

SEASONAL REARING HABITAT IN A LARGE MEDITERRANEAN-CLIMATE RIVER: MANAGEMENT IMPLICATIONS AT THE SOUTHERN EXTENT OF PACIFIC SALMON (*ONCORHYNCHUS* SPP.)

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ABSTRACT

Pacific salmon (*Oncorhynchus*) use a variety of rearing environments prior to seaward migration, yet large river habitats and their use have not been well defined, particularly at the southernmost salmon range where major landscape-level alterations have occurred. We explored juvenile Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss*) presence along the river continuum and in main-channel and off-channel habitats of a regulated California Mediterranean-climate river. Over an 8-year period, off-channels of the lower Mokelumne River exhibited slower and warmer water than the main-channel. Probability of salmonid presence varied by stream reach and habitat types. Steelhead and Chinook salmon both demonstrated transitional responses to the dry season, with juveniles leaving off-channels by midsummer. This corresponded to flow recession, increasing water temperatures, salmonid growth and end of emigration period. Main-channel steelhead observations continued until the following storm season, which brought cool flood flows to reconnect off-channels and the next juvenile cohort of both species to the river. Within arid climates, low-gradient off-channels appear more transiently used than in cooler and more northern humid climate systems. Within a highly regulated Mediterranean-climate river, off-channel habitats become increasingly scarce, disconnected or temperature limiting in low-gradient reaches both seasonally and due to anthropogenic modifications. These observations may provide guidance for future management within large salmon streams. Copyright © 2015 John Wiley & Sons, Ltd.

KEY WORDS: juvenile; habitat use; *Oncorhynchus tshawytscha*; Chinook salmon; steelhead; *Oncorhynchus mykiss*; regulated river; Mediterranean climate

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INTRODUCTION

Rivers are typically large, complex and dynamic streamscapes that are difficult to observe holistically, resulting in mostly piecemeal knowledge of their structure and function. Fausch *et al.* (2002) argued that our fragmented understanding of river ecosystems has accelerated the decline of numerous lotic fish species, including the celebrated salmon of North America. Therefore, analysing large-scale concepts across streamscapes potentially provides important management tools at scales relevant to anthropogenic watershed perturbations (Schlosser, 1991; Fausch *et al.*, 2002).

Pacific salmon (*Oncorhynchus* spp.) are associated with Northern Hemisphere temperate streams from eastern Asia to western North America. Within temperate streams, a variety of environmental parameters can influence salmon production. Additionally, several life stages of more than one species may be present at any given time. Stream com-

plexity, in the form of off-channel habitats and woody debris, may benefit juvenile salmonids by providing refuge from predators, limiting competitive interactions and affording shelter from high, cold winter–spring flows (Swales *et al.*, 1986; Cunjak, 1996; Giannico and Hinch, 2003). This complexity may also provide increased growth opportunities during summer and fall (McMahon and Hartman, 1989; Bell *et al.*, 2001). Growth and survival benefits from seasonally flooded habitats, especially within turbid, tidal regions, have also been observed for juvenile salmon at the southern extent of their North American range (Sommer *et al.*, 2001; Jeffres *et al.*, 2008; Limm and Marchetti, 2009). However, significant climatic differences across the geographic range of Pacific salmonids may lead to variation in habitat use and behaviours.

Unlike temperate regions, annual flooding and drying physically, chemically and biologically shape streams of Mediterranean and semi-arid climates (Gasith and Resh, 1999). Within warmer climates, stream communities are influenced by abiotic controls that dominate during floods (e.g. depth and velocity) and biotic controls when discharge

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declines (e.g. predation and competition). However, as the dry season progresses, abiotic pressures may again become more important regulators of stream populations and community structure as habitat conditions become harsher (Matthews, 1998; Gasith and Resh, 1999).

During the earliest rearing stage, salmon typically use relatively slow, shallow areas and have comparatively small territories. As they grow, salmon move into deeper, faster water and territory sizes increase, affecting habitat use (Grant and Kramer, 1990). However, small-scale habitat preferences vary among salmonid species, reflecting body size (Hasegawa *et al.*, 2012) and morphological adaptations to different environments (Rodnick *et al.*, 2008). Therefore, juveniles of different species and races may utilize habitats differently through space and time, especially within their drier, southern ranges in North America (Roper *et al.*, 1994). Although correlations between juvenile densities and channel margins of large rivers (where main-channel velocities tend to be slower and cover more abundant) have been observed (Beechie *et al.*, 2005), off-channel habitats and their use, especially in regulated Mediterranean and semi-arid climate salmon streams, have not been well defined or examined. Because of their relatively cool water temperature requirements, we hypothesize that Pacific salmon of warmer regions will use off-channel habitats such as backwaters and secondary channels for rearing when seasonal conditions allow but will avoid these environments during the dry season, thus providing a markedly different use pattern compared with northern latitudes (Murphy *et al.*, 1989; Taccogna and Hillaby, 2011).

In this study, we first examine if river reaches and main-channel differ from off-channels in definable terms (e.g. depth, velocity and temperature) within a Mediterranean-climate river supporting Pacific salmon. Secondly, we examine if juveniles of two congener species, Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss*), at the southern extent of their North American range, utilize these habitats differently in time and space. Such information might encourage programmes that re-establish and maintain dynamic river features that inundate at the appropriate magnitude, frequency, duration and time to support the priority species that are examined in this study (Poff *et al.*, 1997; Beechie and Bolton, 1999).

METHODS

Study area

The Mokelumne River is a major Sacramento–San Joaquin river system tributary, entering California's largest delta 48 km south-east of Sacramento. This snow-fed watershed drains 1624 km² of the central Sierra Nevada at the southern native extent of Pacific salmon (Figure 1) and has 16 major

water impoundments; the lowest anadromous fish barrier is Camanche Dam (river kilometre 103; constructed 1963).

