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The influence of land use and Mediterranean seasonality on California stream fishes

By

Kristina Yoshida

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Stephanie M. Carlson, Chair
Professor Mary E. Power
Professor Vincent H. Resh

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ABSTRACT

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Doctor of Philosophy in Environmental Science, Policy, and Management

University of California, Berkeley

Professor Stephanie M. Carlson, Chair

Freshwaters ecosystems support extraordinary biodiversity relative to their extent and provide important societal benefits. As such, freshwater environments and biota are often heavily impacted by anthropogenic activities. Freshwater fishes in Mediterranean-climate regions are especially impacted because of large human populations in these regions and extensive agricultural production, extensive river modification for flood control and to meet societal demands, and because these systems are heavily invaded by non-native organisms. The distribution and ecology of freshwater fishes in Mediterranean-climate regions are also influenced by the distinct wet and dry periods and the high inter-annual variability in precipitation. Thus, efforts to manage and conserve native fishes in Mediterranean-climate regions require understanding both the effects of human disturbance and the strong seasonality that characterizes these regions.

In this dissertation, I examine the relationship between land use and Mediterranean seasonality on freshwater fishes in streams within the greater San Francisco Bay region in California, USA. In my second chapter, I use a multivariate approach to explore variability among fish communities in 25 Bay Area watersheds. I found that a combination of local (water conductivity) and watershed-scale factors (percent forested watershed, watershed area, elevation) were important predictors of fish communities across sites. Furthermore, watershed-scale factors had indirect effects on fish communities through their influence on a local-scale factor, water conductivity. The results of this chapter highlight the importance of considering both the direct and indirect effects of watershed-scale factors on freshwater fish communities.

In my third chapter, I continued my analysis of land use and fish communities with a focus on contemporary land change. For this chapter, I performed a resurvey study, surveying the habitat and fish communities in 32 sites in the Alameda Creek Watershed that had been surveyed by Dr. Robert Leidy in the mid-1990s, including sites in the rapidly urbanizing Livermore Valley region. Again using a multivariate approach, I found that the increase in urbanization across an approximately 16-year period was related to change in fish community

composition, a decline in native species richness, and a decline in a common native cyprinid - changes that were not observed in another part of the watershed that has experienced little land use change in the last 16 years. The relationship between land use change and fish community change was strongest when considering land use change at a local scale. These results suggest that ongoing land change alters fish communities and that contemporary resurveys are an important tool for examining how freshwater taxa respond to recent and ongoing environmental change.

In my final chapter, I assessed how seasonal drought, a characteristic feature of Mediterranean-climate systems, influenced food webs in a small intermittent stream in Marin County, CA that provides rearing habitat for threatened steelhead trout (*Oncorhynchus mykiss*). I used stable isotopes of carbon and nitrogen to characterize food web structure and the trophic position of a suite of predators in this system, including *O. mykiss* and several macroinvertebrate predators. I compared food web snapshots across time, as well as between permanent and temporary pools. I found that the intermittent stream food web remained relatively stable across time and did not differ between pool types. However, I also found significant changes in the trophic position, niche width, and mean $\delta^{13}C$ values for aquatic predators. This study provides an important first look at the trophic ecology of an imperiled fish species in intermittent streams during the summer drought season, and emphasizes that food chain length increases across the drought season, possibly because invertebrate prey are concentrated with declining water levels.

In conclusion, my research shows that anthropogenic factors at the watershed scale influence instream conditions and freshwater fish communities, and emphasizes that contemporary changes in land use can have subtle changes on fish community structure, which may be indicative of future declines of extirpations of native fishes. Finally, my research shows that changing conditions across the summer drought season lead to shifts in the trophic ecology of some, but not all, aquatic predators, including threatened steelhead trout. Overall my research contributes to a growing body of research that demonstrates how multi-scale natural and anthropogenic factors influence freshwater fishes in Mediterranean-climate region

DEDICATION

I dedicate this work to Desiree, mom, dad and Maya, who continuously support, inspire and encourage me – and to Antonia who I hope will one day find as much joy in fish as I do.

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CHAPTER 1

Introduction: The influence of land use and Mediterranean seasonality on California stream fishes

INTRODUCTION

The influence of land use and Mediterranean seasonality on California stream fishes

Freshwater ecosystems make up less than 1% of the Earth's surface (Dudgeon et al. 2006), yet they provide essential resources to humans and support high biodiversity. Indeed, freshwater ecosystems are among the most specious ecosystems on the planet (Balian et al. 2008), containing 10% of all known species and approximately 49% of the world's fishes (Carrizo et al. 2013). However, freshwater systems are also considered one of the most vulnerable ecosystems in the world as they are often subject to modification, water withdrawal, biotic invasions, and contamination (Strayer and Dudgeon 2010). Recent evidence suggests widespread declines of freshwater organisms from invertebrates (e.g., Strong et al. 2008) to amphibians (e.g., Stuart et al. 2004) to fishes (e.g., Smith and Darwall 2006, Strayer and Dudgeon 2010, Warren and Burr 2011), and these systems tend to have a higher proportion of threatened and endangered organisms than terrestrial systems (Richter et al. 1997, Strayer and Dudgeon 2010, Collen et al. 2014) and higher rates of extinctions compared to terrestrial systems (Ricciardi and Rasmussen 1999, Revenga and Kura 2003). Moreover, these extinction rates may be increasing. As an example, a recent analysis by Burkhead (2012) suggests that the extinction rate of North American freshwater fishes has increased by 25% since 1989. These patterns and trends suggest that we have much to learn about how best to manage freshwater ecosystems sustainably. Through this dissertation research, I examined the influence of land use and Mediterranean seasonality on California stream fishes. In this Introduction, I first provide some background on Mediterranean systems, including key characteristics of rivers and river fauna in Mediterranean regions, with a focus on California. Then, I provide an overview of my specific dissertation chapters.

Mediterranean-climate regions

Freshwater systems in Mediterranean-climate regions are especially sensitive to anthropogenic influence due to the high demand for water during the Mediterranean dry season as well as extensive land change to support human populations and agricultural production common in these areas (Cooper et al. 2012). Mediterranean climate regions occur between 31° and 40° north and south of the equator, and are located in the south or west side of their respective continents (Gasith and Resh 1999, Bonada and Resh 2013), including the Mediterranean Basin, central Chile, the Cape region of South Africa, the southwest and southern parts of Australia, and coastal California. Mediterranean systems are characterized by distinct wet and dry seasons. This distinct seasonality leads to limited water supply during the dry season when human demand is high for agricultural needs, which can lead to "water wars" between societal and ecological needs (Poff et al. 2003). In addition to strong seasonality, Mediterranean regions are characterized by

strong inter-annual variability in precipitation (Gasith and Resh 1999), thus exacerbating the competition between human and environmental needs following dry winters.

Water infrastructure

To protect against high flows during the wet season and to provide stable water supplies during the dry season, Mediterranean-climate rivers are highly regulated with complex water infrastructure to meet societal needs (Kondolf and Batalla 2002). As an example, most of California's large rivers are dammed, regulated, and diverted. The most well-known example is from California's Central Valley where massive water projects transfer water from water-rich areas in the north to water-poor areas in the central and southern part of California. These extensive modifications can have deleterious effects on the functioning of rivers and their biota. For example, engineered channels and culverts can impact stream function and biodiversity through changes in natural flow patterns, decrease in water quality, reduction in habitat heterogeneity, reduction in groundwater recharge (Burton et al. 2005), alteration of pool-riffle structure (Lau et al. 2006), and the loss of connection with floodplain and riparian areas which provide natural filtration from runoff (Chung et al. 2004). Similarly, reservoir operations can impair natural flow regimes to which native biota are adapted (Lytle and Poff 2004), create adverse water quality conditions (Santucci et al. 2005), limit fish migrations to upstream areas (Chart and Bergersen 1992), and facilitate the downstream invasion of introduced species (Johnson et al. 2008).

Land cover change

Due to the mild climate conditions, Mediterranean-climate regions have been subject to intense urban and agricultural development (Cooper et al. 2012). Urbanization has several well-documented negative effects on streams and stream biota (Paul and Meyer 2001). Streams in urbanized landscapes have a much higher proportion of impermeable surfaces and are generally associated with poorer water quality (Hatt et al. 2004, Peters 2009), bank instability (Dunne and Leopold 1978), and flashier flows (Konrad and Booth 2005, Schoonover et al. 2006) when compared to streams in more natural landscapes. Even relatively small land change conversions to urban areas can have large effects on freshwater communities (Klein 1980, Wang et al. 2001, Morgan and Cushman 2005). Land change to agriculture can also impact streams through the input of pesticides, nutrients, sediment, and pathogens, all of which can lead to poor water quality and habitat conditions (Lenat 1984). Agricultural activities also directly damage habitat and stream channels, and can decrease stream flow through surface water extraction. Both urban and agricultural land use are associated with reduced number of native and sensitive species and an increase in the number of non-native species (Wang et al. 2000, Genito et al. 2002, Walters et al. 2003, Marchetti et al. 2006, Li et al. 2011, Saalfeld and Reutebuch 2012).

Although the effects of land use on freshwater ecosystems in Mediterranean-climate regions are similar to other regions of the world, the magnitude of these responses may be intensified due to the unique seasonality and inter-annual variability in precipitation

characteristic of these systems (Cooper et al. 2012). During the prolonged dry period when water levels are low, agricultural or urban discharges (e.g., pesticides, sewage, nutrients) can become concentrated without sufficient flushing flows (Cooper et al. 2012). Additionally, water withdrawals during dry periods can intensify drought conditions and negatively impact aquatic biota already experiencing stress due to the seasonal drought conditions (e.g., low water flow, warm stream temperatures).

Invaded rivers

The highly modified landscape and hydroscape of Mediterranean-climate regions have facilitated the introduction of many nonnative freshwater species. In fact, the number of nonnative fishes exceed the number of endemic native fishes in each of the five Mediterranean-climate regions of the world (Marr et al. 2010). A recent synthesis on biotic invasions in Mediterranean-climate regions reported that 136 freshwater fish have been introduced globally, of which 89% of these species belong to the following orders: Cypriniformes, Cyprinodontiformes, Perciformes, Salmoniformes, and Siluriformes. These introductions have subsequently led to increased homogenization among Mediterranean freshwater systems as endemic species have been extirpated or have gone extinct (Marr et al. 2010, 2013). As such, biotic invasions, coupled with habitat degradation, are considered one of the leading threats to native biodiversity in Mediterranean-climate regions (Marchetti et al. 2004, Hermoso et al. 2011).

The predicted decline in native freshwater biota in Mediterranean-climate regions are expected to intensify with climate change (Filipe et al. 2013) and increases in human activities, such as land conversion (Cooper et al. 2012). For example, decreases in precipitation and streamflow and intensification of low flow periods have already been observed (García-Ruiz et al. 2011). Moreover, human populations are expected to become increasingly concentrated in urban areas (Grimm et al. 2008), suggesting that contemporary urbanization will continue to influence the trajectories of native fishes in the impacted regions. My research focuses on understanding the influence of Mediterranean seasonality and land change on stream fish distribution, abundance, and ecology, including both native and non-natives fishes. In the next sections, I introduce the setting and my research questions

Research location

My research is focused on streams in Central California, including within the San Francisco Bay area and in coastal Marin County (Figure 1). This region experiences a Mediterranean climate with cool, wet winters and hot, dry summers. Chapters 2 and 3 focus on streams that drain into the San Francisco Estuary, which is located within the Central Valley ichthyoprovince. This ichthyoprovince supports 40 native and 41 nonnative freshwater fishes (Moyle 2002), which have been introduced into this region for recreational fishing, vector control, the aquarium trade, or accidental releases (Marchetti et al. 2004). Chapter 4 focuses on an intermittent stream within the Golden Gate National Recreation Area in Marin County, which is located within the North Coast ichthyoprovince (Moyle 2002). There are approximately 25 native and freshwater fishes

occurring within North Coast streams (Moyle 2002). This includes two federally-protected salmonid fishes, of which California represents the southern end of their range.

In this region of California, there is a long history of human influence on the landscape and rivers. For example, much of the urban development in the San Francisco Bay region has occurred in lower elevation reaches, creating a common rural to urban gradient from high to low elevation areas; however, in recent years there has been rapid urban expansion into mid-elevation valleys (Gutierrez 2014). Watersheds within the San Francisco Bay region and in west Marin County also have a history of being grazed and agricultural development. Rangelands in this region provide important habitat for native fishes, as the streams are relatively less impacted than lower elevation and urbanized reaches that are common in the San Francisco Bay region (Leidy et al. 2011). With strong Mediterranean seasonality and 7.1 million people living in the greater San Francisco Bay region (US Census 2010), this was an ideal region to explore how land use and Mediterranean seasonality influence the distribution, abundance, and ecology of freshwater fishes.

Chapter 2: Direct and indirect effects of watershed properties on fish communities: an example from San Francisco Bay streams, USA

In chapter two, I explored the relationship between stream fish communities and a suite of environmental factors operating at multiple spatial scales in streams throughout the San Francisco Bay region. Specifically, I examined the direct effects of watershed-scale properties (e.g., land use, hydrologic modification, watershed area) and their indirect effects through changes in local-scale properties (e.g., stream depth, water conductivity) on stream fish communities. For this analysis, I built on local-scale habitat and fish community data collected from 193 sites representing 25 San Francisco Bay Area watersheds by RA Leidy in the mid-1990s (Leidy 2007). I georeferenced all of these sites, delineated individual watersheds for each site, and calculated watershed area, land cover composition, and the degree of hydrologic infrastructure for each site. Using a multivariate approach, I found that a combination of local (water conductivity) and watershed-scale factors (percent forested watershed, watershed area, elevation) explained 41 percent of the fish community variability among sites. Native and more sensitive species such as *Oncorhynchus mykiss* were associated with high forested watersheds and streams with low water conductivity, whereas more tolerant fishes (e.g., *Lavinia exilicauda* and *Gambusia affinis*) were negatively associated with these conditions. I also found evidence that fish communities were influenced indirectly by both natural and human-influenced watershed-scale factors through their effect on stream conductivity (e.g., agriculture and canal density influenced local stream water conductivity). These results suggest that it is important to consider both the watershed and local-scale factors, as well as the direct and indirect effects of watershed-scale properties, on freshwater fish communities. Furthermore, these results highlight the importance of managing water conductivity levels through activities such as storm water management in order to protect sensitive native fishes.

Chapter 3: Contemporary Land Change Alters Fish Communities in a San Francisco Bay Drainage, California, USA

In chapter three, I continued my examination of land use effects on fish communities in the San Francisco Bay streams through a resurvey study. Here I focused on the largest watershed draining directly into the San Francisco Bay: Alameda Creek Watershed (1800km^2) in Alameda and Santa Clara Counties. This rapidly urbanizing watershed, particularly in the mid-elevation reaches (e.g., Livermore Valley, which includes the 3rd fastest growing city in California, Dublin). In contrast, the upper-elevation undeveloped regions of the watershed have remained relatively unchanged in recent decades. This provided an opportunity to ask how recent urbanization has influenced fish communities in this watershed. To answer this question, I resurveyed 32 sites in 2009 that had been surveyed by RA Leidy in the mid-1990s, including 14 sites in the urbanizing region and 18 sites in the "control" region. Using a multivariate approach, I found that downstream of the urbanizing area, fish community composition (as measured by Bray-Curtis dissimilarity) significantly changed between the two survey periods, and native species richness and the relative abundance of a native cyprinid (*Lavinia symmetricus*) decreased. In contrast, I found no change in fish community composition in the control sites. Furthermore, there was a significant relationship between the percent increase in urbanization and the change in community composition, and this relationship was strongest when urbanization occurred close to the sampling site as opposed to further upstream ($r = 0.78$, $p < 0.001$). These results demonstrate that contemporary land change can lead to subtle shifts in freshwater fish communities, and that such studies that may foretell future declines or local extirpations of sensitive freshwater biota.

Chapter 4: Summer drought influences food web structure in an intermittent stream

In Chapter four, I study the effects of Mediterranean-climate seasonality on stream biota in a coastal intermittent stream, with a focus on anadromous *Oncorhynchus mykiss*. *O. mykiss* is a locally threatened species and is the subject of many stream conservation and restoration activities throughout the greater San Francisco Bay Area and in many of California's coastal watersheds. Recent research from the Carlson Lab at UC Berkeley has emphasized the importance of intermittent streams, which cease flowing for part of the year, as spawning and rearing habitat for *O. mykiss* (Bogan et al. 2015, Hwan and Carlson 2015). Here I build on this recent work to ask how food webs that support juvenile *O. mykiss* change across the summer drought season. I collected tissues from juvenile steelhead trout, aquatic invertebrates, terrestrial invertebrates, and primary producers in three permanent and three temporary pools across four months in the John West Fork, a tributary of Olema Creek in Marin County, CA. I then used stable isotopes of carbon and nitrogen to characterize the food web in each pool at each time period to examine shifts in stream food web structure and predator trophic position across the summer drought season. Overall we did not detect a considerable change in food web size or shifts in the mean isotopic carbon range, as most taxa were supported by periphyton and terrestrial detritus. We however found a significant increase in food chain length, and significant

shifts in the trophic position and niche width for a suit of predators. For example, both *O. mykiss* and small predatory midges increased in trophic position across the summer in permanent and temporary pools. Overall, these results provide insight into changes in trophic ecology of the top predator in these systems (*O. mykiss*) and the food web that supports this imperiled fish across the summer drought season.

Conclusion

As the health of our freshwater systems continue to decline, it is vital that we understand how multiple stressors across spatial and temporal scales influence distribution of organisms and ecological function. Through my dissertation, I contribute to this effort by elucidating how anthropogenic (land use and hydrologic modification) and natural (summer drought) conditions affect fish communities and aquatic food webs in Mediterranean-climate California. The results of my research will be useful in conserving native and endemic fish species that are at risk in our local streams, while the general questions and approaches have relevance for fish conservation in other Mediterranean-climate regions of the world.

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CHAPTER 2

Direct and indirect effects of watershed properties on fish communities: an example from San Francisco Bay streams, USA

Direct and indirect effects of watershed properties on fish communities: an example from San Francisco Bay streams, USA

ABSTRACT

Conserving freshwater biodiversity requires understanding the influence of a suite of environmental factors operating at multiple spatial scales, as well as their direct and indirect effects. We used multivariate analyses to evaluate the relationship between fish community composition and watershed- as well as local-scale factors from streams of the San Francisco Bay region, California, USA. We found that a combination of local-scale (water conductivity) and watershed-scale variables (percent of forested watershed, watershed area, elevation) explained 41 percent of the variability in fish community composition. More tolerant fish species, such as native *Lavinia exilicauda* and nonnative *Gambusia affinis*, were associated with low percent forested watersheds and high water conductivity, whereas native *Oncorhynchus mykiss* was negatively associated with these conditions. Structural equation modeling revealed that several watershed-scale factors influenced stream conductivity, including natural factors (elevation, watershed area) and human-influenced factors (land use, canal density), suggesting these factors also had indirect (albeit weak) effects on fish community composition. Our results highlight the importance of considering both the direct and indirect effects of watershed-scale factors on freshwater fish communities. Indeed, neglecting to do so may yield an incomplete picture of how watershed properties influence freshwater biodiversity.

Keywords: freshwater biodiversity; land cover; spatial scale; stream fish; structural equation modeling; watershed

INTRODUCTION

Conserving freshwater biodiversity requires understanding how a suite of environmental factors operating at multiple spatial scales influence freshwater biota (Roy et al. 2003, Strayer et al. 2003, Durance et al. 2006, Dextrase and Mandrak 2006, Johnson and Host 2010, Engman and Ramírez 2012). In-stream ("local") scale factors, such as channel structure and substrate size, have long been considered influential in determining assemblage structure (e.g., Richards et al. 1993, Rosenfeld et al. 2000, Engman and Ramírez 2012)(Erman and Erman 1984, Richards et al. 1993, Rosenfeld et al. 2000). Consequently, early stream restoration efforts were often implemented on small scales (< 1km of stream length; Bernhardt et al., 2005); however, there has been a growing recognition of the influence of the greater watershed area on local biota (Roth et al. 1996, Pease et al. 2011). Indeed, Poff (1997) describes watershed-scale factors as a crucial component of a hierarchical process in which a series of nested filters determine local species abundances and distributions.

Watershed-scale factors that influence streams and stream biota include both natural features, such as elevation and watershed size, as well as watershed modification caused by human activities. As an example, urbanized watersheds are often associated with degraded water quality (Peters 2009), altered flows (Schoonover, Lockaby & Helms 2006), unstable banks (Dunne and Leopold 1978), increased turbidity and suspended sediment (Walters et al. 2003), and assemblages dominated by nonnative or tolerant species (Morgan and Cushman 2005, Marchetti et al. 2006, Wang et al. 2011). Beyond land cover, hydrologic modification of

watersheds can also impact freshwater biodiversity. Reservoirs, for example, alter downstream communities by creating adverse water quality conditions (Santucci et al. 2005), alter the natural flow regime (Poff et al. 1997), and facilitate the downstream invasion of introduced species (Johnson et al. 2008).

Since it is now generally accepted that stream conditions and biota are influenced by watershed properties, there has been a call to incorporate a watershed perspective into stream management and restoration (Fausch et al. 2002, Lake et al. 2007, Beechie et al. 2010). For example, in the 165,759 km^2 Chesapeake Bay Watershed, the recent establishment of the largest Total Maximum Daily Load by the Environmental Protection Agency has led to the development of management plans to curb contaminant and nutrient inputs into focal waterways (U.S. Environmental Protection Agency, 2010). What is less well understood is the mechanism by which these watershed-scale factors influence fish communities, and whether their effects are direct or indirect, that is, mediated through their effect on local-scale factors. Recent research has begun to tackle this question by identifying the causal pathways between land cover and stream biota, including through intermediate factors such as stream water quality (King et al., 2005; Ficetola et al., 2011), sediment and stream channel structure (Burcher et al., 2007), and vegetation (Canessa and Parris 2013).

Here we examine watershed- and local-scale factors influencing the distribution of stream fishes in the San Francisco Bay (SFB) region of California, U.S.A. Our specific objectives were to (1) identify the watershed- and local-scale environmental factors structuring fish communities and (2) test whether watershed-scale factors have both direct and indirect effects on fish community composition.

MATERIALS AND METHODS

Study setting

The study area was located in the San Francisco Bay region of California, U.S.A. We focused on 25 of the approximately 66 smaller watersheds (3-1700 km^2) that drain directly into the San Francisco Estuary (Fig. 2.1), excluding the larger Sacramento and San Joaquin Rivers. Many of the streams flow along a rural-urban gradient, with urban development typically concentrated in the lower elevation zones. The SFB region falls within the Central Valley sub-province of the Sacramento-San Joaquin Ichthyoprovince and supports a diverse fish fauna, including 17 endemic and approximately 14 extant species are endangered, vulnerable, or threatened (Moyle, 2002; Moyle et al., 2011).

Site selection and fish sampling

Fish were collected at 275 sites within 25 watersheds between 1993-1999 (Fig. 2.1; Leidy, 2007). Sample sites were originally chosen to assess the status of native fishes in the region based on historical records of known occurrences, thus sampling was heavily focused on high elevation and less disturbed streams. Site selection was further restricted to accessible, wadeable, and predominately freshwater portions of watersheds. Fish were predominantly captured using single-pass electrofishing (at 250-300 volts), unless the sites were too deep, which required supplemental seine sampling. Regardless of the method, fishes within a study reach were always sampled in a downstream to upstream direction. All captured fish were identified to species, measured for body length (fork length, mm), and released alive. These distributional data

provided an opportunity to explore the influence of watershed properties and land use on fish communities of SFB streams.

Local-scale environmental variables

At each fish sampling location, 21 stream habitat attributes were measured. Our earlier analysis of these data revealed that seven of the local-scale factors had strong associations with fish distributions, including maximum stream depth, wetted channel width, percent canopy cover, dominant substrate, conductivity, stream order, and channel gradient (for details, see Leidy et al., 2011). Consequently, we focused on these local-scale factors in our current study with two modifications: we excluded channel gradient from our analysis due to missing data at multiple sites and we reclassified stream order as a watershed-scale variable.

The five local scale factors retained for analyses were sampled as follows. At each sample site, we measured the maximum depth. We then measured channel width at five equally spaced transects, from which we calculated the average wetted width (m). Dominant substrate size was estimated using the Wentworth particle-size scale. Percent canopy cover was estimated visually at each site. Stream conductivity (umhos/cm) was recorded prior to sampling using a handheld water quality meter (Hach C0150).

