Juvenile fishes of the Lower Feather River: Distribution, emigration patterns, and associations with environmental variables

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Juvenile Fishes of the Lower Feather River: Distribution, Emigration Patterns, and Associations with Environmental Variables

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Abstract.—In the Feather River below Lake Oroville, California, the relative importance of water temperature and flow regimes on fish populations was assessed by comparing two distinct river segments, the low flow channel (LFC) and high flow channel (HFC). Rotary screw traps and beach seining surveys were used to assess distribution, abundance, and emigration patterns of fishes between 1997 and 2001. Both sampling methods revealed similar patterns in species composition. Chinook salmon *Oncorhynchus tshawytscha* dominated seining (46%) and rotary screw trap (99%) catch by number. More than 80% of Chinook salmon captured were less than 50 mm, demonstrating that most Feather River Chinook salmon emigrate before smolting. In multiple linear regression models, Chinook salmon spawn timing ($P < 0.001$) and water temperature ($P = 0.036$) were statistically significant predictors of weekly Chinook salmon catch in the LFC, while Secchi depth was statistically significant ($P = 0.007$) for the HFC catch. Most steelhead *Oncorhynchus mykiss* were captured in the LFC, particularly in 2001, which accounted for 82% of all steelhead collected. The total relative abundance of alien fishes was low, 7.2% and 0.1% from beach seining and rotary screw trap sampling, respectively. Alien fishes were more abundant in the HFC. Native fish species were found throughout the study area. Canonical correspondence analysis suggested that river kilometer, water temperature, and year were highly significant ($P = 0.001$), while season ($P = 0.01$) and flow ($P = 0.01$) were significant to observed fish assemblages within LFC. Water temperature, river kilometer, year, and season were highly significant ($P = 0.001$) to observed fish assemblages within the HFC. Our results demonstrate that native fishes can be successful in a regulated river environment, despite an unnatural flow regime. These findings provide valuable information in assessing the impacts of dam operations and in implementing river restoration actions by flow and water temperature manipulation.

Introduction

The river systems of California have been extensively dammed and modified to provide water storage, flood control, and power generation (Mount 1995). Rivers draining the west slope of the Sierra Nevada, which historically supported large populations of anadromous fishes (Yoshiyama et al. 2001), have been particularly affected. Nearly all major west-slope tributaries are presently impounded by large dams located along the transition between the Central Valley and upland, foothill regions. Being the furthest downstream and located at a major transition between landforms, terminal dams impact anadromous fishes as well as fish assemblages typical of valley bottom,

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foothill, and mountain regions. Changes in flow regime, water temperature, and geomorphic process that result from river regulation (Ward and Stanford 1983; Ligon et al. 1995) are known to impact downstream fish assemblages (Brown 2000; Brown and Ford 2002; Moyle 2002). Despite these effects, California's terminal dams can be operated to partially ameliorate negative impacts and may even serve as tools for stream ecosystem improvement. However, effectively using these dams as implements of restoration requires a thorough understanding of how river conditions drive the distribution, abundance, and behavior of downstream fish assemblages.

Flow regime is widely recognized as a critical factor affecting stream ecosystems, but in regulated rivers, natural patterns of seasonal runoff are modified or lost. Instead, flow regime is dictated by demands for flood control, irrigation, hydropower, and recreation. The absence of a natural flow regime has often been linked with the decline of native fish assemblages. Several California studies have shown that invasion success of alien fishes and the decline of native fish species are related to altered flows, particularly the loss of spring flood pulses (Baltz and Moyle 1993; Brown 2000; Marchetti and Moyle 2000; Brown and Ford 2002). Similar patterns have been observed in the Columbia River system (Li et al. 1987) and in rivers of the southwestern United States (Meffe 1984; Minckley and Meffe 1987). In California's Sacramento–San Joaquin Delta, high-flow events are also thought to be important for cueing emigration and enhancing survival of juvenile Chinook salmon *Oncorhynchus tshawytscha* (Stevens et al. 1984). Recent work shows that high flows inundating floodplains create high-quality rearing habitat that enhances the growth of juvenile Chinook salmon (Sommer et al. 2001). In consideration of these and other findings, efforts to restore or enhance native fish populations in regulated rivers increasingly focus on the use of natural flow regimes (Stanford et al. 1996; Poff et al. 1997; Brown and Ford 2002).