The anadromous portion of the watershed, the lower Mokelumne River (LMR), ranges in elevation from ~30 m at Camanche Dam to sea level at Thornton, California. Gradient varies from 0.10% near Camanche Dam to 0.02% near the Cosumnes River confluence (Merz *et al.*, 2006). Tidal influence is observed up to river kilometre 53. Similar to many other system tributaries, hydraulic mining, gravel extraction, damming, diversions, regulation, deforestation, bank armoring, channelization and levee construction have altered sediment transport and greatly reduced floodplain connection and channel complexity (Edwards *et al.*, 2004).

Pre-Camanche Dam mean monthly flow had a typical snowmelt hydrograph, with the highest flow during May and June, well after peak precipitation. The post-dam hydrograph exhibits a significant reduction in late spring run-off (Pasternack *et al.*, 2003). Average annual pre-dam discharge (period 1905–1963) was 26.3 m³ s⁻¹ (minimum = 0 m³ s⁻¹, maximum = 761.7 m³ s⁻¹) at the town of Clements (Figure 1). Post-dam average daily flow (period 1964–2000) is 22.6 m³ s⁻¹ (minimum = 0.7 m³ s⁻¹, maximum = 162.8 m³ s⁻¹) with flood flows set at 142.0 m³ s⁻¹. Edwards *et al.* (2004) found that 80% of seasonal lakes and 23.8 ha (100%) of secondary LMR channels were lost between 1910 and 2001.

Lower Mokelumne River Chinook salmon (Chinook) and steelhead populations are supplemented by Mokelumne River Fish Hatchery production. During 1990–2002, average annual Chinook escapement estimates were 5506 Chinook (minimum = 280, maximum = 10 757), whereas average annual steelhead estimates were 27 steelhead (minimum = 0, maximum = 81) (Workman, 2003).

Life history strategies of these two congeners exhibit considerable overlap, but also inherent differences. The LMR supports a fall-run Chinook population, which exhibits an ocean-type juvenile life stage. Adults enter freshwater from August through December, peaking in late October, and juveniles primarily emigrate in their first year (Healey, 1991). Age 0 Chinook first appear in seine samples during late December, and although a remnant number of yearlings can be found during fall and winter fish community sampling, typically over 95% of juveniles leave the non-tidal LMR by July (Workman *et al.*, 2007). In comparison, steelhead exhibit perhaps the most complex suite of life history traits of any Pacific salmonid. They can be anadromous, rearing in fresh water for one or more years (McEwan, 2001), or live their entire life in freshwater. Because of these complex strategies, multiple life stages are found in the river/tributary environment all year (Sogard *et al.*, 2012). Adult immigrants are observed from October through March and typically Age 0 steelhead first appear in February with most emigration occurring from February to July (Workman *et al.*, 2007). A

PACIFIC SALMON-REARING IN A LARGE MEDITERRANEAN-CLIMATE RIVER

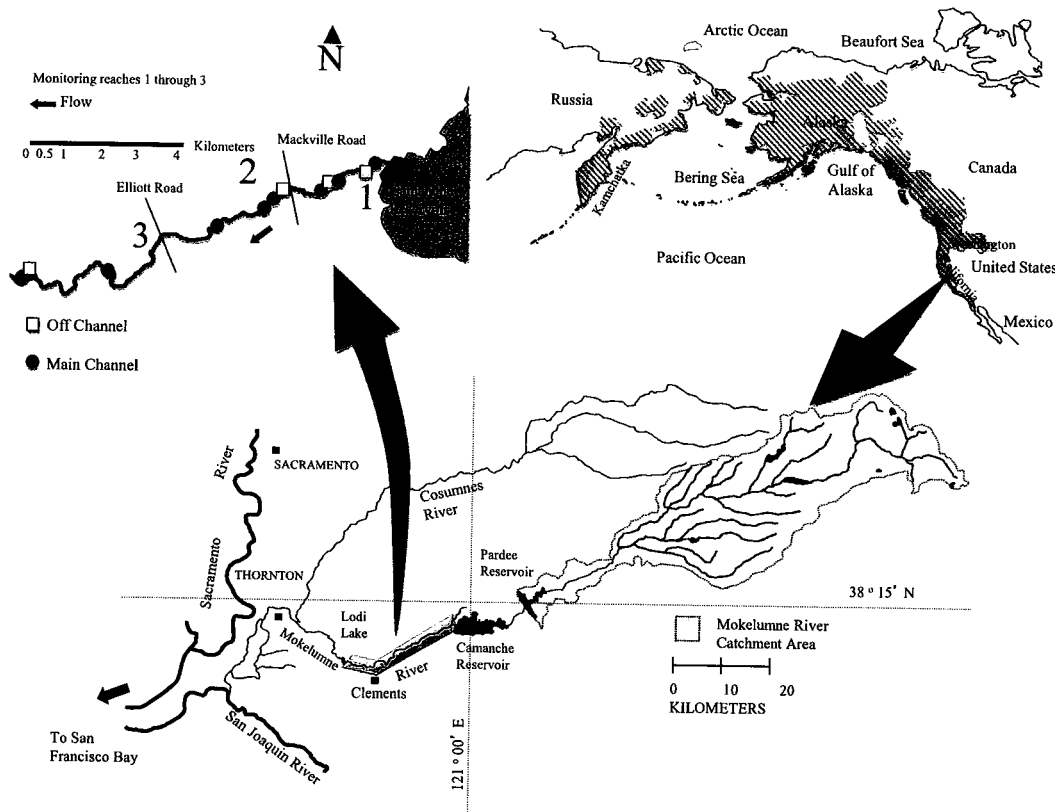


Figure 1. Present natural distributions of Chinook salmon (cross hatch) and steelhead (green) associated with Russia and North America (upper right); study area (orange) of the Mokelumne River watershed in relationship to San Francisco Bay (bottom) and sample sites associated with the three study reaches of the lower Mokelumne River, California. Distributions adapted from Behnke (2002) and Augerot *et al.* (2005). This figure is available in colour online at wileyonlinelibrary.com/journal/trr

relatively large portion of LMR *O. mykiss* appears to be non-anadromous (Del Real *et al.*, 2012).

