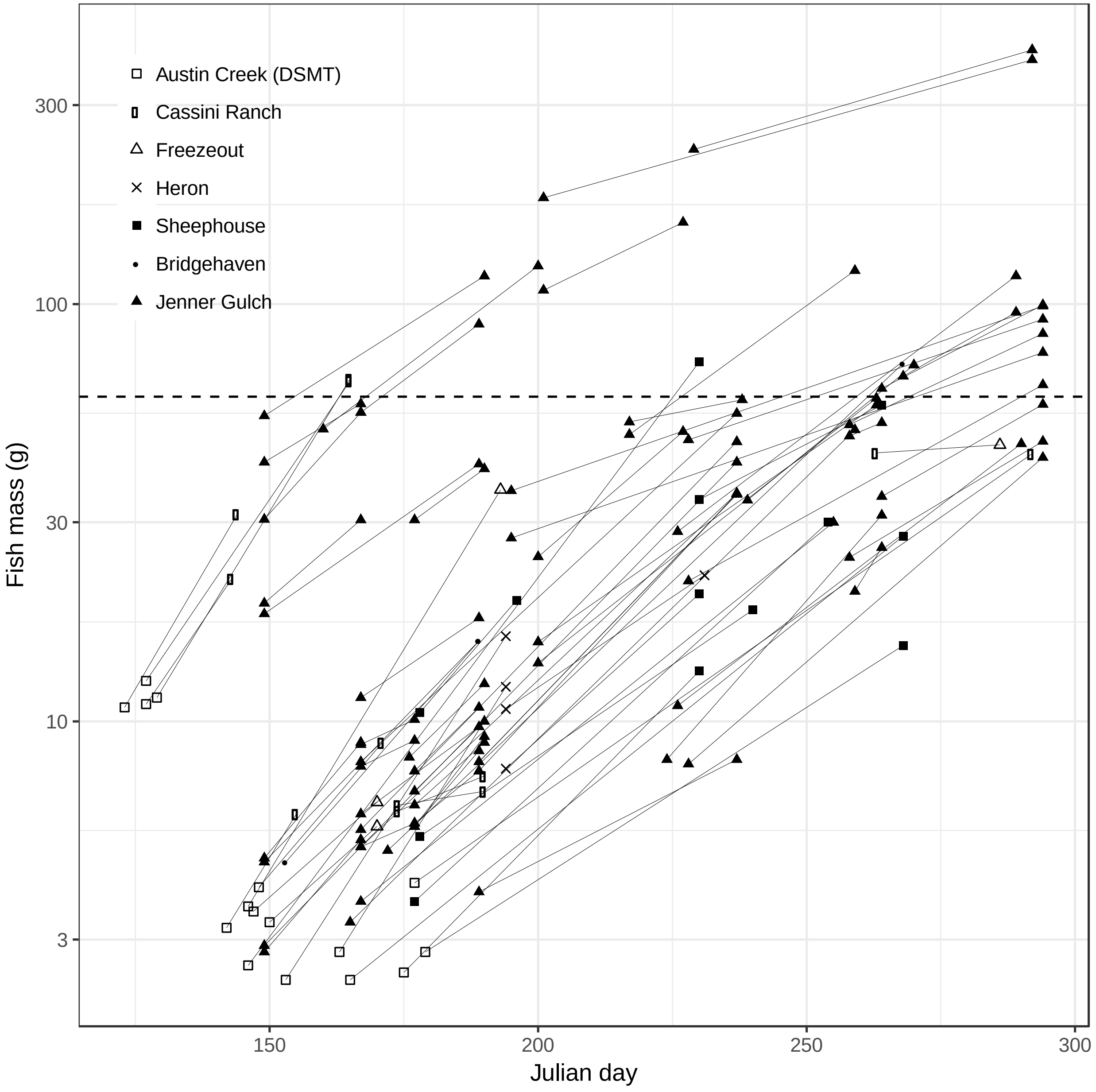

Figure 5.4. The initial weight at capture and recapture of juvenile steelhead in the Russian River estuary. The symbol represents the location of capture, which was either Austin Creek or in the Estuary. The dotted horizontal line represents the 60 g threshold where juvenile steelhead have increased marine survival (Osterback et al. 2014).

