

**Life History Diversity and Resiliency of Steelhead Trout (*Oncorhynchus mykiss*):
A Case Study from the Pescadero Watershed**

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ABSTRACT

Life history diversity provides population resilience to fish stocks via the portfolio effect. To investigate the potential evolutionary pressure of a recurrent fish kill of steelhead salmon (*Oncorhynchus mykiss*) in the seasonally closed Pescadero estuary in central California, I assessed juvenile life history using fyke net sampling and otolith samples. A fyke net continuously trapped downstream migrants above the estuary, and I measured otolith Strontium:Calcium (Sr:Ca) and Barium:Calcium (Ba:Ca) ratios of two incidental mortalities. I also analyzed otoliths from mortalities of fish kills in November 2011 and February 2014. Larger juveniles migrate downstream and exit the estuary in early spring (March median FL = 200 mm), and smaller individuals migrate downstream later in the spring (May median FL = 121 mm). The small fyke net mortality (FL = 86 mm) had no evidence of previous estuary entry but the larger mortality (FL = 213 mm) had Sr:Ca >1.5 mmol/mol and Ba:Ca <2 μ mol/mol for several months of its ontology, indicating previous estuary residence. Thus at least some larger downstream migrants had previously lived in the estuary, exhibiting the rare smolting twice life history, however, none of the fish kill otoliths analyzed (n=7) indicated the smolting twice life history. Smaller downstream migrants remaining in the estuary after sandbar closure are vulnerable to fish kills occurring during bar breach. Due to the heritability of life history strategies, the fish kill exerts selective pressure against the life history that overwinters in the estuary.

KEYWORDS

portfolio effect, otolith microchemistry, smolting twice, phenotypic plasticity, seasonally closed estuary

INTRODUCTION

Just as species diversity provides ecosystem stability (MacArthur 1955, Tilman and Downing 1994), interpopulation diversity affords stability of stock complexes by buffering against variability of individual populations. This process is called the portfolio effect (Hilborn et al. 2003, Hutchinson et al. 2008, Schindler et al. 2010), as an analogy to diverse assets stabilizing a financial portfolio in economic volatility. Furthermore, population resiliency, or the ability to persist following environmental disturbances, is increased by diversity of life histories within the population (Hilborn et al. 2003, Secor 2007). Pacific salmon (*Oncorhynchus* spp.), an economically and environmentally important taxon, exhibit tremendous life history variation, which is hypothesized to increase population resilience. Population resilience is of particular interest in California, where 78% of native salmonid taxa are likely to be extirpated in the next century (Katz et al. 2013). Resilience buffers against both anthropogenic impacts (e.g., logging, dams, and invasive species) and California's Mediterranean climate, whose interannual fluctuations will become more severe under climate change predictions (Wood and Armitage 1997, Cook et al. 2004, Waples 2009). Therefore it is critical to understand the factors which maintain or threaten life history variation and by consequence population resilience.

Some habitats that display significant life history diversity are estuaries, which are vital nursery habitat for many anadromous Pacific salmon. These productive habitats support rapid somatic growth of juveniles and can thereby improve ocean survival by decreasing size selective ocean mortality (Ward et al. 1989, Bond et al. 2008). Salmon use these habitats with many temporally and spatially distinct life history strategies, often categorized by age, size, and duration of estuary residence. In California bar-built estuaries, which lose connectivity with the ocean in fall when low flows allow sandbar formation, larger, older steelhead (*Oncorhynchus mykiss*) juveniles migrate straight through the estuary in early spring and smaller, younger juveniles migrate downstream later in the spring (Shapovalov and Taft 1954, Hayes et al. 2011). A small portion (~20%) of these smaller juveniles remain in the estuary past bar closure (Bond et al. 2008, Hayes 2011), but comprise about 60-90% of the returning anadromous population (Shapovalov and Taft 1954, Bond et al. 2008, Atkinson 2010). A portion (~45%) of the juveniles remaining in the estuary after sandbar closure migrate upstream when estuary water quality deteriorates, a life

history called “smolting twice” (Hayes et al. 2011). Such diverse life history patterns provide the buffering capacity against the variable Mediterranean climate and other disturbance.

Disturbance can exert selective pressure on fish life histories in the span of only a few generations (Williams et al. 2008). Both physiological (e.g., metabolism) and behavioral (e.g., parental care and juvenile migration patterns) traits can undergo natural selection in wild fish populations (Cooke et al. 2007, Hegg et al. 2013). These studies focus on chronic selective pressure by fisheries or altered habitat, but there is a variety of disturbances. Four key attributes of disturbance regimes are frequency, magnitude, duration, and predictability, and these may be altered in a variety of ways (Waples et al. 2009). For example, dams reduce magnitude and frequency of flood events for an indefinite period, but logging and road construction increase magnitude and frequency of flooding (Waples et al. 2009). It is unclear how disturbances of shorter duration and higher unpredictability may exert selective pressure on juvenile life history and affect population resilience.

This paper investigates whether a recurrent estuary fish kill of approximately yearly frequency, short duration, and low predictability exerts selective pressure on juvenile steelhead life histories. I will first determine the different juvenile life histories by examining fyke net sampling of downstream migrants and using otolith microchemistry to confirm life history assignment. Second, I will assess if the life histories of the fish kill mortalities differ from the total assortment of juvenile life histories. Otolith microchemistry will determine previous habitat use of juveniles killed in the estuary. If juvenile life histories resemble those of nearby estuaries, I predict that smaller individuals remaining in the estuary and not migrating upstream will be disproportionately affected by the fish kill, indicating the presence of selective pressure on juvenile life history strategies.

METHODS

Study site

The fish kills occur in the seasonally closed estuary at Pescadero State Beach (37°15'43"N 122°24'48"W), 15 miles south of Half Moon Bay, California (Figure 1). The estuary extends between the confluence of Butano and Pescadero Creeks and the Pacific Ocean and experiences a

Mediterranean climate regime. In the fall during low flows, a sandbar forms, separating the estuary from the ocean and creating a lagoon (in this paper, the term “estuary” will refer to either the open or closed state). Since 1994, hypoxic conditions following sandbar breaches have caused fifteen fish kills of steelhead and other species including threespine stickleback (*Gasterosteus aculeatus*), prickly sculpin (*Cottus asper*), staghorn sculpin (*Leptocottus armatus*), and topsmelt (*Atherinops affinis*). Steelhead carcasses were collected after the kill and frozen for tissue samples. A fyke net was operated in Pescadero Creek two kilometers upstream of the estuary at 1805 Pescadero Creek Road (37°15'08"N 122°23'11"W).