Natural flow regime is appealing as a restoration concept because it is consistent with the current understanding of river ecosystem function and because it fits perceptions that native fish species are uniquely adapted to natural or historic conditions. However, natural flow regimes may not be a restoration panacea for all regulated rivers in California. At least some California streams seem to benefit from temperature and flow modifications (Moyle 2002). Despite unnatural flow regimes, many Sacramento Basin rivers support relatively strong and intact native fish populations (May and Brown 2002). Many regulated Central Valley rivers also appear to produce relatively large populations of emigrating juvenile Chinook salmon (e.g., Williams 2001). However, in the Feather River, and in other rivers influenced by anadromous fish hatcheries, inriver spawning of hatchery Chinook salmon may contribute significantly to resulting juvenile populations. The unknown, but potentially large contribution of hatchery Chinook salmon to wild, fall-run Chinook salmon populations is a primary reason this stock currently has candidate status under the federal Endangered Species Act (NMFS 1999).

Here we present data from 5 years of study on the Feather River downstream of Oroville Dam. The Feather River is significant because it is the largest tributary to the Sacramento River system, it is home to two federally listed endangered species (Central Valley spring-run Chinook salmon and Central Valley steelhead *Oncorhynchus mykiss*), and the Oroville Dam-Thermalito Complex is currently undergoing a review for relicensing by the Federal Energy Regulatory Commission (FERC). Anticipation of studies instituted as part of FERC relicensing provided an opportunity to evaluate project effects on downstream fish assemblages and to develop potential enhancement measures. Furthermore, the unusual design of flow-release structures from the Oroville Dam-Thermalito Complex provides a unique setting to evaluate the relative importance of temperature and flow regime on fish species composition and distribution. The objectives of this paper were to (1) provide information on species composition, distribution, relative abundance, and migration timing of Feather River fishes; (2) provide an assessment of fish assemblage response to environmental conditions, particularly flow regime and water temperature; and (3) interpret these findings to aid in decision-making policies related to regulated river restoration and management.

Study Area

The Feather River drainage is located within the Central Valley of California, draining approximately 9,324 km^2 of the western slope of the Sierra Nevada (Figure 1). Oroville Dam impounds the Feather River as it leaves the foothills. Lake Oroville, created by completion of the dam in 1967, has a capacity of about 430,000 hectare-meters of water, and is the centerpiece of the State Water Project, California's principal water storage and conveyance system. Oroville Dam is equipped with a temperature control device capable of selecting water from various depths within the reservoir. The temperature of water released from Oroville Dam is determined by needs of the Feather River Fish Hatchery, river temperature requirements, and local agricultural water users. Under normal operations, the majority of water released from Lake Oroville is diverted into the Thermalito Complex (Figure 1). Excluding local diversions, water is returned to the Feather River through the Thermalito Afterbay Outlet, then flows southward through the valley to the confluence with the Sacramento River at Verona. The purpose of the Thermalito Complex is to provide warm water for local agricultural users and to provide additional storage and operational flexibility. The remainder of the water, typically 20 m^3/s, flows through the historic river channel locally known as the low flow channel (LFC).

Field activities occurred in a 72-km river segment between the Fish Barrier Dam, which directs Chinook salmon and steelhead into the Feather River Hatchery, and Boyd's Pump, 3.2 km downstream of Yuba City (Figure 1). This portion of the river is composed of two distinct river segments, the LFC and the high flow channel (HFC), which exhibit distinct physical and environmental conditions (Table 1). This collective river segment (LFC and HFC) is referred to as the lower Feather River. The LFC extends from the Fish Barrier Dam at river kilometer (rkm) 108 to the Thermalito Afterbay Outlet (rkm 95). Flow regime in the LFC is stable and exceeds 20 m^3/s only during flood events, such as those that occurred in February/March 1999 (Figure 2). The LFC temperature regime, channel morphology, and geomorphic process are strongly influenced by the proximity to Oroville Dam and the city of Oroville, which is separated from the river by flood control levees. Water temperatures in the LFC tend to be cooler year-round than those found downstream. Mean daily summer temperatures for the LFC during the study period were 15.9°C, with a maximum hourly temperature of 21.5°C (Table 1).

The HFC, which extends from the Thermalito Outlet to Boyd's Pump (rkm 37), is subject to different thermal, hydrologic, and geomorphic conditions. Because the HFC is further downstream, water temperatures are influenced less by dam releases and exhibit more diel and seasonal fluctuations. Also, due to the warming effect of the shallow Thermalito Complex, waters released from the Thermalito Outlet (at the upstream extent of the HFC) tend to be warmer than those of the LFC (Table 1). Flow regime in the HFC is more variable (Figure 2), since this segment, unlike the LFC, is regularly affected by flood control, water storage and water delivery operations at the Oroville Dam and Thermalito Complex. The river below Thermalito Outlet is generally less confined by levees, with a broader active channel and floodplain.