Watershed-scale environmental variables

To quantify the influence of watershed-scale factors on fish communities, we first delineated individual upstream watershed boundaries for each sample site using United States Geological Survey (USGS) 10m National Elevation Data and hydrology tools in ArcGIS 9.2 (ESRI, 2009). From this we determined the elevation at each sample site and quantified the watershed area upstream of the site (hereafter "watershed area"). Land cover for each upstream watershed boundary was quantified using National Land Cover Data (NLCD), a USGS product with a 16 land cover classification scheme at a 30 m resolution (Vogelmann et al. 2001). We used NCLD data from 1992 to correspond with the time period when fish data were collected. We collapsed these land cover classifications into four new categories: grassland, forested, urbanized, and cultivated (Table 2.1), and added another land cover layer of road density calculated from the1992 United States Census road data. Next we identified reservoirs with surface areas greater than 6000 m^2 that were connected to our sampled streams using the USGS National Hydrography Dataset and calculated engineered canal density using Bay Area Aquatic Resource Inventory stream data (Table 2.1; SFEI, 2011). Strahler stream order (Strahler 1957) was determined using USGS topographic maps. In total, we considered 10 watershed-scale variables in our analysis: elevation (m), watershed area upstream of each sample site (km^2), stream order, number of upstream reservoirs, canal density (m/km^2), road density (km/km^2), percent grassland, percent forested, percent urbanized, and percent cultivated land in the watershed (Table 2.1).

Statistical analyses

Prior to analysis, we removed several sites to avoid pseudoreplication and spatial autocorrelation. We used a Mantel correlogram to quantify the correlation between community composition (Bray-Curtis distance) and spatial (Euclidean) distance. At a threshold distance of 525 m, we observed a substantial decrease in the Pearson's correlation value (from 0.05 to 0.01). Consequently, we identified sites that were within 525 m of a neighboring site (n = 63), and randomly selected one site to retain for analyses. If, however, sites were within 525 m of one another but separated by a tributary confluence, both sites were retained for analyses (n = 6), as

these sites experienced different watershed inputs. Finally, we excluded 23 sites that were estuarine, had missing data missing, where no fish were captured, or were extreme outliers in terms of fish community composition (± 2 standard deviations in Bray-Curtis distance). Following these exclusions, we retained data from 193 sites in our analyses.

Beyond the above site exclusions, we also excluded rare species that were found at fewer than 3% of sites (Table 2.2). For the rest of the species (n = 14), we calculated relative abundance within sites as a response variable for our analyses because raw abundances were highly variable across sites. We also conducted several transformations on the environmental variables to improve normality: all percentage data were transformed using arcsin square root and all continuous data were log transformed (Table 2.1). Finally, we excluded variables that were highly correlated with other variables by calculating Pearson's correlation coefficients and identifying pair-wise correlations > 0.8 (Legendre and Legendre, 1998). Stream order and road density were highly correlated with watershed area and percent urbanized, respectively (Table 2.3), so we retained only watershed area and percent urbanized for analyses.

To visualize differences in fish community composition among sites, we used nonmetric multidimensional scaling (NMDS) with the Bray-Curtis dissimilarity index. To explore the association between the environmental variables and fish community composition, we calculated Spearman correlation coefficients between our environmental factors and the scores on NMDS axes one and two and plotted these factors as vectors on the NMDS plot. Next we identified a subset of environmental variables that best explained the community composition using BIO-ENV (Clarke and Ainsworth 1993). This approach quantifies the correlations between a community dissimilarity matrix and multiple environmental dissimilarity matrices, including every possible combination of environmental variables. The goal of BIO-ENV is to identify the combination of environmental variables that maximizes the Spearman correlation with the community dissimilarity matrix. We used Bray-Curtis and Euclidean distance for our community and environmental variable distance matrices, respectively. NMDS, BIO-ENV, and correlation analyses were all performed using the vegan package in R (Oksanen et al. 2012, R Core Team 2014).

While the BIO-ENV procedure identified a subset of watershed and local-scale factors that were correlated with community composition, it did not consider the possibility that watershed-scale factors *indirectly* influence community composition through their influence on local-scale factors. For this, we used structural equation modeling (SEM; Anderson & Gerbing, 1988). This method is used to examine complex ecological relationships by testing if a representative model including direct and indirect effects is a reasonable explanation of the data. The strength of the direct and indirect effects of particular variables in the SEM is assessed using standardized path coefficients. Direct effects are measured as the path coefficients between a predictor and the response variable. Indirect effects are represented by the effect of one predictor variable on the response variable as mediated by a second predictor variable (e.g., in our model the pathway from watershed area to conductivity to community composition represents the indirect effect of watershed area on community composition via its effect on conductivity). Indirect effects are calculated as the product of the indirect paths towards the response variable. Finally, total effects are calculated by summing the direct and indirect effects.

We used SEM to explore the possibility that watershed-scale variables had indirect effects on fish communities through their influence on local-scale variables. Consequently, we included only those local-scale variables that emerged as important from our BIO-ENV results (i.e., water conductivity). However, we included the full suite of watershed-scale variables-

regardless of whether they or not they were identified as important via BIO-ENV because the BIO-ENV procedure tested only the direct influence of these variables on fish community composition. It is therefore possible that additional watershed-scale variables might indirectly influence fish communities by influencing water conductivity. Thus, we considered all of the watershed-scale variables, including natural (watershed area and elevation) and human-influenced (land use and hydrologic modification) variables. However, because most of the human-influenced factors were correlated with one another (mean correlation r = 0.30), we generated synthetic variables to describe the factors. Here we conducted a principal component analysis (PCA) including all land cover and hydrologic modification variables, and retained principle components (PCs) with eigenvalues > 1 for our SEM analysis. Finally, we used NMDS axis values to represent our response variable, community composition (see also Tylianakis et al., 2008; García-Palacios et al., 2011). As indicators of model fit, we used a chi-square test with an associated p-value > 0.05, a root mean square error of approximation (RMSEA) < 0.05, and a goodness of fit (GFI) > 0.95 (Kline 2010). Structural equation modeling was conducted using the lavaan package in R (Rosseel 2012, R Core Team 2014).

RESULTS

Fish assemblages

Across all sampling sites, we captured a total of 31 species from 24 genera and 14 families. Seventeen of these species however were not widely distributed nor in high abundance (< 3% of sites). The 14 more common species that were the focus of this analysis were from 11 genera and 9 families, including 8 native species and 6 nonnative species (Table 2.2). The most widely distributed fishes, each found at greater than 40% of study sites, were all native fishes: California roach (*Lavinia symmetricus*), rainbow trout (*Oncorhynchus mykiss*), Sacramento sucker (*Catostomus occidentalis*), and threespine stickleback (*Gasterosteus aculeatus*). Four other native species had more limited distributions (found at < 30% of sites), including prickly sculpin (*Cottus asper*), riffle sculpin (*Cottus gulosus*), Sacramento pikeminnow (*Ptychocheilus grandis*), and hitch (*Lavinia exilicauda*). Mean native species richness per site was 2.7 (range = 0 to 6), the mean density of native fishes was 1.1 fish/m^2 (range = 0 to 43.7), and the mean relative abundance of native fishes was 0.94 (range = 0 to 1). Overall, the six nonnative fishes were rare and comprised only a small proportion of fishes captured at any given site (Table 2.2); these included common carp (*Cyprinus carpio*), western mosquitofish (*Gambusia affinis*), green sunfish (*Lepomis cyanellus*), bluegill (*Lepomis machrochirus*), rainwater killifish (*Lucania parva*), and inland silverside (*Menidia beryllina*).

Nonmetric multidimensional scaling analyses resulted in a significant two-dimensional ordination (Fig. 2.2; stress = 0.16). Axis 1 represented a gradient from sites characterized by high relative abundances of native rainbow trout (negative correlation coefficient with Axis 1) to those characterized by high relative abundances of native *L. exilicauda, C. asper, C. occidentalis* and a few nonnative fishes including *G. affinis* (positive correlation coefficients with Axis 1; Table 2.2). Axis 2 represented a gradient from sites characterized by a by high relative abundances of native *L. symmetricus* and lower relative abundances of the native *G. aculeatus* and *C. asper* (Table2. 2).

Watershed properties

Our 193 study sites were distributed across 25 watersheds that differed in several watershed properties, both natural and anthropogenic (Table 2.1). The mean elevation was 104 m (range = 2 to 809 m) and the mean total watershed size was 677.8 km^2 (range = 7.9 to 1714.3 km^2; Table 2.1). Overall, the watersheds upstream of our study sites were dominated by forest and grassland (Table 2.1), reflecting our focus on upstream areas (see Methods). Although most sites had some degree of cultivated or urbanized lands upstream of the site, these tended to comprise only a small proportion of the total watershed land cover (Table 2.1). Forty-three percent of sites had major reservoirs upstream, and canals and engineered channels were present in the majority of the sampled watersheds (70%) but at relatively low densities (0.11 m/km^2). Some watershed-scale variables were significantly correlated with local-scale variables, suggesting the possibility of indirect effects of watershed-scale factors on fish communities via their influence on local-scale factors. For example, water conductivity was positively correlated with watershed area upstream of each site and percent cultivated watershed, and negatively correlated with elevation and percent forested watershed (Pearson $r > 0.4$; Table 2.3).

Influence of local-scale and watershed-scale factors on fish communities

Six environmental factors exhibited relatively strong correlations ($r \geq 0.40$) with NMDS ordination Axis 1: water conductivity ($r = 0.61$), percent forested watershed ($r = -0.56$), watershed area ($r = 0.44$), upstream canal density ($r = 0.42$), percent canopy cover ($r = -0.41$), and elevation ($r = -0.40$; Fig. 2.2). None of the environmental factors were strongly correlated with Axes 2 (i.e., all correlations < 0.4). The BIO-ENV procedure indicated that the correlation between community and environmental dissimilarity matrices was maximized (Spearman correlation = 0.41) when four of these environmental factors were included in the model: percent of forested watershed, elevation, watershed area, and water conductivity.

SEM of watershed-scale factors on fish communities

For the structural equation model, we included water conductivity as our local-scale variable as well as two natural watershed-scale factors (elevation and watershed) that were identified through BIO-ENV as factors influencing fish communities. Additionally, we included two principal component (PC) axes that together explained 63% of the variation in variables related to land cover and hydrologic modification. PC1 represented watersheds with low percent forested land, high percent cultivated land, and with high canal density, while PC2 represented watersheds with low percent urbanized lands and a high percent of grassland. As a response variable for our SEM, we used only the first NMDS axis to represent community composition, as the direct and indirect effects of our environmental variables were not significantly associated with the second NMDS axis. Although we considered the direct and indirect effects of all of the environmental factors listed above, our main focus was on the indirect effect of watershed land cover and hydrologic modification on community composition mediated through water conductivity.

Our SEM model explaining the community composition gradient was a good fit and explained a substantial amount of the variance in community composition ($\chi^2 = 1.47$, df = 1, $P = 0.23$; RMSEA = 0.05; GFI = 0.99; $R^2 = 0.62$). The largest contribution to this variance was due to the direct effect of water conductivity (Table 2.4, Fig. 2.3), consistent with the BIO-ENV results (Fig. 2.2). PC1 also had a moderately strong direct effect on community composition as well as significant indirect effect acting through water conductivity. Overall, this suggests that watersheds with low forested land cover, high cultivated land cover, and high canal density had a

weak positive indirect effect on the relative abundance of nonnative fishes and *L. exilicauda*, and a negative effect on *O. mykiss*, mediated through the influence of these variables on water conductivity. PC2 did not have significant direct or indirect effects on community composition (Fig. 2.3, Table 2.4). The direct effects of watershed area explained a moderate proportion of the variation, but had a larger effect through its indirect effect on PC1 and water conductivity. Elevation did not have a significant direct effect, but did have significant indirect effects mediated through other variables (Fig. 2.3, Table 2.4).

DISCUSSION

We used multivariate analyses (NMDS) to characterize fish community composition across 193 sites from 25 San Francisco Bay Area watersheds. We then correlated variation in fish communities and environmental conditions to explore the effects of watershed- and local-scale environmental variables on fish community structure (using the BIO-ENV procedure). The top supported model indicated that water conductivity, percent of forested watershed, elevation, and watershed area all influenced fish community composition. We then investigated the *indirect* effects of watershed land cover and hydrologic modification on fish communities using structural equation modeling (SEM). We found that canal density, percent of forested watershed, and percent of cultivated land cover had both direct and indirect effects on fish community composition mediated through their influence on water conductivity. Our study also highlighted patterns in species-environment relationships, particularly the importance of high percent of forested watershed and low water conductivity for native *O. mykiss*. Overall, our results re-affirm the importance of considering both local-scale and watershed-scale properties for explaining variation in fish communities and underscores the need to consider both the direct and indirect effects of watershed properties on freshwater biota.

Watershed- and local-scale factors influence fish communities

Our results highlight the importance of both local- and watershed-scale factors in influencing fish community composition in San Francisco Bay streams. A local-scale factor, water conductivity, had the strongest correlation with fish community composition (Spearman correlation with NMDS axes: 0.61). At the species level, we found that high water conductivity was negatively associated with the abundance of the native salmonid *O. mykiss* but positively associated with the abundance of nonnative *G. affinis* and *M. beryllina*. One native species, *L. exilicauda*, was found in watersheds with high water conductivity levels, highlighting that some native species are more robust than others to altered stream conditions. Although high water conductivity/total dissolved solids can cause direct mortality of stream biota (Weber-Scannell and Duffy 2007, Herbst et al. 2008, Kimmel and Argent 2009), the levels in our study were likely not high enough to cause mortality. However, high water conductivity levels are commonly correlated with other stressful water conditions (e.g., metal toxins, Wang and Yin 1997), suggesting that the levels found in our study might reflect deteriorated water quality conditions more generally.

Beyond the high correlation between water conductivity and fish communities, water conductivity was also correlated with a suite of watershed-scale environmental variables, including percent of forested and percent of cultivated land. These correlations suggest that land use might be influencing water quality conditions among our study sites. Indeed, artificially high

water conductivity (and associated total dissolved solids; TDS) has commonly been linked to runoff from agriculture (Lenat 1984), industry, and urban nonpoint source pollution such as sewage leakage (Rose 2007). Local geology (e.g., marine sediments) can also influence water conductivity; however our preliminary exploration of the influence of geology on water conductivity in our study watersheds revealed no correlation between the two within our data set ($p = 0.364$).

In addition to the influence of local-scale water conductivity, watershed-scale factors also influenced fish communities. For example, the percent of forested land cover in a watershed was highly correlated with fish community composition (Spearman correlation with NMDS axes: 0.56). Forested land cover may have emerged as the most influential of the four land cover types because it was the most common among our study sites (Table 2.1), given our focus on upper elevational areas. Additionally, this correlation may have been driven by strong associations between the percent of forested watershed and the distribution and abundance of certain species. For example, native *O. mykiss* and *C. asper* were strongly associated with highly forested watersheds, while native hitch *L. exilicauda* were negatively associated with these conditions. However, other native fishes were more ubiquitous and inhabited watersheds dominated by multiple land cover types (e.g., *C. occidentalis*), which would serve to diminish the correlation between land cover and community composition. Overall, our results support earlier studies that have found forested land cover to be an important factor influencing stream biota (Strayer et al. 2003, Allan 2004, Urban et al. 2006).

Finally, two natural watershed properties had moderate influences on fish communities, elevation and watershed area. The majority of the fish species included in our study (with the exception of native *O. mykiss* and *C. asper*) were negatively associated with elevation. Similarly, fishes were structured along a gradient of watershed area, with native *C. occidentalis* and nonnative *C. carpio* associated with larger watershed areas. These results are expected as distinct fish assemblages, as well as overall patterns of species diversity, often emerge along gradients of elevation and watershed area (e.g., Rahel and Hubert 1991, Quist et al. 2004).

Indirect effects of watershed-scale factors on fish communities

Because streams are structured in a complex hierarchical manner (Frissell et al. 1986), watershed-scale factors are often correlated with local-scale factors making it difficult to tease apart their relative influence on stream biota (Allan, 2004; Roy et al., 2005; Gido et al., 2006). We used structural equation modeling (SEM) to estimate the direct and indirect effects of watershed-scale properties on fish community composition.

Simple correlations between watershed-scale factors and water conductivity (Table 2.3) hinted that watershed-scale land cover might be indirectly influencing fish communities. Using SEM to explore this possibility, we found that a composite variable derived from a principal component analysis including canal density, percent forested, and percent cultivated watersheds had significant indirect effects on fish community composition, mediated through its influence on water conductivity. Canal density may be important because of the common association between modified stream channels and the loss of connection with floodplain and riparian areas which provide natural filtration from runoff (Chung et al. 2004). Land cover can also influence water conductivity. For example, forested watersheds are commonly associated with higher water quality than regions with significant agricultural influence (e.g., Lenat, 1984; Marzin et al., 2012). Similar to our results, a study in the North Lakes region of the United States reported that local-scale variables explained most of the variation in fish presence in relatively undisturbed

regions, but that these local processes were controlled by watershed and riparian land use (Wang et al. 2003).

Finally, our SEM results revealed the indirect effect of elevation and watershed area through their influence on water conductivity. This result was not too surprising given that both elevation and watershed area were correlated with water conductivity (r= 0.53 and 0.49, respectively). Importantly, patterns in human modification of watersheds are often structured along elevational gradients (Maloney and Weller 2011), which may have strengthened this result. In the San Francisco Bay study region, for example, urban development has largely been concentrated in low to mid-elevation regions fringing the bay similar to other systems (e.g., Iberian Peninsula, Matono and Bernardo 2014). The indirect effects of watershed area were also highlighted by Infante and Allan (2010), who reported that watershed area indirectly influenced certain fish species through its correlation with stream width and volume.

Overall, the indirect effects identified in our study were weaker than the direct effects (Table 2.4). Nevertheless, failure to consider such indirect effects could lead to an incomplete picture of the total effect of watershed-scale properties on freshwater biota. By not considering such indirect effects, otherwise influential environmental factors might be underestimated or overlooked altogether (e.g., Maloney and Weller 2011). Including the indirect effects of watershed-scale factors might be especially important for implementing effective restoration and management of aquatic biota (Cooper et al. 2012).

Conclusions

Our study identified key environmental factors influencing fish communities in streams of the San Francisco Bay region, including watershed- and local-scale factors. We considered the direct as well as indirect effect of the watershed on stream fish communities by assessing how watershed-scale properties and hydrologic modification influenced water conductivity, a key factor influencing fish communities in this system. These results support the common perception that reductions in water conductivity from stormwater management projects should favor sensitive freshwater biota (Walsh et al. 2005). Many cities around the globe have established such programs to curb urban runoff into waterways and manage water conductivity and total dissolved solids levels (Dietz 2007). However many regions of the world still lack adequate stormwater management and treatment methods that could benefit stream ecosystems (Marsalek and Chocat 2002). Our results also re-affirm the importance of incorporating a watershed-scale perspective into stream management (e.g., Fausch et al., 2002; Lake et al., 2007), specifically management actions that minimize land conversion and that manage urban stormwater to reduce water conductivity levels. Finally, our study contributes to the growing body of research highlighting how watershed properties can directly and indirectly influence freshwater biodiversity.

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Table 2.1. Name, description, transformation, and source of the variables used in analyses. Included are the summary statistics of continuous variables from all of the sites included in the analysis (mean, standard deviation, and range).

Variable	Category	Description	Transformation	Mean (SD)	Range	Source
fish species	response	relative abundance	-	-	-	Leidy 2007
elevation	natural	sample site elevation (m)	log (x)	104 (23)	2-809	Nat'l Elevation Dataset 10m
watershed area	natural	total drainage area upstream of sites (km^2)	log (x)	193.9 (371.9)	1-1692	ArcGIS 9.2 hydrology tool calculation
stream order	natural	Strahler stream order	-	3.4 (1.2)	1-6	Leidy 2007
reservoir	hydrologic modification	number of upstream reservoirs	-	0.8 (1.5)	0-9	Nat'l Hydrography Dataset
canal	hydrologic modification	density of ditches, engineered channels, or culverts (m/km^2)	log (x)	0.1 (0.1)	0-.0.5	SFEI BAARI
road	land cover	road density within a watershed (km/km^2)	log(x)	1.9 (0.1)	0-13.9	TIGER, US Census
forested	land cover	% of watershed that is forest or shrubs	arcsine sqrt	56.3 (20.3)	4.2-94.5	Nat'l Land Cover Dataset
grassland	land cover	% of watershed that is grassland	arcsine sqrt	29.9 (17.2)	1.7-88.8	Nat'l Land Cover Dataset
cultivated	land cover	% of watershed that is orchards, pasture, row crops, small grain, or recreational grasses	arcsine sqrt	2.2 (5.7)	0-70.1	Nat'l Land Cover Dataset
urban	land cover	% of watershed that is residential, commercial, or industrial	arcsine sqrt	9.2 (15.4)	0-93.1	Nat'l Land Cover Dataset
wetted width	reach	average wetted channel width (m)	log (x)	5.3 (3.2)	1.3-17.6	Leidy 2007
max depth	reach	maximum depth (m)	log (x)	74.9 (38.6)	3.5-240	Leidy 2007
canopy cover	reach	% of the wetted channel covered by vegetation	arcsine sqrt	41.1 (32.4)	0-90	Leidy 2007
water conductivity	reach	average conductivity (umhos/cm)	log (x)	370.4 (218.2)	77-1200	Leidy 2007
dominant substrate	reach	based on Wentworth particle size	log (x)	-	-	Leidy 2007

Table 2.2. Species collected in the dataset listed in order of the percentage of sites they are found, including the common name, whether native (N) or introduced (I), percent and number of sites where a species was captured, mean relative abundance per site (± standard error), the labeling code used in the NMDS plot (first letter of the genus followed by the first two letters from the species name), and the Pearson product correlation between species relative abundance and scores on NMDS Axes 1 and 2. Rare species listed below the dotted line were not included in the analyses.