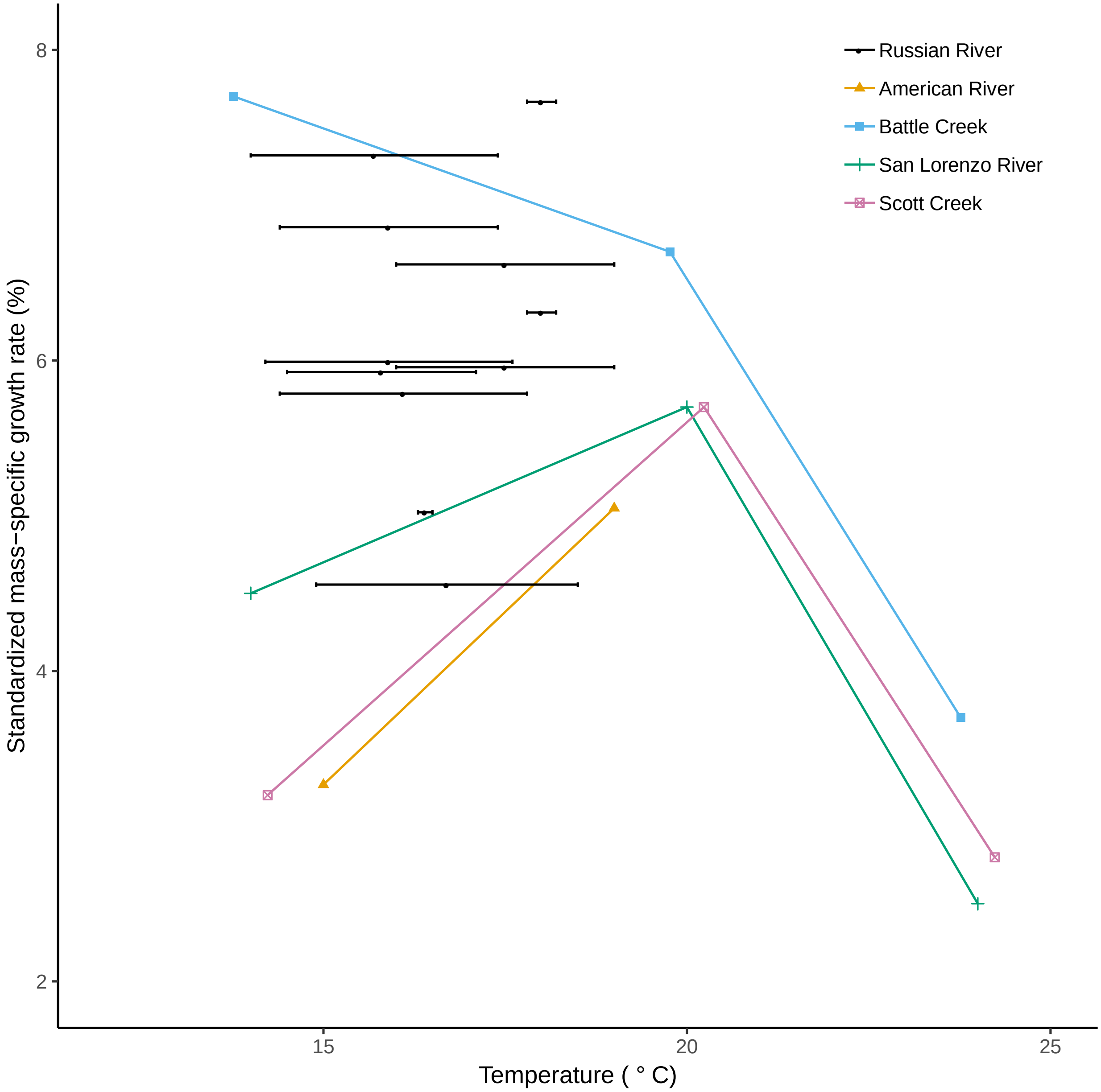

Figure 5.5. Comparisons of empirical growth with other systems. The standardized mass-specific growth (%) and temperature (mean ± SD; Matsubu et al., 2017) of recaptured juvenile steelhead tagged with sensor encoded acoustic telemetry in the Russian River estuary (Black). The coloured lines represent the relationship between the standardized mass-specific growth rate and temperature for juvenile steelhead from American River, CA (Myrick & Cech 2005), Battle Creek, CA, San Lorenzo River, CA, and Scott Creek, CA (Heady 2012).

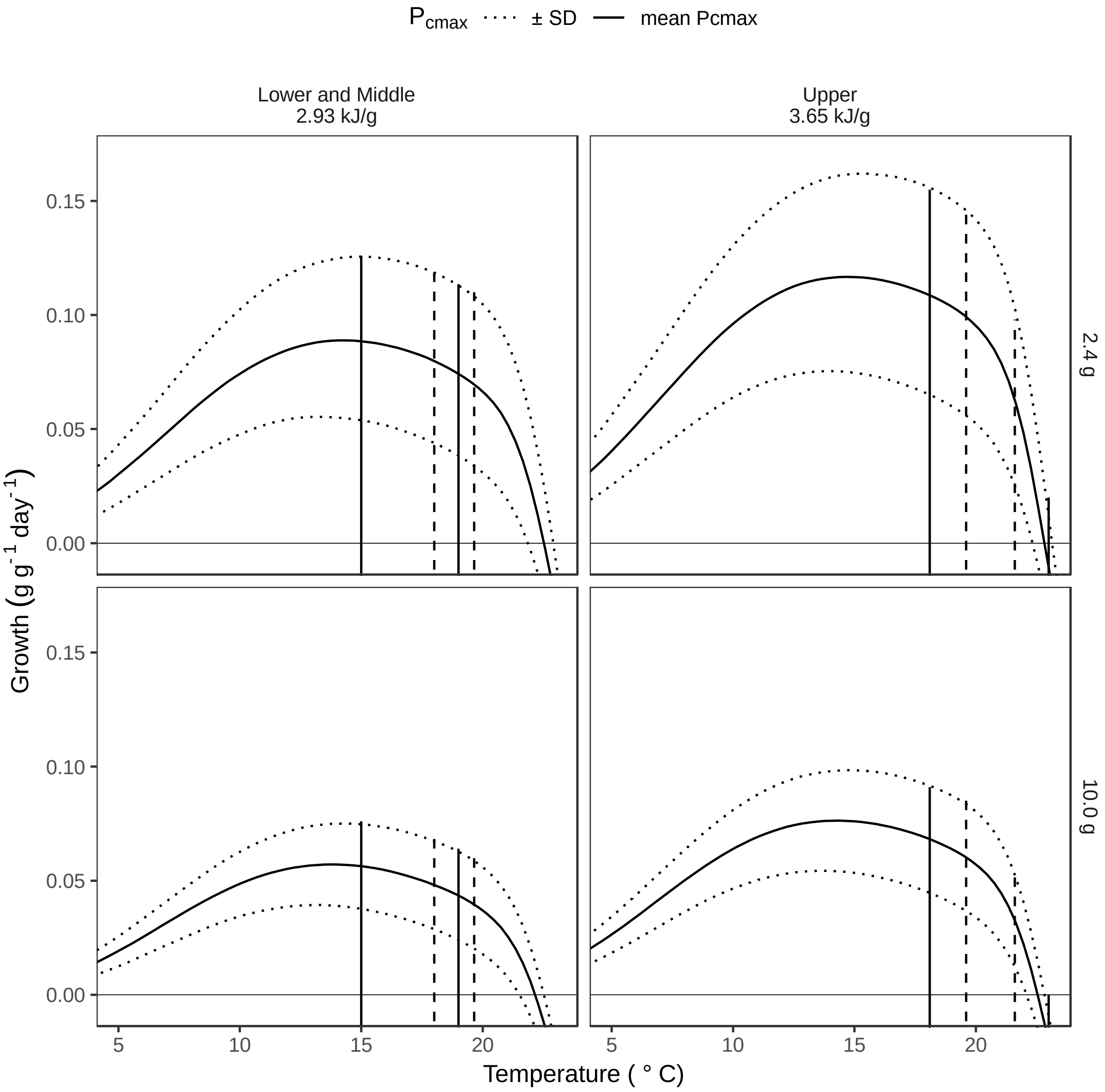

Figure 5.6. The temperature-dependent growth curves for juvenile steelhead. The top two panels were simulations for 2.4g steelhead and the bottom two were simulations for 10.0g steelhead. The left panels were simulations of juvenile steelhead foraging on a 2.93 kJ/g diet and the right panels were of juvenile steelhead foraging on a 3.65 kJ/g diet. The $P_{cmax}$ was 0.49 (± 0.10). The dotted curves represent growth at $P_{cmax}$ ± SD. The dashed vertical lines represent temperatures fish were exposed to during closed mouth conditions and the solid vertical lines represent the range of temperatures fish were exposed to during open mouth conditions in the respective reaches.