Both the LFC and HFC are very low gradient, less than or equal to 0.1% (Table 1). Composition of macrohabitat types (i.e., riffles, pools, and glides) between river segments is also similar, although glides may be more commonly found in the HFC (Table 1). Substrates in the LFC consist of large gravel and cobble, which is also the predominate substrate through the upper 25 rkm of the HFC. Downstream of Honcut Creek (rkm 70), the substrate is increasingly composed of sand and silt materials.

The California Department of Fish and Game has stocking programs in Lake Oroville and the Thermalito Forebay, which is part of the Thermalito Complex. Rainbow trout *Oncorhynchus mykiss* are the most commonly stocked fish in the forebay. Brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta* have been stocked intermittently in the past. While Chinook salmon and brown trout were previously stocked in Lake Oroville, currently coho salmon *Oncorhynchus kisutch* are the only stocked salmonid. Florida strain

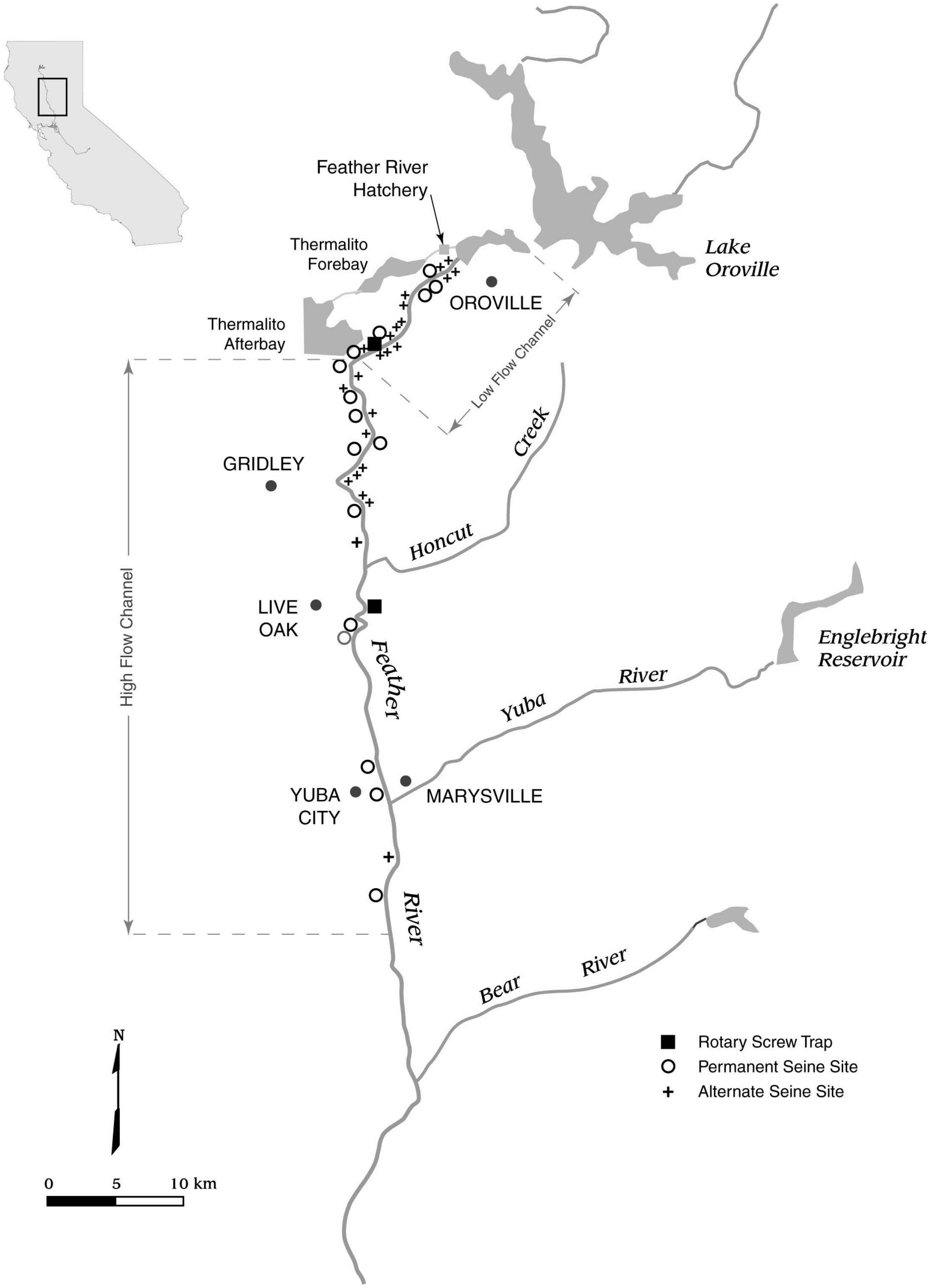

FIGURE 1. The Feather River in California's Central Valley and sampling locations.