Species	Common name	N/I	% (#) of sites	Mean relative abundance	code	NMDS 1 corr.	NMDS 2 corr.
Lavinia symmetricus	California roach	N	59(112)	30.0 ± 2.6	LSY	0.14	-0.80
Oncorhynchus mykiss	rainbow trout	N	52(99)	24.0 ± 2.6	OMY	-0.87	0.13
Catostomus occidentalis	Sacramento sucker	N	49(94)	9.4 ± 1.3	COC	0.35	-0.16
Gasterosteus aculeatus	threespine stickleback	N	44(84)	16.7 ± 2.2	GAC	0.20	0.70
Cottus asper	prickly sculpin	N	31(60)	8.6 ± 1.5	CAS	0.30	0.35
Cottus gulosus	riffle sculpin	N	16(30)	2.7 ± 0.6	CGU	-0.10	-0.06
Ptychocheilus grandis	Sacramento pikeminnow	N	14(27)	1.1 ± 0.4	PGR	0.05	-0.17
Lepomis cyanellus	green sunfish	I	13(25)	1.5 ± 0.4	LCY	0.22	-0.07
Gambusia affinis	western mosquitofish	I	11(21)	3.2± 1.0	GAF	0.36	-0.05
Lavinia exilicauda	hitch	N	8(16)	1.5 ± 0.6	LEX	0.26	-0.02
Cyprinus carpio	common carp	I	5(10)	0.1 ± 0.0	CCA	0.17	-0.13
Lepomis machrochirus	bluegill	I	4(9)	0.5 ± 0.2	LMA	0.10	0.04
Lucania parva	rainwater killifish	I	4(8)	0.5 ± 0.2	LPA	0.18	0.21
Menidia beryllina	inland silverside	I	4(7)	0.5 ± 0.3	MBE	0.21	0.01
Hysterocarpus traski	tule perch	N	2(4)	0.2 ± 0.1			
Morone saxitilis	striped bass	I	2(4)	0.1 ± 0.1			
Lampetra tridentata	Pacific lamprey	N	2(3)	0.03 ± 0.02			
Orthodon microlepidotus	Sacramento blackfish	N	2(3)	0.1 ± 0.1			
Leptocottus armatus	staghorn sculpin	N	2(3)	0.2 ± 0.2			
Micropterus dolomieu	smallmouth bass	I	2(3)	0.1 ± 0.1			
Micropterus salmoides	largemouth bass	I	2(3)	0.06 ± 0.05			
Acanthogobius flavimus	yellow fin goby	I	2(3)	0.06 ± 0.04			
Lepomis gibbosus	pumpkinseed	I	1(2)	0.02 ± 0.02			
Mylopharodon conocephalus	hardhead	N	1(2)	0.5 ± 0.5			
Lepomis microlophus	redear sunfish	I	1(2)	0.01 ± 0.01			
Carassius auratus	goldfish	I	1(2)	0.01 ± 0.01			

Oncorhynchus mykiss	steelhead	N	0.5(1)	0.01 ± 0.01
Notemigonus crysoleucas	golden shiner	I	0.5(1)	1.2 ± 1.2
Percina macrolepida	bigscale logperch	I	0.5(1)	0.01 ± 0.01
Pimephales promelas	fathead minnow	I	0.5(1)	0.03 ± 0.03
Tridentiger trigonocephalus	chameleon goby	I	0.5(1)	0.04 ± 0.04

Table 2.3. Pearson correlation coefficient for each pair of environmental variables, with significant values bolded ($p < 0.05$)

	water-shed area	elev-ation	stream order	max depth	wetted width	cond-uctivity	canopy cover	reser-voir	canal density	road density	% urban-ized	% cult-ivated	% for-ested
elevation	**-0.18**												
order[b]	**0.86**	**-0.15**											
max depth	**0.16**	-0.06	0.14										
wetted width	**0.67**	**-0.15**	**0.63**	**0.25**									
conductivity	**0.53**	**-0.49**	**0.51**	0.13	**0.36**								
canopy cover	**-0.39**	**0.28**	**-0.33**	**-0.16**	**-0.43**	**-0.42**							
reservoir	**0.47**	**-0.20**	**0.47**	0.14	**0.38**	**0.24**	-0.13						
canal density	**0.15**	**-0.57**	**0.25**	0.02	0.14	**0.37**	**-0.19**	**0.22**					
road density	-0.04	**-0.61**	-0.05	-0.01	0.00	**0.23**	**-0.18**	-0.04	**0.42**				
% urban	0.01	**-0.60**	0.07	0.04	0.05	**0.29**	**-0.24**	-0.01	**0.47**	**0.85**			
% cultivated	**0.48**	**-0.41**	**0.41**	0.04	**0.29**	**0.44**	**-0.21**	**0.24**	**0.44**	**0.15**	0.12		
% forest	**-0.35**	**0.52**	**-0.24**	-0.04	**-0.16**	**-0.46**	**0.41**	-0.11	**-0.45**	**-0.42**	**-0.56**	-0.40	
% grassland	**0.41**	-0.07	**0.22**	0.01	0.12	**0.26**	**-0.26**	0.09	-0.01	**-0.24**	**-0.20**	0.26	-0.65

Table 2.4. Results from a structural equation model for community composition (NMDS Axis 1) including direct, indirect, and total standardized effects (n.s. = non-significant models, $P > 0.05$).

Predictor	Pathway	Effect
conductivity	direct	0.46
land cover and hydrologic modification (PC1)	direct	0.21
	indirect via conductivity	0.08
	total effect	0.29
land cover (PC2)	direct	n.s.
	indirect via conductivity	n.s.
	total effect	n.s.
watershed area	direct	0.19
	indirect via PC1	0.07
	indirect via PC2	n.s.
	indirect via conductivity	0.19
	total effect	0.45
elevation	direct	n.s.
	indirect via PC1	-0.13
	indirect via PC2	n.s.
	indirect via conductivity	-0.13
	total effect	-0.26

Figure 2.1. Location of study sites in the San Francisco Bay region, California, U.S.A., including the 193 sites included in analyses.

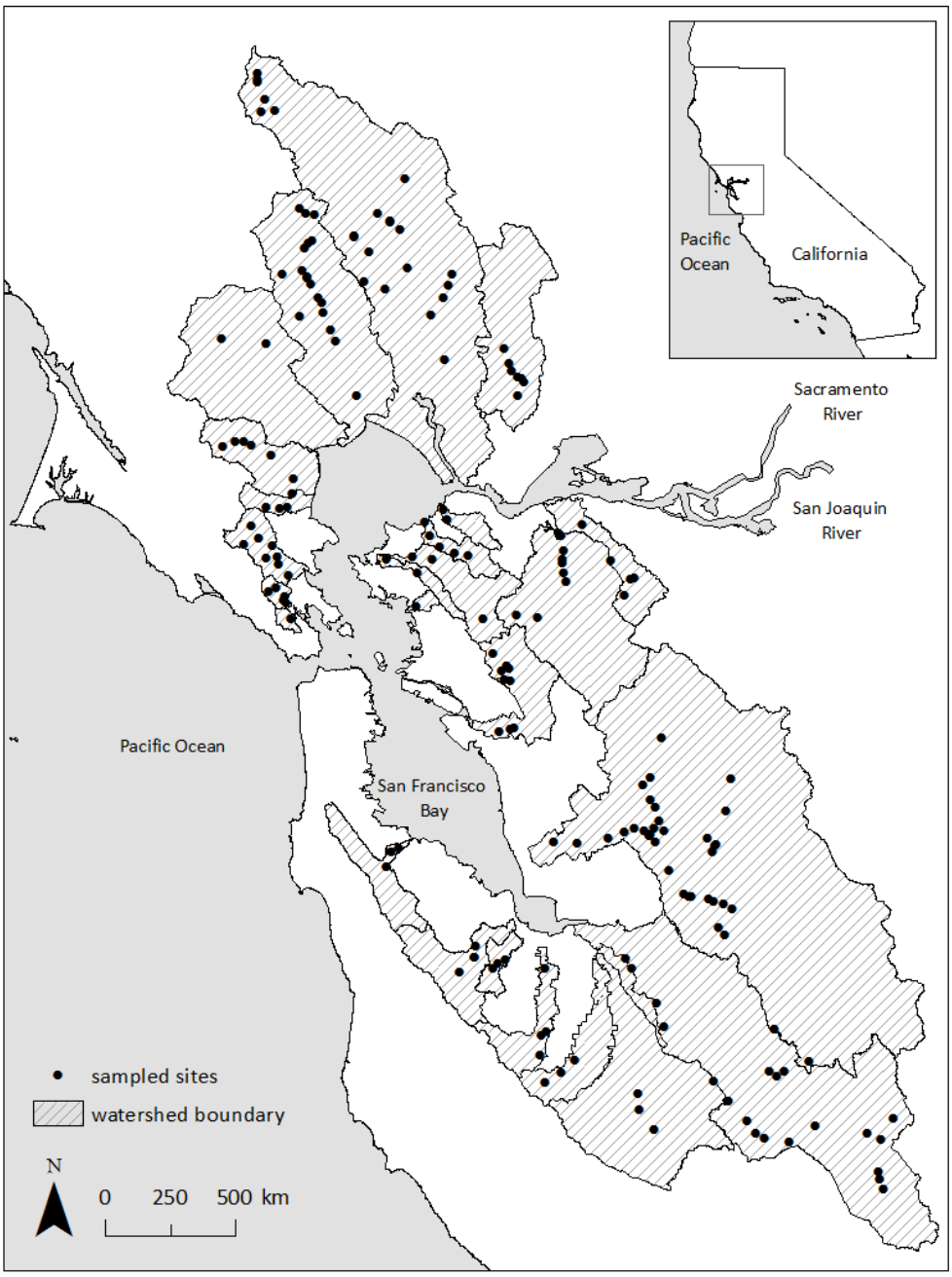


Figure 2.2. Two-dimensional NMDS plots of stream sites, fish species, and environmental variables from the top model as identified via the BIO-ENV procedure. The angles and lengths of the vectors indicate the direction and strength of relationships of the variables with the ordination scores. Species are labeled by their species code (see Table 2.2). Native species are shown in plain black font, and nonnative species are denoted by gray italicized font.

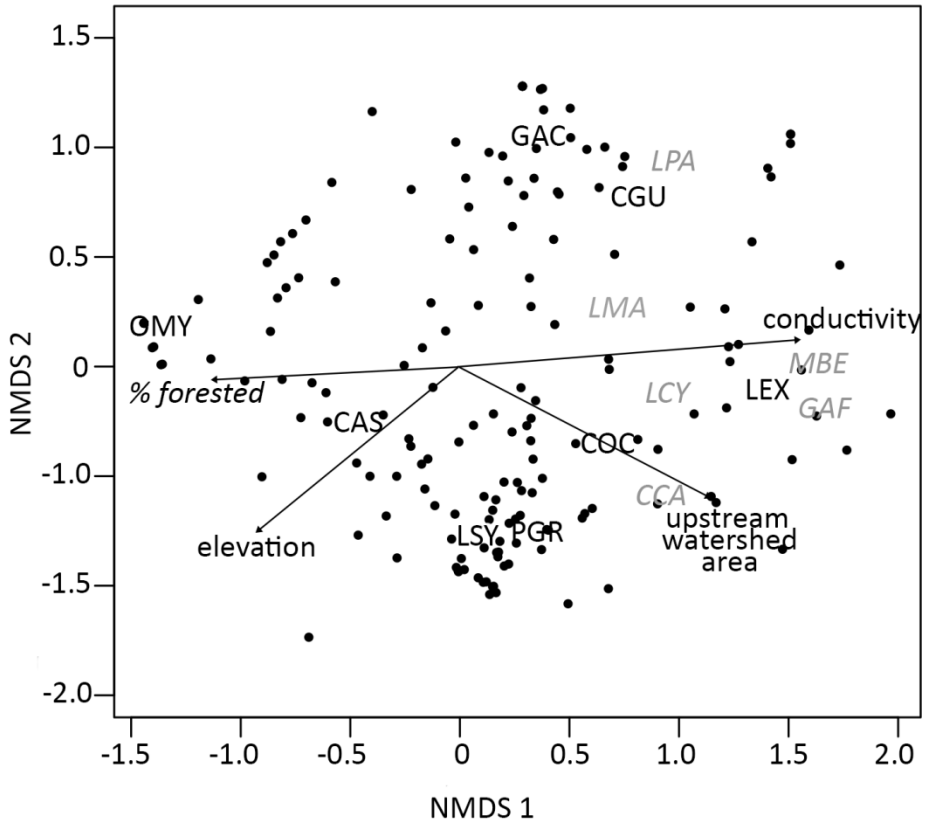
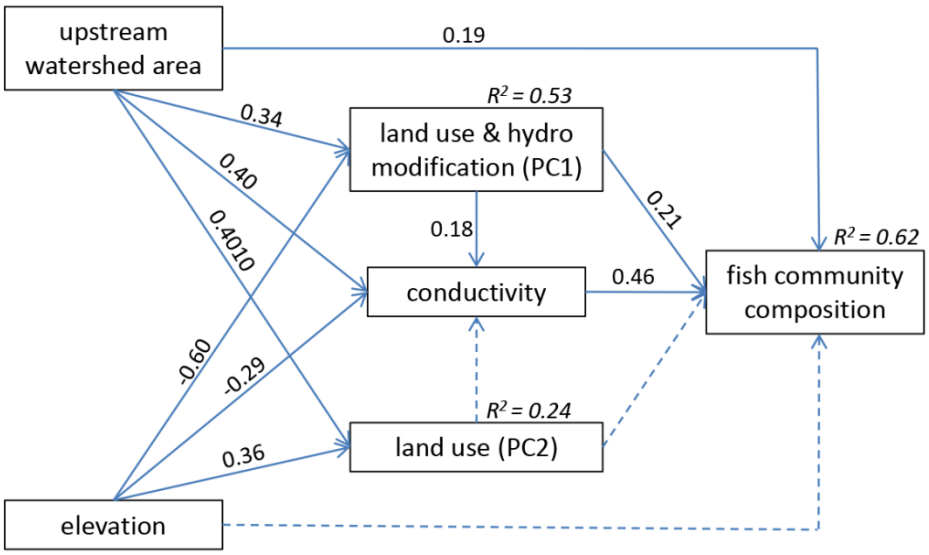


Figure 2.3. Structural equation model showing the pathways of upstream watershed area, elevation, water conductivity, and land use and hydrologic modification (represented by PC1 and PC2) on fish community composition (i.e., NMDS Axis 1). The standardized coefficients for each direct pathway are shown along arrows. Indirect effects and total effects are given in Table 2.4. Above each response variable, R^2 values are shown and signify the proportion of variance explained. Dashed lines represent non-significant relationships ($P > 0.05$).



CHAPTER 3

Contemporary Land Change Alters Fish Communities in a San Francisco Bay Drainage, California, U.S.A.

Contemporary Land Change Alters Fish Communities in a San Francisco Bay Drainage, California, U.S.A.

ABSTRACT

Urbanization is one of the leading threats to freshwater biodiversity, and urban regions continue to expand globally. Here we examined the relationship between recent urbanization and shifts in stream fish communities. We sampled fishes at 32 sites in the Alameda Creek drainage, near San Francisco, California, in the 1990s and in 2009, and we quantified univariate and multivariate changes in fish communities between the sampling periods. Sampling sites were classified into those downstream of a rapidly urbanizing area ("urbanized sites"), and those found in less impacted areas ("low-impacted sites"). We calculated land cover changes between 1993 and 2009 at two scales for each site (the entire drainage basin and a 3km buffer zone immediately upstream of each site). Neither the mean relative abundance of native fish nor nonnative species richness changed significantly between the survey periods. However, we observed significant changes in fish community composition (as measured by Bray-Curtis dissimilarity) and a decrease in native species richness between the sampling periods at urbanized sites, but not at low-impacted sites. Moreover, the relative abundance of one native cyprinid (*Lavinia symmetricus*) decreased at the urbanized sites but not at low-impacted sites. Increased urbanization was associated with changes in the fish community, and this relationship was strongest at the smaller (3km buffer) scale. Our results suggest that ongoing land change alters fish communities and that contemporary resurveys are an important tool for examining how freshwater taxa are responding to recent environmental change.

Keywords: urbanization; land cover; resurvey; stream fish; watershed

INTRODUCTION

The conversion of natural to urban land cover is one of the greatest threats to species diversity and ecosystem function in freshwater ecosystems (Sala 2000, McDonald et al. 2013). Urbanization degrades water quality and alters hydrology, channel structure, and bed composition (Paul and Meyer 2001, Walsh et al. 2005), all of which have the potential to impact native biota. Indeed, urbanization has been linked to decreased native species diversity (Riley et al. 2005, Helms et al. 2009) as well as the expansion of tolerant and/or nonnative species (Morgan and Cushman 2005, Roy et al. 2005, Marchetti et al. 2006). With continuing human population growth (Gerland et al. 2014) and the anticipated expansion of urban areas in the next few decades (Seto et al. 2011), there is a pressing need to understand the consequences of contemporary (e.g., 1-2 decades) land change on freshwater biodiversity.

To evaluate the influence of changing land cover on freshwater communities, several approaches have been employed. Most research has focused on single time periods to evaluate how present day community patterns relate to present day land (e.g., Lammert and Allan 1999, Fitzpatrick et al. 2001, Sály et al. 2011, de Jesús-Crespo and Ramírez 2011). This approach is useful for elucidating the legacy effects of land use, but provides little insight into the time scale of community shifts. Another approach involves resurveying communities after a given period of time. Historical resurvey studies that span multiple decades have yielded valuable insights into community change in response to land cover change (e.g., Harding et al. 1998, Wenger et al. 2008, Johnston and MacEina 2009, Maloney and Weller 2011, Johnson et al. 2011). Likewise, contemporary resurvey studies following 1-2 decades can be useful for revealing how quickly biotic communities respond to recent land cover change and can provide insight into the dynamics of declining species (Patton et al. 1998, Poole and Downing 2004, Gibbs et al. 2005, Labay et al. 2011, Matthews et al. 2013).

Beyond considering the effects of recent environmental change, effective freshwater conservation also requires identifying the appropriate spatial scale for examining biotic responses to land cover change. Local stream assemblages are influenced by a hierarchy of nested environmental filters that operate at multiple scales from the watershed to the microhabitat scale (Frissell et al. 1986, Poff 1997). However, the relative importance of any particular scale on freshwater biota can vary depending of the drainage size, the degree of human disturbance, and other regional differences (Strayer et al. 2003, Stanfield and Kilgour 2012). Similarly, the impacts of land change at different scales and locations within a drainage basin may have different effects on freshwater communities.

Here, we evaluate the impact of contemporary land change on stream fish communities in a San Francisco Bay drainage in California, USA through a resurvey study. The fish community was originally surveyed in the mid-1990s (described in (Leidy 2007), which provided an opportunity to resurvey 32 sites after approximately 16 years to determine how recent urbanization in the region has influenced local fish communities. Our specific objectives were to (1) characterize recent land change within the drainage, (2) characterize fish community change at each sampling site, and (3) explore the influence of land change on fish community change between the two survey periods. We predicted that regions with a greater land cover change would be associated with greater fish community change. We tested this hypothesis using land cover data collected at two scales: a local (3km) buffer immediately upstream of each sampling site and the larger total drainage basin upstream of each site.

METHODS AND MATERIALS

Study sites

We conducted our study in the Alameda Creek watershed, the largest drainage basin of the San Francisco Bay in California, USA, excluding the greater Sacramento and San Joaquin Rivers

(Fig. 3.1). This region falls within the Sacramento-San Joaquin Ichthyoprovince, which supports a diverse assemblage of native and nonnative fish species (Moyle 2002). The Alameda Creek drainage basin is approximately 1800 km^2 and encompasses multiple land cover types, from upper watershed oak savannas and grasslands, to mid-watershed mixed suburban-low intensity agricultural regions, to low elevation and densely urbanized floodplains. Although much of the upper drainage has remained relatively intact, as much as 78% of the mid- and lower regions of the drainage basin has been converted to agriculture, urban areas, or salt ponds since the early 1880s (Stanford et al. 2013). The majority of the contemporary land cover change in the drainage basin has occurred in the Livermore Valley region (see Fig. 3.1). This region includes the city of Dublin, which was recently identified as the third fastest growing city in the state of California (Gutierrez 2014).

Sample sites were originally chosen to assess the status of native fishes in the drainage, thus sampling was heavily focused on high elevation and less disturbed regions of the basin. We further restricted our sampling sites to those sites that were wadeable, accessible, and predominately freshwater regions. Sixty-nine sites were initially surveyed by one of us (RAL) between April-October in 1992-1996, with the majority of sites sampled between May and August of 1993 and 1994 (Leidy 2007, Leidy et al. 2011). In 2009, we resurveyed these sites between May and August, excluding sites that were no longer accessible (n = 1) or were seasonally dry (n = 2). We also excluded sites that were directly upstream and downstream of a small impoundment that was removed between the two sampling periods (n = 5). In some cases, the earlier sample sites were within a short distance of one another (<500 m). In these cases, we randomly selected one site to resample, and excluded the other sites (n = 29). After this selection process, 32 sites remained that were sampled in both time periods.

We then classified these 32 sites into one of two categories: (1) those downstream of the developing Livermore Valley (hereafter "urbanized sites"; n sites = 14) and (2) those that were either upstream of Livermore Valley or in adjacent sub-drainages (hereafter "low-impacted sites"; n sites = 18; Fig. 3.1). These low-impacted sites experienced little land cover change between the two sampling periods (e.g., < 0.2% change to urban land cover, see Results). This allowed us to compare fish community change in a rapidly urbanizing portion of the drainage basin to a "control" region that has experienced little land change in recent decades.

Fish species abundance and distributions

Fish distribution and abundance data were collected by the same lead scientist (RAL) in both the 1990s and 2009. Prior to revisiting sites in 2009, we reviewed the associated data sheets from the mid-1990s for details of site descriptions and sampling methodology. Here we were able to reconstruct an approximately identical study design and effort based on these field notes and from input from RAL. Each site was sampled in same location, and there was no difference in site reach length between the two time periods (paired t-test, P = 0.534). At each site, we sampled fishes using single-pass electrofishing in a downstream to upstream direction, using a single-pass to minimize stress on fish during California's summer drought season. For both

sampling periods we used shallow riffles or elevational barriers to delimit site boundaries (i.e. to prevent fish escaping upstream from sampled reaches). At deeper sites, we additionally used seine nets to sample the deeper habitat. All captured fish were identified to species, measured for body length (fork length, mm), and released alive at the place of capture. Full details on sampling methodology can be found in (Leidy 2007).

Our fish collection protocol was approved by the University of California Office of Animal Care and Use (permit # R343), and scientific collection permits specific to this project were obtained from the California Department of Fish and Wildlife. Additionally, we acquired the necessary permits to sample fishes located on land managed by various government agencies (East Bay Regional Park District, San Francisco Public Utilities Commission, Alameda County Flood Control, Livermore Area Recreation and Parks District). No sites in our study were within protected areas, and no listed species were handled.

Land cover data

Landsat TM Imagery at 30m resolution for two dates (July 5, 1993 and June 17, 2009 - the median dates for each sample period) were combined to produce a stacked multi-temporal land cover change layer. We performed a supervised classification using maximum likelihood to create a thematic map representing pairwise land cover change classes that included 4 change classes (natural land cover to urban areas, natural land cover to agriculture/lawns, agriculture/lawns to urban areas, urban areas to agriculture/lawn) and 3 classes that represented no land cover change (i.e., natural land cover, urban areas, agriculture/lawn in both time periods).

Supervised classification training samples were located based on the first author's knowledge of the region, and on United States Geological Survey (USGS) and United States Department of Agriculture (USDA) high resolution aerial imagery available on Google Earth for June-July of both 1993 and 2009. To assess the accuracy of our land cover change map, we generated 1000 random points to visually compare our derived land cover map with the remote imagery used in the supervised classification. We then calculated standard accuracy metrics including a confusion matrix and kappa statistic (Congalton 1991). The kappa statistic is a commonly used measurement of accuracy that represents the agreement between the classification and the reference data after removing the proportion of the agreement that might be expected to occur by chance. All land cover classification and accuracy assessments were performed using ERDAS Imagine (Atlanta, USA). Overall we found that the accuracy for our land cover change product was 98.2% and the kappa statistic was 0.93. These values are well within acceptable ranges (Foody 2002), and are considerably more accurate than commonly used land cover classification data such as the National Land Cover Dataset, which has an accuracy less than 81% for our sample period.

Next we generated individual upstream drainage basin boundaries for each sample site using USGS 10 m National Elevation Data and hydrology tools in ArcGIS 9.2 (ESRI: Environmental Systems Resource Institute 2009). We also delineated a 3km buffer upstream of

each site to assess the effect of local land cover (see also Wang et al. 2001; Fig. 3.2). We then overlaid the derived land cover change data onto each drainage basin boundary to determine the degree of land cover change that has occurred upstream of each individual sample site.

Statistical Analyses

Fish community change

We characterized the fish community by calculating the following univariate metrics: 1) native species richness, 2) nonnative species richness, 3) relative abundance of native individuals, and 4) the relative abundance of individuals of the most common species (i.e., species present at greater than 10% of sites). We tested for differences in these metrics between the two time periods using paired t-tests. When the estimated proportional data were not normally distributed, we applied a logit transformation. We performed these analyses separately for the urbanized and low-impacted regions.

We also examined fish community change using ordination and other multivariate methods. Prior to multivariate analyses, we removed rare species (i.e., those found at less than two sites) and abundance data were transformed to log(x+1) to reduce the influence of highly abundant taxa. We used nonmetric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity to visualize differences in community composition between the two sampling periods, again conducting separate analyses for the urbanized and low-impacted sites. Bray-Curtis dissimilarity values range from 0 to 1, where communities that have identical species composition have a value of 0 and communities that share no species have a value of 1. Next we tested for significant differences in community composition between the two sampling periods using permutation-based analysis of variance (PERMANOVA) with Bray-Curtis dissimilarity (Anderson 2001). When significant community differences were found, we used indicator-species analysis (ISA; Dufrene and Legendre 1997) to identify which species were indicative of a given time period. We considered species with indicator values > 0.50 and $P < 0.05$ as good indicators of a given time period. Finally, we used a Wilcoxon Signed-Rank test to assess if paired urban sites experienced more community change across time (paired Bray-Curtis dissimilarity values) compared to paired low-impacted sites. All statistical analyses were performed using R (R Core Team 2014).

Relationship between the change in land cover and fish communities

We used nonparametric Spearman's rank correlation to determine the statistical significance (p-values < 0.05) and relative strength of correlations (r) between fish community change between the two sampling periods and percent change to urban land cover. To characterize land cover change, we used the percentage of the land cover that changed to urban areas at two scales (within the total drainage basin and within the 3km buffer area for a particular site). Percent land cover data were logit transformed to improve normality prior to analyses. We used the Bray-Curtis distance to describe the pairwise similarity of the fish community composition at a given

site between the two sampling periods. Finally, we assessed the relationship between land cover change and a subset of univariate fish measures that differed significantly between the sampling periods. The changes in univariate fish measurements were assessed by calculating the difference in values of each time period, where a negative (positive) value represented a decrease (increase) in the relative abundance of a given species across time.