Study reaches and habitat units

To describe physical differences in LMR habitat associated with juvenile salmonid observations, we performed study area habitat classification during LMR base flow of $7-8.5 \text{ m}^3 \text{ s}^{-1}$. We identified three reaches within the primary non-tidal juvenile-rearing area (Table I) based on stream gradient (Merz, 2001) and channel width. Reaches 1 and 2 support lateral cobble and gravel bars and support Chinook and steelhead spawning (Merz and Setka, 2004). No spawning occurs in Reach 3. Reach 1 has an average elevation above mean sea level of 24.7 m, with a mean low-flow channel width of 29.7 m and the highest Chinook and steelhead spawning densities. Reach 2 has an average elevation of 20.4 m, with a mean low-flow channel width of 25.3 m and lower spawning densities than in Reach 1. Reach 3 is downstream from the spawning area, has average elevation of 16.1 m and a mean low-flow channel width of 23.8 m, bed substrates of primarily

Table I. Total estimated surface area (hectares) of the lower Mokelumne River by river reach, and main-channel and off-channel habitats

Reach	Main-channel	Off-channel	Total
1	25.9	5.2	31.1
2	22.7	<0.1	22.7
3	37.6	0.1	37.7
Total (percent total)	86.2 (94)	5.3 (6)	91.5 (100)

Habitats mapped at base flow of $7-8.5 \text{ m}^3 \text{ s}^{-1}$.

sand and mud. Each study reach included main-channel and off-channel habitats (Figure 1). We randomly selected main-channel habitat within each reach. Off-channel areas include backwaters and secondary channels, which may contain riffles, glides and pools (Beechie *et al.*, 2005). Reach 1 has two off-channel and three main-channel sites. Reach 2 has one off-channel and three main-channel sites. Reach 3 has one off-channel and two main-channel sites. The total off-channel surface area during low flow was estimated to be 16.7% in Reach 1, <0.1% in Reach 2 and 0.1% in Reach 3.

Environmental monitoring

Between January 1997 and June 2004, we sampled 12 habitat units selected to represent available main-channel and off-channel features along the stream gradient (Figure 1). When sampling fish, we measured point estimates of water depth, temperature and velocity between approximately 0900 and 1400 hours. Depth was recorded from a top-setting velocity rod, and depth-averaged velocity was approximated by taking a measurement at 60% of the depth with an electromagnetic Marsh McBirney Flo-Mate velocimeter (Flo-Mate Model 2000, Marsh-McBirney Inc., 4539 Metropolitan Court Frederick, Maryland). Water temperature measurements were taken 0.1 m below the water surface with a YSI model 55 meter (Yellow Springs, Ohio) at each fish sampling location.

Fish sampling

We sampled habitat units monthly during daylight hours (~0900–1400 hours) by seine. Camanche Dam discharge ranged from $141.7 \text{ m}^3 \text{ s}^{-1}$ in January 1997 to $5.3 \text{ m}^3 \text{ s}^{-1}$ in September 2001 (Figure 2). On sampling days, a $15.3 \text{ m} \times 1.8 \text{ m}$ beach seine with 1.6-mm mesh was used to make one to six hauls within each sample site. Individual site hauls during each day at a site were averaged to produce a single data point. The seine was deployed along a transect extending 15.3 m from shore or to a water depth of 1.8 m, whichever came first, and then retrieved to shore. Depth and velocity were recorded at three points along the seine haul transect: (1) maximum distance from shore; (2) half-distance from shore; and (3) at shore. Temperature was recorded at each haul transect.

All captured fish were identified to species and then released alive. All salmonids $< 200 \text{ mm}$ Fork Length (FL) and not demonstrating secondary sexual characteristics

(e.g. releasing milt and spawning colouration) were designated 'juvenile'. Catch per unit effort was calculated as number of fish captured per total volume sampled (m^3) and converted to binary presence/absence data (0 = species not detected/1 = species were detected). Data were recorded separately for each species.

Data analysis

We conducted multilevel mixed-effects modelling on the data collected. To account for the lack of independence, we used a statistical approach (Zuur *et al.*, 2009) that modelled the data with both exchangeable and unstructured correlation matrices. An exchangeable correlation matrix (also known as compound symmetry) uses homogenous correlations between elements, which assumes correlations between elements to be the same over time (Heck *et al.*, 2012). An unstructured matrix provides a separate coefficient for each covariance (Heck *et al.*, 2012). The results from models using both exchangeable and unstructured correlation matrices were the same overall, so we used the former for all subsequent analyses.

We conducted multilevel mixed-effects modelling on the data. The data collected lack independence, and this is accounted for by the statistical approach we used. We modelled the data with both unstructured and exchangeable correlation matrices, and the results were unchanged, so we used the latter for all analyses.