TABLE 1. Summary of physical characteristics in the low flow channel (LFC) and high flow channel (HFC) of the lower Feather River. Temperature and Secchi depth were measured during the 1999–2001 sampling period.

	LFC	HFC
Habitat type		
Riffle (%)	40	34
Glide (%)	20	35
Pool (%)	40	31
Stream gradient (%)	0.10	0.07
Temperature (°C)		
Winter (Nov–Jan)		
Daily mean	9.8	10.5
Hourly max	11.0	15.1
Hourly min	8.5	8.0
Spring (Feb–Apr)		
Daily mean	10.6	12.3
Hourly max	17.1	17.7
Hourly min	7.8	8.4
Summer (May–Jul)		
Daily mean	15.9	18.1
Hourly max	21.5	23.5
Hourly min	10.9	12.8
Fall (Aug–Oct)		
Daily mean	14.2	16.7
Hourly max	21.0	21.0
Hourly min	9.9	10.0
Secchi depth (m)		
Mean	3.5	2.3
SD	0.9	0.9

largemouth bass *Micropterus salmoides* are also periodically stocked.

Methods

Field methods

We used beach seines and rotary screw traps (RST) to assess the abundance and distribution of fishes in the lower Feather River. Because larger fish are more evasive and utilize different habitats, these two sampling techniques primarily captured juvenile fishes (including young of year). The intensity and distribution of seining effort were modified over the period of study January 1997–August 2001. Seining was originally conducted monthly at 11 core stations throughout the lower Feather River study area (Figure 1). The core stations were augmented with 6 sites in the LFC and 4 in the HFC between March and October 1997. In late 1998, 5 permanent and 14 alternative sites were added to provide more thorough sampling. The 16 permanent stations were sampled monthly along with as many alternate sites as time allowed.

One to three hauls were conducted at each sample site using a 3-mm-mesh seine that was 1.6 m in height and either 9 m or 15 m in length. All fish were removed from the seine, identified to species, and counted. Fork length (mm) was measured for the first 50 individuals of