RESULTS

Land cover change

In both 1993 and 2009, the majority the Alameda Creek drainage basin was comprised of natural land cover (grassland and forested areas). Overall the upstream portion of the drainage remained relatively unchanged, whereas contemporary urbanization was concentrated in low elevation reaches and mid-elevation reaches of the Livermore Valley region (Fig. 3.1). This was reflected in our results, where the average percent conversion to urban areas was greater among the sites in the "urbanized" region than the "low-impacted" region at both the total drainage (3.75%, 0.03%, respectively) and at the 3km buffer scale (3.70% and 0.36%, respectively).

Fish change

Over 3106 individual fish were captured between the two sample periods, representing 12 families and 23 species (Table 3.1). Fourteen species were captured in both sample periods, while three species were captured in 2009 that were not captured in the 1990s, and four other species captured in the 1990s that were not captured in 2009. Species captured in only one time period were also in low abundance, and were subsequently excluded from analyses (see Methods). The most widely distributed species during both sample periods was *Lavinia symmetricus* (California roach). *L. symmetricus* was also the numerically dominant species in the 1990s, while *Catostomus occidentalis* (Sacramento sucker) was the numerically dominant species in 2009 (Fig. 3.3). Other common species during both time periods included *Oncorhynchus mykiss* (rainbow trout), *Cottus asper* (prickly sculpin), and *Ptychocheilus grandis* (Sacramento pikeminnow; Table 3.1). The remaining native species and all of the nonnative species comprised a relatively small proportion of the total catch at any given site.

In low-impacted sites, native species richness did not significantly differ between the 1990s and 2009 (natives: 2.33 and 2.00, respectively; paired t-tests, $P = 0.33$). Native fish comprised the vast majority of the catch at low-impacted sites during both time periods (98.0% and 99.1% for the mid-1990s and 2009, respectively; Table 3.2), with no difference in relative abundance of natives between the two sample periods for low-impacted sites (paired t-test, $P = 0.34$). The two dominant species during both time periods at low-impacted sites were *L. symmetricus* and *O. mykiss* (Fig. 3.3a), and there were no significant differences in the relative abundance of individual native species between the two time periods at low-impacted sites

(paired t-test, $P > 0.05$). Non-native species richness was low and did not differ among years (0.16 and 0.11, respectively, $P = 0.29$).

At urbanized sites, there was a significant decrease in the richness of native species between the 1990s and 2009 (2.86 and 2.00, respectively, paired t-test, P = 0.002; Table 3.2). The relative abundance of native species also decreased (from 90.2% to 72.7%), but this difference was not statistically significant (paired t-test, $P = 0.18$). The numerically dominant native species in urbanized sites in the 1990s was *L. symmetricus* (Fig. 3.3b). However, the relative abundance of *L. symmetricus* was significantly lower in 2009 than in the 1990s (paired t-test, $P = 0.004$), leaving *C. occidentalis* as the new numerically dominant species for urbanized sites in 2009 (Fig. 3.3b). The average nonnative species richness increased slightly between the 1990s and 2009 for urbanized sites (0.43 and 0.86, respectively), but again this result was not statistically significant (paired t-test, $P = 0.29$).

Multivariate analyses revealed that the fish community composition did not change at the low-impacted sites between the two sample periods ($_{\text{PERMANOVA}}$, pseudo-$F_{1,33} = 0.44$, $P = 0.65$). Indeed, the NMDS plot (stress = 0.10), with convex hulls enclosing sites for a given sample period, revealed considerable overlap of fish communities during the two time periods for low-impacted sites (Fig. 3.4a). In contrast, fish community composition at the urbanized sites changed significantly between the two sample periods ($_{\text{PERMANOVA,}}$ pseudo-$F_{1,26} = 2.2$, $P = 0.04$). The NMDS plot of urbanized sites for each time period suggested a directional change of the communities between sampling periods, with nonnative species and native *C. occidentalis* more strongly associated with 2009 samples and native *L. symmetricus* more strongly associated with 1990s samples (stress = 0.12; Fig. 3.4b). For our urbanized sites, we also found that *L. symmetricus* was a significant indicator species in the 1990s (Indicator value = 0.60, $P = 0.03$). No significant indicator species were found for urbanized sites in 2009. When comparing low-impacted and urban sites, we found that fish communities in urban sites were significantly more different between the two time periods than those in low-impacted sites (mean Bray-Curtis dissimilarity values = 0.60 and 0.33, respectively, Wilcoxon Rank test, p = 0.002; Fig. 3.5).

Relationship between the changes in land cover and the fish communities

To assess the relationship between the change in land cover and fish communities, we focused on the fish metrics that had significant changes between the two sample periods. The change in fish community composition among paired sites (measured as Bray-Curtis dissimilarity) was positively related to land cover change to urban land cover. This relationship was significant at both scales, though it was stronger at the local 3km scale (r = 0.78, p < 0.001; Fig. 3.6a) compared to the total drainage basin scale (r = 0.64, p < 0.001; Fig 3.6b). Overall, sites in the urbanized portion of the drainage basin experienced the highest land cover change and the largest change in fish community composition. Additionally we found that the relative abundance of *L. symmetricus* was negatively related to land cover change, a result that was consistent at both scales (3km watershed watershed, r = -0.42, p = 0.01, total watershed r = -0.49, p = 0.004; Fig.

3.7a, 3.7b). We did not find a significant relationship between native species richness and land cover change at either scale.

DISCUSSION

Our results showed that contemporary urbanization (i.e., over an approximately 16 year period) in the 1800 km^2 Alameda Creek drainage was associated with contemporary fish community change. Importantly, we found significant changes in fish communities only in those portions of the basin that had experienced recent urbanization, while no such changes were detected in regions that experienced little land cover change during this same time period. The relationship between land cover change and fish community change was the strongest at the local scale (i.e., 3km buffer) as opposed to the land change in the total drainage basin upstream of our sampling sites.

Fish community changes

While our study focused on contemporary change, earlier research in the study basin provides a longer time scale perspective on fish community change due to human impacts. Leidy (2007) compiled a time series of fish extirpations and introductions in the Alameda Creek drainage from 1855-2012 using diverse data sources, including direct sampling, historical literature, and museum specimens (Table 3.3; Leidy 2007, Stanford et al. 2013). His results indicated that four fish species have been extirpated from this drainage basin, including one that is now globally extinct (*Gila crassicauda*, thicktail chub). Two anadromous species were extirpated from the system, likely due to the construction of three major dams (between 1925 and 1968) which blocked access to upstream areas. The extirpation of *Pogonichthys macrolepidotus* (Sacramento splittail), an estuarine fish, may have occurred following the draining of a major wetland and the degradation of tidal wetlands in the lower reaches of the drainage basin (Stanford et al. 2013). In contrast, nonnatives have been steadily increasing through time in this basin, with nonnative richness nearly doubling from 1953-1969 to the present day (Table 3.3).

Our examination of contemporary fish community change provided little evidence of new introductions or extirpations between the mid-1990s and 2009, although there were seven species that were found during one time period but not the other. All nine of these species were rare and encountered at just a few sampling sites. Moreover, all of these species have been detected in other surveying efforts by the authors in different locations within the same watershed, although in low abundances and with limited distributions. These patterns may reflect the fact that all of the sensitive species were already extirpated from the watershed prior to our study (see above). These results also suggest that despite continued degradation of the watershed, the extant native species are relatively resilient (Leidy et al. 2011).

Although we did not detect any recent extirpations, our analyses revealed a decrease in native species richness and shifts in the dominance and co-occurrences of extant species. These

shifts occurred at sites experiencing recent urbanization, but not at sites with little recent land change. Specifically, we found that the distribution of the native *Lavinia symmetricus* (California roach) decreased over time in urbanized sites (detected at 85.7% of sites in the 1990s but only 50.0% of sites in 2009). This finding was not surprising because common species are often the first species within communities to be intensely affected by environmental perturbations (Gaston 2010). Although *L. symmetricus* is widespread in streams of the region, they are vulnerable to human disturbances and nonnative predators. In fact they are often absent from sites invaded by the nonnative *Lepomis cyanellus* (Moyle 2002), which is a cause for concern since this and other nonnative centrarchids species were captured at more sites in 2009 than in the 1990s.

Other studies have shown that native cyprinids can be replaced by other cosmopolitan species following environmental perturbation (Johnston and MacEina 2009). Here we found that native *Catostomus occidentalis* (Sacramento sucker) emerged as the numerically dominant fish species at sites experiencing recent urbanization. This may be due to their wide salinity and temperature tolerances and their ability to tolerate drought conditions (Moyle 2002). Unlike many native cyprinids with which they co-occur, *C. occidentalis* are commonly found in waters dominated by nonnatives (Moyle 2002). This remarkable ability to persist in altered habitats is apparent in the results of our study, and further increases in their relative abundance might be expected as urbanization increases - to a point - over time. Both the decrease in *L. symmetricus* and the increase in *C. occidentalis* may have broader impacts for the ecosystem, as common species often are involved in many biotic interactions (Gaston 2010) and can thus have cascading effects on other organisms.

While long-term historical resurveys commonly report extirpations or range shifts (Tingley and Beissinger 2009, Magurran et al. 2010), contemporary resurveys across shorter time periods are important for detecting subtle shifts in communities that may foretell future changes in dominance. For example, a survey of aquatic macroinvertebrates in Central Australia across a contemporary 12-year period showed slight shifts in species richness following major disturbances in the drainage (Brim-Box et al. 2014). Likewise, Heard et al. (Heard et al. 2012) found shifts in the ratio of native and nonnatives species in shoreline plant communities across a contemporary 10-year period.

Contemporary resurveys studies are also useful in identifying patterns in community trajectories. For example, a recent study spanning a 27-year period found that fish communities followed a directional trajectory with a return to a former state following various flow disturbances (Matthews et al. 2013). Our documentation of the subtle shifts in the community dynamics may also be part of a longer-term directional trajectory and may foretell future conservation challenges, and could help identify species in decline prior to extirpation. For example, our results suggest a decline in a tolerant native species in rapidly urbanizing reaches, a result which warrants further study. Moreover, some native species in our study were encountered at too few sites to be included in analyses (e.g., Pacific lamprey, *Entosphenus tridentatus*), while other rare species were not captured in our surveys despite being known to be occur in the drainage basin (e.g., Sacramento perch, *Hysterocarpus traskii*; (Moyle et al. 2011).

Monitoring rare species such as these require additional effort because of issues with detection, but such efforts are clearly needed to monitor status and trends and to identify threats to the viability of rare species and how these patterns change with ongoing urbanization.

Influence of scale

We found that fish community shifts were more strongly associated with local land cover change (3km buffer) than changes at the scale of the entire drainage basin. This finding may be explained by the spatial pattern of urbanization within our study basin, i.e., it is concentrated in the mid and lower regions. For example, when focusing on the urbanized sites, the influence of local land change (e.g., degraded water quality, excess nutrients, altered hydrology) was possibly diluted when considering the larger drainage scale, where – in this system – most of the upper drainage has experienced little land change. Similarly, urban and agricultural development in the upper drainage may also have been dampened by the relatively intact riparian areas in the upper drainage that may, for example, allow for the infiltration of pollutants. Other studies have also suggested regional factors such as drainage size, the degree of human disturbance, and the configuration of land cover change within the drainage basin are important factors influencing stream biota (Strayer et al. 2003, Kearns et al. 2005, Esselman and Allan 2010, Stanfield and Kilgour 2012), and may determine the dominant scale of influence in a particular system. This suggests that the dominant scale of influence of land change may be context specific, thus highlighting the need for regionally-based studies to fully understand how land cover change influences freshwater biota.

The relationship between land cover change and changes in aquatic biota may also vary across time. For example, certain land use practices may have legacy effects on stream biota. Harding et al. (Harding et al. 1998) found that the diversity of freshwater taxa had a stronger relationship with agricultural land cover from forty years prior compared to recent land cover change, despite recent restoration efforts in the drainage basin. There may also be lag times between land cover change and the subsequent effect on stream biota downstream (Meals et al. 2010), which can vary among different water stressors. For example, dissolved pollutants (e.g., nutrients) can quickly disperse downstream, while sediment and attached pollutants may take many years to move downstream and influence biota (Meals et al. 2010). Lag time responses may also differ among species with r- and K-selected life histories, with the prediction that r-selected species should respond faster to perturbation (Alford 2014). Other patterns may emerge across time, such as the recovery of the physical stream and subsequent recovery of the biota following periods of land cover change. For instance, Henshaw and Booth (Henshaw and Booth 2001) found that stream banks restabilized in one to two decades following a period of active urbanization in the drainage. These results suggest that re-surveys after varying periods of time may help reveal lag effects in the relationship between land conversion and stream biota.

Management implications

As freshwater fish populations continue to decline both locally (e.g., Moyle et al. 2011) and globally (Burkhead 2012), research exploring causes of decline are needed to guide conservation and management efforts. Urbanization is considered one of the leading factors influencing freshwater biodiversity (Sala 2000), and urban areas are expected to expand significantly across the globe in the coming decades (Angel et al. 2011). Between 1993 and 2009, the percent of urban land cover in our study drainage basin increased from 6.86% to 10.38%, but it was much higher for many of our sample sites within the rapidly urbanizing region of the watershed (e.g., from 8.44% to 13.75%). Previous research has shown that even a relatively low percentage of urbanization in a drainage basin can have a disproportionately large effect on stream biota. King et al. (2011) found that 80% of stream macroinvertebrates declined in drainages with as little as 0.5-2% urbanization. Likewise, a meta-analysis on land cover change reported that across multiple systems there was an approximate 5.9% loss of aquatic species richness for 10% loss of natural land cover (Weijters et al. 2009). Hence, if the current rate of land cover change in Alameda Creek Watershed continues, future declines or even extirpations are likely to occur.

Finally, our results support a conservation strategy of protecting existing undeveloped regions in urbanizing drainages. These regions support several of the endemic and threatened fishes found in our focal drainage, including one native fish (*L. symmetricus*) that has declined in the urbanizing portions of the basin. Overall our results suggest that contemporary land change is associated with subtle changes in fish communities that may foretell future declines, and highlight the need for additional surveys to understand these effects on fish communities.

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Table 3.1. Information on the species collected. Species table includes origin, family, species, the labeling code used in the NMDS plot (first letter of the genus followed by the first two letters from the species names), the proportion of sites where a species was captured among all sites for each sample period and site type (urbanized or low-impacted), and the mean relative abundance of a species for each sample period and site type. Species found in fewer than 2 sites were excluded from the analyses and are denoted with a "–" under NMDS code column.

Origin	Family	Species	NMDS code	Proportion of sites (relative abundance)			
				1990s low-impacted	2009 low-impacted	1990s urbanized	2009 urbanized
Native	Catostomidae	*Catostomus occidentalis*	COC	0.39(0.06)	0.45(0.14)	0.79(0.29)	0.79(0.40)
	Cyprinidae	*Ptychocheilus grandis*	PGR	0.06(0.02)	0.11(0.04)	0.79(0.13)	0.64(0.20)
	Cottidae	*Cottus asper*	CAS	0.28(0.12)	0.56(0.11)	0.36(0.05)	0.36(0.08)
	Cottidae	*Leptocottus armatus*	-	0	0.01(0.01)	0.07(0.01)	0
	Cyprinidae	*Lavinia symmetricus*	LSY	0.72(0.43)	0.78(0.47)	0.86(0.32)	0.50(0.06)
	Cyprinidae	*Lavinia exilicauda*	LEX	0.17(0.10)	0.11(<0.01)	0.43(0.05)	0.29(0.01)
	Cyprinidae	*Orthodon microlepidotus*	-	0	0	0.07(0.01)	0
	Gasterosteidae	*Gasterosteus aculeatus*	GAC	0.11(0.02)	0	0.14(0.06)	0.07(0.01)
	Petromyzontidae	*Entosphenus tridentatus*	-	0	0.06(<0.01)	0	0
	Salmonidae	*Oncorhynchus mykiss*	OMY	0.61(0.24)	0.50(0.25)	0	0
Nonnative	Centrarchidae	*Lepomis cyanellus*	LCY	0.17(0.01)	0	0.29(0.01)	0.21(0.07)
	Atherinopsidae	*Menidia beryllina*	-	0	0	0.14(0.01)	0.07(0.01)
	Centrarchidae	*Micropterus dolomieu*	MDO	0	0	0.07(0.02)	0.29(0.05)
	Centrarchidae	*Lepomis machrochirus*	-	0.06(<0.01)	0	0.07(<0.01)	0
	Centrarchidae	*Micropterus salmoides*	MSA	0	0.06(<0.01)	0	14(0.01)
	Cyprinidae	*Cyprinus carpio*	CCA	0.06(<0.01)	0	0.14(0.01)	0.01(<0.01)
	Cyprinidae	*Notemigonus crysoleucas*	-	0	0	0.07(0.02)	0
	Cyprinidae	*Carassius auratus*	-	0	0	0	0.14(0.04)
	Fundulidae	*Lucania parva*	-	0	0	0.07(<0.01)	0.07(0.01)
	Gobiidae	*Tridentiger bifasciatus*	-	0	0	0	0.07(<0.01)
	Gobiidae	*Acanthogobius flavimus*	-	0	0	0	0.07(<0.01)
	Percidae	*Percina macrolepida*	-	0	0	0.07(<0.01)	0
	Poeciliidae	*Gambusia affinis*	GAF	0.11(0.01)	0.06(<0.01)	0	0.29(0.08)

Table 3.2. Community and land cover metric values for each sampling period (1990s, 2009) and the change between sampling periods for urbanized sites and low-impacted sites.

		Low-impacted sites			Urbanized sites		
		1990s	**2009**	**Δ**	**1990s**	**2009**	**Δ**
community metrics	native species richness	2.33	2.00	-0.33	2.86	2.00	-0.86
	nonnative species richness	0.16	0.11	-0.05	0.43	0.86	0.43
	% natives species per site	98.0	99.1	1.1	90.2	72.7	-17.5
	% *L. symmetricus* per site	43.1	47.0	3.9	31.58	5.76	-25.82
	L. symmetricus (proportion of sites)	72.2	77.8	5.56	85.7	50.0	-35.7
land cover: total watershed	% natural (e.g., forest, grass)	99.7	99.6	-0.1	89.5	85.7	-3.8
	% agriculture/lawn	0.22	0.30	0.08	4.43	4.52	0.09
	% urban	0.09	0.12	0.03	6.03	9.78	3.75
land cover: 3km buffer	% natural (e.g., forest, grass)	97.5	97.0	-0.5	71.1	68.2	-2.9
	% agriculture/lawn	1.58	1.81	0.23	7.39	6.66	-0.73
	% urban	0.88	1.24	0.36	21.5	25.2	3.70

All values are based on averages from sites for a given time period and region.

Table 3.3. Historical changes in fish fauna of the Alameda Creek drainage 1865-2012 (Leidy 2007, Stanford et al. 2013). Criteria were developed to assess the reliability of the data, where X denotes definite occurrences determined by observations made from stream surveys, published and unpublished literature and reports, and museum collections (see Leidy, Becker & Harvey 2005 for more details). Occurrences that are not recorded but are likely present are denoted by P, and species with unknown status are denoted by U.

Scientific name	Period of Record				
	1855-1860	1895-1948	1953-1969	1972-1987	1992-2012
Native species					
Gila crassicauda	X1				
Pogonichthys macrolepidotus	X	P	X		
Oncorhynchus kisutch	P	P	X		
Oncorhynchus tshawytscha	X	U	U	U	X
Rhinichthys osculus	P	X	U	U	U
Cottus gulosus	P	X	U	U	X
Mylopharodon conocephalus	P	X	X	P	X
Hysterocarpus traskii	X	X	P	X	X
Cymatogaster aggregata	P	P	P	X	X
Lampetra ayresii	P	P	X	X	X
Lampetra cf. pacifica	P	P	P	P	X
Entosphenus tridentatus	X	X	X	X	X
Lavinia exilicauda	P	X	X	X	X
Lavinia symmetricus	X	X	X	X	X
Orthodon microlepidotus	P	X	X	X	X
Ptychocheilus grandis	P	X	X	X	X
Catostomus occidentalis	X	X	X	X	X
Oncorhynchus mykiss	P	X	X	X	X
Gasterosteus aculeatus	X	X	X	X	X
Archoplites interruptus	X	X	X	X	X
Cottus asper	X	X	X	X	X
Leptocottus armatus	P	P	P	X	X
Gillichthys mirabilis	P	P	P	X	X
Platichthys stellatus	P	P	P	P	X
Non-native species					
Micropterus dolomieu		X	X	X	X
Salmo trutta		X	X		
Cyprinus carpio			X	X	X
Ameiurus catus			X	X	X
Ameiurus nebulosus			X	X	X
Gambusia affinis			X	X	X
Pomoxis nigromaculatus			X	X	X

Lepomis cyanellus	X	X	X
Lepomis macrochirus	X	X	X
Micropterus salmoides	X	X	X
Carassius auratus	X	X	X
Notemigonus crysoleucas	X	X	X
Lucania parva	X	X	X
Dorosoma petenense		X	X
Ictalurus punctatus		X	X
Ameiurus melas		X	X
Menidia beryllina		X	X
Morone saxatilis		X	X
Lepomis microlophus		X	X
Percina macrolepida		X	X
Acanthogobius flavimanus		P	X
Micropterus coosae			X
Gila bicolor			X
Tridentiger bifasciatus			X

[1]exact date unknown, source from archeological excavations of Native American middens in the Alameda Creek drainage (Gobalet et al. 2004)

Fig. 3.1. Map of study area showing major streams, sample sites, and the change in land cover to urban areas between 1993 and 2009.

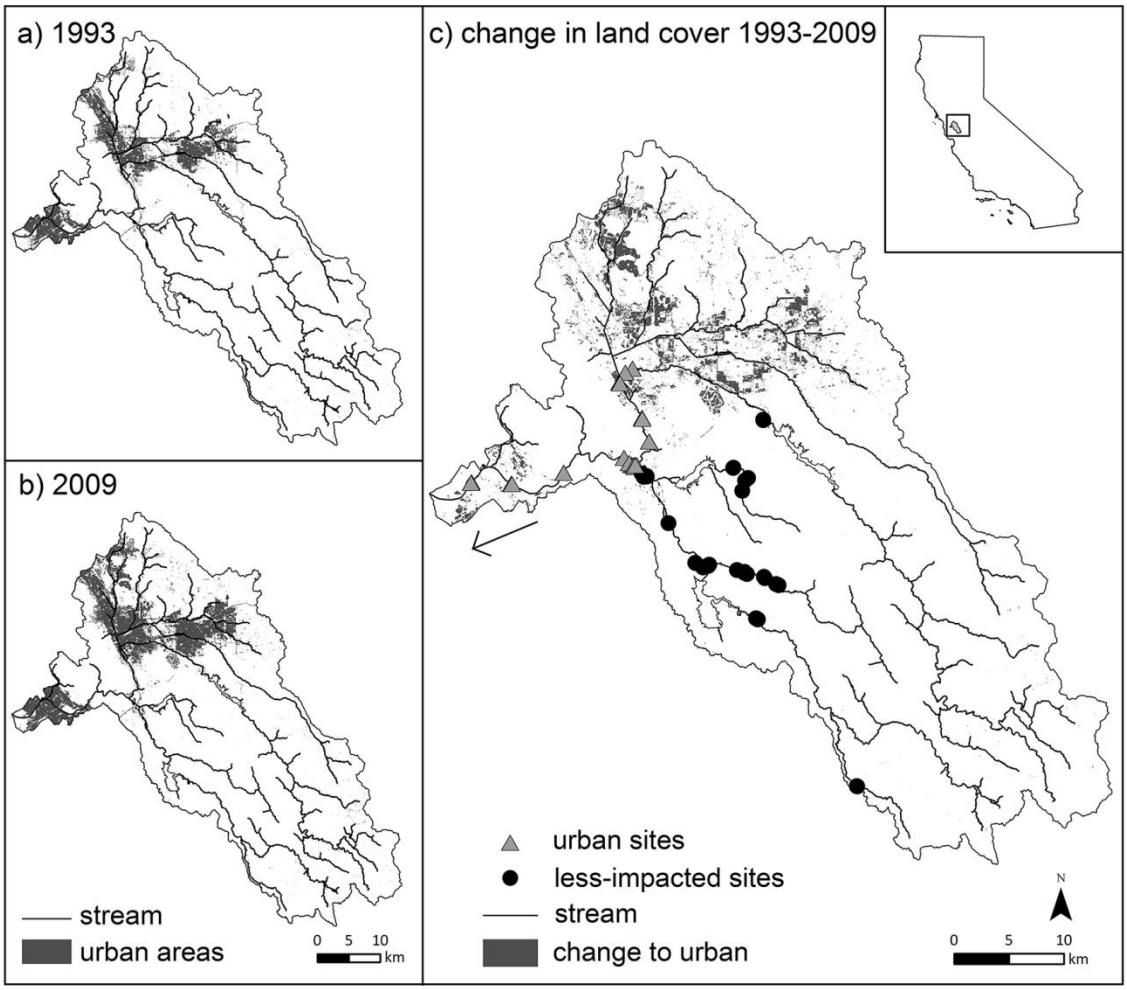


Fig. 3.2. Illustration showing how the 3km upstream buffer was determined (shaded in gray) for a given site.