We conducted analyses on response variables that are continuous (water temperatures, velocities and depths) or binary (fish species detected or not detected); therefore, we used different statistical approaches to handle the different data types. For the environmental data that were continuous, we conducted linear mixed-effects regressions fit with restricted maximum likelihood with observations nested within study sites ($N = 12$ sites). In these regressions, we

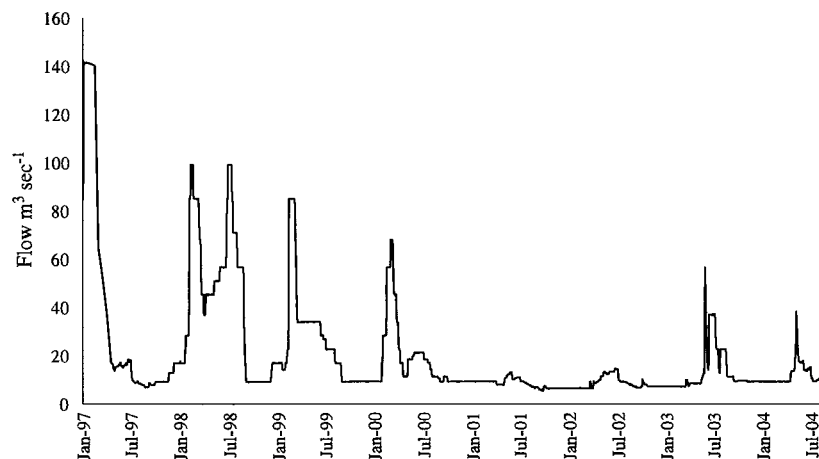


Figure 2. Flow released from Camanche Dam to the lower Mokelumne River, California, 1 January 1997 through 15 July 2004

examined if mean water temperature, velocity and depth varied between study reaches, seasons (winter: data from January, February and March; spring: data from April, May and June; summer: data from July, August and September; fall: data from October, November and December) and/or main-channel and off-channel habitats. Given that the analyses examining juvenile salmonid presence used a binary outcome, we used mixed-effects logistic regressions with observations nested by study site. In these mixed-effects models, we examined if juvenile salmonid presence varied between reaches, seasons, main or off-channel and with environmental conditions (water temperature, velocity and depth). Each species (Chinook salmon and steelhead) was analysed separately. For all mixed-effects models, we examined the effect size and significance of the independent variables (reach, season, main-channel and off-channel), and we reported the *p*-values, effect size and its 95% confidence interval. For estimating where significant differences occurred, we compared the first season (winter) with all other seasons, Reach 1 with the other reaches and main-channel with off-channel habitats. The mixed-effects modelling analyses were conducted in STATA/SE 13 (StataCorp, College Station, Texas). STATA provides the coefficients and odds ratio for statistical tests that have continuous and binary dependent variables, respectively. For coefficients of tests using a continuous dependent variable, positive coefficient estimates represent increasing values, and negative values represent decreasing values. For mixed-effects models with a binary dependent variable, we report the odds ratios that are estimated by the model and can range from 0 to positive infinity. Odds ratios from 0 to 1 indicate a lower probability of presence (PoP), and odds ratios greater than 1 indicate a higher PoP.

To display how the presence of a juvenile salmonid species varied across months, reaches and habitat types, we quantified the PoP as the number of samples where the species was detected divided by the total number of samples taken within that reach and time period (e.g. all samples collected in Reach 1 during the month of January). Mean PoP values for each species in the main-channel and off-channel were plotted for the 12 months and three river reaches that were surveyed in this study.

RESULTS

Study period flows varied from 5.3 to 141.7 m³. We executed 986 seine hauls that sampled an estimated 77 327.8 m³ of water and collected 15 013 juvenile Chinook salmon and 664 steelhead from the 12 study sites. This sampling design provided 669 data points, and we documented the number of data points collected by site, reach, season, main-channel and off-channel (Table II).

Table II. The number of data points sampled on the lower Mokolumne River by reach, habitat and season

Reach	Habitat	Winter	Spring	Summer	Fall	Total
1	Main-channel	15	31	4	8	58
1	Main-channel	12	28	4	8	52
1	Main-channel	15	37	6	8	66
1	Off-channel	12	32	5	9	58
1	Off-channel	14	38	6	8	66
2	Main-channel	18	39	6	9	72
2	Main-channel	16	41	4	8	69
2	Main-channel	13	24	3	5	45
2	Off-channel	14	28	5	9	56
3	Main-channel	13	32	6	6	57
3	Main-channel	18	5	0	4	27
3	Off-channel	0 ^a	31	7	5	43
	Total	160	366	56	87	669

^aHabitat not available.

Environmental data

Reaches and seasons. Between reaches and seasons, we observed significant differences in water temperature and velocity. Overall, mean monthly water temperature generally increased from January to September and decreased from September to January. The linear mixed-effects regression, fit by restricted maximum likelihood, found that water temperatures varied significantly between all seasons (Table III). Water temperature point estimates recorded in this study varied from 7.0°C (Reach 1) to 19.6°C (Reach 3). Overall, the average monthly water temperatures sampled increased in downstream reaches; we found a significant difference (*p*=0.048; Table III) in water temperatures between Reach 1 [mean=12.2°C,

Table III. Association between main-channel and off-channel habitats, and reaches, seasons and water temperatures^a (*N*=656)

	Coefficient ^b [95% confidence interval]	<i>p</i> -value
Location		
Main-channel	Reference	
Off-channel	0.907 [0.329, 1.485]	0.002
Reach		
1	Reference	
2	0.211 [-0.417, 0.839]	0.510
3	0.699 [0.006, 1.391]	0.048
Season		
Winter	Reference	
Spring	2.073 [1.829, 2.318]	<0.001
Summer	3.748 [3.341, 4.154]	<0.001
Fall	3.634 [3.296, 3.972]	<0.001
Constant	10.151 [9.659, 10.643]	<0.001

^aEstimates were obtained with linear mixed-effects regression fit with restricted maximum likelihood.