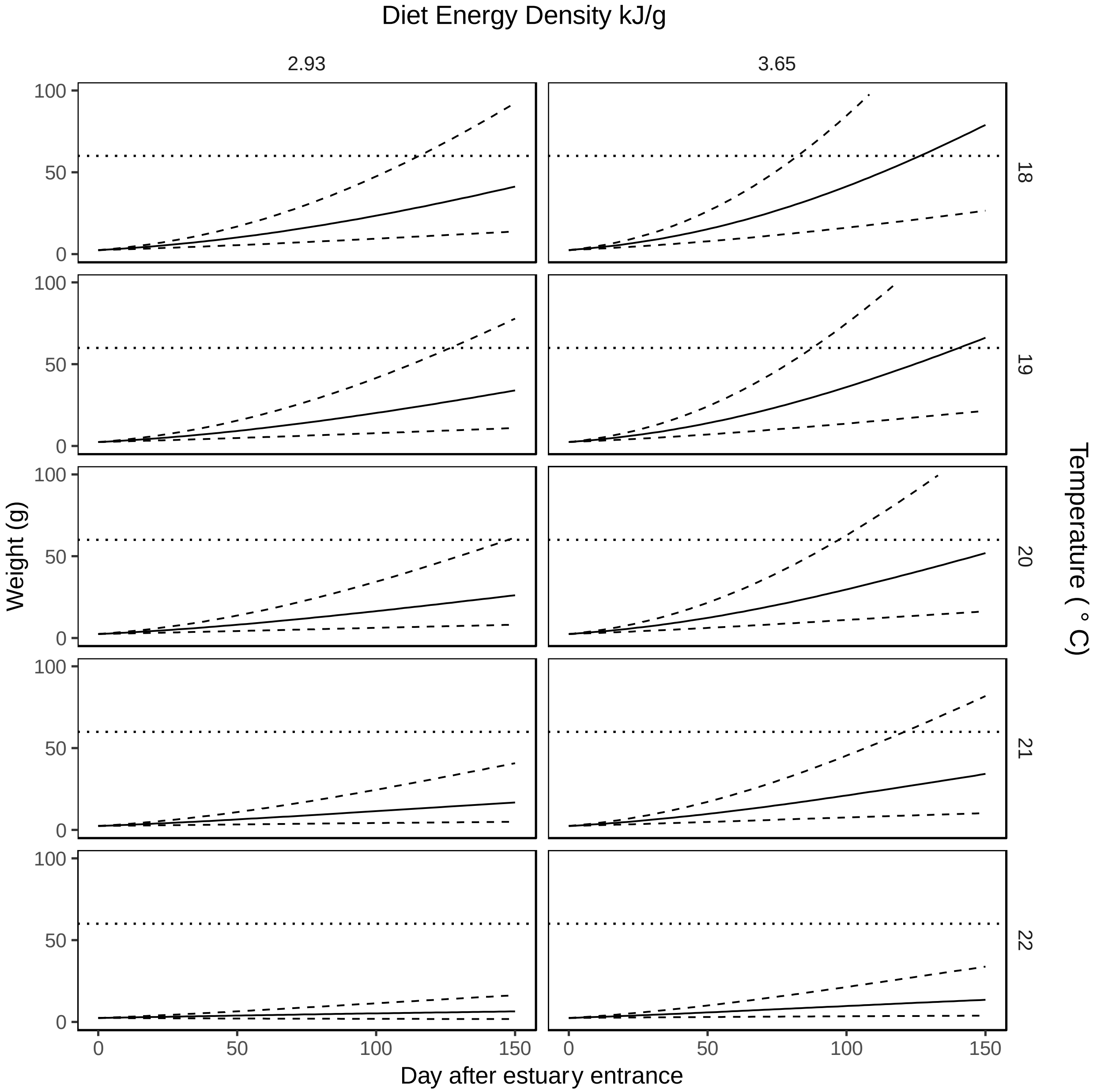

Figure 5.7. Output from bioenergetics simulations of juvenile steelhead. Simulations were conducted for 18 °C, 19 °C, 20 °C, 21 °C and 22 °C for 2.4 g fish foraging on a 2.93 kJ/g (left panels) and a 3.65 kJ/g (right panels) diet. The dotted horizontal line represents the 60 g threshold where juvenile steelhead have increased marine survival. The solid black line represents fish foraging at mean $P_{cmax}$ of 0.49. The dashed curves represent growth at $P_{cmax}$ ± SD (0.10).

## 5.9 SUPPLEMENTAL TABLES

Table 5.1. Table of prey taxa found in more than 1% of the juvenile steelhead lavage samples pooled across all months and sizes of steelhead. Energy density values were obtained from Grey 2005; Cordell et al. 2011; David et al. 2014 and McCarthy et al. 2009.