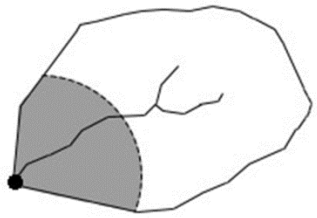


Fig. 3.3. Bar plots of the mean relative abundance of species and taxa for (a) low-impacted sites, and (b) urbanized sites for each sample period. Individual species are plotted for three native species: *C. occidentalis*, *O. mykiss*, and *L. symmetricus*. Other species were combined into the following groups (see Table 3.1 for listing): other cyprinids, other natives, other nonnatives, and piscivorous nonnatives (centrarchids and *A. flavimanus*).

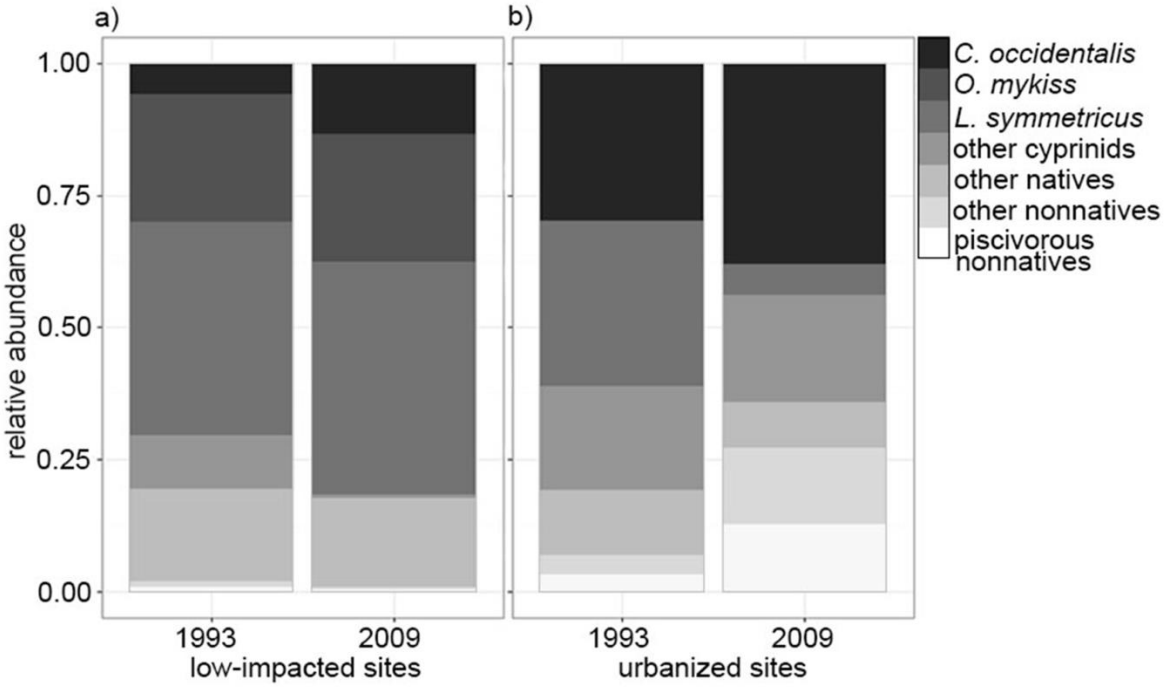


Fig. 3.4. Nonmetric multidimensional plot of species abundance for (a) low-impacted sites, and for (b) urbanized sites. Species are labeled by their species code (see Table 3.1). Native species are shown in plain black font, and nonnative species are denoted by gray italicized font. Sites sampled in the 1990s are denoted with black triangles and sites sampled in 2009 are denoted with gray circles. Sites closer to one another in the plot represent sites more similar species assemblages. Convex hulls enclose sites for the two time periods.

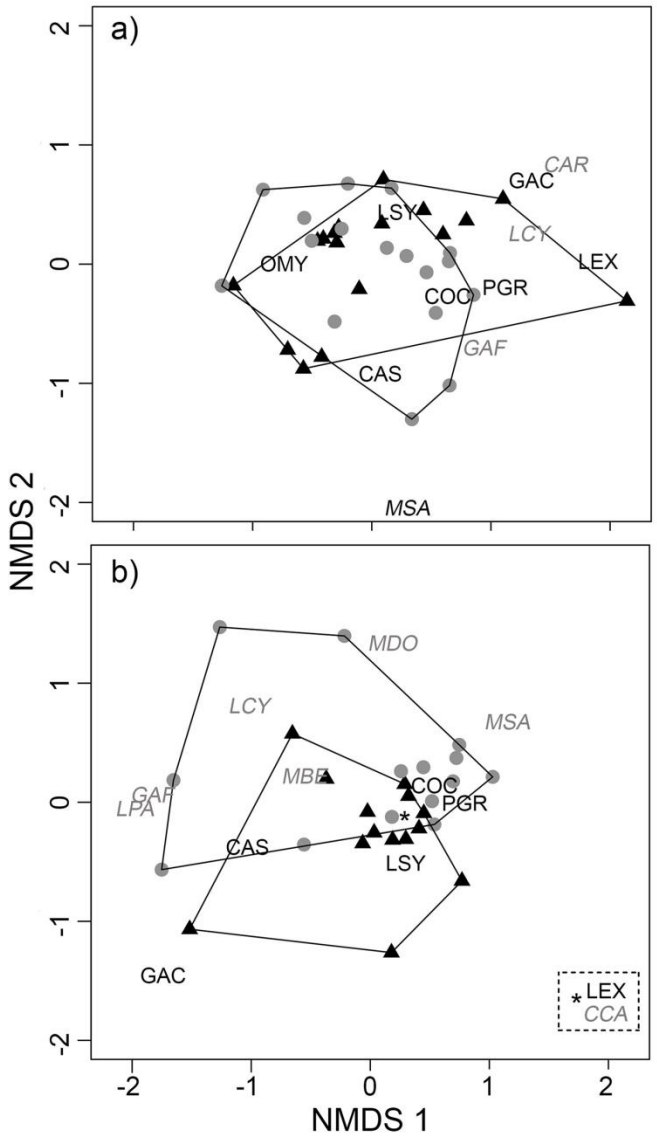


Fig. 3.5. Boxplots comparing Bray-Curtis dissimilarity distances between 1990s and 2009 paired sample sites in low-impacted and urbanized sites.

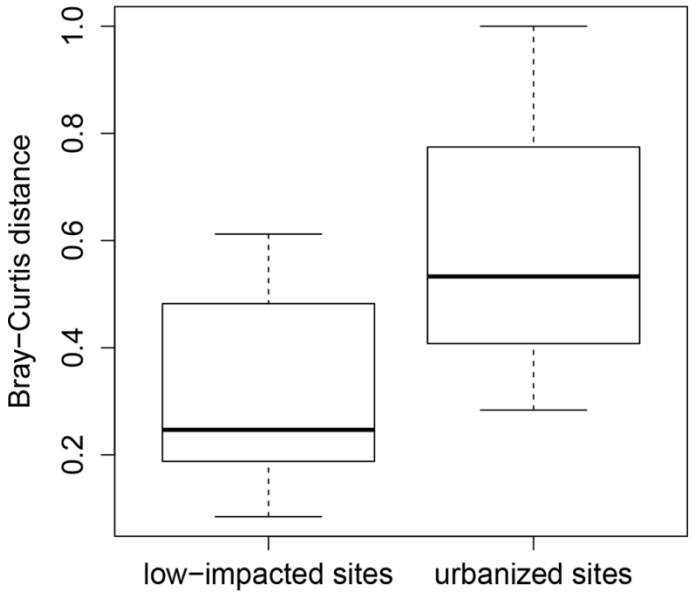


Fig. 3.6. Correlation between the change in community composition using Bray-Curtis dissimilarity and the change to urban areas. The first plot (a) shows the change to urban areas in the 3km upstream drainage area (logit transformed), and (b) the total drainage area (logit transformed). Bray-Curtis values closer to one indicate that communities have a high degree of dissimilarity. Black triangles represent urbanized sites and gray triangles represent low-impacted sites. Spearman's rank correlation coefficient (r) and level of significance (p) are indicated within each graph.

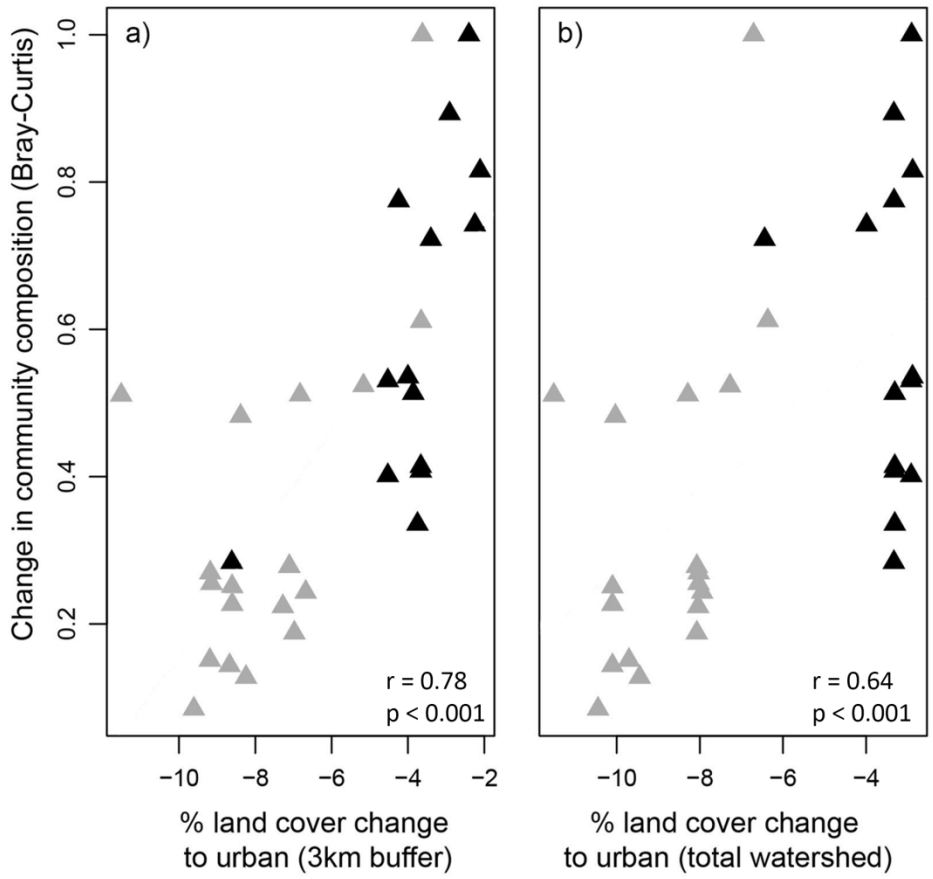
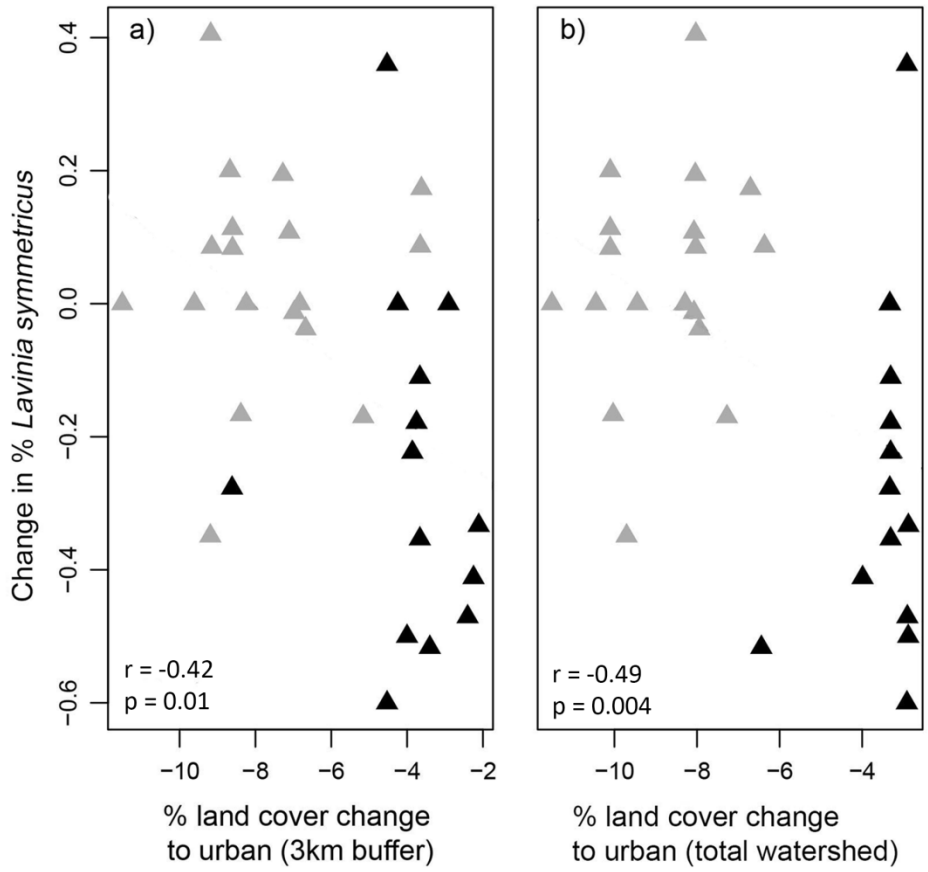


Fig. 3.7. Correlation between the change in the relative abundance of *Lavinia symmetricus* (California roach) and the change to urban areas. The first plot (a) shows the change to urban areas in the 3km upstream drainage area (logit transformed), and (b) the total drainage area (logit transformed). Black triangles represent urbanized sites and gray triangles represent low-impacted sites. Spearman's rank correlation coefficient (r) and level of significance (p) are indicated within each graph.



CHAPTER 4

Summer drought influences food web structure in an intermittent stream

Summer drought influences food web structure in an intermittent stream

ABSTRACT

In many regions of the world, seasonal drought disturbances cause the cessation of flow in intermittent streams, resulting in a series of isolated pool habitats. Some of these pools inevitably dry while others persist and provide refuge for aquatic biota until flow resumes during the wet season. Climate change, along with the increasing societal demand for freshwater, will lead to more intense and longer droughts, leading to a growing interest in understanding how drought conditions will influence aquatic taxa and food web structure. We sampled replicate pools in a California coastal intermittent stream each month across the drought season to explore how the food web changed across the drought season, including both temporary and permanent pools. We used stable isotope analysis of carbon and nitrogen to characterize food web structure and the trophic position of a suite of predators in this system, including juvenile steelhead (*Oncorhynchus mykiss*) and several macroinvertebrate predators. Temporary pools dried by early-September while permanent pools remained wetted across the entire drought season. We detected subtle changes in niche width size and basal carbon range, but most taxa appeared to be supported by periphyton and terrestrial detritus across the drought period. With advancing drought conditions, we detected a significant increase in food chain length, and increases in trophic position for three predators, which was reflected in moderate shifts in predator niche width across the drought period. The apex predator at our site, *O. mykiss*, increased in trophic position in both temporary and permanent pools, perhaps due to an increase in prey availability and a decrease in intraspecific competition as steelhead densities decreased. Overall, we were surprised that there were only moderate changes in temporary pools between early summer and our last sampling event which occurred approximately seven days before the pool dried completely. We, suspect that aquatic taxa in our study system are relatively resistant to drought conditions until they reach a threshold of low water level and the food web collapses.

Keywords: food web; intermittent stream; drought; trophic position; niche width; steelhead

INTRODUCTION

Climate change scenarios predict that droughts will increase in frequency and intensity in many regions around the globe (Kundzewicz et al. 2008, Overpeck and Udall 2010). Moreover, human demand for water resources will likely increase with continued population growth. As a consequence of both drought and water resource development , freshwater systems, which are already considered one of the most imperiled ecosystems on the planet, are at risk for further declines in biodiversity and ecological function (Strayer and Dudgeon 2010).

Increased drought will alter river flows, leading to more extreme flow contraction during drought periods. Accordingly, the number of intermittent streams is predicted to increase as formally perennial streams fragment under more extreme or longer duration droughts (Brooks 2009, Larned et al. 2010). Although many aquatic organisms have adaptations to drought and stream intermittency (Hershkovitz and Gasith 2013), changes from permanent to intermittent flow represent an extreme disturbance that can lead to local extirpations of aquatic taxa (Bogan and Lytle 2011).

Previous studies have shown that cessation of flow in intermittent streams can have multiple ecological consequences. At the reach-level, fragmentation can lead to changes in the flow of nutrients (e.g., Dent et al. 2001, von Schiller et al. 2011), decreased invertebrate drift (e.g., Delucchi 1989), and reduced longitudinal movement of stream fishes (e.g., Fischer and Kummer 2000, Hwan and Carlson 2015). At the pool-level, contraction of remnant pools is associated with a suite of changes including a deterioration of water quality (e.g., increased temperature and reduced dissolved oxygen) and a loss of habitat and pool complexity as volume decreases (Lake 2003, Boulton 2003, Hwan and Carlson 2015). These habitat changes subsequently affect aquatic biota, altering species richness, density, species interactions, all of which can lead to restructuring of communities (Acuña et al. 2005, Bêche et al. 2009, Bogan and Lytle 2011, Ledger et al. 2013). Indeed, drought disturbance is considered a key factor shaping stream food webs (e.g., Power et al. 2008).

The effects of drought and stream intermittency on freshwater food webs are variable, likely due in part to differences in drought severity or duration. Previous studies have shown that drought conditions can cause minimal (Walters and Post 2008), partial (Ledger et al. 2013), or complete (McHugh et al. 2014) food web collapse. In a recent experiment, Ledger et al. (2013) found that while consumers' diets and the basal resources supporting a stream food web did not change following stream drying events, linkages between trophic levels were reduced. Drought can also cause decreases in food web size (Woodward et al. 2012) or reductions in food chain length (e.g., Power et al. 2008). For example, in a study examining food chain length across a gradient of flow conditions, Sabo et al. (2010) found that intermittent streams that experience frequent drought disturbances may have shorter food chain lengths compared to perennial streams.

Shifts in food web structure can be driven by changes in the abundance and behavior of particular food web elements or entire trophic levels. Top predators appear particularly sensitive to the effects of drought as their large body sizes and rarity make them susceptible to hydrologic disturbance and local extirpation (Woodward et al. 2012). For example under intense drought conditions, large-bodied predators can be extirpated and replaced by smaller mesopredators (Bogan and Lytle 2011). The loss of predators during drought may also have large ecological consequences due to their direct and indirect effects on food webs (Holomuzki et al. 2010, Boersma et al. 2014, Rodríguez-Lozano et al. 2015). Despite these studies, it remains difficult to predict the trophic response of predators to changing water levels in streams. Previous research has shown that densities of aquatic invertebrates and fishes tend to increase during drying (Pires

et al. 1999, Acuña et al. 2005, Bogan and Lytle 2011), as organisms are concentrated into shrinking habitat. This concentration could lead to increased encounters between predators and prey, but the consequences for predator niche width is not clear. Predators may switch their diet during drying as certain prey species become more available (e.g., due to increased density) while others become less available (e.g., due to mortality or dispersal). Few studies have described shifts in predator feeding ecology during drying, and fewer have explored how responses differ among predators that differ in body size and abundance.

The objectives of our study were to examine how drought influences (1) food web structure (food web size, food chain length, and isotopic carbon values) during stream drying and (2) the trophic position and niche width of a suite of predators from small midges to top predatory fish (steelhead trout, *Oncorhynchus mykiss*). We addressed these objectives via monthly food web sampling from six intermittent stream pools, including three temporary and three permanent pools, across the summer drought season in a small intermittent stream in coastal California, USA. Remnant pools in intermittent streams provide a natural unit of replication for exploring the ecological effects of drought (Perkin and Gido 2012). We used stable isotope analyses of carbon and nitrogen to characterize food web structure, food chain length, and trophic niche width. We hypothesized that food web size would contract and food chain length would decrease as the drought season progressed, and that these changes would be more pronounced in temporary pools as abiotic conditions deteriorate compared to permanent pools. Similarly, we predicted that prey diversity and niche width of a suite of predators would decrease as drying progressed, with more pronounced changes in temporary relative to permanent pools and stronger changes in larger bodied predators.

MATERIALS AND METHODS

Site description

Our study was conducted in the John West Fork (JWF), a tributary of Olema Creek in the Golden Gate National Recreation Area (Marin County, California, USA; Fig. 4.1). The watershed is approximately 3.1km^2 and the creek is approximately 3km in total length. It is dominated by grass and rangeland, and has a dense riparian canopy consisting of California bay laurel (*Umbellularia californica*), beaked hazelnut (*Corylus cornuta*), big leaf maple (*Acer macrophyllum*), and other native riparian vegetation. Typical of small streams in Mediterranean-climate regions, JWF experiences peak flows in the winter and early spring. During the summer and extending through fall, the stream predictably fragments into a series of isolated pools. However, due to the inter-annual variability in precipitation, the timing and magnitude of fragmentation and pool contraction varies among years (Hwan and Carlson 2015). There are only two species of fish in our focal stream, *Oncorhynchus kisutch* (coho salmon) and *O. mykiss* (steelhead trout). We focused on juvenile *O. mykiss* because *O. kisutch* were not present at the site in the year we conducted this study (2012). The steelhead in JWF are designated as part of

the Central California Coast Distinct Population Segment (CCC DPS) and are listed as federally threatened (NMFS 2011).

Our study was conducted between July 6 – October 14, 2012 along a 110m section of the creek. To test for differences in food web metrics between fast drying and permanent habitats, we chose three permanent and three temporary pools based on drying patterns observed at this site in previous years (Hwan and Carlson 2015). The three isolated pools within the two pool types (permanent and temporary) were then treated as replicates in analyses. Fish, aquatic invertebrates, terrestrial invertebrates, and primary producers were sampled from each wetted study pool once per month. Permanent pools were sampled four times (July-October), and temporary pools were sampled three times before they dried in September (July-September). Maximum pool depth was monitored each week across the four month study using a stationary meter stick affixed to rebar that was anchored in the deepest part of each study pool.

Biotic sampling

We sampled tissue from predators, consumers, and primary producers for stable isotope analyses. First we sampled juvenile steelhead using either electrofishing (June, September) or seining (July, August). We measured each captured fish (fork length [mm]) and took a small non-lethal caudal fin clip from each fish. Previous studies have shown that caudal fin tissue from juvenile steelhead has a fast turnover rate (13 days), providing an opportunity to characterize recent diet through stable isotope analysis (Heady and Moore 2013). Fin clips were stored in coin envelopes and dried prior to analysis.

We sampled aquatic invertebrates using a combination of methods to ensure that we captured a complete representation of the pool community. To collect benthic invertebrates we used a Surber sampler for 90 seconds in two random locations in each pool. We also performed a timed (10 sec/m^2) D-frame net sweep through the water column. Invertebrates were stored in 95% ethanol for further analysis. We did not adjust our isotopic values as previous studies have shown that fixing samples in ethanol does not significantly alter the isotopic values of carbon and nitrogen of tissue (Feuchtmayr and Grey 2003).

We sampled terrestrial invertebrates by placing three large 30x35mm white pan traps along the bank of each pool. Trays were filled with strained creek water and a few drops of biodegradable dish soap to keep trapped insects from escaping. We deployed trays for approximately 48 hours and then sieved, rinsed, and stored the collected invertebrates in 95% ethanol. The collection from each tray was stored in a separate vial leading to three replicates per pool per month.