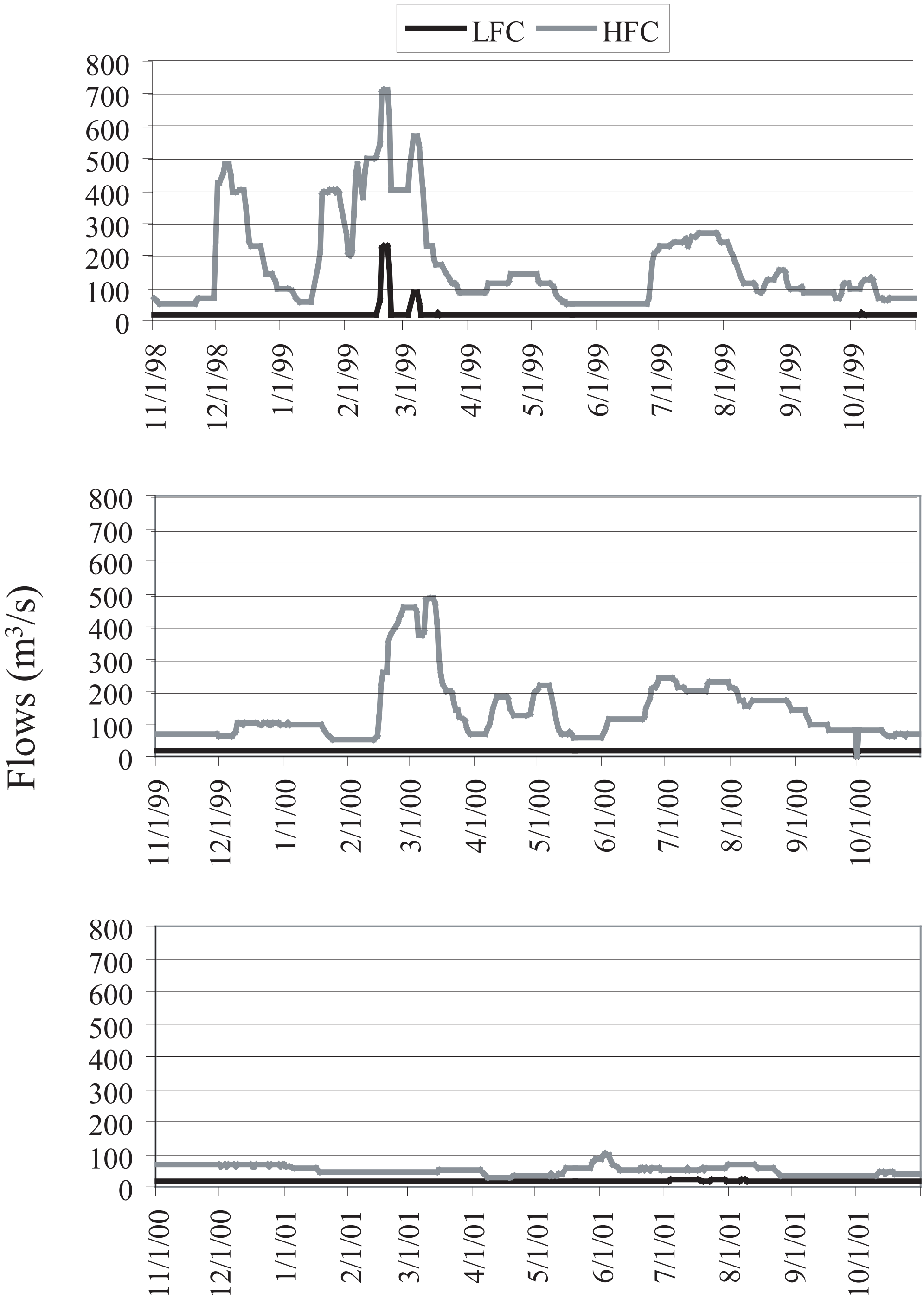

FIGURE 2. Daily mean river flows (m^3/s) for the low flow channel (LFC) and high flow channel (HFC). The LFC discharge was obtained by adding the Thermalito Diversion Dam flow (California Department of Water Resources [CDWR] gauge AO 5191) to the Feather River Fish Hatchery Outflow (CDWR gauge AO 5990). HFC discharge was obtained by adding LFC flow to the Feather River Outlet-Thermalito Afterbay flow (CDWR gauge AO 5975).

each species. Water temperature was also recorded. Daily mean river flow (m^3/s) for the LFC was obtained by adding the flow through the Thermalito Diversion Dam (California Department of Water Resources [CDWR] gauge AO 5191) to the Feather River Fish Hatchery Outflow (CDWR gauge AO 5990). River flow for the HFC was obtained by adding LFC flow to the Feather River Outlet-Thermalito Afterbay flow (CDWR gauge AO 5975). Yuba River flow (U.S. Geological Survey gauge 11421000) was added to the HFC flow for the Boyd's Pump sampling sites.

Two 2.4-m-diameter RSTs with 3-mm screens were used to sample emigrating fishes from 1998 to 2001. One RST was located at the downstream end of the LFC and the second in the HFC near the town of Live Oak (Figure 1). The RSTs were fished continuously for approximately 7 months (mid-November through June), except for short periods at Live Oak when river conditions became unsafe due to high flows. Both RSTs were serviced at least once per day and more often when a high debris load occurred. During servicing, trapped fish were removed from the live box, identified to species, and counted. When juvenile salmonids were abundant, a volume displacement method was used to estimate numbers in increments of 1,000. All live salmonids that were measured were also inspected for characters such as presence of parr marks, silvery appearance, and deciduous scales to determine life stage. Based on these criteria, Chinook salmon and steelhead were categorized as parr, smolt, or intermediate between parr and smolt. Other measurements collected daily at each RST included water clarity (Secchi depth), water temperature, length of the sample period, average trapping cone revolutions per minute, and total number of trapping cone revolutions during the sample period.

Seine and RST sampling techniques did present some potential biases. First, seining is a difficult method to employ successfully in a river environment. Seine samples are typically limited to shallow waters with a fairly uniform substrate to prevent snags. Low water velocities are also needed in order to prevent the net from inverting during deployment. As might be expected, seines were more effective in capturing species common in slow moving habitats (e.g., hitch *Lavinia exilicauda*, Sacramento pikeminnow *Ptychocheilus grandis*, and tule perch *Hysterocarpus traski*) while RSTs were more effective in sampling more open water migrants like salmonids and lamprey *Lampetra* spp. Neither sampling technique was effective in sampling for larval or postlarval cyprinids and catostomids. Despite these potential biases, results from these two methods presented together should provide a sufficiently reliable account of species composition and abundance.