| Taxon | Percent occurrence (%) | Numerical composition (%) | Gravimetric composition (%) | Energy Density (kJ/g) |
|---|---:|---:|---:|---:|
| *Americorophium spinicorne* | 63.49% | 16.51% | 7.93% | 3.04 |
| *Gnorimosphaeroma insulare* | 45.50% | 14.59% | 13.54% | 2.65 |
| *Eogammarus confervicolus* | 45.14% | 20.50% | 42.44% | 2.65 |
| Corixidae | 22.39% | 2.00% | 0.80% | 7.97 |
| Chironomidae pupa | 19.27% | 9.00% | 5.03% | 3.83 |
| Ephemeroptera nymph | 18.90% | 7.48% | 2.48% | 3.66 |
| Chironomidae larva | 14.13% | 5.21% | 1.85% | 2.58 |
| Hydrobiidae adult | 13.76% | 2.35% | 1.74% | 0.68 |
| *Neomysis mercedis* | 13.03% | 3.89% | 6.23% | 3.55 |
| *Americorophium stimpsoni* | 5.87% | 0.92% | 0.30% | 3.04 |
| Chironomidae adult | 5.50% | 1.38% | 0.52% | 3.83 |
| Ephemeroptera adult | 5.32% | 11.59% | 11.71% | 5.07 |
| Ephydridae adult | 5.14% | 0.39% | 0.07% | 8.92 |
| Nereididae | 5.14% | 0.85% | 2.57% | 1.98 |
| Empididae adult | 4.22% | 0.48% | 0.05% | 8.98 |
| Fish | 3.67% | 0.22% | 1.52% | 6.83 |
| Aphididae adult | 2.57% | 0.07% | 0.01% | 10.93 |
| Psocoptera adult | 2.57% | 0.59% | 0.02% | 7.41 |
| Araneae adult | 2.20% | 0.07% | 0.01% | 5.32 |
| Cicadellidae adult | 2.20% | 0.38% | 0.09% | 10.93 |
| Diptera adult | 2.20% | 0.05% | 0.01% | 8.92 |
| Formicidae adult | 1.83% | 0.19% | 0.13% | 5.68 |
| Lygaeidae adult | 1.47% | 0.06% | 0.02% | 10.93 |
| Nematoda adult | 1.47% | 0.07% | 0.00% | 3.00 |
| Chalcidoidea adult | 1.10% | 0.03% | 0.00% | 12.67 |
| Coleoptera adult | 1.10% | 0.03% | 0.02% | 7.97 |

Table 5.2. Summary of bioenergetics inputs for recaptured steelhead with the dates of capture and recapture, the weights (g), the $P_{cmax}$, total consumption, and standardized mass-specific growth rate (SMSGR).

| Fish ID | Tagging Date | Recapture Date | Tagging location | Recapture Location | Initial weight (g) | Final weight (g) | $P_{cmax}$ | Total consumption (g) | SMSGR (% body wt day) |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 8/27/07 | 9/27/07 | Jenner gulch | Jenner gulch | 33.9 | 71.5 | 0.66 | 178.55 | 8.07 |
| 2 | 6/26/08 | 7/14/08 | Sheephouse | Sheephouse | 10.5 | 19.5 | 0.55 | 41.56 | 7.86 |
| 3 | 8/4/08 | 8/25/08 | Jenner gulch | Jenner gulch | 52.2 | 59.0 | 0.40 | 88.06 | 2.03 |
| 4 | 6/26/08 | 8/27/08 | Sheephouse | Sheephouse | 5.3 | 18.5 | 0.39 | 79.86 | 4.13 |
| 5 | 8/4/08 | 9/15/08 | Jenner gulch | Jenner gulch | 48.7 | 120.4 | 0.76 | 424.08 | 8.30 |
| 6 | 8/4/08 | 8/25/08 | Jenner gulch | Jenner gulch | 52.2 | 59.0 | 0.40 | 88.06 | 2.03 |
| 7 | 8/12/09 | 9/21/09 | Jenner gulch | Jenner gulch | 8.1 | 31.2 | 0.69 | 125.59 | 8.01 |
| 8 | 5/26/10 | 8/18/10 | Austin Creek | Sheephouse | 2.6 | 72.7 | 0.62 | 293.66 | 9.34 |
| 9 | 5/26/10 | 7/12/10 | Austin Creek | Freezeout | 3.6 | 35.9 | 0.71 | 139.57 | 10.62 |
| 10 | 6/2/10 | 7/13/10 | Austin Creek | Heron | 2.4 | 16.0 | 0.57 | 59.42 | 8.26 |
| 11 | 6/12/10 | 7/13/10 | Austin Creek | Heron | 2.8 | 12.1 | 0.56 | 40.06 | 8.22 |
| 12 | 6/14/10 | 9/16/10 | Jenner gulch | Jenner gulch | 3.3 | 50.0 | 0.59 | 274.92 | 6.57 |
| 13 | 6/24/10 | 8/18/10 | Austin Creek | Sheephouse | 2.5 | 13.2 | 0.40 | 49.35 | 5.26 |
| 14 | 7/13/10 | 8/19/10 | Heron | Heron | 10.7 | 22.4 | 0.42 | 66.76 | 4.68 |
| 15 | 7/13/10 | 8/18/10 | Heron | Sheephouse | 7.7 | 20.2 | 0.43 | 56.89 | 5.88 |
| 16 | 7/14/10 | 10/21/10 | Jenner gulch | Jenner gulch | 35.7 | 99 | 0.49 | 494.35 | 3.67 |
| 17 | 7/14/10 | 10/21/10 | Jenner gulch | Jenner gulch | 27.5 | 76.6 | 0.46 | 388.03 | 3.40 |
| 18 | 8/16/10 | 10/21/10 | Jenner gulch | Jenner gulch | 7.9 | 42.9 | 0.57 | 177.69 | 6.40 |
| 19 | 8/16/10 | 10/21/10 | Jenner gulch | Jenner gulch | 21.7 | 64.1 | 0.52 | 252.48 | 5.06 |
| 20 | 8/16/10 | 10/21/10 | Jenner gulch | Jenner gulch | 47.3 | 92.0 | 0.48 | 335.54 | 3.70 |
| 21 | 8/18/10 | 9/21/10 | Sheephouse | Sheephouse | 34.0 | 57.3 | 0.42 | 121.90 | 4.97 |
| 22 | 9/15/10 | 10/21/10 | Jenner gulch | Jenner gulch | 24.7 | 46.9 | 0.49 | 119.02 | 5.32 |
| 23 | 9/15/10 | 10/21/10 | Jenner gulch | Jenner gulch | 51.4 | 85.0 | 0.51 | 194.53 | 5.13 |
| 24 | 9/15/10 | 9/21/10 | Jenner gulch | Jenner gulch | 48.3 | 52.0 | 0.43 | 26.20 | 4.14 |
| 25 | 9/16/10 | 9/21/10 | Jenner gulch | Jenner gulch | 20.5 | 26.1 | 0.79 | 24.01 | 12.79 |
| 26 | 9/20/10 | 10/13/10 | Cassini Ranch | Freezeout | 44.0 | 46.0 | 0.32 | 66.03 | 0.63 |
| 27 | 9/21/10 | 10/21/10 | Jenner gulch | Jenner gulch | 34.6 | 57.5 | 0.51 | 123.06 | 5.50 |
| 28 | 9/21/10 | 10/21/10 | Jenner gulch | Jenner gulch | 62.8 | 99.6 | 0.56 | 201.70 | 5.96 |
| 29 | 5/7/11 | 5/23/11 | Austin Creek | Cassini Ranch | 11.0 | 22.0 | 0.62 | 43.61 | 10.16 |
| 30 | 5/7/11 | 6/14/11 | Austin Creek | Cassini Ranch | 12.5 | 65.5 | 0.79 | 220.94 | 12.46 |
| 31 | 5/9/11 | 6/14/11 | Austin Creek | Cassini Ranch | 11.4 | 66.3 | 0.86 | 221.88 | 13.83 |
| 32 | 6/9/11 | 7/19/11 | Jenner gulch | Jenner gulch | 50.2 | 123.5 | 0.73 | 379.30 | 8.74 |
| 33 | 7/19/11 | 9/20/11 | Jenner gulch | Jenner gulch | 13.8 | 59.5 | 0.63 | 271.73 | 6.62 |
| 34 | 7/19/11 | 8/15/11 | Jenner gulch | Jenner gulch | 24.8 | 49.5 | 0.69 | 142.64 | 7.72 |
| 35 | 7/19/11 | 9/20/11 | Jenner gulch | Jenner gulch | 15.5 | 57.3 | 0.60 | 260.81 | 5.99 |