We collected periphyton (a combination of algae, bacteria, and detritus) by randomly choosing 10-15 rocks in each pool, gently wiping off any invertebrates, scrubbing periphyton from each rock with a toothbrush, and capturing the resultant slurry in a tray. We cleaned each toothbrush and tray with ethanol and deionized water in between samples. We also collected leaf litter and filamentous algae in each pool by hand when either was visibly present. All producer material was kept in a dark cooler in the field and then stored in a freezer until further analysis.

Stable isotope preparation

To measure changes in food web structure, we used stable carbon and nitrogen isotope values. The ratio of ^{13}C to ^{12}C ($\delta^{13}C$) is a useful indicator of the basal source of carbon to a consumer, whereas the ratio of ^{15}N to ^{14}N ($\delta^{15}N$) in animal tissue is typically enriched by 3.4‰ (± 1‰) from their food source (Post 2002) and can thus be used to estimate trophic position. Together, $\delta^{13}C$ and $\delta^{15}N$ values of individuals can be used to compare trophic niche width (i.e., diet diversity) among populations or for entire food webs across time or among habitats (e.g., Layman et al. 2007).

Aquatic invertebrates were first identified to the lowest taxa possible (usually genus) and placed into functional feeding groups based on Merritt et al. (2008). We then selected two representative taxa for each of the following functional feeding groups: collector, scraper/grazer, shredder, and predator (Table 4.1). Additionally, we included a fourth predator (*Gerridae*) to represent a surface feeder. We selected these taxa because they were consistently present across most pools and time periods, and because their ecology and functional feeding types are well known. Next we ran preliminary samples to determine the average number of individuals needed to meet the mass requirements for stable isotope analysis. These numbers varied from 1-30 individuals depending on the organism size and on the number of individuals we were able to collect (Appendix 4.1).

To prepare producer material, we first thawed, rinsed with deionized water, and inspected the collected material under a dissecting scope to remove any debris or invertebrates. We also tested if there were inorganic carbonates in our periphyton samples, a result of scrapping rocks. We fumigated a subset of samples with concentrated hydrochloric acid for 24 hours (Harris et al. 2001), and found that there was no statistical difference in the $\delta^{13}C$ values between fumigated and unfumigated samples (paired t-test, $p < 0.01$). We therefore assumed that the amount of inorganic carbonate in our periphyton samples was insignificant and thus we used unfumigated samples for our analysis.

All invertebrate samples were rinsed with deionized water multiple times prior to analyses. The entire bodies of most aquatic invertebrates were used for stable isotopes, but we first removed the shells of the gastropods to avoid possible contamination from non-dietary carbonates. Our main interest in including the terrestrial invertebrates was to determine if they were a significant prey source for predators at our site. Consequently, we identified terrestrial invertebrates to order and then combined all individuals from a given tray into one sample for stable isotope processing (for a total of three samples per pool/time period).

All animal and plant material were placed in sterilized glass vials and dried at 60°C for 24 hours or until the samples were completely dry. The samples were then ground into a fine powder using a mortar and pestle, weighed to the nearest 0.001mg, and placed in pre-weighed Costech tin capsules. Our samples were analyzed using elemental analyzer/continuous flow isotope ratio mass spectrometry stable isotope analyses (Thermo Finnigan DeltaPlus XL gas phase isotope ratio mass spectrometer; Bremen, Germany) at the University of California

Berkeley Center for Stable Isotope Biochemistry Lab. The isotope ratios were reported in conventional delta (δ) notation as parts per mil (‰) relative to the international standards for carbon and nitrogen (Peedee Belemnite Carbonate and atmospheric nitrogen, respectively).

Statistical analyses

To account for variability among taxa within a pool at a given sample period, we included 8-15 replicates of steelhead, three replicates for aquatic and terrestrial invertebrates, and one replicate for primary producers. In some instances however, we were unable to collect enough individuals or mass, especially late in the summer, therefore the number of replicates for each taxon varied (Appendix 4.1). For each of our analyses, we used average values of $\delta^{15}N$ and $\delta^{13}C$ from our replicate taxa samples and then among pool type (three permanent and three temporary pools) for approximately nine replicates of each taxa per pool type and time period (Appendix 4.2).

We first constructed biplots of $\delta^{15}N$ and $\delta^{13}C$ values of steelhead, aquatic macroinvertebrates, terrestrial invertebrates, periphyton, leaf litter, and algae samples to compare isotopic patterns across time and between pool types. We did not use mixing models to estimate the percent assimilation of food sources for consumers because we were not confident that we had sufficient representation of potential prey sources. Instead, we used our biplots to visually assess the relative importance of sources of organic carbon for consumers and prey sources for predators.

To estimate the food web niche width (a proxy of overall food web size) for a given pool type and time period, we used the bivariate isotope signatures ($\delta^{15}N$ and $\delta^{13}C$) for all aquatic taxa (excluding primary producers) and generated standard ellipse areas (SEA_c) and alpha hulls. These metrics represent the total amount of niche space occupied by the sampled community, and thus is a representation of the extent of trophic diversity within our sampled food web. SEA_c are commonly used for small sample sizes and unbalanced designs and they are calculated using a Bayesian framework (Jackson et al. 2011). Convex hulls (Layman et al. 2007) are also commonly used, however they are sensitive to outliers and dependent on sample size (Syväranta et al. 2013). Consequently, we used alpha hulls which are similar to convex hulls but more conservative and reduce the influence of outliers (Burgman and Fox 2003). They are produced with Delauney triangulations of bivariate data where all sides that are α times longer than the average of the original sides are removed (Pateiro-Lopez and Rodriguez-Casal 2010). After preliminary analyses, we chose an α value of 4, which is within range of other ecological studies (e.g., Rutan et al. 2012, Davies et al. 2013). SEA_c and α-hulls were calculated using the SIBER function in the "Siar" and "Alphahull" packages in R, respectively (Pateiro-Lopez and Rodriguez-Casal 2010, Parnell et al. 2010). Next, we applied these same methods to calculate the predator niche width for *O. mykiss* and three aquatic invertebrate predators for each pool type and time period. To estimate food web and predator niche widths, we merged data from individuals from a given pool into our two pool type groups (permanent and temporary) for each time period.

We estimated food chain length using the trophic position of the predator that held the highest trophic position (in our system, steelhead trout). We estimated the trophic position (TP) for steelhead trout and three predatory aquatic invertebrates using the equation described in Post (2002): $TP = \lambda + (\delta^{15}N_{predator} - \delta^{15}N_{base\ consumer})/ 3.4‰$, where λ is the assumed trophic position of the baseline taxa (i.e., 1 for primary consumer) and 3.4‰ is the mean $\delta^{15}N$ fractionation rate based on Post (2002). For the base consumer, we used the mean $\delta^{15}N$ value for a given pool and time period of the most common primary consumer in our sites, a caddisfly shredder (*Heteroplectron* sp.).

Lastly, we calculated the mean $\delta^{13}C$ value for each taxon to measure changes in the diversity of basal resources across time and among perennial and temporary pools. These values were then visually compared to the mean $\delta^{13}C$ values of the producers to estimate their approximate basal source.

To test for differences in the trend of food chain length, and trophic position, and $\delta^{13}C$ across time and between pool types (permanent and temporary), we used linear mixed-models (ANCOVA) that accounted for repeated measures in each pool. Time (continuous variable), pool type (categorical variable), and their interaction were included as fixed factors and pool number (three replicates per pool type) was included as a random factor. When we did not find linear trends over time, we also computed mixed 2-way ANOVA to control for non-linear effects in time, i.e., we computed the same models, but used time as a categorical factor rather than a continuous one. Finally, when there was an interaction between pool type and time, i.e., when the time trends differed between pool types, we performed mixed-linear regression in each pool type, with time as a fixed effect and pool number as a random effect. Models were computed with the lmer function (Bates et al. 2014) and p-values were computed with the lmerTest package (Kuznetsova et al. 2015) that uses Satterthwaite's approximation to estimate the degrees of freedom when performing F-test and t-tests. The alpha threshold were set to 0.05 and all statistical analyses were performed using R (R Core Team 2014).

RESULTS

Pool drying patterns

On average, the three temporary pools dried at a faster rate (slope = -2.30 ± 0.19 mm/day, t=-12.01) than the three permanent pools (-0.837± 0.12 mm/day; $t = -7.77$, $p < 0.05$). All three temporary pools dried completely by September 12, 2012, whereas permanent pools persisted through the first rain event in mid-October 2012 (Fig. 4.2).

Food web structure

Based on the $\delta^{13}C$ and $\delta^{15}N$ isotopic biplots representing food web snap shots across time, we found that there was considerable overlap in isotopic space for many of the aquatic invertebrates, although some patterns emerged (Fig. 4.3). Invertebrate predators were tightly grouped together

and were generally associated with higher $\delta^{13}C$ and $\delta^{15}N$ values. In contrast, shredders, scrappers, and collectors were distributed lower in $\delta^{15}N$ space and spread across $\delta^{13}C$ space. Although there were some minor shifts of individual taxa across time (e.g., *Lepidostoma* sp.) overall there was little change in the food web structure through time (Fig.4.3). Specific differences in the values of isotopic carbon and nitrogen for taxa across time or among pools type are discussed below.

Food web size

The isotopic niche of the food web (excluding producers and terrestrial invertebrates) overlapped considerably across time and between pool types (Fig. 4.4). Overall, the two niche width metrics gave different directional and magnitude values, making interpretations difficult. First, both permanent and temporary pools showed a slight increase in isotopic niche width between the July and August, regardless of method used to calculate the niche width area (i.e., ellipses vs alpha hulls, Fig. 4.5). Overall, the ellipse-based metric showed a slight decrease in niche width from early summer to late summer for both pool types, whereas the alpha hull metric showed an increase in niche width between early and late summer. In general, the ellipse-based metric method was more conservative for calculating niche width compared to the alpha hull metric (i.e., for any given comparison, the ellipse area was smaller than the associated alpha hull area; Fig. 4.5).

Food chain length

We used the trophic position (TP) of *O. mykiss* to estimate food chain length as it was the apex predator at our study site. There was moderate variation in the food chain length (TP of *O. mykiss*) across pools and time (Fig.4.6a). Using linear mixed-regression models, we found that food chain length increased across time for both permanent (slope 0.004 ± 0.001, $t = -3.0$, $p < 0.05$) and temporary pools (slope $= 0.007 \pm 0.002$, $t = -0.04$, $p < 0.05$), but there was no difference in the trend across time between the pool types (mixed-ancova, $F_{1, 76} = 1.47$, $p = 0.23$). Figure 4.6a, also suggests that there may have been a threshold effect with an increase in TP between July and August, and with less change after that point. Additionally, we found no evidence that trophic position of *O. mykiss* was related to trout size across the range of sizes encountered in our study (slope $= -0.01 \pm 0.004$, $t = -1.73$, $p = 0.12$).

$\delta^{13}C$ of aquatic taxa

The mean $\delta^{13}C$ value for leaf litter was -28.56 (range: -33.26 to -28.56) and for periphyton was 31.94 (range: -35.02 to -27.64). Algae had a mean $\delta^{13}C$ value of -35.06 (range: -36.9 to -33.22), but note that this was based on only two samples. We found that the $\delta^{13}C$ values of primary producers did not vary across time nor pool types; therefore we used their mean values to approximate their relative importance as a food source for consumers. All of the consumers (with the exception of *Leucrocuta* sp. and *Lepidostoma* sp.) were closer in range to periphyton and leaf litter, suggesting that these were likely important carbon sources. However, over half of the

aquatic consumers had isotopic carbon values higher than the average or range of the producers included in our analysis (Fig. 4.7). These taxa were situated between leaf litter and terrestrial invertebrate $\delta^{13}C$ values, perhaps indicating that their carbon source was terrestrially based.

To determine if $\delta^{13}C$ values varied across time or among pool types, we used mixed-linear regression models, unless otherwise noted. The mean $\delta^{13}C$ values for the shredder *Lepidostoma* sp. decreased for temporary pools (slope = -0.05±0.02, t = -2.52, $p < 0.05$, Fig 4.7b) but not significantly for permanent pools (slope = -0.01±0.01, t = -0.81, p = 0.43), and there was no difference in the trend among the pool types (mixed-ancova, $F_{1,42} = 2.17$, p = 0.15). Conversely, the $\delta^{13}C$ of the collector *Paraleptophlebia* sp. increased across time for temporary pools (slope = 0.04±0.01, t = 3.99, $p < 0.05$) and had significant differences in the linear trend between the pool types (mixed-ancova, $F_{1,55} = 15.61$, $p < 0.05$, Fig. 4.6c). The $\delta^{13}C$ trends for *Physidae* sp. differed among pool types (mixed-ancova, $F_{1,42} = 4.26$, $p < 0.05$). Specifically, the trend in $\delta^{13}C$ values increased over time in temporary pools (slope = 0.04±0.01, t =2.59, $p < 0.05$), but decreased in permanent pools (although not significantly; slope = -0.004±0.004, t = -0.82, p = 0.42, Fig. 4.7d). The results were similar for the other scrapper, *Leucrocuta* sp., where the trends were different between the pool types (mixed-ancova, $F_{1,35} = 35.02$, $p < 0.05$) and permanent pools significantly decreased (slope = -0.03±0.01, t = -4.23, $p < 0.05$) but not temporary pools (slope = 0.02±0.01, t = 2.03, p = 0.06, Fig. 4.7e).

For the predatory midge, *Paramerina* sp., we found that the trend in $\delta^{13}C$ differed between pool types (mixed-ancova, $F_{2,40} = 4.49$, $p < 0.05$), where permanent pools decreased over time (mixed-anova, $F_{3,24} = 7.12$, $p < 0.05$), but not in temporary pools (mixed-anova, $F_{2,15} = 0.147$, p = 0.86, Fig. 4.7g). There was a significant difference in the $\delta^{13}C$ trend between pool type for the predator *Sialis* sp. (mixed-ancova, $F_{1,42} = 11.03$, $p < 0.05$), where temporary pools increased across time (slope = -0.03±0.008, t = 3.01, $p < 0.05$), and decreased in permanent pools (although not significantly; slope = 0.01±0.005, t = -1.62, p = 0.11, Fig. 4.7h). The trend in $\delta^{13}C$ for a surface predator, *A. remigis* differed for each pool type (mixed-ancova, $F_{1,45} = 4.96$, $p < 0.05$), where but there were no significant trends across time for both pool types (all $p > 0.05$, Fig. 4.7i). Lastly, there were no significant differences in $\delta^{13}C$ among pool types or across time for *Heteroplectron* sp., and *O. mykiss* (linear-mixed effects model, $p > 0.05$, Fig.4.7a,f). *Polypedilum* sp. and algae were excluded from this analysis due to limited sample numbers.

Predator trophic position and niche width

Predator niche width

Beyond an examination of how the food web shifted through time, we were also interested in understanding how seasonal drought influenced a suite of aquatic predators. There was substantial overlap in the niche width of *O. mykiss* across time for both permanent and temporary pools (Fig 4.6a, Fig.4.8a), although *O. mykiss* in temporary pools had larger niche widths at any given time compared to permanent pools. Additionally, for both pool types, there was a moderate upward trend for *O. mykiss* (increase in $\delta^{15}N$) from early to late summer. In permanent pools, *O.*

mykiss niche width (based on the ellipse-based metric) was larger in October compared to early July, a pattern that was also observed - but to a lesser extent - in temporary pools. These results differed considerably from the alpha hull metric which instead suggested that the niche width of *O. mykiss* in temporary pool decreased across the summer drought season. For both temporary and permanent pools, the ellipses showed a considerable increase in niche width in August due to the influence of outliers which were associated with high trophic positions (Fig.4.6a), whereas the alpha hull metric was more conservative and did not show an upward tick in August.

The niche area of *Paramerina* sp. in permanent and temporary pools appeared to diverge from one another along the $\delta^{13}C$ axis, and both were associated with an upward shift along $\delta^{15}N$ axis through time (Fig. 4.8b; see trophic position results below). The ellipse areas showed no significant differences in size between July and September/October for both pool types whereas the alpha hull method showed moderate decreases in niche width (Fig. 4.6b). The niche width of *Sialis* sp. (Fig. 4.8c) had similar patterns to *Paramerina* sp. where permanent and temporary pools appeared to moderately diverge from each other along the $\delta^{13}C$ axis (Fig. 4.8c). The niche width of *A. remigis* appeared to collapse over time, leading to a decrease in niche width area between the early and late summer (Fig. 4.6d, Fig.4.8d). Results were similar regardless of method (ellipses vs alpha hulls), with one exception: the ellipses showed a greater increase in August due to an outlier.

Trophic position of predators

The results for the trophic position (TP) of *O. mykiss* are reported above under the food chain length section. To determine if TP varied across time or among pool types for the invertebrate predators, we again used mixed-linear regression models, unless otherwise noted. The trend in TP for *Paramerina* sp. differed between pool types (mixed-anova, $F_{2,39} = 4.87, p < 0.05$), where it increased across time in both temporary (mixed-anova, $F_{2,15} = 8.29$, $p < 0.05$) and permanent pools (mixed-anova, $F_{3,24} = 9.44$, $p < 0.05$, Fig. 4.6b). There were no differences in the trend of TP between pool type for *Sialis* sp. (mixed-ancova, $F_{1,43} = 0.26$, $p = 0.25$), and there was no significant relationship between time and TP for temporary pools (slope = -0.015±0.005, t= 3.01, $p = 0.85$), but there were significant non-linear trends for permanent pools (mixed-anova, slope = 0.03±0.01, $F_{1,27} = 0.55$, $p < 0.05$, , Fig. 4.6c). Lastly, there were no significant differences between pool types for *A. remigis* (mixed-ancova, $F = 0.17$, df = 1,45, $p = 0.68$), nor were there any time effects (all $p > 0.05$, , Fig. 4.6d).

DISCUSSION

We studied the influence of stream drying on an intermittent stream food web across the drought season, including in pools that eventually dried completely (temporary) and those that persisted through the drought season (permanent). Our results revealed subtle shifts in overall food web structure, including shifts in isotopic niche width and increases in food chain length, whereas

mean carbon did not shift considerably. When we looked closer at the response of individual predators, we detected stronger changes, including increase in the trophic position for the top predator at our site (steelhead trout) and niche width collapse of a surface-feeding invertebrate predator. We also report that some of these shifts in food web structure differed among temporary and permanent pools, which we elaborate on further below.

The influence of stream drying on an intermittent stream food web

As our study stream contracted across the drought season, residual pools were created, which provided a natural unit of replication for our study. We found only subtle shifts in food web structure during stream drying, and no consistent differences among temporary and intermittent pools as we had predicted. This interpretation was apparent from visual assessments of $\delta^{13}C$ and $\delta^{15}N$ biplots and isotopic niche width of food webs, where there were we detected no clear changes in the overall shape or niche area across time or among pool types. One possible explanation for food web stability in our study is the relatively low food chain length (average = 2.53) among our pools. Short food chain lengths are common in intermittent streams (Sabo et al. 2010) and may be more stable than long, complex food webs (Pimm and Ktiching 1987). The moderate stability in our food webs may also be attributed to the high density of detritus in our pools, compared to other studies on food web stability that are conducted in regions with more variable and/or less dense riparian coverage (e.g., Bunn et al. 2003, Balcombe et al. 2005). Detritus-based food webs are often considered more stable than autotrophic-based food webs (Moore et al. 2004), and habitats with a large continuous source of detritus have increased resistance to disturbances (DeAngelis 1992, Closs and Lake 1994). Lastly, our monthly sampling study design may have missed the period of rapid change in temporary pools that occurred immediately before they dried completely. We sampled approximately seven days before temporary pools dried, suggesting that catastrophic food web collapse did not occur until the pools nearly dried. Boersma et al. (2013) found similar thresholds of community stability up until the point of complete pool desiccation, supporting their drought-resistance hypothesis that species adaptations make them resistant to drought conditions. At our study site, Hwan and Carlson (in review) report that steelhead mortality is concentrated in the late summer during dry years when pool conditions begin to deteriorate, providing further support for the importance of this late summer period. There is no question that the food webs in temporary pools eventually collapse, and future work should concentrate on this during advanced drought stages.

Weak fluctuations in food web structure across a drought disturbance have been previously observed (e.g., experimental flow reduction, Walters and Post 2008), while others have reported catastrophic food web shifts or collapses, where taxa are eliminated, links are severed (experimental flow reduction, Ledger et al. 2013), and trophic levels are reduced (space for time substitution, Woodward et al. 2012). We suspect differences among studies are attributed to the variation in food web metrics used to assess food web changes, study design (experimental vs. observational), the severity of the drought conditions, type of drought

(seasonal vs. supra-seasonal drought, Lake 2003), and the drought stage when observations on food web state were recorded.

One counterintuitive result from our study relates to the increase in food chain length and the trophic position of the top predator in our system, juvenile steelhead trout. Although steelhead are inevitably removed (suggesting a reduction in food chain length) from temporary pools prior to drying, it is curious that prior to this point, we found that their trophic position *increased* across the drought season. We suspect that this increase may be due to either the concentration of prey with declining water levels and associated decrease in encounter time. Another possibility is that as sensitive prey were eliminated during drought conditions, they were replaced by other taxa that may have held higher trophic positions and could withstand harsher drought conditions. Although we did not statistically test for it, terrestrial invertebrates, which on average held a high trophic position, fell within range of steelhead $\delta^{13}C$ and $\delta^{15}N$ and therefore could have become an important food source for *O. mykiss* as pool habitat contracted. The trajectory of trophic level and food chain length during drought disturbance is interesting and warrants further exploration.

Our results also suggest that the food webs in our study were supported primarily by terrestrial subsidies, and did not shift from allochthonous to autochthonous sources across the drought period as was detected by Reid et al. (2008) and McHugh et al. (2014). For one, most of the taxa were centered closest to leaf isotopic carbon values (-30.54‰), and secondly to periphyton (-31.90‰), which is known to gain a significant portion of its mass from terrestrial sources (Rasmussen 2010). These results may be due to the consistent supply of nutrients from riparian detritus or terrestrial invertebrates across the drought period. Secondly, we did not observe a substantial change in conditions that may otherwise encourage algal or macrophyte growth (e.g., increased sunlight penetration). Third, even if allocthonous source material was available, the main consumers of this material may not have been available to predators. For example, the only aquatic invertebrate in our study site with a strong autochthonous signal (*Leucrocuta* sp.) dramatically declined from July to September/October.

Lastly, we observed that a number of the taxa had $\delta^{13}C$ lighter than any of the primary producers that we sampled. We expected that the $\delta^{13}C$ values of the consumers would reflect the proportional assimilation of carbon from the producers because stable isotopes of carbon do not fractionate more than approximately 1‰ between trophic levels (DeNiro and Epstein 1978). Winemiller et al. (2011) hypothesized that this may due to missing relevant basal sources during sampling, or due to temporary shifts in consumer $\delta^{13}C$ values from physio-chemical environmental factors. We may have also underestimated the importance of algae as a carbon source in our food webs as we did not have sufficient samples to obtain an accurate $\delta^{13}C$ range. In fact, stream algae can have a wide $\delta^{13}C$ range as a consequence of factors such as watershed size, water velocity (Finlay et al. 1999), thus the lighter carbon values in our consumers may still reflect an algal base.

The influence of stream drying on aquatic predators

Predators are thought to be especially sensitive to the effects of drought (Bogan and Lytle 2011), so we also explored how drought influenced a suite of predators that range in feeding types (i.e., surface and benthic feeders) and vary in body size (from midges to steelhead trout). As previously mentioned, steelhead trout (*O. mykiss*) increased in trophic position though time. Although it was unclear if steelhead niche width increased or decreased over time, there was a distinct separation in their niche between early and late summer in both temporary and permanent pools. This shift in niche width was primarily along the $\delta^{15}N$ axis (as observed in the increase in trophic position) with little change in $\delta^{13}C$. This may indicate that *O. mykiss* were either feeding on different prey items that share a similar basal carbon source, or they are feeding on similar prey that increased in trophic position across time. This change in diet may also be due to a change in availability of potential prey. A separate community analysis on the macroinvertebrates during this same drought season found that the density and species richness of macroinvertebrates increased significantly in temporary pools before drying (Bogan et al. in prep.). Moreover, *O. mykiss* density decreased though time at our site suggesting that individuals died faster than habitat contracted (Hwan and Carlson, unpublished), thus decreasing competition and potentially giving the remaining individuals access to prey that were previously difficult to capture.