Figure 1. Field site location. Pescadero State Beach is on Highway 1, 15 miles south of Half Moon Bay, California.

Fyke net sampling

To determine the juvenile life histories, a fyke net captured all downstream migrants in late spring of 2013. Species identity and fork length (FL) were recorded for 39 days between March 27 and May 31. Fishing time varied between 20 and 27 hours for each sampling day.

Incidental mortalities were stored in ethanol for tissue samples.

Otolith preparation

To prepare the otoliths for analysis, I dissected the otoliths from the fish, then sanded and polished thin sections. I cut a transverse section through the brain case and removed the sagittal otoliths with forceps. I rinsed the otoliths with deionized water to remove organic material and allowed them to air dry. I glued otoliths sulcus side up on glass slides with Krazy Glue. Using

sandpaper between 400 and 2000 grit, I gently sanded down to the plane of growth increments, and polished using 3um alumina oxide lapping film (Ted Pella, inc.).

Otolith microchemistry

To determine previous habitats of individual juvenile steelhead, I measured otolith Strontium:Calcium (Sr:Ca) and Barium:Calcium (Ba:Ca) ratios with quadrupole inductively coupled plasma-mass spectrometry (ICP-MS). First, I sought to confirm life history designations of the fyke net by analyzing two incidental mortalities from the fyke net: a smaller individual (FL = 86mm) and a larger individual (FL = 213 mm), whose sizes correspond to those of an age 1+ and age 2+/3+ (Shapovalov and Taft 1954). Second, to determine the juvenile life histories of fish kill individuals, I measured Sr:Ca and Ba:Ca ratios of selected estuary mortalities of various sizes (n=7).

To measure chemical habitat markers throughout the fish' life, I took spot element measurements along a transect from the primordial to the outer edge of the otolith, within 30° from the perpendicular to the long axis on the ventral side (Figure 2). The laser ablated 40µm spots at 60µm intervals, giving resolution of approximately one month. Calcium measurements were set to an otolith standard in GLITTER (Gemoc Initiative) (Gry Barfod, *unpublished data*), and I recorded Sr, Ba, and Ca composition of each spot. Sr composition increases and Ba composition decreases with increasing salinity, but Ca is constant (Miller et al. 2010). I calculated Sr:Ca and Ba:Ca ratios and determined previous habitats using accepted values for freshwater, brackish, and marine environments (Table 1) (Miller et al. 2010).

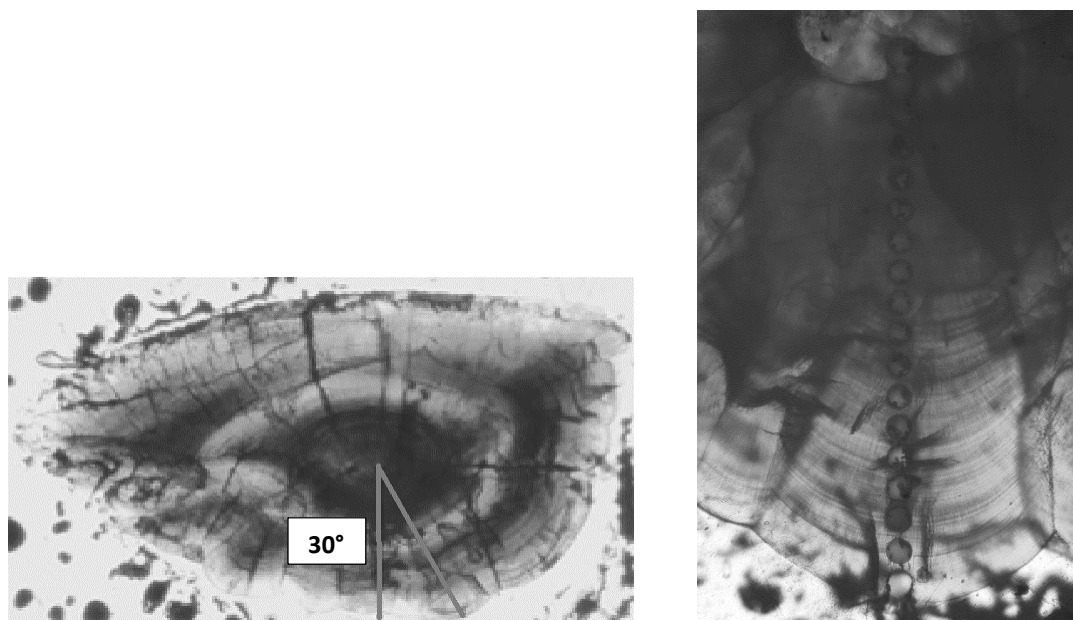


Figure 2. Transect of spot element measurement. Sr, Ba, and Ca were measured along a transect drawn within a (a) 30° wedge from the perpendicular to the long axis on the ventral side. The transect consisted of (b) 40 μ m diameter spots spaced at 60 μ m intervals for a resolution of approximately one month.

Table 1. Expected otolith element ratios for different water types. Sr composition increases and Ba decreases with increasing salinity, but Ca is constant (Miller et al. 2010).

Water Type	Sr:Ca (mmol/mol)	Ba:Ca (μ mol/mol)
Freshwater	< 1.5	> 2
Brackish	> 1.5	Either > 2 or < 2
Marine	> 1.5	< 2

RESULTS

Fyke net sampling

The fyke net captured downstream migrating fish of all size classes. FL ranged from 65mm to 760mm, but most migrants were juveniles (median FL = 112mm). I assigned fish to age classes as follows: FL <140mm as age 0+/1+ juveniles, FL between 140mm and 270mm as

age 2+/3+ juveniles, and FL >270mm as adults (Shapovalov and Taft 1954). Adults were not included in further analyses of juvenile life histories. Age 2+/3+ juveniles migrated downstream earlier than age 0+/1+ juveniles (March median FL = 200mm, May median FL = 121mm) (Figure 3). The majority of age 2+/3+ juveniles entered the estuary before sandbar closure, but the majority of age 0+/1+ juveniles entered after sandbar closure on April 24, 2013 (Figure 3). In most years, the sandbar closes in fall when discharge decreases (Eric Huber, *unpublished data*), after all juveniles have migrated downstream.