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|---|---|---|---|---|---|---|---|---|---|
| 36 | 7/20/11 | 8/15/11 | Jenner gulch | Jenner gulch | 108.0 | 157.1 | 0.72 | 357.97 | 6.53 |
| 37 | 7/20/11 | 10/19/11 | Jenner gulch | Jenner gulch | 179.9 | 385.5 | 0.66 | 1710.49 | 4.72 |
| 38 | 8/17/11 | 10/19/11 | Jenner gulch | Jenner gulch | 235.0 | 407.0 | 0.68 | 1328.54 | 5.16 |
| 39 | 5/2/12 | 5/23/12 | Austin Creek | Cassini Ranch | 10.8 | 31.4 | 0.8 | 83.90 | 12.60 |
| 40 | 6/13/12 | 9/24/12 | Austin Creek | Sheephouse | 2.4 | 27.8 | 0.37 | 128.57 | 4.67 |
| 41 | 6/20/12 | 9/24/12 | Jenner gulch | Bridgehaven | 4.9 | 72.2 | 0.6 | 344.76 | 7.16 |
| 42 | 6/25/12 | 10/18/12 | Austin Creek | Cassini Ranch | 4.1 | 43.8 | 0.46 | 228.94 | 4.71 |
| 43 | 6/27/12 | 9/24/12 | Austin Creek | Sheephouse | 2.8 | 15.2 | 0.31 | 69.99 | 3.44 |
| 44 | 8/13/12 | 10/15/12 | Jenner gulch | Jenner gulch | 28.5 | 116.9 | 0.69 | 480.95 | 7.94 |
| 45 | 8/13/12 | 10/16/12 | Jenner gulch | Jenner gulch | 10.9 | 46.3 | 0.54 | 198.06 | 5.98 |
| 46 | 9/24/12 | 10/15/12 | Jenner gulch | Jenner gulch | 67.2 | 95.6 | 0.61 | 169.71 | 6.54 |
| 47 | 5/27/13 | 6/19/13 | Austin Creek | Freezeout | 3.5 | 6.4 | 0.75 | 19.85 | 4.25 |
| 48 | 5/28/13 | 6/20/13 | Austin Creek | Cassini Ranch | 4.0 | 8.9 | 0.53 | 25.73 | 6.06 |
| 49 | 5/30/13 | 6/19/13 | Austin Creek | Freezeout | 3.3 | 5.6 | 0.72 | 15.82 | 4.16 |
| 50 | 5/22/14 | 6/4/14 | Austin Creek | Cassini Ranch | 3.2 | 6.0 | 0.38 | 15.55 | 7.66 |
| 51 | 5/29/14 | 6/16/14 | Jenner gulch | Jenner gulch | 2.8 | 5.2 | 0.45 | 13.28 | 5.22 |
| 52 | 5/29/14 | 6/16/14 | Jenner gulch | Jenner gulch | 4.7 | 8.9 | 0.52 | 22.28 | 6.34 |
| 53 | 5/29/14 | 8/25/14 | Jenner gulch | Jenner gulch | 2.9 | 41.8 | 0.57 | 213.76 | 6.56 |
| 54 | 5/29/14 | 7/9/14 | Jenner gulch | Jenner gulch | 54.0 | 116.8 | 0.66 | 355.41 | 7.32 |
| 55 | 5/29/14 | 6/16/14 | Jenner gulch | Jenner gulch | 41.8 | 57.7 | 0.56 | 94.99 | 5.99 |
| 56 | 5/29/14 | 6/16/14 | Jenner gulch | Jenner gulch | 19.2 | 30.4 | 0.45 | 71.85 | 6.86 |
| 57 | 5/29/14 | 7/8/14 | Jenner gulch | Bridgehaven | 4.6 | 15.6 | 0.56 | 58.29 | 5.96 |
| 58 | 5/29/14 | 6/16/14 | Jenner gulch | Jenner gulch | 30.5 | 55.0 | 0.78 | 116.57 | 10.37 |
| 59 | 5/29/14 | 7/8/14 | Jenner gulch | Jenner gulch | 18.1 | 41.4 | 0.54 | 134.19 | 5.79 |
| 60 | 6/2/14 | 7/8/14 | Bridgehaven | Bridgehaven | 4.6 | 15.6 | 0.55 | 57.91 | 6.62 |
| 61 | 6/16/14 | 8/25/14 | Jenner gulch | Jenner gulch | 8.0 | 54.7 | 0.62 | 254.21 | 7.15 |
| 62 | 6/16/14 | 6/26/14 | Jenner gulch | Jenner gulch | 8.8 | 10.1 | 0.35 | 11.18 | 2.76 |
| 63 | 6/16/14 | 8/25/14 | Jenner gulch | Jenner gulch | 5.5 | 46.8 | 0.62 | 218.58 | 7.36 |
| 64 | 6/16/14 | 6/26/14 | Jenner gulch | Jenner gulch | 7.8 | 9.0 | 0.35 | 10.17 | 2.77 |
| 65 | 6/16/14 | 9/12/14 | Jenner gulch | Jenner gulch | 3.7 | 30.0 | 0.48 | 156.91 | 5.02 |
| 66 | 6/16/14 | 8/25/14 | Jenner gulch | Jenner gulch | 5.0 | 35.2 | 0.55 | 166.63 | 6.31 |
| 67 | 6/16/14 | 7/8/14 | Jenner gulch | Jenner gulch | 6.0 | 9.7 | 0.42 | 23.88 | 4.10 |
| 68 | 6/16/14 | 7/8/14 | Jenner gulch | Jenner gulch | 11.4 | 17.7 | 0.45 | 39.58 | 4.56 |
| 69 | 6/16/14 | 6/26/14 | Jenner gulch | Jenner gulch | 5.0 | 5.7 | 0.32 | 6.83 | 2.20 |
| 70 | 6/16/14 | 7/8/14 | Jenner gulch | Jenner gulch | 55.0 | 89.6 | 0.71 | 187.94 | 8.29 |
| 71 | 6/23/14 | 7/9/14 | Cassini Ranch | Cassini Ranch | 6.1 | 7.4 | 0.37 | 13.33 | 2.18 |
| 72 | 6/23/14 | 7/9/14 | Cassini Ranch | Cassini Ranch | 6.3 | 6.8 | 0.31 | 11.06 | 0.85 |
| 73 | 6/25/14 | 7/9/14 | Jenner gulch | Jenner gulch | 8.2 | 12.3 | 0.51 | 22.87 | 5.92 |
| 74 | 6/26/14 | 7/9/14 | Jenner gulch | Jenner gulch | 6.8 | 10.0 | 0.49 | 17.88 | 5.71 |
| 75 | 6/26/14 | 7/9/14 | Jenner gulch | Jenner gulch | 5.6 | 9.2 | 0.55 | 18.27 | 7.04 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 76 | 6/26/14 | 7/9/14 | Jenner gulch | Jenner gulch | 6.3 | 8.9 | 0.45 | 15.37 | 4.96 |
| 77 | 6/26/14 | 7/8/14 | Jenner gulch | Jenner gulch | 5.6 | 8.5 | 0.51 | 15.33 | 6.33 |
| 78 | 6/26/14 | 7/8/14 | Jenner gulch | Jenner gulch | 7.6 | 10.8 | 0.49 | 17.52 | 5.80 |
| 79 | 6/26/14 | 7/8/14 | Jenner gulch | Jenner gulch | 5.7 | 7.6 | 0.43 | 12.47 | 4.30 |
| 80 | 6/26/14 | 7/9/14 | Jenner gulch | Jenner gulch | 30.4 | 40.3 | 0.56 | 55.51 | 6.53 |
| 81 | 7/8/14 | 8/25/14 | Jenner gulch | Jenner gulch | 8.0 | 35.0 | 0.61 | 139.38 | 7.43 |
| 82 | 7/8/14 | 8/25/14 | Jenner gulch | Jenner gulch | 3.9 | 8.1 | 0.33 | 32.74 | 2.61 |
| 83 | 7/8/14 | 8/25/14 | Jenner gulch | Jenner gulch | 7.6 | 35.2 | 0.65 | 149.84 | 7.67 |