Seine data analysis

Seine catch data were standardized as fish captured per seine haul. A seining year began in November, corresponding to the start of a new Chinook salmon spawning and emigration season. Seasons were defined as November–January (Winter), February–April (Spring), May–July (Summer), and August–October (Fall). Species caught upstream of the Thermalito Outlet (>rkm 95) were categorized as LFC and those downstream (≤rkm 95) as HFC. For detailed analysis of juvenile salmonid emigration and distribution trends, only seining years 1998–1999, 1999–2000, and 2000–2001 were assessed, as they represent complete sampling seasons. Monthly histograms of length frequency and catch per seine haul were prepared to determine fish size, relative abundance, and distribution.

Canonical correspondence analysis (CCA) was performed using the CANOCO software program to correlate fish assemblages with environmental variables (ter Braak and Verdonschot 1995; ter Braak and Smilauer 1998). All seine hauls conducted at a site within the same month were incorporated into and analyzed as a sample. For data analysis, fish catches were categorized into groupings that occurred in 5% or more of the samples (combined for LFC and HFC): sculpin *Cottus* spp., native cyprinids, alien cyprinids, centrarchids, Chinook salmon, Sacramento sucker *Catostomus occidentalis*, steelhead, tule perch, wakasagi *Hypomesus nipponensis*, and western mosquitofish *Gambusia affinis*. Species data were log transformed to improve normality.

The explanatory variables used in the CCA were average monthly river flow and water temperature, seining year, season, and river kilometer. A CCA was conducted on both the LFC and the HFC due to the differences in temperature and flow regimes. Manual selection was used to select the environmental factors ($P \leq 0.05$) to include in the final CCA models.

Rotary screw trap data analysis

Species catch was summed by sample year and RST location. A trapping year was defined as November–June. Daily and weekly catch were used to assess emigration timing for Chinook salmon and steelhead. Monthly average fork length (±2 SD) was used to assess fish size at emigration and apparent residence time in the river.

Multiple linear regression was used to assess the effects of environmental variables on juvenile Chinook salmon emigration timing from 1999 to 2001. Analysis of the 1998–1999 RST catch was conducted separately because there was insufficient data on Chinook salmon spawn timing for that year. Chinook salmon catch was standardized as weekly average catch per unit effort (h sampled). Environmental variables included weekly average flow, water temperature, and water clarity. At the Live Oak RST, Secchi depth and flow were the only variables found to have a significant positive correlation ($r = 0.648$; $P < 0.001$). Correlations between explanatory variables were not considered further in the analysis. To assess the possible role of Chinook salmon spawn timing on emigration timing of juvenile Chinook salmon, we also included weekly escapement survey estimates as an explanatory variable. This was accomplished by offsetting weekly Chinook salmon spawning escapement estimates by the time required for eggs to develop into 35-mm fry and by the time required to reach a downstream RST by active migration. Based on ambient water temperatures and data from the Feather River Hatchery, we allowed roughly 90 d (13 weeks) for eggs to develop into 35-mm fry. For travel time to the Thermalito RST, we then added an additional week (14 weeks total) to LFC spawning escapement estimates. For the Live Oak RST, we combined escapement estimates from both the LFC and HFC. LFC escapement estimates were offset by 14 weeks, while HFC escapement estimates were offset by one additional week (15 weeks total) to account for additional migration time for fish traveling from the LFC to Live Oak. Time allowed for downstream migration to RSTs was based upon trap efficiency mark–recapture experiments (CDWR 2002).