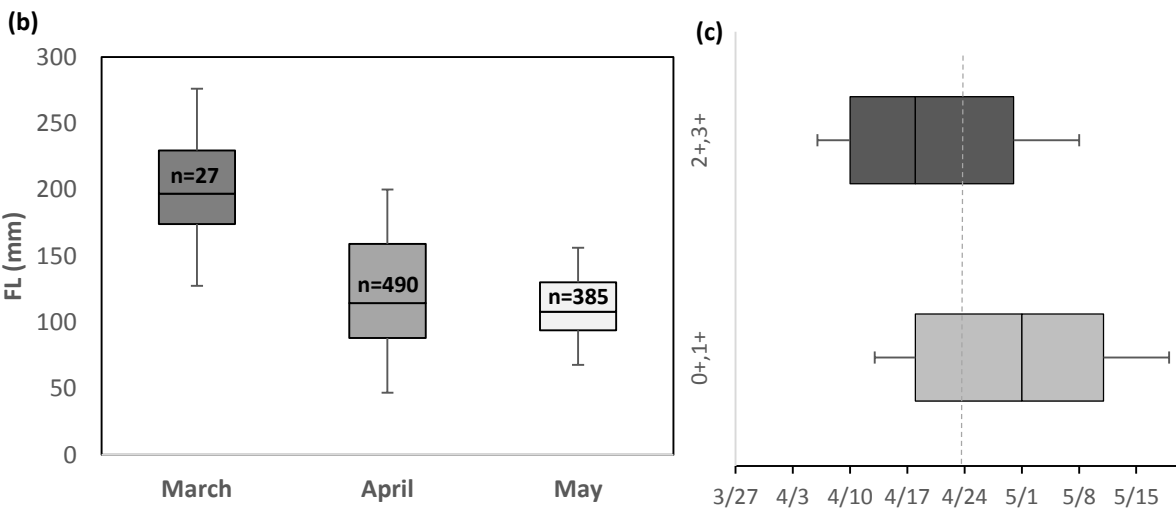
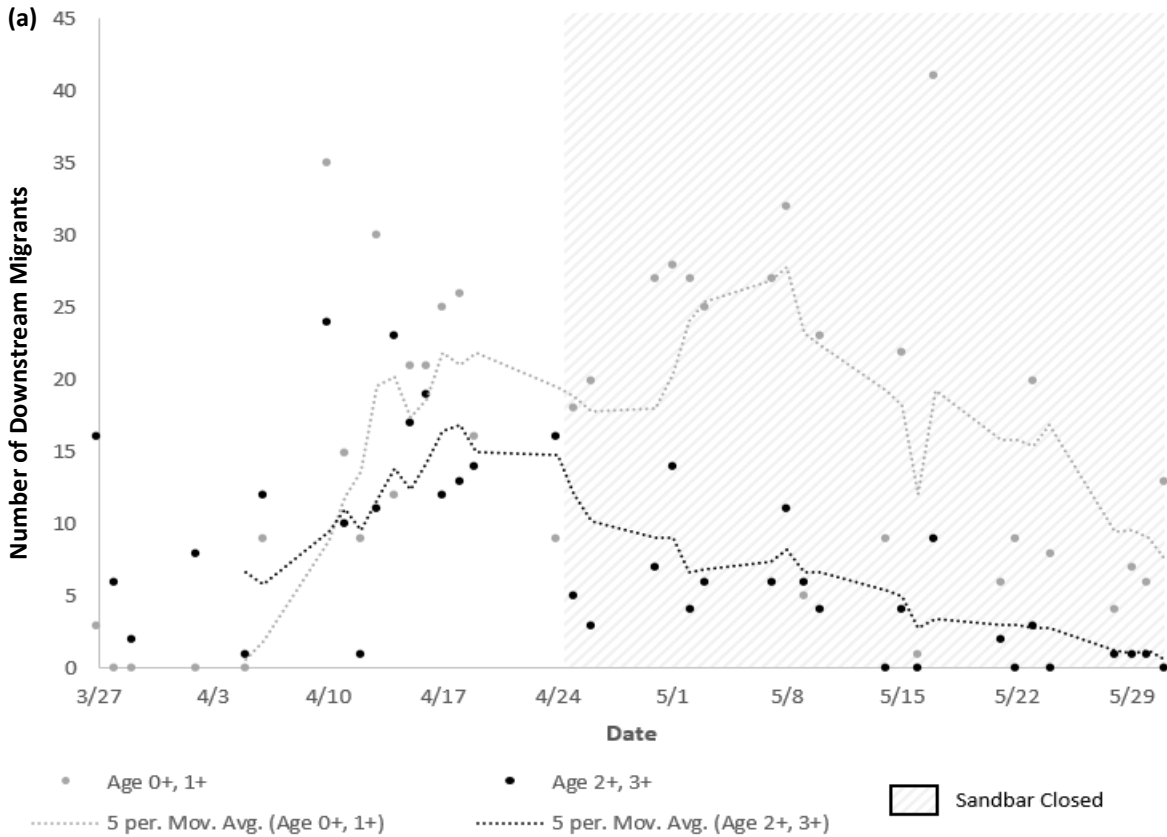


Figure 3. Juvenile Downstream Migration in 2013. Downstream migration of juveniles (FL < 270 mm) captured by the fyke net depicted as (a) scatterplot of the daily capture numbers of juveniles of different age classes, age 0+/1+ (FL < 140 mm) and age 2+/3+ (140 mm < FL < 270 mm), with five day running average (dotted lines), (b) box plot comparison of juvenile FLs of each month, whiskers showing standard deviation, and (c) migration timing of 0+/1+ and 2+/3+ age classes, whiskers showing range of 75% of migrants. 2013 sandbar closure is represented by (a) hatched-bar box or (c) dashed line. The sandbar generally forms in fall, as discharge decreases. In 2011, the bar closed on August 22. In 2014, the bar closed on February 21.