# Chapter 6. SYNTHESIS

This dissertation explored the ecological and physiological trade-offs for juvenile steelhead and assessed the consequences of estuary mouth closures and management interventions affecting the intermittently closed Russian River estuary (RRE). These investigations have revealed insights about the variable conditions juvenile steelhead are exposed to, specific movement patterns and behaviours, their diet composition, trends regarding prey abundance, and how these impacts their growth. Most evidence suggests the behavioural plasticity of steelhead and the physiological tolerances or mobility of macroinvertebrates are uniquely fitted to benefit from the high productivity of intermittently closed estuaries (ICEs) while mediating the dynamic abiotic conditions. Evidence of this is the high growth of juvenile steelhead, but there are still many uncertainties regarding how juvenile steelhead and their prey will respond to extended closures.

In chapter two, I took advantage of technological advances in sensor encoded acoustic telemetry to locate and determine the temperature of juvenile steelhead as small as 93 mm FL. I inferred the overall water quality exposure of juvenile steelhead by linking the temperature of individually-tagged fish with water quality profiles of temperature, salinity, and dissolved oxygen collected in close proximity. Under open mouth conditions, juvenile steelhead experienced primarily brackish and saline water in the lower and middle reaches and warm fresh water in the upper reach, whereas under closed mouth conditions, juvenile steelhead experienced warm fresh water in the middle and upper reaches. During closed mouth conditions, juvenile steelhead moved greater distances, resulting in the aggregation of fish near thermal refugia. This chapter shows the importance of recognizing these strategies when contemplating changes to estuary management and highlights the significance of tributary hydrogeomorphic processes and groundwater linkages in sub-watersheds that are sources of cool water for thermal refugia in ICEs.

To understand how the stochastic abiotic conditions in ICEs affect juvenile steelhead, chapter three expanded on the acoustic telemetry and simultaneous water quality sampling in chapter two. These results indicated the depth of fish varied in response to the present abiotic conditions, but this sometimes depended on fish size. Overall, the depth of fish reflected the occupation of more energetically and physiologically ideal habitats. When coincident temperatures were warmer, fish were deeper, but if coincident DO levels were lower, fish were shallower. Also, higher salinities led to smaller juvenile steelhead (<150mm FL) occupying shallower depths, while larger steelhead (>150mm FL) were deeper in the water column. Furthermore, smaller fish (99-144 mm FL) readily moved across the halocline and made forays into the deeper more saline conditions and returned into shallower less saline water. While this behaviour increases the foraging opportunities of juvenile steelhead that are not tolerant of high salinities, there are likely tradeoffs with increased vulnerability to avian predation and energetic costs.