Beyond changes to the apex predator at our site, our results also showed a decrease in niche width and increase in trophic position of our smallest predator (*Paramerina* sp.). This could be due the rapid growth of midges (Benke 1998) and a corresponding shift in diet. Earlier in the season, small midges may have fed on a wider variety of small prey and then switched to a more size-selective diet later in the summer. We also found a decrease in niche width for *A. remigis* across the drought period for both temporary and permanent pools. The decrease in diet diversity may be due to changes in their behavior or in prey availability. A large proportion of their carbon comes from consuming terrestrial invertebrates that fall into the stream (Jardine et al. 2008), therefore, future studies should investigate if there are shifts in terrestrial prey diversity that might explain the decrease in *A. remigis*' niche width across the summer drought. Another explanation may be that emerging aquatic insects account for a significant portion of *A. remigis*' diet. The peak emergence period in the region is in early summer; therefore we would expect the wane in emergence to coincide with a decrease in diet diversity. Likewise, the cessation of flow across the summer would have decreased the potential rheophilic prey that drift down from upstream riffles, again suggesting reduced prey diversity in later summer. Finally, we observed an increase in niche width for *Sialis* sp. That may have also been due to an increase in prey availability as pools contracted. Future studies are needed to explore the mechanisms driving these shifts in trophic position and niche width for our suite of aquatic predators.

A comparison of niche width metrics

We found that there were substantial differences in our niche width estimates using the ellipse vs. alpha hulls metrics, making it difficult to interpret our results in some cases (i.e., the trend

across time and differences among pool types). For example, a steelhead outlier in in a temporary pool in August resulted in an increase in niche width according to the ellipse metric, whereas it decreased in this same time period using the alpha hull method, which is less sensitive to the influence of outliers. As such, for predator niche width estimates, alpha hulls tended to be more conservative with lower niche areas (by being less sensitive to outliers) and less overlap among sample periods. Conversely, when we calculated the niche width of all of the consumers (food web size) the ellipse method was far more conservative. Although these metrics were developed to decrease the influence of outliers and correct for sample size (Burgman and Fox 2003, Jackson et al. 2011), our results show that these metrics can lead to inconsistent estimates of niche widths, confounding interpretation. We suggest that future studies further explore the usefulness and precision of other metrics, such as those used in estimating species' home ranges (e.g., local convex hulls, Getz et al. 2007).

Implications

Overall, our results suggest that changes in food web structure are subtle across a 'typical' summer drought, but that individual predator taxa may have more distinct trajectories in trophic position or niche width. Our study occurred in the above-normal water year of 2011-12, therefore it is probable that we would have observed even stronger changes had our study occurred in an even drier year. Beginning the following year (2013-14), California entered into an extended, multi-year drought with intensifying drought conditions each year for the past four years and continuing through the present. These kinds of conditions are expected to become more common in the future with climate change, which should lead to increased duration of low flow periods (Larned et al. 2010). At our study site, for example, the "fall" rains of the 2013-14 water year did not arrive until February 2014, extending the "summer" drought season by over four months.

The intensified drought conditions predicted with climate change will lead to altered flow regimes. It is likely that there will be shifts from permanent to intermittent flow, as well longer zero-flow periods within existing intermittent streams, which may lead to some formerly permanent pools shifting to temporary ones (Larned et al. 2010). Intermittent streams can support high biodiversity in coastal California (Bogan et al.in prep.) and many taxa found at these sites show adaptations to seasonal drought, which can lead to resilient communities and moderately stable food webs as we have demonstrated here. However, intensified drought conditions due to climate change and/or water withdrawals may lead to declines or even extirpations of ecologically important species (e.g., top predators, Boersma et al. 2014), such as juvenile salmonids *O. mykiss* and coho salmon (*O. kisutch*) that are found in many intermittent streams in this region (Boughton et al. 2009, Grantham et al. 2012, Hwan and Carlson 2015). Experimental studies using mesocosms and artificial water withdrawals have provided insight into how freshwater streams will react to drought (e.g.,Walters and Post 2008, Woodward et al. 2012, Ledger et al. 2013, Boersma et al. 2013). Future studies however, should also incorporate multi-year studies in natural systems to understand the resistance and resilience of entire food

webs to drought, which depends on the resistance and resilience of individual elements and the degree of functional redundancy within the food web.

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Table 4.1. List of taxa included in our sampled food web, including organism type, order, family, genus or species, functional feeding group (FFG), and the code used in the $\delta^{15}N$ and $\delta^{13}C$ biplots.

Type	Order	Family	Genus/spp	FFG	Code
fish	Salmoniformes	Salmonidae	Oncorhynchus mykiss	predator	omy
aquatic invertebrate	Diptera	Chironomidae	Paramerina sp.	predator	pre1
aquatic invertebrate	Megaloptera	Sialidae	Sialis sp.	predator	pre2
aquatic invertebrate	Hemiptera	Gerridae	Aquarius remigis	predator	pre3
aquatic invertebrate	Trichoptera	Calamoceratidae	Heteroplectron sp.	shredder	shr1
aquatic invertebrate	Trichoptera	Lepidostomatidae	Lepidostoma sp.	shredder	shr2
aquatic invertebrate	Ephemeroptera	Leptophlebiidae	Paraleptophlebia sp.	collector	col1
aquatic invertebrate	Diptera	Chironomidae	Polypedilum sp.	collector	col2
aquatic invertebrate	Gastropoda	Physidae	Physidae	scraper	scr1
aquatic invertebrate	Ephemeroptera	Heptageniidae	Leucrocuta sp.	scaper	scr2
terrestrial invertebrates				various	terr
periphyton				producer	peri
terrestrial plants				producer	leaf
algae				producer	alg

Figure 4.1. Location of the sample sites along John West Fork in the Golden Gate National Recreation Area, Marin County, California, USA.

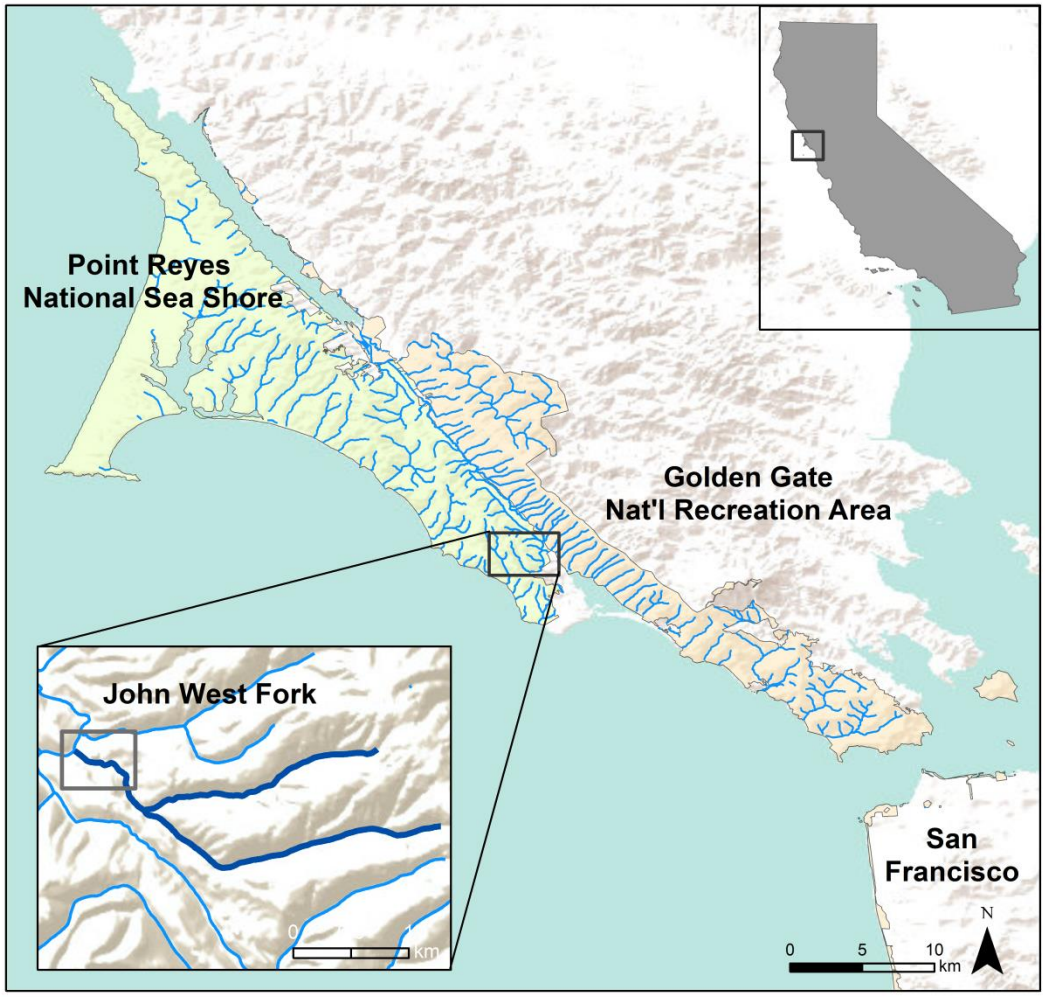


Figure 4.2. Change in water level in each of our study periods measured at weekly intervals over the course of the 2012 summer drought season. The dashed vertical gray lines represent our sampling dates of the study pools. Note that the temporary pools dried in September, so our October sample included only permanent pools.

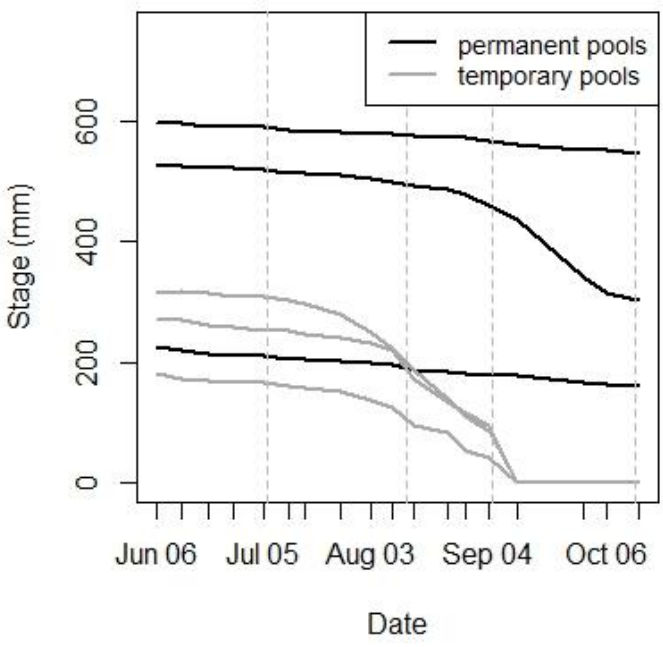


Figure 4.3. Stable isotope biplots of mean $\delta^{15}N$ and $\delta^{13}C$ values for aquatic taxa, potential terrestrial prey, and producers at each sampling time period. The top row represents permanent pools and the bottom row represents temporary pools.

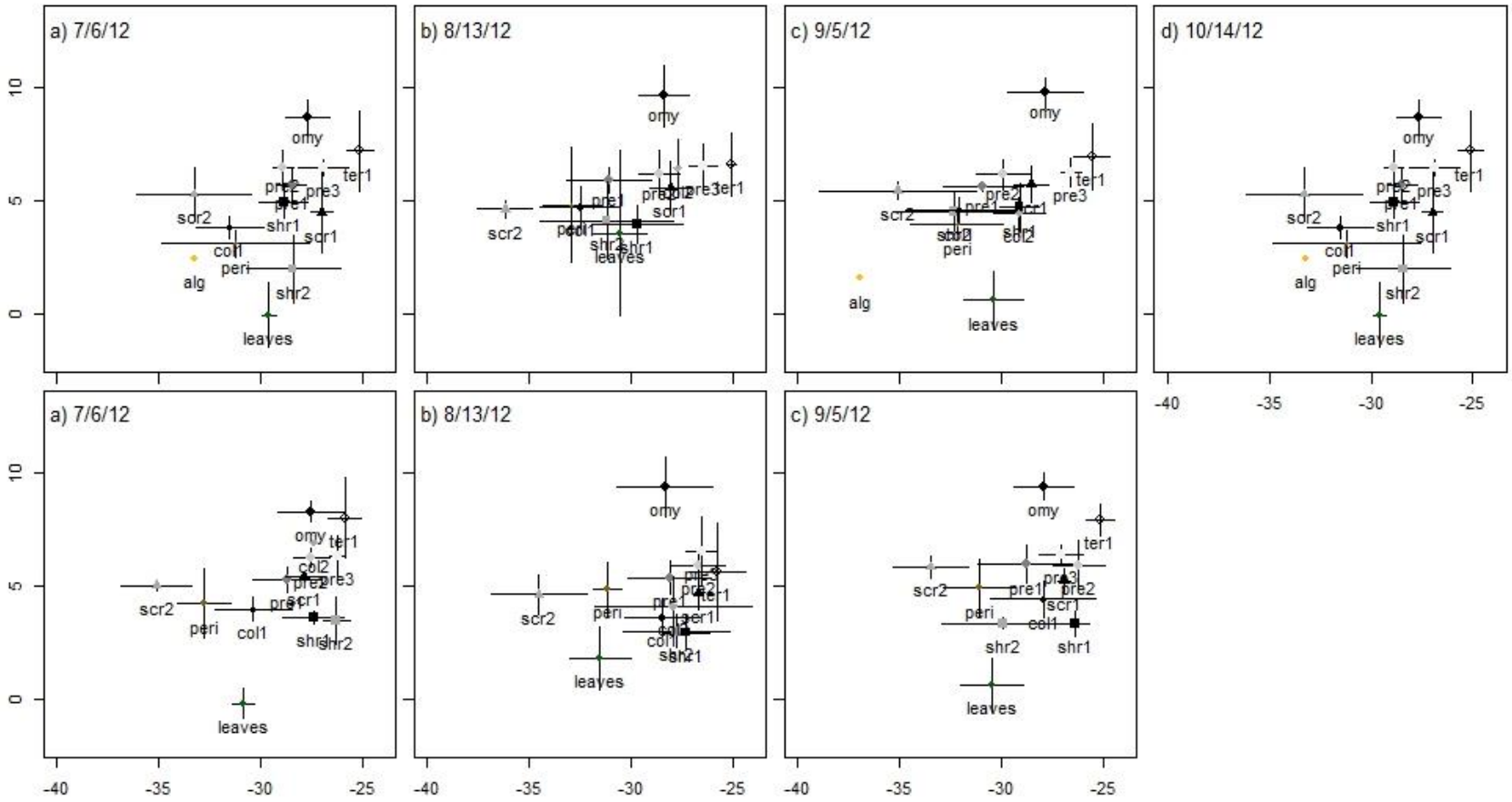


Figure 4.4. Niche width of all consumers, including two methods for calculating niche width: the top row represents the results using the SEA_c metric and the bottom row represents the results using the alpha hull metric. The left column (cool colors) represents permanent pools and the right column (warm colors) represents temporary pools. Each sample period is represented by a different color polygon, with lighter colors representing early summer and dark colors representing late summer.

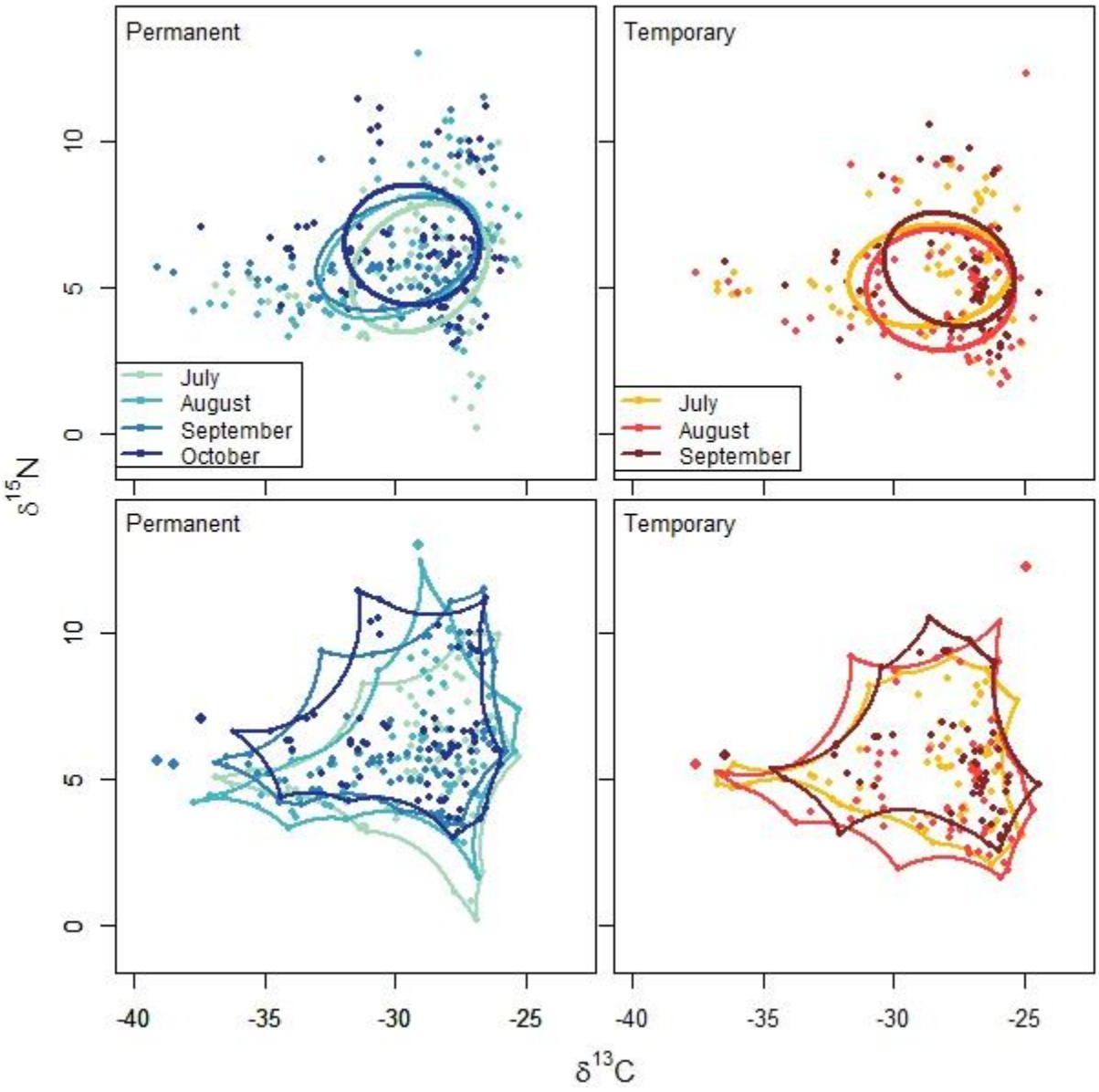


Figure 4.5. Changes in niche width values across the drought period for a) all consumers, b) *O. mykiss*, c) *Paramerina* sp., d) *Sialis* sp., and e) *A. remigis* based on the SEA_c and alpha hull metrics.

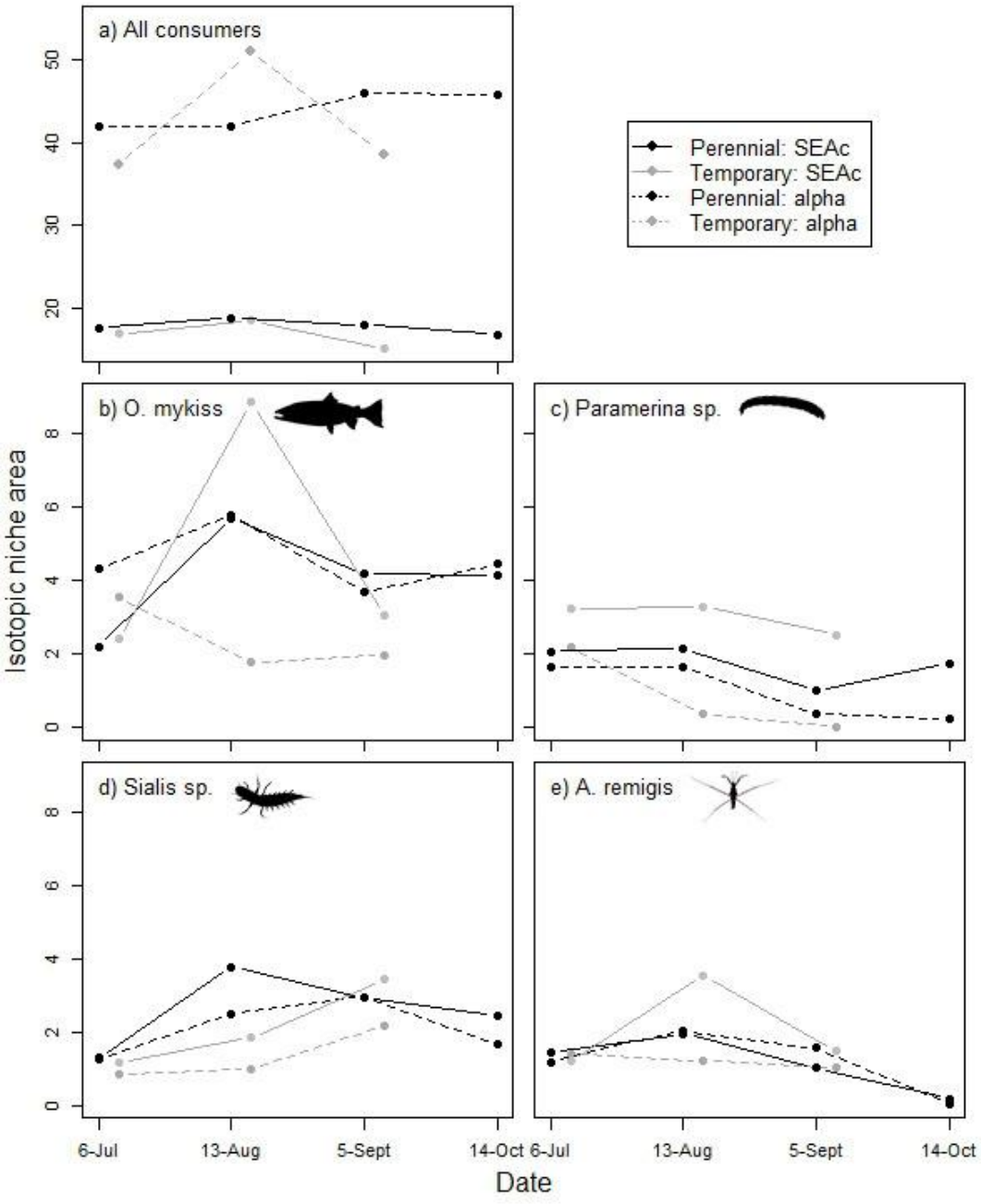


Figure 4.6. Changes in predator trophic position with associated standard error bars in permanent pools (black dashed line) and temporary pools (gray dashed line) across the drought period for a) *O.* mykiss, b) *Paramerina* sp., c) *Sialis* sp., and d) *A. remigis*. The apex predator for all sites was *O. mykiss*, thus its trophic position also provides insight into changes in food chain length.