Otolith microchemistry

Of the two analyzed otoliths of fyke net incidental mortalities, only the larger downstream migrant (FL = 213 mm) had elevated Sr:Ca and decreased Ba:Ca ratios (Figure 4). After the first few ablated spots, which represent yolk sac chemistry (Kalish 1990), the otolith of the smaller downstream migrant (FL = 86 mm) had Sr:Ca < 1.5 mmol/mol and Ba:Ca > 5 μ mol/mol for all ablated spots. The larger migrant had seven ablated spots after yolk sac absorption with Sr:Ca > 1.5 mmol/mol and Ba:Ca < 2 μ mol/mol. Otolith Sr:Ca > 1.5 mmol/mol and Ba:Ca < 2 μ mol/mol indicates marine or brackish residence (Miller et al. 2010).

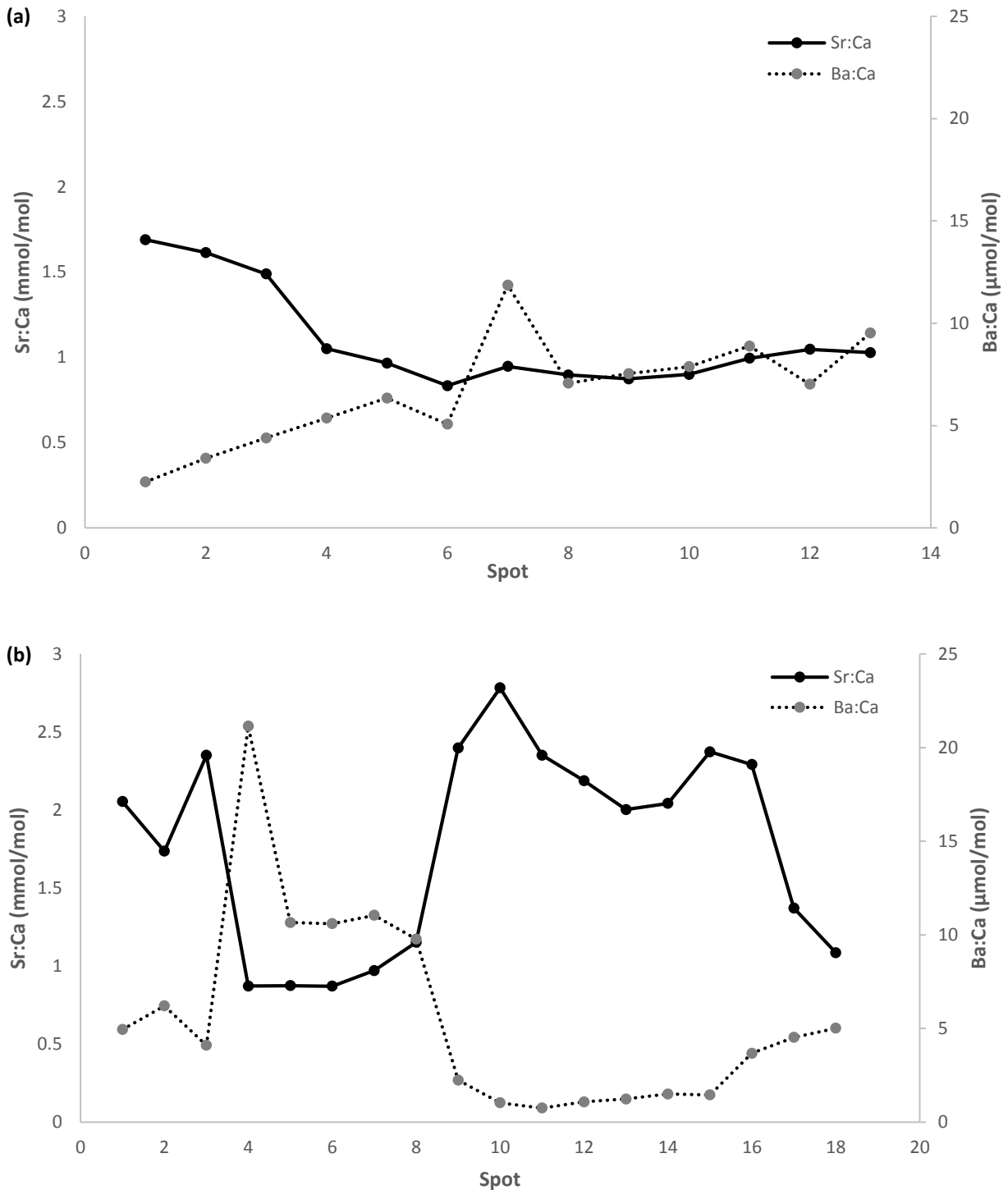


Figure 4. Otolith microchemistry of juvenile fyke net mortalities. Comparison of Sr:Ca and Ba:Ca ratios from the primordia (Spot 1) to the outer edge of the otoliths of (a) small and (b) large fyke net mortalities. The small mortality (FL = 86 mm) did not have Sr:Ca > 1.5 mmol/mol after yolk sac absorption. The large mortality (FL = 213 mm) had spots with Sr:Ca > 1.5 mmol/mol and Ba:Ca < 2 μmol/mol. Otolith Sr:Ca > 1.5 mmol/mol and Ba:Ca < 2 μmol/mol indicates marine or brackish residence (Miller et al. 2010).

Of the otoliths analyzed from juvenile estuary fish kill mortalities (n=7), none had decreased Sr:Ca levels after initial Sr:Ca increase (Figure 5). Within otolith regions of elevated Sr:Ca, Ba:Ca was less than 2 $\mu\text{mol/mol}$ for three of seven individuals (Appendix A).