To assess the impact of management activities on macroinvertebrates in the RRE, Chapter four analyzed the effects of mouth condition and closure duration on the assemblage compositions and abundance of macroinvertebrates important to the food web. Only some macroinvertebrate assemblages at specific sites differed between open and closed mouth conditions. Similar to other ICEs, the macroinvertebrate assemblage is primarily composed of taxa that can deal with the variability, either physiologically or behaviourally. Furthermore, the key food web taxa are abundant during both open and closed mouth conditions and were found in large aggregations in habitat only inundated during closed mouth conditions. These increased densities in the closure-inundated habitat may reflect more expansive aggregations of food web taxa, leading to more efficient foraging for juvenile steelhead.

In Chapter five, I employed a bioenergetics model to investigate the biotic and abiotic conditions that influence the growth of juvenile steelhead in the RRE. I identified that the growth rates of juvenile steelhead in the RRE rival the highest in literature both in the wild and under laboratory conditions. Fish had relatively high consumption rates and, in habitats with elevated temperatures, foraged on more energy dense taxa. These results would suggest that growth in the estuary is likely not limiting the recovery of threatened steelhead in the Russian River watershed. If growth became limiting (e.g., crashes of prey resources, density dependence, or increased temperatures from climate change), the increased stratification (e.g., thermal refugia) and increased habitat available during closed mouth conditions could buffer some of the limitations. With many populations of salmonids imperiled near their southern range, efforts for recovery could benefit from protecting habitats in intermittently closed estuaries and considering the impacts of management activities to the water quality conditions (Moyle et al., 2017).

Although the behavioural and life-history plasticity of steelhead makes them uniquely fitted to use ICEs, the trade-offs for salmonids with more fixed life-histories in ICEs may be different. ESA-listed populations of Chinook salmon and Coho salmon also occur in the Russian River (NMFS, 2008), but these salmonids have different life histories and timing of migrations (Quinn, 2018). The Russian River is the most southern watershed used by California Coast (CC) Chinook salmon (NMFS, 2016). Interestingly, most coastal rivers south of the Russian River have prolonged or seasonal closures (Heady et al., 2014) but do not support persistent populations of Chinook salmon. This Evolutionary Significant Unit only consists of fall-run ocean-type Chinook salmon (NMFS, 2016) such that the timing of downstream migration (April-

July) and return migration (fall) can be impeded during a prolonged closure common in estuaries south of the Russian River.

In contrast, Central California Coast (CCC) Coho salmon, like steelhead, use coastal rivers south of the Russian River (NMFS, 2012). CCC Coho salmon begin their upstream migration to the spawning habitat later (December – March) than CC Chinook salmon. Furthermore, the later spawning time leads to CCC Coho salmon spending more than a year rearing in upstream and estuarine habitats and out-migrating the following spring (March-June) as yearlings (NMFS 2012). Osterback et al. (2018) monitored the abundance and ecology of juvenile steelhead and Coho salmon in an ICE that was disconnected from the ocean two months earlier than average, essentially trapping fish that out-migrate in the spring. Although both species were able to persist and showed similar patterns in abundance throughout the closure, growth rates of Coho salmon were much lower than steelhead, likely because the growth of Coho salmon is less tolerant of higher temperatures (Richter & Kolmes, 2005).

## 6.1 FUTURE RESEARCH.

With 84% of anadromous salmonid populations in California expected to be negatively impacted by climate change (Moyle et al., 2017), identifying essential habitats and restoring the functions and access to habitats will allow salmonids to express life history diversity that can assist in mediating adverse impacts from climate variability (Katz et al., 2013; Moore et al., 2014; Manhard et al, 2017). The main effects of climate change on California salmonid populations include increased temperatures, decreased streamflow, and loss of habitat availability and suitability (Moyle et al., 2017). The results of bioenergetics modeling in Chapter 5 indicate even slight increases (+1.0-2.0 °C) in temperature as expected from climate change will eventually eliminate all growth potential in the upper reach of the RRE if cool water refugia is not available. With cool water refugia from hyporheic flow or groundwater inputs only accessed by juvenile steelhead during closed conditions (Chapter 2), management activities that promote closed mouth conditions and maintaining water table levels can marginalize the effects of climate change on growth. Considering that groundwater inputs are an important factor in the hydrological patterns and water quality conditions of ICEs around the world (Chikita et al., 2012; Sadat-Noori et al., 2016; Menció et al., 2017; Alcolea et al., 2019) and groundwater was the source of cool refugia for juvenile steelhead in the RRE (Chapter 2), future research regarding water quality conditions in the RRE should consider groundwater inputs (Alcolea et al., 2019).

The survival of juvenile salmonids in intermittent streams, common in Mediterranean climates where ICEs occur, is directly linked to flow (Grantham et al., 2012; Woelfle-Erkine et al., 2017; Obedzinski et al., 2018). Water extraction is expected to increase with population growth (Koniecski & Heilman, 2004; Grantham et al., 2010), and the changes to projected summer stream flows due to climate change (Mannion, 1995; Karl et al., 2009) will negatively impact the juvenile salmon rearing habitat upstream, especially in intermittent streams (Grantham et al., 2012; NMFS, 2012). When considering impacts to upstream and ICE salmonid habitats, dams are a double-edged sword. In addition to eliminating access to spawning and rearing habitat for anadromous salmonids in the upper watershed (NRC, 1996; Moyle et al., 2017), they also alter the hydrologic patterns and, as a result, the connectivity of ICEs to the ocean (Behrens et al., 2015). For example, the artificially high inflows in the Russian River due to water releases from dams during the naturally dry season has decreased the duration of estuary mouth closures (Behrens et al., 2013). While these impacts negatively affect salmon habitats in tributaries, habitats and prey communities in ICEs (Chapter 4) may be more robust. The potential increased robustness of habitat quality in ICEs highlights the importance of addressing uncertainties regarding the ecological and physiological trade-offs of extended mouth closures, as this dissertation was constrained to sampling during short-term mouth closures.