^bPositive values represent increasing values, and negatives values represent decreasing values.

standard error (SE)=0.113°C, *n*=295] and Reach 3 (mean=12.9°C, SE=0.234°C, *n*=125), which were the coldest and warmest reaches, respectively. There was no significant difference (*p*=0.510; Table III) in water temperatures between Reaches 1 and 2 (mean=12.3°C, SE=0.123°C, *n*=236). Sampled water velocities varied from <0.001 to 1.448 ms⁻¹. Reach 1 water velocities (mean=0.143 ms⁻¹, SE=0.012 ms⁻¹, *n*=300) did not differ significantly from those sampled in Reach 2 (*p*=0.390; Table IV, mean=0.239 ms⁻¹, SE=0.016 ms⁻¹, *n*=242) or Reach 3 (*p*=0.844, Table IV, mean=0.180 ms⁻¹, SE=0.016, *n*=127). Sampled depths varied from 0.061 to 1.829 m. Depths sampled also did not differ significantly between Reach 1 (mean=0.570 m, SE=0.013 m, *n*=299) and Reach 2 (*p*=0.553; Table V, mean=0.601 m, SE=0.019 m, *n*=242) or Reach 3 (*p*=0.889; Table V, mean=0.570 m, SE=0.015 m, *n*=126). Finally, significant differences occurred between all or some of the seasons in a year depending on the environmental factor examined (Tables III-V). Based on these results, the warmest temperatures were found in the off-channel habitat of Reach 3 during summer and the coldest water temperatures in the main-channel of Reach 1 in winter (Table III).

Main-channels and off-channels. Overall, mean water temperatures were significantly (*p*=0.002; Table III) cooler in the main-channel (mean=12.000°C, SE=0.090, *n*=435) than in the off-channel habitats (mean=13.070°C, SE=0.154°C, *n*=221). Main-channel velocities (mean=0.252 ms⁻¹, SE=0.010 ms⁻¹, *n*=446) were significantly (*p*<0.001; Table IV) faster than in off-channels (mean=0.051 ms⁻¹,

Table IV. Association between main-channel and off-channel habitats, reaches, seasons and water velocities^a (*N*=669)

	Coefficient ^b [95% confidence interval]	<i>p</i> -value
Location		
Main-channel	Reference	
Off-channel	-0.190 [-0.296, -0.085]	<0.001
Reach		
1	Reference	
2	0.050 [-0.064, 0.165]	0.390
3	0.012 [-0.113, 0.138]	0.844
Season		
Winter	Reference	
Spring	0.059 [0.026, 0.091]	<0.001
Summer	-0.004 [-0.057, 0.049]	0.886
Fall	0.030 [-0.014, 0.075]	0.184
Constant	0.190 [0.102, 0.278]	<0.001

^aEstimates were obtained with linear mixed-effects regression fit with restricted maximum likelihood.

^bPositive values represent increasing values, and negatives values represent decreasing values.

Table V. Association between main-channel and off-channel habitats, reaches, seasons and water depths^a (*N*=667)

	Coefficient ^b [95% confidence interval]	<i>p</i> -value
Location		
Main-channel	Reference	
Off-channel	0.018 [-0.090, 0.127]	0.738
Reach		
1	Reference	
2	0.036 [-0.082, 0.154]	0.553
3	-0.009 [-0.139, 0.121]	0.889
Season		
Winter	Reference	
Spring	0.024 [-0.016, 0.066]	0.242
Summer	-0.046 [-0.115, 0.022]	0.184
Fall	-0.063 [-0.120, -0.005]	0.032
Constant	0.567 [0.475, 0.659]	<0.001

^aEstimates were obtained with linear mixed-effects regression fit with restricted maximum likelihood.

^bPositive values represent increasing values, and negatives values represent decreasing values.

SE=0.009 ms⁻¹, *n*=223). Sampled depths were not significantly (*p*=0.738, Table V) different between the main-channel (mean=0.578 m, SE=0.011 m, *n*=445) and off-channel (mean=0.588 m, SE=0.019 m, *n*=222). While off-channel habitats were available in each reach during the wetter season, some sites desiccated by July and were often unavailable until the following November or December.

Fish observations

Chinook salmon. Juvenile Chinook salmon were only detected from October through June (Figure 3). Densities (catch per unit effort) ranged from 0.0 to 0.02718 Chinook per cubic metre and on average were 0.00041 Chinook per cubic metre (SE=0.00008 Chinook per cubic metre, *N*=669). Chinook salmon PoP varied significantly between seasons as the species was not detected during summer and was significantly lower in spring (*p*=0.001; Table VI) and fall (*p*<0.001; Table VI). The highest probability of Chinook presence was observed in winter (Table VI) with both the highest mean monthly density and PoP occurring in February (mean=94.81%, SE=2.55%, *n*=77; Figure 3). Overall, Chinook salmon PoP was significantly lower (*p*=0.001; Table VI) in Reach 1 (mean=51.00%, SE=2.89%, *n*=300) than in Reach 3 (mean=63.78%, SE=4.28%, *n*=127). There was no significant difference (*p*=0.786; Table VI) in Chinook salmon PoP between Reaches 1 and 2 (mean=55.79%, SE=3.20%, *n*=242).