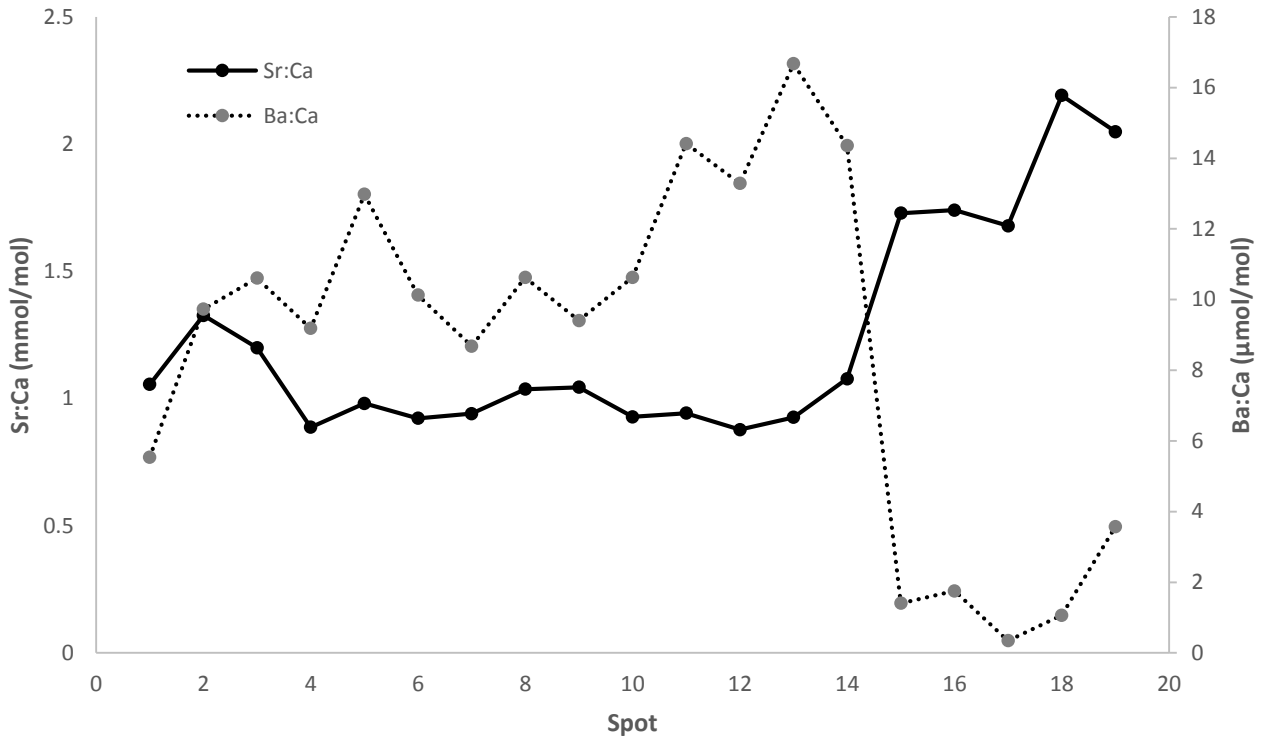


Figure 5. Example of otolith microchemistry of estuary fish kill mortality (FL = 375 mm). None of the analyzed otoliths of fish kill mortalities (n=7) had Sr:Ca < 1.5 mmol/mol after the initial increase above 1.5 mmol/mol. Ba:Ca ratios during elevated Sr:Ca levels were usually but not always under 2 $\mu\text{mol/mol}$. Otolith Sr:Ca > 1.5 mmol/mol and Ba:Ca < 2 $\mu\text{mol/mol}$ indicates marine or brackish residence (Miller et al. 2010).

DISCUSSION

The resiliency of the Pescadero watershed's steelhead population is jeopardized by selective pressure of the recurrent anoxic fish kill on different juvenile life histories. Fyke net sampling shows a distribution of juvenile sizes clustered around FL of 100 mm and 200 mm. Otolith microchemistry analysis reveals that at least some of the larger juveniles had previously resided in the estuary, using the smolting twice life history. However, none of the seven juvenile fish kill mortalities were of the smolting twice life history. Pescadero juvenile steelhead show a

diversity of spatial and temporal habitat use, and certain life histories are more susceptible to the fish kill. California watersheds show estuaries to be an important nursery habitat enhancing ocean survival (Bond et al. 2008, Atkinson 2010), but benefits of estuary rearing may be limited here by an anthropogenic fish kill. The selective pressure against certain life histories may decrease life history diversity, which is integral to population resilience (Schindler et al. 2010, Carlson and Satterthwaite 2011).

Juvenile life history strategies

Juveniles display variation in the spatial and temporal habitat use, with estuary rearing being an important parameter. Fyke net sampling shows larger juveniles (estimated age 2+/3+) migrating downstream earlier in the spring, with peak numbers in mid-April, and smaller individuals (estimated age 0+/1+) migrating downstream later, with peak numbers in early-May (Figure 3). Monthly population sampling of the estuary indicate that most larger downstream migrants move out to the ocean without extended estuary residence (E. Huber, *unpublished data*). The temporally separated downstream migration of different age classes has been documented in physiographically similar Scott and Waddell Creeks, where larger downstream migrants move through the estuary in early spring while smaller individuals enter later in the spring and are more likely to remain in the estuary after sandbar formation (Shapovalov and Taft 1954, Atkinson 2010, Hayes et al. 2011).

Some juvenile steelhead in Pescadero exhibit the rare strategy of smolting twice, in which fish move back upstream in fall in response to deteriorating estuarine water conditions (Hayes et al. 2011). Age 0+ and 1+ downstream migrants are too small to have lived in the estuary the previous fall, but larger age 2+ and 3+ individuals may have. The smaller (FL = 86 mm) fyke mortality showed no chemical evidence of previous estuary residence (Sr:Ca > 1.5 mmol/mol) after yolk sac absorption. However, the larger (FL = 213 mm) fyke mortality had smolted twice. Otolith element ratios indicate extended estuarine residence (Sr:Ca > 1.5 mmol/mol, Ba:Ca < 2 μ mol/mol) before returning to freshwater levels previous to fyke net capture. Smolting twice is further evidenced by monthly population sampling, in which emigration from the estuary is observed while the sandbar is closed (E. Huber, *unpublished data*).

None of the juvenile fish kill mortalities examined displayed the smolting twice life history. Of the seven otoliths tested for element ratios, none displayed signs of freshwater re-entry ($\text{Sr:Ca} < 1.5 \text{ mmol/mol}$) after estimated estuary entry. Otoliths had $\text{Sr:Ca} > 1.5 \text{ mmol/mol}$ for several spots near the primordia, which represents the yolk sac chemistry before yolk sac absorption (Kalish 1990). Ba:Ca ratios were less robust in determining juvenile habitat than Sr:Ca because Sr:Ca ratios cannot easily distinguish between freshwater and brackish water (Miller 2010).