Results

Species composition and distribution

A total of 31 fish species, 13 native and 18 alien, were collected over the study period. Juvenile Chinook salmon and Sacramento sucker dominated seine catches, composing 46% and 35%, respectively, of the total fish captured per seine haul (Table 2). Although other species accounted for a relatively small proportion of the total catch, two native cyprinids, Sacramento pikeminnow and hardhead *Mylopharodon conocephalus*, were common, with a rank abundance of third and fifth, respectively. Steelhead and tule perch were also relatively common, occurring in at least 4 of 5 years and collectively composing 1.0% of the total catch (Table 2). Other native fishes, including hitch, prickly sculpin *Cottus asper,* riffle sculpin *Cottus gulosus,* speckled dace *Rhinichthys osculus*, splittail *Pogonichthys macrolepidotus,* and lamprey, occurred either infrequently across sampling years or in low numbers (Table 2). Alien fishes composed a small proportion of total relative abundance (7.2%) and were generally less common in terms of rank abundance relative to native fishes (Table 2). Among the top 10 fish species in rank abundance, only 3 were alien, wakasagi, western mosquitofish, and golden shiner *Notemigonus crysoleucas*. Wakasagi was the only alien species found in the top 5 of rank abundance. Various centrarchids (bluegill *Lepomis macrochirus*, redear sunfish *L. microlophus*, largemouth bass, and smallmouth bass *Micropterus dolomieui*) were the only other alien fishes occurring regularly in seine samples from the lower Feather River. Alien fathead minnow *Pimephales promelas*, threadfin shad *Dorosoma petenense*, common carp *Cyprinus carpio*, green sunfish *Lepomis cyanellus*, inland silverside *Menidia beryllina*, white crappie *Pomoxis annularis*, and American shad *Alosa sapi-*

TABLE 2. Mean catch per seine haul by species and seining season in the low flow channel (LFC) and the high flow channel (HFC) of the lower Feather River. Number in parenthesis following HFC or LFC indicates number of hauls conducted that seining year. Native fish species are indicated with an asterisk.

Common name	1996–1997 HFC (6)	1996–1997 LFC (8)	1997–1998 HFC (61)	1997–1998 LFC (27)	1998–1999 HFC (132)	1998–1999 LFC (61)	1999–2000 HFC (112)	1999–2000 LFC (57)	2000–2001 HFC (96)	2000–2001 LFC (53)	Mean %
Chinook salmon*	18.3	5.6	4.2	2.3	60.8	56.9	91.0	84.6	80.9	31.0	45.6
Sacramento sucker*	0.3	0.3	77.9	31.1	115.8	12.4	34.8	18.0	16.6	24.0	34.6
Sacramento pikeminnow*	0.3	0.6	8.8	14.8	13.8	5.2	11.6	1.5	13.5	0.6	7.4
Wakasagi	36.3	10.8	1.3	0.7	0.9	0.3	1.6	0.1	2.8	–	5.7
Hardhead*	0.7	0.9	2.0	1.0	11.5	0.3	5.0	0.5	2.1	–	2.5
Hitch*	–	–	7.4	–	–	–	–	–	–	–	0.8
Steelhead*	–	–	<0.1	0.1	<0.1	2.5	<0.1	3.3	0.3	0.6	0.7
Western mosquitofish	–	0.1	2.8	1.7	0.6	<0.1	0.3	0.2	0.2	0.2	0.6
Prickly sculpin*	0.5	0.5	0.0	0.7	0.2	1.1	0.4	0.8	0.4	0.3	0.5
Golden shiner	0.2	–	2.6	0.0	0.3	<0.1	0.2	<0.1	<0.1	<0.1	0.4
Tule perch*	–	–	0.0	2.6	0.1	<0.1	0.1	–	0.1	<0.1	0.3
Unid. sculpin*	–	–	0.7	0.6	0.1	0.6	<0.1	0.1	<0.1	0.1	0.2
Bluegill	0.2	–	0.7	–	0.1	<0.1	0.1	–	<0.1	–	0.1
Largemouth bass	–	–	0.5	0.1	<0.1	–	<0.1	<0.1	0.1	<0.1	0.1
Riffle sculpin*	–	–	–	<0.1	–	0.3	<0.1	0.4	<0.1	0.1	0.1
Unid. sunfish	–	0.6	0.1	–	<0.1	–	–	–	0.1	–	0.1
Speckled dace*	–	–	–	–	0.4	<0.1	<0.1	<0.1	<0.1	<0.1	0.1
Redear sunfish	–	–	<0.1	–	–	–	0.3	–	<0.1	–	<0.1
Unid. bass	–	–	0.2	0.1	<0.1	–	<0.1	–	–	–	<0.1
Splittail*	–	–	0.3	–	–	–	<0.1	–	–	–	<0.1
Smallmouth bass	–	–	<0.1	–	0.1	–	<0.1	–	0.2	–	<0.1
Fathead minnow	–	0.1	–	–	–	–	–	–	–	–	<0.1
Unid. lamprey*	–	–	<0.1	–	–	<0.1	–	–	–	<0.1	<0.1
Threadfin shad	–	–	<0.1	–	–	–	–	–	–	–	<0.1
Common carp	–	–	<0.1	–	–	–	–	–	–	–	<0.1
Green sunfish	–	–	<0.1	–	–	–	–	–	–	–	<0.1
Inland silverside	–	–	<0.1	–	–	–	–	–	–	–	<0.1
White crappie	–	–	–	–	–	–	<0.1	–	–	–	<0.1
American shad	–	–	–	–	<0.1	–	–	–	–	–	<0.1

dissima were rare and ranked at the bottom of overall abundance (Table 2).