Probability of Chinook salmon presence was significantly higher (*p*=0.007; Table VI) in the main-channel

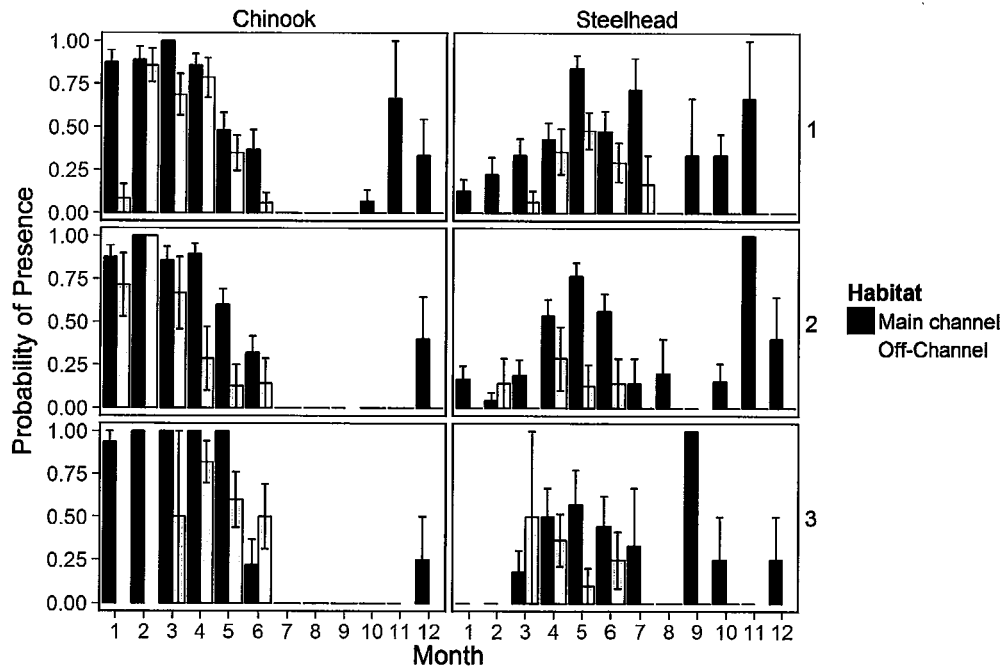


Figure 3. The mean probability of presence by habitat area for Chinook salmon and steelhead for Mokelumne River Reach (1, 2 and 3) and month. Error bars indicate the standard error of the mean. No bar = habitat not available

Table VI. Association between main-channel and off-channel habitats, reaches, seasons, environmental data and detection of Chinook salmon^a (*N* = 599)

	Odds ratio ^b [95% confidence interval]	<i>p</i> -value
Location		
Main-channel	Reference	
Off-channel	0.425 [0.229, 0.791]	0.007
Reach		
1	Reference	
2	1.089 [0.590, 2.009]	0.786
3	3.720 [1.701, 8.136]	0.001
Season		
Winter	Reference	
Spring	0.392 [0.222, 0.691]	0.001
Summer ^c	(empty)	NA
Fall	0.039 [0.015, 0.104]	<0.001
Water measurement		
Temperature	0.665 [0.565, 0.784]	<0.001
Velocity	2.256 [0.659, 7.727]	0.195
Depth	1.738 [0.654, 4.615]	0.267

^aEstimates were obtained with mixed-effects logistic regression.

^bOdds ratios from 0 to 1 indicate lower probability of presence, and odds ratios greater than 1 indicate higher probability of presence.

^cChinook salmon were not detected at any site in the summer (July–September).

(mean = 63.90%, SE = 2.28%, *n* = 446) than in the off-channel (mean = 37.67%, SE = 3.25%, *n* = 223). The odds of detecting Chinook salmon in the off-channel was 0.425

(95% confidence interval 0.229, 0.791; Table VI) after statistical adjustment for reach, season and environmental characteristics. Juvenile Chinook salmon were detected in the main-channel every month that they were detected (October through June) but were only detected in the off-channel from January to June (Figure 3). Several off-channels were no longer available after this time.

Chinook salmon were detected at depths of 0.061–1.829 m (mean = 0.595 m, SE = 0.014 m, *n* = 368), water temperatures of 8.267–16.600°C (mean = 11.361°C, SE = 0.084°C, *n* = 362) and velocities of <0.001–1.448 m s⁻¹ (mean = 0.212 m s⁻¹, SE = 0.012 m s⁻¹, *n* = 369). Chinook salmon presence was not significantly related to water depth (*p* = 0.267; Table VI) or velocity (*p* = 0.195; Table VI) but was significantly related to water temperatures (*p* < 0.001; Table VI). Given that the odds ratio (0.665; Table VI) is less than 1, the probability of Chinook presence decreases as water temperatures increase.

Steelhead. Juvenile steelhead were captured during every month, and densities ranged from 0.0 to 0.00031 steelhead per cubic metre and on average was 0.000011 steelhead per cubic metre (SE = 0.000001 steelhead per cubic metre, *N* = 669). Steelhead PoP was significantly higher (*p* < 0.001; Table VII) in spring than in winter, with both highest mean monthly density and PoP in May (mean = 59.22%, SE = 4.87%, *n* = 103; Figure 3), but steelhead PoP was not significantly different between winter and summer (*p* = 0.317; Table VII) or fall (*p* = 0.467;

Table VII. Association between main-channel and off-channel habitats, reaches, seasons, environmental data and detection of steelhead^a ($N=654$)

	Odds ratio ^b [95% confidence interval]	<i>p</i> -value
Location		
Main-channel	Reference	
Off-channel	0.296 [0.179, 0.489]	<0.001
Reach		
1	Reference	
2	0.635 [0.407, 0.990]	0.045
3	0.454 [0.259, 0.798]	0.006
Season		
Winter	Reference	
Spring	6.789 [3.856, 11.953]	<0.001
Summer	1.628 [0.627, 4.223]	0.317
Fall	1.383 [0.578, 3.308]	0.467
Water measurement		
Temperature	1.077 [0.934, 1.242]	0.307
Velocity	4.082 [1.508, 11.045]	0.006
Depth	1.389 [0.584, 3.303]	0.457

^aEstimates were obtained with mixed-effects logistic regression.

^bOdds ratios from 0 to 1 indicate lower probability of presence, and odds ratios greater than 1 indicate higher probability of presence.