Selective pressure

The kill exerts selective pressure on the overall population by disproportionately affecting the life histories predominantly present in the estuary at the time of bar breach: age 0+/1+ downstream migrants overwintering in the estuary (ie, age 2+/3+ ocean migrants). Juvenile life history strategies with no extended estuary residence, the age 0+/1+ ocean migrants, generally move out the ocean before the sandbar closes. However, the sandbar can form as early as February in extreme drought years such as 2014 (E. Huber, *unpublished data*), trapping fish of all life histories who enter the estuary intending to outmigrate (Figure 3). The smolting twice life history is not present in the estuary during the kill, having already migrated upstream to avoid deteriorating water quality in fall and migrating straight through the estuary the following spring (Hayes et al. 2011).

The magnitude of selective pressure depends largely on the extent to which life history diversity is resultant of phenotypic plasticity or hereditary traits. Both phenotypic plasticity and evolution likely played a “significant role” in changing juvenile outmigration patterns following anthropogenic habitat disturbance (Williams et al. 2008, Hegg et al. 2013). A behavioral plasticity model explains the large interannual variability in observed life histories in an East Coast estuary (Kerr and Secor 2012). Others have estimated very high heritabilities and genetic correlations for migration and maturation date suggesting rapid responsiveness of life history to selection (Quinn et al. 2000). One possible explanation for life history heritability is differential growth rates, because growth rate is a heritable trait responsive to natural and artificial selection (Olsen et al. 2012, Biro and Post 2008). Upstream juvenile growth rates likely play a role in determining life history strategies regarding estuary habitat use, because larger fish tend to migrate earlier and not reside in the estuary. Indeed, it appears that juvenile steelhead enter the estuary predisposed toward

a specific life history; larger migrants had higher Na^+, K^+ -ATPase activity levels indicating greater marine readiness (Hayes et al. 2011). Although individual fish may alter habitat use due to factors such as predation, density dependence, and water quality, the genetic component to life history may be susceptible to selective pressures such as the Pescadero fish kill.

Limitations and future directions

My assessment of life histories and natural selection is limited by restricted sampling due to ecological and funding constraints. Concern for sensitive adult steelhead limited fyke net sampling in the early spring, when mostly larger juveniles are migrating downstream. Thus, I cannot estimate the relative proportions of the different ages and sizes of downstream migrants. Furthermore, I cannot estimate the proportion of the larger migrants that have smolted twice because the grant only funded microchemistry analyses on two fyke net mortalities. I am uncertain what proportion of the larger migrants had previously migrated to the estuary and which grew faster or longer in upstream habitats.

Funding constraints also limited me to seven otolith microanalyses on estuary fish kill mortalities. Without having an estimate of the prevalence of the smolting twice life history in downstream migrants, I cannot rule out the possibility that this life history was too rare to detect with a limited sample size. However, in nearby Scott Creek 45% of PIT-tagged individuals observed in the estuary after sandbar closure were later observed in upstream habitats (Hayes et al. 2011), so it is unlikely that the smolting twice life history is rare but proportionately represented in the fish kill mortalities.

Besides conducting further costly microchemistry analyses of both downstream migrants and estuary residents, habitat selection could be measured by PIT tags and scale analysis. Fish were PIT tagged in the estuary but there were no upstream PIT tag readers. Some individuals were tagged in the estuary and not observed again until the following spring, suggesting upstream movement (Eric Huber, *unpublished* data), but upstream migration cannot be confirmed and its prevalence cannot be estimated without upstream PIT tag readers. Scale increment spacing can reveal previous steelhead habitat selection (Bond et al. 2008) because increment spacing is correlated to body growth (Bhatia 1932, Fukuwaka and Kaeriyama 1997, Fukuwaka 1998, Fisher

and Pearcy 2005). Scale analysis, in addition to being cheaper and easier than otolith microchemistry analysis, is a nonlethal sampling technique.

Adult scales could be analyzed to determine the contribution of different life histories to the adult spawning population. Juveniles rearing in California estuaries are strongly overrepresented in adult populations (Shapovalov and Taft 1954, Bond et al. 2008, Atkinson 2010). The composition of juvenile life histories in the Pescadero adult population is of particular interest because there may be opposing selective pressures on estuary rearing juveniles by size selective ocean survival and estuary fish kill mortality (Ward et al. 1989).

The strength of selective pressure is uncertain because the heritability of life history is poorly understood. Studies on genotypic differences could better assess the heritability of life history strategies such as smolting twice (Hegg et al. 2013). Only with a better understanding of heritability can we understand the contributions of behavioral adaption and genetic diversity to the adaptive plasticity of Pacific salmonids.

Broader implications

Given the rapid pace of extirpation of native California salmonid taxa (Katz et al. 2013), greater efforts should be made to understand and preserve the life history diversity of salmonids. Special adaptations such as smolting twice are integral to resilience in fringe populations subject to drought (Hayes et al. 2011), as well as other current habitats predicted to suffer from increased drought frequency and intensity under climate change models (Cook et al. 2004). Smolting twice is just one of many life history strategies, the diversity of which provides a portfolio effect that buffers against disturbance and California's variable Mediterranean climate to maintain long-term population stability (Schindler et al. 2010, Carlson and Satterthwaite 2011). To preserve this diversity, management should bring current disturbance regimes in line with the historical template (Waples et al. 2009), and restoration efforts should preserve or restore life history diversity (Bottom et al. 2005, Carlson and Satterthwaite 2011). In this light, active management of the Pescadero system should aim to prevent future fish kills. Since Pescadero wetland restoration efforts in the 1990s, there have been 15 fish kills following prolonged estuary closure and no kill after the 2012 managed breach (E. Huber, *unpublished data*). Natural and artificial breaches following shorter closure periods (<30 days) have not resulted in major kills (E. Huber,

unpublished data), thus state agencies should intervene when the estuary is closed for 30 days to protect this federally listed species.