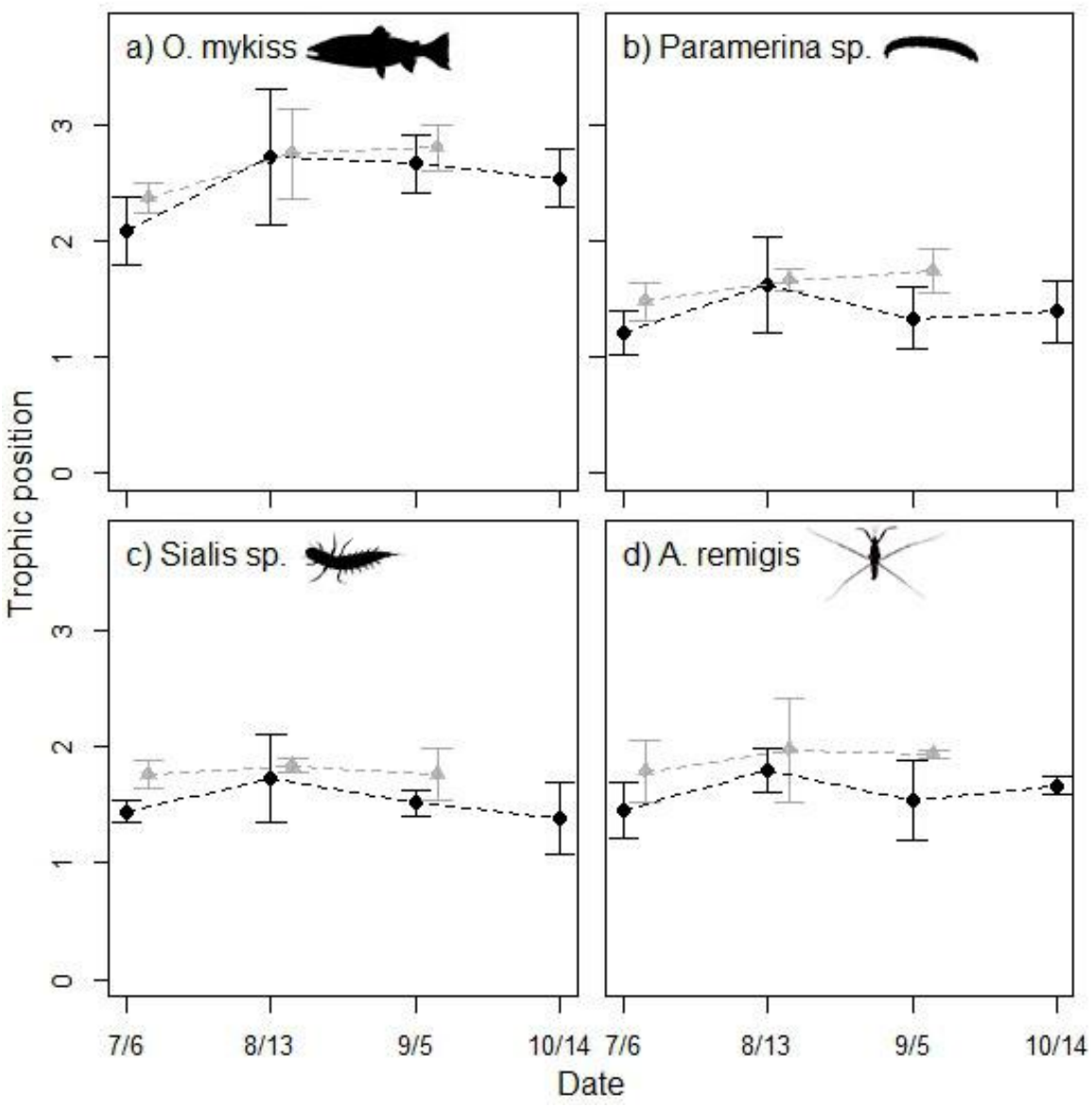


Figure 4.7. Changes in mean $\delta^{13}C$ values with standard error bars in permanent (black line) and temporary pools (gray dashed line) for our sampled organisms, including: a) *O. mykiss*), b) *Paramerina* sp., c) *Sialis* sp., d) *A. remigis*, e) *Heteroplectron* sp., f) *Lepidostoma* sp., g) *Paraleptophlebia* sp., h) *Physidae* sp., and i) *Leucrocuta* sp.. Also included are mean $\delta^{13}C$ values for leaf litter (dark green solid line), periphyton (brown solid line), and algae (yellow solid line).

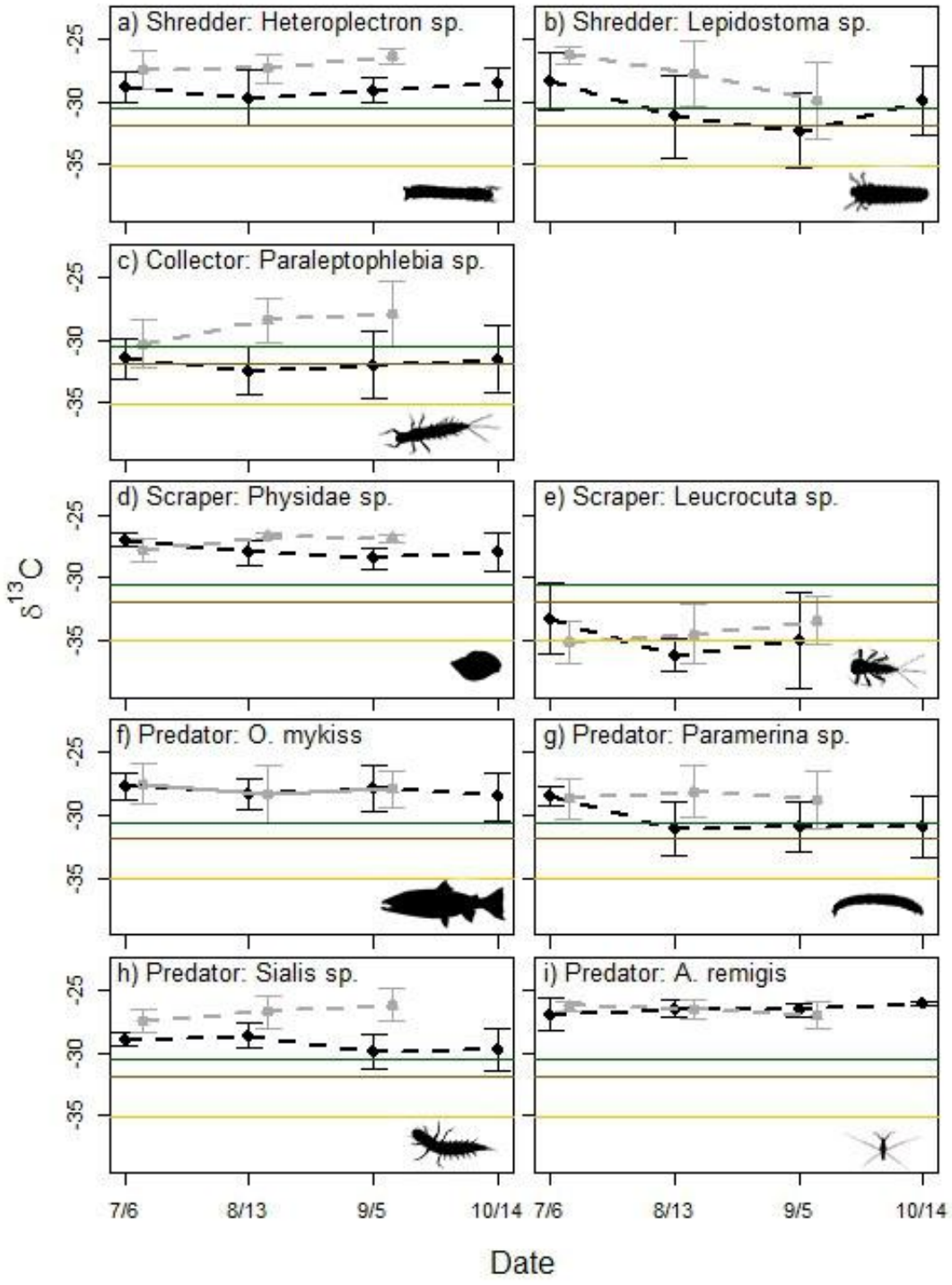
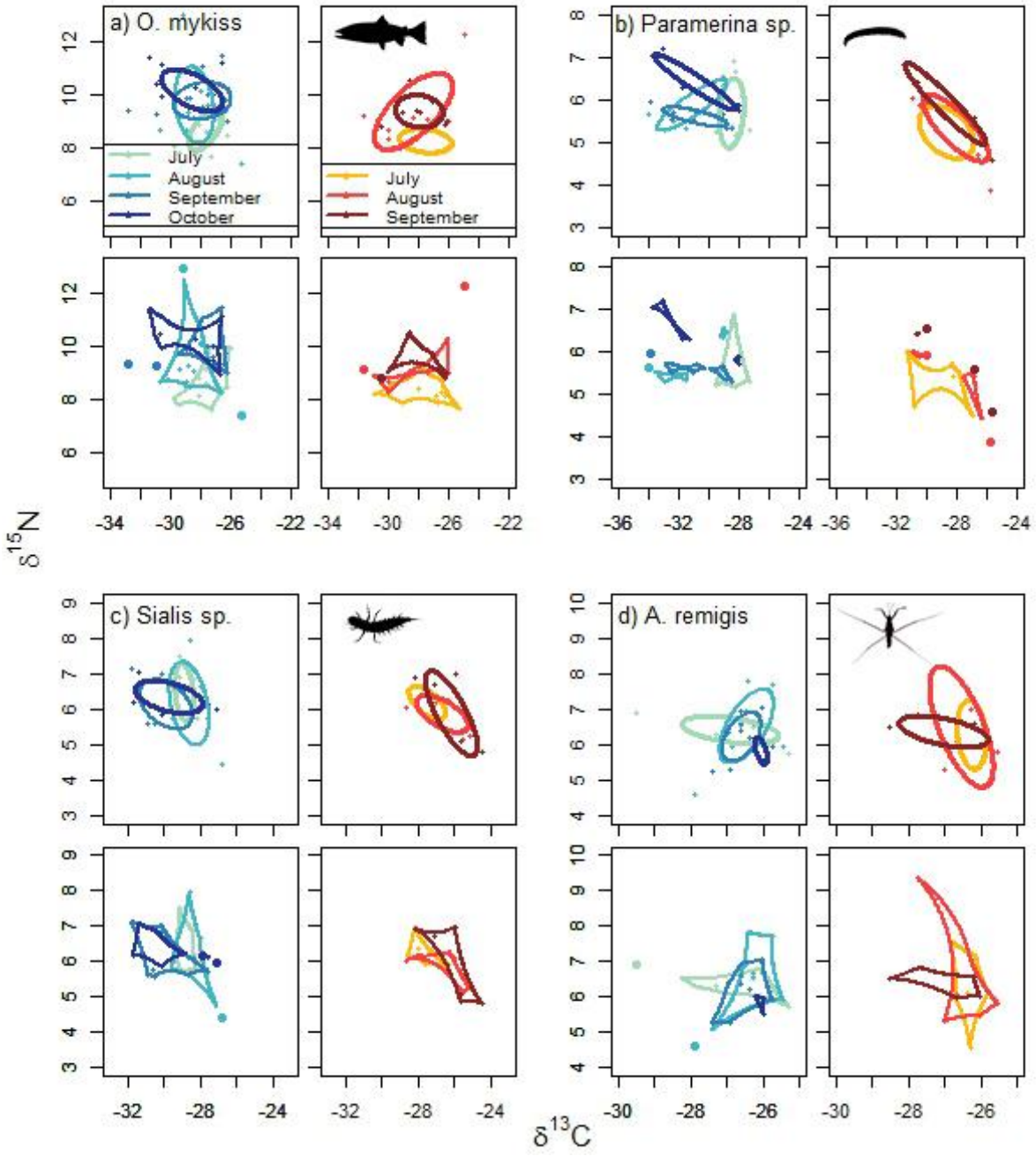


Figure 4.8. Predator niche width plots of four predators, a) *O. mykiss*, b) *Paramerina* sp., c) *Sialis* sp., and d) *A. remigis*. For each predator there are four plots, where the top row represents the results using the SEA_c metric and the bottom row represents the results using the alpha hull metric. The left column (cool colors) represents permanent pools and the right column (warm colors) represents temporary pools. Each sample period is represented by a different color polygon, with lighter colors representing early summer and dark colors representing late summer.



Appendix 4.1. List of taxa (see Table 1 for code), sample size (n), mean $\delta^{15}N \pm sd$, mean $\delta^{13}C \pm sd$ for each sample period (time) and pool type (per = perennial, temp = temporary).

Taxa	Time	Type	n	$\delta^{15}N$	$\delta^{13}C$
omy	July	per	14	8.67±0.75	-27.66±1.07
terr	July	per	9	7.18±1.79	-25.11±0.62
col1	July	per	9	3.80±0.47	-31.50±1.63
shr1	July	per	4	4.90±0.69	-28.87±1.20
shr2	July	per	7	1.97±1.47	-28.41±2.31
scr1	July	per	4	4.46±1.78	-27.00±0.52
scr2	July	per	9	5.26±1.19	-33.27±2.84
pre1	July	per	7	5.70±0.75	-28.48±0.75
pre2	July	per	6	6.48±0.73	-28.88±0.47
pre3	July	per	9	6.42±0.36	-26.90±1.25
omy	August	per	13	9.61±1.37	-28.35±1.24
terr	August	per	9	7.38±1.76	-25.20±0.61
col1	August	per	9	4.70±0.94	-32.47±1.96
col2	August	per	2	6.41±1.29	-27.70±0.18
shr1	August	per	7	3.94±0.82	-29.69±2.23
shr2	August	per	7	4.11±1.70	-31.17±3.29
scr1	August	per	8	5.57±1.16	-28.03±1.04
scr2	August	per	5	4.61±0.38	-36.17±1.34
pre1	August	per	7	5.88±0.55	-31.07±2.11
pre2	August	per	7	6.17±1.07	-28.59±1.01
pre3	August	per	9	6.53±0.98	-26.44±0.70
omy	September	per	15	9.76±0.67	-27.85±1.86
terr	September	per	9	7.38±1.15	-25.43±0.78
col1	September	per	9	4.54±0.58	-32.04±2.67
col2	September	per	4	4.41±0.73	-29.09±1.25
shr1	September	per	6	4.68±1.09	-29.09±0.99
shr2	September	per	8	4.50±0.86	-32.30±2.99
scr1	September	per	9	5.70±0.81	-28.49±0.86
scr2	September	per	7	5.43±0.36	-35.07±3.83
pre1	September	per	8	5.60±0.21	-30.87±1.96
pre2	September	per	9	6.14±0.65	-29.86±1.37
pre3	September	per	9	6.23±0.64	-26.58±0.50
omy	October	per	13	10.17±0.76	-28.53±1.94
terr	October	per	9	7.19±1.01	-25.74±0.76
col1	October	per	9	5.22±0.96	-31.55±2.72
col2	October	per	3	4.65±0.59	-27.21±0.65
shr1	October	per	9	5.05±1.44	-28.54±1.30
shr2	October	per	9	4.67±1.27	-29.84±2.74
scr1	October	per	9	6.42±0.31	-27.96±1.47
scr2	October	per	1	7.08±0.00	-37.42±0.00
pre1	October	per	8	6.42±0.60	-30.90±2.50
pre2	October	per	9	6.36±0.43	-29.73±1.76
pre3	October	per	3	5.84±0.26	-26.06±0.12
pgs	October	per	2	7.09±0.60	-30.98±1.21
omy	July	temp	12	8.27±0.43	-27.50±1.65

Taxa	Time	Type	n	$\delta^{15}N$	$\delta^{13}C$
terr	July	temp	9	7.99±1.79	-25.86±0.80
col1	July	temp	9	3.96±0.53	-30.35±1.91
col2	July	temp	1	6.89±0.00	-27.37±0.00
shr1	July	temp	7	3.60±0.29	-27.41±1.51
shr2	July	temp	9	3.46±1.03	-26.28±0.63
scr1	July	temp	3	5.38±0.21	-27.86±0.91
scr2	July	temp	9	4.99±0.25	-35.12±1.71
pre1	July	temp	7	5.25±0.56	-28.69±1.66
pre2	July	temp	6	6.19±0.42	-27.50±0.92
pre3	July	temp	8	6.29±0.89	-26.26±0.37
omy	August	temp	7	9.38±1.31	-28.31±2.37
terr	August	temp	9	6.15±2.18	-25.81±0.91
col1	August	temp	9	3.57±0.83	-28.45±1.82
col2	August	temp	2	4.06±1.32	-27.89±3.85
shr1	August	temp	8	2.92±0.72	-27.31±1.14
shr2	August	temp	8	2.98±0.73	-27.76±2.60
scr1	August	temp	8	4.64±0.70	-26.67±0.25
scr2	August	temp	7	4.60±0.86	-34.50±2.34
pre1	August	temp	8	5.34±0.73	-28.08±2.03
pre2	August	temp	7	5.88±0.47	-26.67±1.31
pre3	August	temp	6	6.52±1.53	-26.54±0.79
omy	September	temp	8	9.38±0.57	-27.93±1.47
terr	October	temp	8	6.55±1.75	-25.48±0.69
col1	November	temp	9	4.39±0.77	-27.93±2.55
shr1	December	temp	8	3.33±0.55	-26.33±0.65
shr2	January	temp	2	3.33±0.22	-29.90±3.01
scr1	February	temp	9	5.19±0.57	-26.87±0.31
scr2	March	temp	5	5.81±0.46	-33.44±1.88
pre1	April	temp	5	5.92±0.83	-28.77±2.33
pre2	May	temp	6	5.89±1.07	-26.17±1.29
pre3	June	temp	5	6.38±0.38	-27.03±1.08

Appendix 4.2. Results from the mixed-linear models testing for a trend in $\delta^{13}C$ through time, and trophic position for predators, including the mean, range, intercept and slope for permanent and temporary pools (Type).

		$\delta^{13}C$				Trophic position			
Taxa	**Type**	**Mean**	**Range**	**Intercept (±SE)**	**Slope (±SE)**	**Mean**	**Range**	**Intercept (±SE)**	**Slope (±SE)**
omy	per	-28.08	-32.82 to -25.26	-27.81±0.47	-0.01±0.01	2.5	1.63 to 3.97	2.26±0.14	0.004±0.001
omy	temp	-27.84	-31.60 to -24.94	-27.53±0.86	-0.0003±0.01	2.6	2.19 to 3.62	2.38±0.07	0.007±0.002
pre1	per	-30.37	-33.93 to -27.25	NA	NA	1.39	0.92 to 2.08	NA	NA
pre1	temp	-28.47	-31.26 to -25.68	NA	NA	1.62	1.26 to 1.90	NA	NA
pre2	per	-26.77	-28.64 to -24.48	-29.05±0.70	-0.015±0.005	1.51	0.99 to 1.51	1.55±0.13	-0.001±0.001
pre2	temp	-29.35	-31.81 to -26.77	-27.58±0.61	0.03±0.01	1.79	1.48 to 2.01	1.78±0.06	-26.78
pre3	per	-26.58	-29.52 to -25.3	-26.87±0.25	0.01±0.01	1.6	1.08 to 2.09	1.54±0.08	0.002±0.002
pre3	temp	-26.55	-28.54 to -25.53	-26.21±0.25	-0.01±0.01	1.89	1.29 to 2.74	1.80±0.10	0.003±0.003
shr1	per	-29.03	-31.94 to -26.72	-29.42±0.80	0.01±0.01				
shr1	temp	-26.99	-29.28 to -25.45	-27.58±0.42	0.02±0.01				
shr2	per	-30.45	-35.63 to -26.41	-29.86±1.43	-0.01±0.01				
shr2	temp	-27.28	-32.03 to -24.65	-26.13±0.63	-0.05±0.02				
col1	per	-31.89	-35.26 to -28.08	-31.19±01.43	0.01±0.004				
col2	temp	-28.9	-32.3 to -25.61	-30.29±1.17	0.04±0.01				
scr1	per	-28.01	-31.43 to -26.3	-27.85±0.66	-0.004±0.004				
scr1	temp	-26.94	-28.7 to -26.19	-27.52±0.26	0.01±0.004				
scr2	per	-34.51	-37.57 to -30.59	-33.14±2.1	-0.03±0.01				
scr2	temp	-34.69	-39.1 to -28.18	-35.01±1.17	0.02±0.01				

DISCUSSION AND CONCLUSIONS

In this dissertation, I explored how land use, hydrologic infrastructure, and seasonality influence freshwater fish communities and food web structure in a Mediterranean-climate region. My methods included multivariate community analyses, GIS spatial analyses, stable isotope analyses, and fish and habitat surveys. As freshwater systems continue to decline (Strayer and Dudgeon 2010), it is important that future research consider how both anthropogenic and natural factors influence freshwater biota across multiple spatial and temporal scales (e.g., Roy et al. 2003b, Durance et al. 2006, Johnson and Host 2010, Engman and Ramírez 2012).

In Chapter two, I built on a large dataset of local-scale habitat and fish community data from streams across the San Francisco Bay region to assess the influence of large-scale watershed properties on stream fishes. Specifically, using GIS, I delineated the watershed boundaries for 193 sites, determined the land use within each and the extent of hydrologic infrastructure. I then used multivariate community analyses to ask questions about the relative importance of watershed-scale properties versus local-scale stream properties on freshwater fish communities. I found that freshwater fish communities are associated with a combination of local (instream) and watershed-scale factors. Sensitive native fishes were primarily found in high elevation reaches with low water conductivity and within watersheds dominated by forests, whereas more tolerant native and nonnative fishes were negatively associated with these conditions. Structural equation modeling revealed that community composition was in part influenced by watershed properties indirectly through their effects on water quality (namely, water conductivity). From an applied perspective, these results suggest that conserving sensitive native species (e.g., rainbow trout, *Oncorhynchus mykiss*) requires maintaining undeveloped high elevation habitat, which is often associated with good water quality and forested watersheds.

In Chapter three, I used a resurvey approach to show that contemporary urbanization in the largest watershed of the San Francisco Bay region (Alameda Creek Watershed) was correlated with changes in fish community structure and, specifically, a decrease in the number of native fish species and a decline in a common native cyprinid (California roach, *Lavinia symmetricus*). Furthermore, this relationship was strongest when urbanization occurred in the vicinity of the sampling site as opposed to further upstream in the watershed. While the changes we documented were subtle, they may foretell future declines or extirpations if urbanization continues in this region. Together, the results of my first two chapters support the common perception that maintaining the integrity of freshwater systems requires a basin-wide perspective (Lake et al. 2007), such as limiting upstream development. Much of the urbanization in the greater San Francisco Bay region is concentrated in low elevation regions surrounding the bay. However, urbanization continues to expand upslope as the demand for residential and commercial development is high. My results suggest that efforts to reduce contaminants, fine sediments, and altered hydrographs through storm water management programs (e.g., bio-retention devices, public education) in newly urbanized regions will be critical for conserve native fishes in urbanizing landscapes (Bernhardt and Palmer 2007). My research also highlights

the value of contemporary resurvey studies, which provide insights into how freshwater communities are responding to ongoing environmental change.

In Chapter four, I shifted my focus to an exploration of the influence of Mediterranean seasonality on stream food webs that support an imperiled salmonid fish (*O. mykiss*). For this study, I sampled the stream food web in 6 replicate pools, including 3 temporary and 3 permanent pools, each month across the summer drought season in a small intermittent stream in Marin County, California. I collected tissues from primary producers, aquatic and terrestrial invertebrates, and fishes and used analyses of stable isotopes of nitrogen and carbon to visualize food web snapshots for each pool type-month combination. My results showed that food web structure did not change considerably across the summer, or between permanent and temporary pools. However, I did observe changes in predator feeding ecology, including noting that *O. mykiss* and a predatory midge both increased in trophic position across the summer drought season, possibly as a result of increased density of potential prey as pools contract.

Seasonal drought is characteristic of Mediterranean-climate regions, however the severity of these events varies among years (Gasith and Resh 1999) and are predicted to intensify with climate change and continued human demand for freshwater (Filipe et al. 2013). More generally, climate change is expected to decrease hydrologic connectivity in arid and semi-arid regions, which may result in increased intermittency or complete stream drying (Larned et al. 2010, Jaeger et al. 2014), leading to intense interest in understanding the effects of drought on river food webs. Our study occurred in an 'above-normal' water year and we found that food web structure remained relatively stable through the summer. Beginning the following year, California has experienced an extreme multi-year drought. How our results would have differed under more extreme drought conditions is unclear, but food web collapse due to drought has been observed in other systems (e.g., McHugh et al. 2014). Future studies should encompass multiple years with a broader range of drought intensity to better understand the effects of drought on intermittent stream food webs. This is important as many threatened fish species rely on intermittent streams for rearing (e.g., Labbe and Fausch 2000, Hwan and Carlson 2015).

In summary, the results of my dissertation research show that land use conversion, extensive water infrastructure, and drought conditions have strong effects on freshwater fish communities. However, my research also suggests that these communities are remarkably resilient, persisting in many San Francisco Bay Area rivers and streams despite the substantial impact we have had on the landscape, our natural resources, and the climate. For example, I showed that while urbanization can influence water quality and fish community structure, native fishes continue to dominate in the mid- to upper elevation regions around the San Francisco Bay region. Likewise, despite approximately 15 years of rapid urban expansion in the largest watershed of the region, I found only moderate shifts in the dominance of common fishes and slight decreases in the number of native species. Finally, I found that while individual taxa do show trophic shifts in response to drought and pool contraction, the larger food web was remarkably stable across the summer drought season. Overall, these results suggest that native fishes of the region are relatively resilient to perturbation when suitable habitat is available to

support them and highlights the importance of conserving key habitats (e.g., upper elevational reaches) for conserving native fishes in heavily modified, heavily invaded, drought prone regions- features typically of most Mediterranean-climate rivers.

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