Table VII). Steelhead PoP was significantly higher ($p=0.006$; Table VII) in Reach 1 (mean=31.00%, SE=2.67%, $n=300$) than in Reach 3 (mean=21.26%, SE=3.64%, $n=127$) and also significantly different ($p=0.045$; Table VII) between Reaches 1 and 2 (mean=31.40%, SE=2.99%, $n=242$).

Steelhead PoP was significantly higher ($p<0.001$; Table VII) in the main-channel (mean=35.87%, SE=2.27%, $n=446$) than in the off-channel (mean=16.14%, SE=2.47%, $n=223$). The odds of steelhead detection was 0.296 (95% confidence interval 0.179–0.489; Table VII) in the off-channel, after statistical adjustment for reach, season and environmental characteristics. Steelhead were detected in the main-channel during all months but were only detected in off-channel habitats from February to July (Figure 3).

Steelhead were found at depths of 0.152–1.524 m (mean=0.597 m, SE=0.014 m, $n=196$), water temperatures of 8.400–15.900°C (mean=12.581°C, SE=0.110°C, $n=193$) and velocities of <0.001–0.991 m s⁻¹ (mean=0.259 m s⁻¹, SE=0.016 m s⁻¹, $n=196$). Steelhead PoP was not significantly related to water temperature ($p=0.307$; Table VII) or depth ($p=0.457$; Table VII) but was significantly and positively related to water velocities ($p=0.006$; Table VII).

DISCUSSION

Although North American Pacific salmon streams are found from the Canadian polar region into California's Mediterranean climate, large river habitat utilized by rearing salmonids

has not been well defined or studied, especially at the southern extent of their range where major anthropogenic disturbance has occurred. Within larger Pacific Northwest rivers, preferred rearing depths and velocities occur mostly in edge habitats rather than mid-channels as evidenced by higher densities and more consistent use of off-channel habitats throughout the year (Moore and Gregory, 1988; Beechie *et al.*, 2005; Morley *et al.*, 2005). However, in general, rivers in more arid climates of the Pacific Southwest typically have greater flow and temperature regime variability than further north (Gasith and Resh, 1999; Kondolf *et al.*, 2013).

We contrasted main-channel and off-channel habitat conditions within a large California Mediterranean-climate river using parameters known to influence juvenile salmonids. Abiotic conditions differed between main and off-channel habitats. In turn, juvenile Chinook and steelhead were observed to use habitats differently. Specifically, both species were not detected in off-channels during warmer months. Although the study area was markedly altered by anthropogenic changes, our results demonstrate off-channel habitats of Mediterranean-climate rivers are important salmon-rearing areas but are more ephemerally used than their temperate counterparts.

Stream basins are hierarchically organized systems, and the greatest variation in temporal and spatial habitat use by salmonids typically occurs at lower levels (e.g. stream segment and microhabitat) (Frissell *et al.*, 1986; Urban *et al.*, 1987). Not surprisingly, we observed variation in physical attributes and juvenile presence of two salmonid species over time and space within a large river at the southern extent of North American Pacific salmon. Physical variables of streams also exhibit a continuous gradient of conditions and biological responses from headwaters to mouth (Vannote *et al.*, 1980; Poole *et al.*, 2001). As expected, a lower gradient and warmer temperatures were observed as we sampled from upstream to downstream. However, we also observed reduced channel width and fewer off-channel and overall habitats, which is counterintuitive to a Mediterranean-climate river. Historically, the LMR would have demonstrated from upstream to downstream, an anastomosing channel with increasing complexity including braids and backwater sloughs (Florsheim and Mount, 2003). Within the urbanized California Central Valley, channelization and levees have simplified riverine habitats, converting much of the valley floor to farmland and urban uses. Additionally, reduced sediment transport from dams and mining has promoted channel incision (Kondolf, 1997). Even so, these habitats still persist along the stream gradient, providing variability in the physical environment juvenile salmonids are exposed to.

We observed significant differences between Chinook and steelhead habitat utilization at the reach scale as well. One possible reason is that compared with Chinook salmon,

steelhead often seek higher velocities in warmer water with high food availability (Smith and Li, 1983). Another possibility is related to rearing timing and duration, and stream temperatures. Fall-run Chinook generally emigrate during their first spring, before conditions start to warm. In contrast, LMR steelhead emerge later than Chinook and may remain for several years before emigration, exposing them to warmer temperatures for a longer time period (Sogard *et al.*, 2012). Because of Camanche Reservoir solar heat exchange and seasonal air temperatures, LMR water temperatures increase from upstream to downstream and January to September and then decrease to January (Merz and Setka, 2004). Optimal rearing temperatures (10–16°C; US EPA, 2003) were not exceeded by mean monthly averages in Reaches 1 and 2 but surpassed them in Reach 3 during September. Only steelhead occupied Reach 3 at measurable levels during this period, and Chinook typically emigrated from the LMR by this time (Workman *et al.*, 2007). Lower PoP in Reach 3 suggests steelhead concentrate in areas where water temperatures, and possibly velocities, are more optimal. We assume relatively rapid Central Valley steelhead growth (Sogard *et al.*, 2012) enables them to move to cooler, faster main-channel waters or move upstream to avoid adverse conditions if they are not ready to emigrate. Our results illustrate significantly different life history strategies for these two species demonstrated by dissimilar responses to environmental conditions. These observations suggest temperature exceedances may influence specific rearing habitat use and densities, but not necessarily prohibit reach presence. Steelhead temperature tolerances vary depending on life stage, stock characteristics and ecological conditions such as acclimation time, food availability and access to cold-water refugia (Nielsen *et al.*, 1994; Brewitt and Danner, 2014). Future studies of temperature, food availability and cold-water refugia may further our understanding of seasonal Mediterranean-climate river dynamics.