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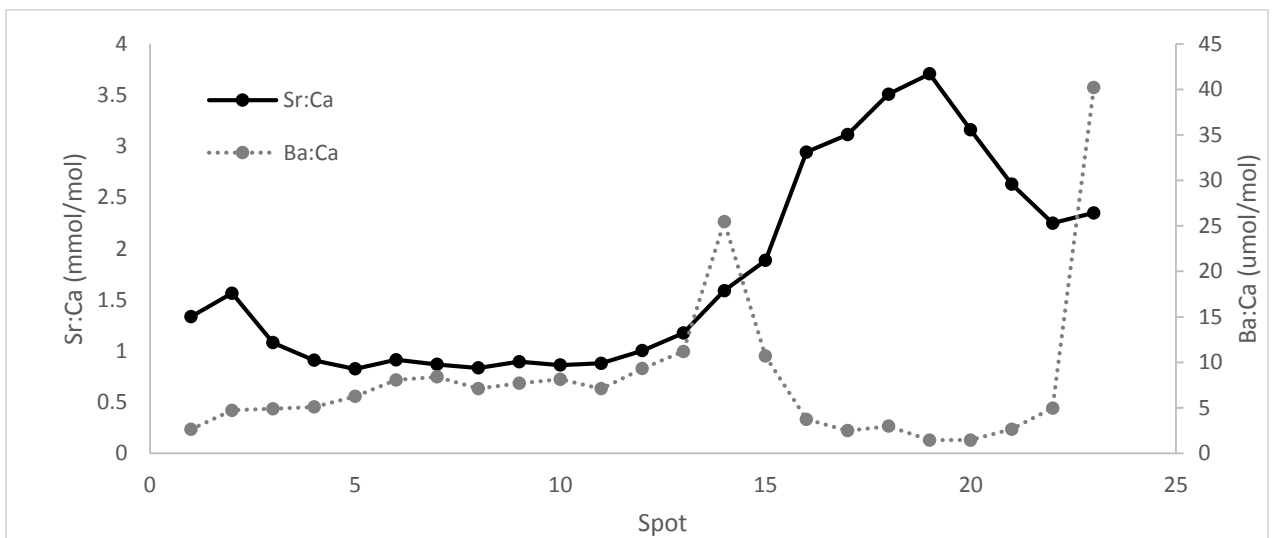
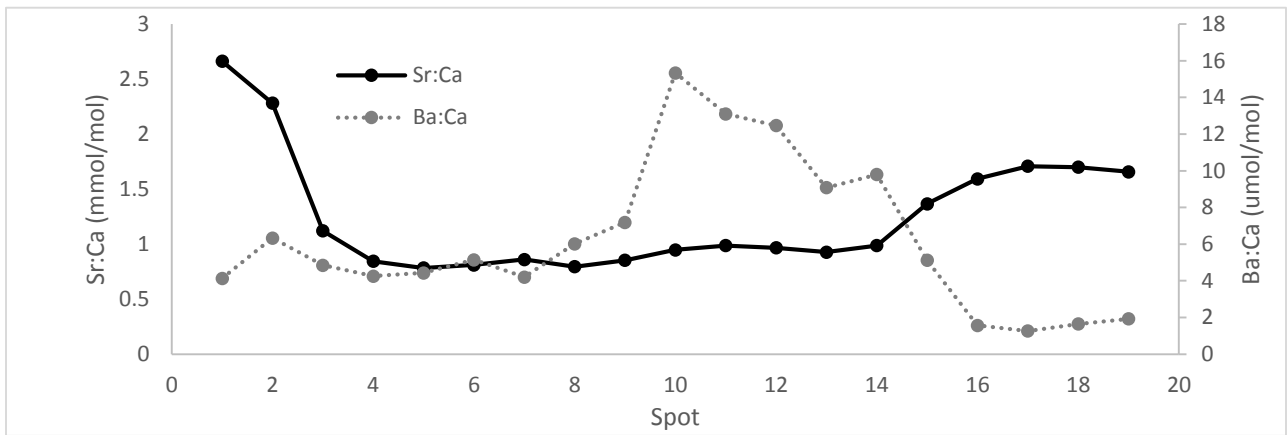
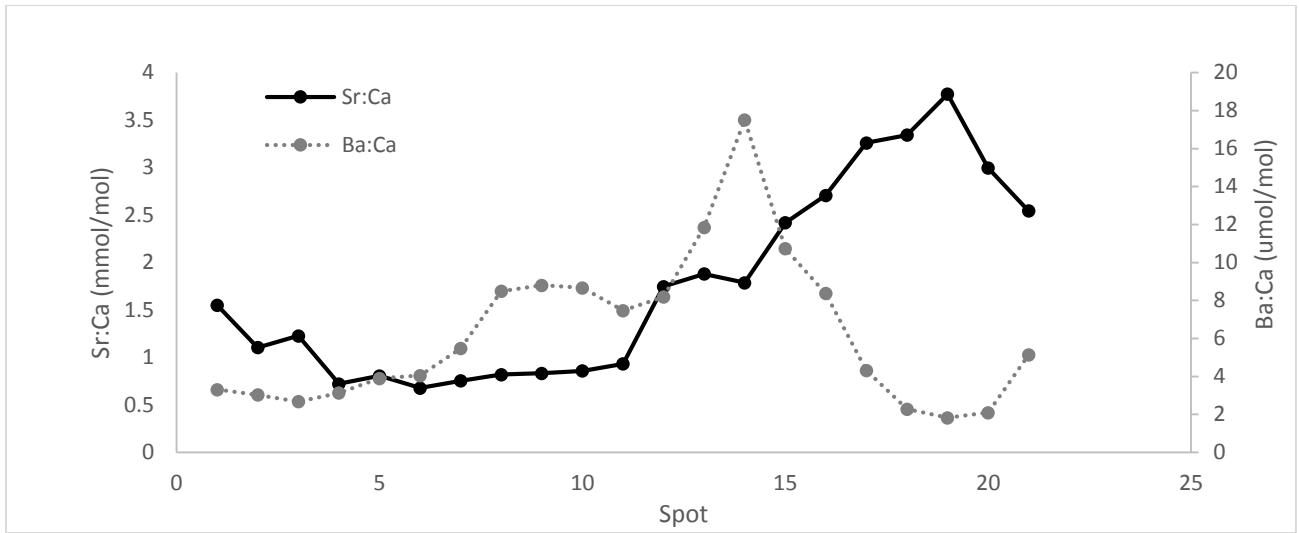
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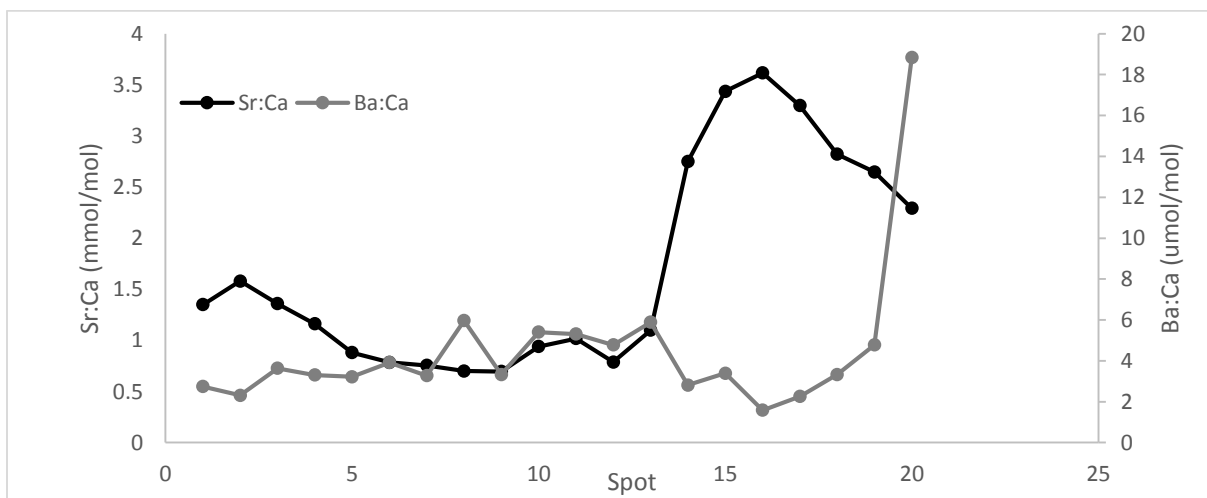