I propose a comprehensive study evaluating the survival of steelhead life history trajectories in response to estuary mouth dynamics, flow, and increasing temperatures throughout the watershed, including upstream tributaries, in the river, in the estuary, and for adults returning from the ocean. Further advances in the technology of acoustic telemetry has decreased the size of transmitters (tag weight as small as 0.216 g) with increased battery life (up to 432 days), allowing the tagging of smaller steelhead prior to entering the estuary (e.g., in upstream habitats). Combining this technology with data gathered from the current Passive Integrated Transponder (PIT) tag studies in the RRE (Manning & Martini-Lamb, 2014; Martini-Lamb & Manning, 2015) and analyzing the scales from returning adults would identify major sources of mortality.

A major source of mortality for juvenile steelhead in ICEs is avian predation (probability of predation up to 0.82; Osterback et al., 2013). Direct observations of this predation are common at shallow mouths of ICEs by Western Gulls (*Larus occidentalis*) (Osterback et al., 2013). NMFS (2008) has required the Sonoma County Water Agency to manage the RRE in a manner that promotes a “perched lagoon” where water outflows over the sandbar with the elevation of the estuary staying higher than the ocean. These conditions may actually increase the vulnerability to predation due to the shallow flow through the mouth forcing any fish transiting through the mouth more available to birds (Osterback et al., 2013). Additionally, avian predators will selectively forage on larger salmonids (Collis et al., 2001), but Osterback et al. (2014) found that intermediate-sized juvenile steelhead (140-180 mm FL) had a higher risk of avian predation than smaller and larger individuals. Although the mechanism of increased predation on the intermediate-size fish is unknown, one possibility is that the small and intermediate-sized juvenile steelhead are modifying their behaviour (Chapter 3) in response to salinities, and birds are selectively foraging on the larger of those as in Collis et al. (2001). In contrast, the larger steelhead are not as susceptible to predation because the larger steelhead were deeper when higher salinities are present (Chapter 3). With avian predation strongly affecting populations of steelhead in ICEs (Osterback et al., 2013), research should be conducted to identify factors that influence the vulnerability to avian predation and consider these when making management decisions.

There are still many uncertainties regarding the macroinvertebrate assemblages that could be resolved with changes to the sampling design. Despite revisions to the study design, little is known about the immediate responses of assemblages or their abundance to estuary closures or berm breaches. Changes to the sampling design would provide the ability to investigate hypotheses such as: (a) extant epibenthic prey populations volitionally expand and disperse into the increasing areas of shallow water habitats; (b) increased production of epibenthic organisms is a function of increased availability of organic detritus and other food resources; and (c) rapid decrease in water elevation after re-opening of the closed estuary imposes mortality to epibenthic prey populations in occupied shallow water habitats.

The previously used fixed sampling with large temporal intervals between each sampling event is incapable of fully capturing distributional changes to the assemblage. For example, Lill et al. (2012) found that breaching the mouth affected the assemblage composition with daily sampling, but these changes were almost imperceptible when analyzed across weekly sampling. I propose increased temporal and spatial resolution at one “intensive” study site as the water level increases directly after a closure and just before and after a breach. For example, sampling would occur every day for the first week after the mouth closure, every other day for the following week, and then weekly after that. Furthermore, keeping fixed locations of benthic cores near the water's edge and adding additional cores as water levels rise and then resampling all sites after a berm breach will provide the ability to measure the colonization rate of tube dwelling *Americorophium* spp. and quantify the number of individuals killed after a breach.

## 6.2 CONCLUSIONS

This dissertation highlights the importance of ICEs for juvenile steelhead and reveals tradeoffs of management decisions for their behaviour and abundance of prey. Juvenile steelhead would benefit from closed mouth conditions by an increased capability to move longitudinally (Chapter 2) and the ability to occupy thermal refugia (Chapter 2), smaller individuals have more access to deeper depths (decreased avian predation and increased access to prey; Chapter 3), and expansive aggregations of prey taxa would lead to more efficient foraging for juvenile steelhead (Chapter 4). The fifth chapter confirmed the importance of access to cool water refugia and abundant foraging opportunities. Regardless of how of the RRE is managed, preserving access to and restoring the habitat throughout the watershed is essential to the recovery of steelhead in the Russian River upper watershed and would benefit conditions in the RRE. An example of this includes access to cool water refugia (Chapter 2). In addition to benefiting juvenile steelhead in the RRE, protecting groundwater inputs would benefit salmonids throughout the watershed (Lake, 2011; Woelfle-Erskine et al., 2017; Obedzinski et al., 2018), including the two tributaries connected to the RRE (Austin Creek, Willow Creek) where juvenile steelhead were detected using cool water refugia from groundwater inputs (Chapter 2). With climate change and human demands expected to impact salmonids negatively (Moyle et al., 2017), preserving habitats and making informed decisions is essential to restoring imperiled salmonid populations.

Globally and regionally, ICEs span a broad spectrum of environmental settings, including intermittency, climate, hydrogeology, and anthropogenic demands (Dürr et al., 2011; McSweeney et al., 2017). Due to the diversity of ecological pressures among and within ICEs, comparisons among estuaries are limited, especially when considering management decisions affecting threatened species with specific physiological tolerances. As a result, a processed-based approach to management (Largier et al., 2019) should be used in ICEs, including the RRE. This includes understanding and quantifying the abiotic and biotic processes, identifying ecosystem functions and how management activities affect these functions, and incorporating active monitoring programs into management decisions. Understanding how threatened species respond to the ecological pressures within each ICE is critical when considering the major implications of management decisions to habitats in ICEs.

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# VITA

William Carson Matsubu is originally from Citrus Heights, California. His family was supported by commercial fishing until population declines forced his family to switch industries. He graduated from Humboldt State University with a Bachelor of Science in Fisheries Biology with a Marine Fisheries emphasis and a minor in Applied Statistics in 2010. During the course of his undergraduate studies, William worked at a salmon cannery for Ocean Beauty Seafoods in Naknek, Alaska; as a deck hand on the Humboldt State University Research Vessel in Arcata, California; and as a technician at the South West Fisheries Science Center in Santa Cruz, California. After graduating from Humboldt State, William worked as a fisheries technician on the Russian River for California Sea Grant, and the Sonoma County Water Agency. In 2013, he moved to Seattle to pursue a graduate degree at the University of Washington School of Aquatic and Fishery Sciences.