Floods provide physical linkages between main and ephemeral off-channel habitats that control biogeochemical cycles and community structure of floodplain river systems (Stanford *et al.*, 2005). We hypothesized that physical parameters known to influence rearing habitat use would vary significantly between main and off-channel habitats, and juvenile salmonids would respond to them. Although depths did not differ significantly between sampled main-channel and off-channel areas, off-channels exhibited slower and warmer water than the main-channel. As expected, we observed differences in timing and habitat use of both species between the reaches, and main-channels and off-channels, supporting the idea that habitat complexity allows for behavioural differences within individual species (Bellmore *et al.*, 2013).

Chinook salmon were observed in off-channel habitats from January to June, and steelhead from February to July. Highest Chinook PoP was observed in February when at

their smallest size and water temperatures were relatively cool and flows high. Off-channel habitat could provide relatively warm, slow water and enhanced rearing opportunities before increased temperatures become limiting (Jeffres *et al.*, 2008; Limm and Marchetti, 2009). In contrast, the highest steelhead densities and PoP were observed in May. As LMR flows recede after June, many off-channel habitats become warmer, become isolated and may desiccate. Therefore, LMR off-channel habitats may not provide optimum conditions for steelhead during their densest rearing period. It is important to note that LMR snowmelt historically peaked in May and steelhead behaviour may have been quite different (Brown and Bauer, 2010). Even so, steelhead were observed using off-channel habitats early in their respective rearing seasons, demonstrating the value of these habitats. Variability in depth, velocity and temperature suitability between these species most likely supports overlap in their specific habitat use (Gratwicke and Speight, 2005).

Mediterranean-climate rivers are physically, chemically and biologically shaped by sequential, predictable flooding and drying events over the annual cycle (Gasith and Resh, 1999). As flood transitions to dry season, ambient habitat conditions become progressively harsher drivers of stream populations. Even within the dampened LMR hydrograph, both study species exhibited a transitional response to the dry season, using main-channel and off-channel habitats early in the rearing season but avoided off-channel areas by July. This corresponds to flow recession from off-channel habitats and increasing water temperatures, fish growth and end of emigration. Similar observations have been observed within emergent wetlands of the Pacific Northwest (Henning *et al.*, 2006).

Juvenile steelhead observations continued in main-channel habitats until the following storm season, which brought the next cohort to the river, and cooler water temperatures and flooding flows to reconnect off-channel habitats. This synergy of flood and temperature appears important. We observed a stranding event in March 1997 where juveniles of both species were stranded in a small pool with instantaneous water temperature recorded at 17.6°C. However, when only contiguous habitat was examined, the warmest temperatures in which Chinook and steelhead were both observed at a site was 13.8°C (off-channel) and 15.7°C (main-channel) even though we sampled in temperatures as high as 19.6°C. Taylor (1988) indicates juvenile Chinook salmon increase their use of low-velocity areas when water temperatures are low. However, as temperatures increase, many salmonids respond to these changes by moving to areas with more preferable temperatures (Bjornn and Reiser, 1991). Additionally, as temperatures increase, so do metabolic rates and greater drift feeding tends to occur in faster waters (Smith and Li, 1983). We hypothesize that during warmer months, remaining Chinook salmon and

steelhead move to cooler waters of the main-channel. Therefore, habitat connectivity may allow juveniles to select for optimum rearing conditions. This should be evaluated more fully.

According to Zeug and Winemiller (2008), both hydrology and habitat heterogeneity interact with fish life history strategies to determine optimal recruitment conditions, and all three factors must be considered in river management. The two species we studied utilize the river through space and time differently because of dissimilar life histories and affinities. Everest and Chapman (1972) found significant correlations between fish size and both water depth and velocity where juvenile salmonids occur. Additionally, slight variations in metabolism and related temperature requirements may further influence site selection (Brett, 1971).

Consequently, species' concentrations change along the river gradient depending on season, life history and abiotic parameters such as depth, velocity and temperature. Even within a species, habitat heterogeneity is vital for life history diversity, which in turn is important for population resilience (Watters *et al.*, 2003; Miller *et al.*, 2010; Carlson and Satterthwaite, 2012). This demonstrates the need to avoid overgeneralizations about habitat use. We recommend future studies that help predict spatial and temporal salmonid habitat use patterns to support more effective management actions including the support of variable life history traits.

Although we observed that juvenile salmonid presence was highest in the main-channel, several things should be taken into consideration. Main-channel habitat was estimated at over 78% of available habitat at base flows. However, using hydraulic modelling (East Bay Municipal Utility District; unpublished data), at the highest observed rearing flows ($\sim 142 \text{ m}^3 \text{ s}^{-1}$), off-channel habitat increased the available inundated area almost ninefold (from an estimated 91.5 to 823 ha). These observations suggest potentially significant seasonal benefits to rearing salmonids from off-channel habitats even at their southern extent.

Management implications

According to Beechie *et al.* (2005), a primary limitation in estimating habitat impacts on salmonid populations is limited knowledge of large river habitat use. This inhibits our ability to predict how large river restoration might contribute to salmonid recovery (Beechie *et al.*, 2002). The information we gathered appears valuable for identifying future habitat restoration needs including timing of seasonal habitat inundation to meet juvenile salmonid requirements within drier and warmer climates (Waples *et al.*, 2009).

Building upon past large river salmonid habitat classification schemes (Beechie *et al.*, 2005), we more clearly define how environmental conditions and fish presence differ between main-channel and off-channel habitats, which exhibit

significant variability in conditions known to influence juvenile salmonids. Our observations indicate that within a highly regulated Mediterranean-climate river, off-channel habitats become increasingly scarce, disconnected or temperature limiting in low-gradient reaches both seasonally and due to anthropogenic modifications. These observations may provide guidance for future management within large salmon-bearing streams.

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