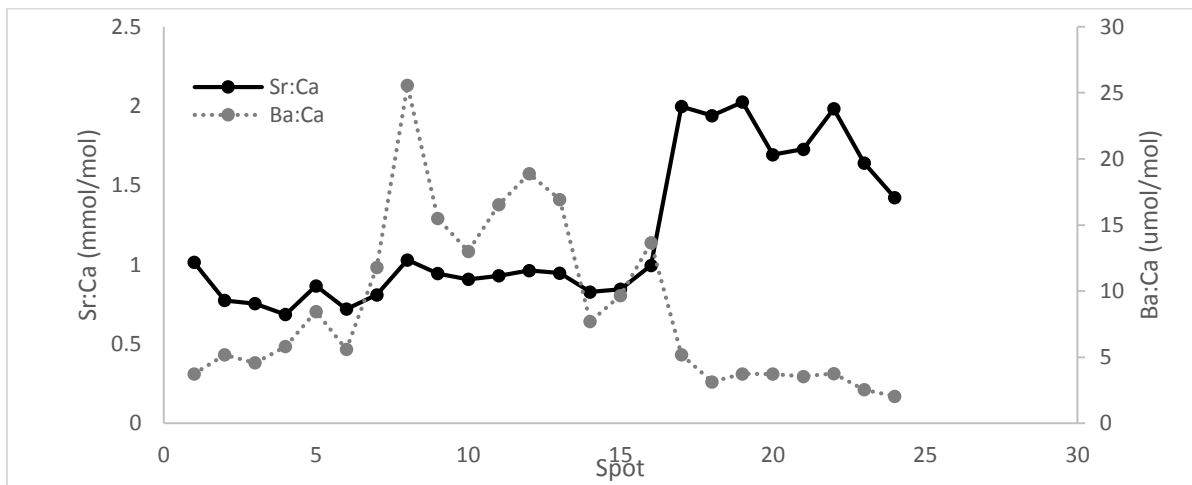
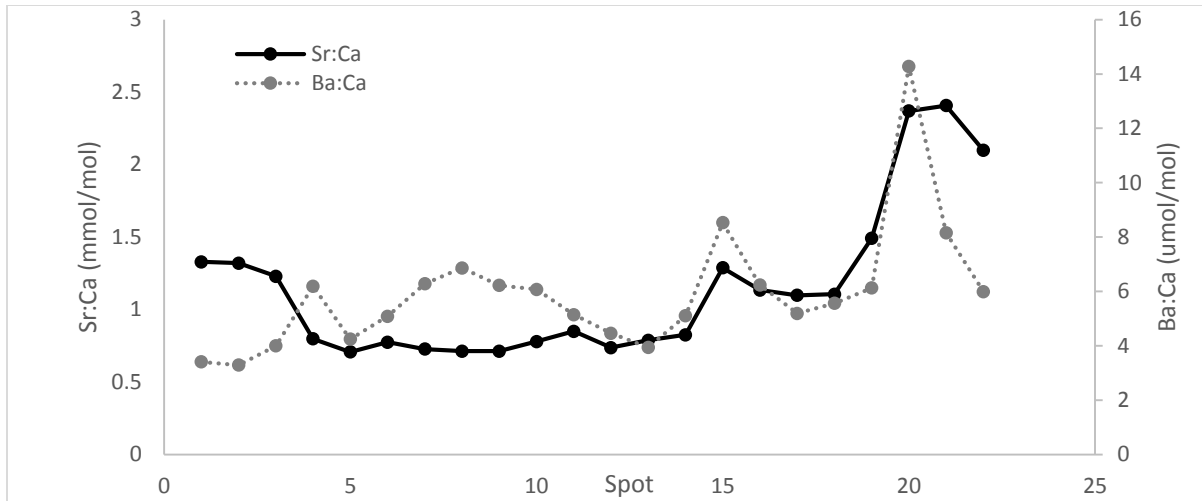
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APPENDIX A: Fish Kill Mortality Microchemistry





Appendix A. Microchemistry analyses of estuary fish kill mortalities.