Chinook salmon were extremely abundant in RST sampling, comprising more than 99% of the total catch (Table 3). Among native species, the next most common group of fishes included Pacific lamprey *Lampetra tridentata*, steelhead, and Sacramento sucker. Sacramento pikeminnow, prickly sculpin, hardhead, river lamprey *L. ayresi*, and tule perch were also sampled consistently and were in the upper half of rank abundance (between 7th and 16th). Splittail, speckled dace, and hitch were present in low numbers (23rd, 25th, and 27th ranks respectively), and in only two of three sample years (Table 3). Alien fishes accounted for a very small proportion of the fishes captured in RSTs (0.1%). As with seining, waka-

TABLE 3. Total catch by species and year at Live Oak (L) and Thermalito (T) rotary screw traps. Native fish species are indicated with an asterisk.

Common name	1998–1999 L	1998–1999 T	1999–2000 L	1999–2000 T	2000–2001 L	2000–2001 T	Total (%)
Chinook salmon*	318,058	155,946	100,652	389,922	207,571	473,540	1,645,689 (99.4)
Pacific lamprey*	235	135	142	827	715	77	2,131 (0.13)
Steelhead*	1	82	21	263	14	1,143	1,524 (0.09)
Wakasagi	512	12	160	–	185	548	1,417 (0.09)
Sacramento sucker*	1,064	94	132	39	23	1	1,353 (0.08)
Unid. lamprey*	378	114	253	178	114	134	1,171 (0.07)
Sacramento pikeminnow*	153	22	174	14	44	7	414 (0.03)
Unid. sculpin*	28	382	3	–	1	–	414 (0.03)
Prickly sculpin*	12	268	22	–	17	–	319 (0.02)
Hardhead*	62	2	158	4	77	5	308 (0.02)
Largemouth bass	137	59	23	9	27	21	276 (0.02)
Unid. bass	61	62	48	22	–	–	193 (0.01)
Riffle sculpin*	2	31	3	76	2	36	150 (0.01)
Bluegill	76	7	29	4	9	1	126 (0.01)
River lamprey*	3	–	17	–	67	4	91 (0.01)
Tule perch*	13	1	50	–	22	2	88 (0.01)
Western mosquitofish	19	6	21	12	16	2	76 (<0.01)
Golden shiner	33	2	17	1	18	–	71 (<0.01)
Warmouth *Lepomis gulosus*	10	5	11	2	13	2	43 (<0.01)
Unid. sunfish	19	1	9	–	12	–	41 (<0.01)
American shad	15	–	2	–	8	–	25 (<0.01)
Redear sunfish	7	1	4	–	4	–	16 (<0.01)
Splittail*	–	–	12	–	2	–	14 (<0.01)
Green sunfish	1	–	–	–	11	–	12 (<0.01)
Speckled dace*	6	–	2	–	–	–	8 (<0.01)
Black crappie *Pomoxis nigromaculatus*	2	–	4	–	1	–	7 (<0.01)
Hitch*	2	–	4	–	–	–	6 (<0.01)
Brown bullhead *Ameirus nebulosus*	1	–	1	–	1	–	3 (<0.01)
Smallmouth bass	1	–	1	–	1	–	3 (<0.01)
Brook trout	1	–	–	–	–	–	1 (<0.01)
Common carp	1	–	–	–	–	–	1 (<0.01)

sagi was the most common alien species, ranking fourth in overall abundance. Other alien fishes occurring in moderate to low rank abundance include various cen-trarchids (largemouth bass, bluegill, redear sunfish, green sunfish, and warmouth), western mosquitofish, and golden shiners. Black crappie, brown bullhead, smallmouth bass, brook trout, and common carp were the six species lowest in rank abundance from RST sampling in the lower Feather River (Table 3).

Occurrence and relative abundance of fish species differed between HFC and LFC river segments. Chinook salmon were extremely common in seine and RST sampling from both river segments, whereas steelhead were primarily captured in the LFC (Tables 2 and 3). Of all steelhead collected by seining, 90% were in the LFC, and 78% were found in the upper 2 km of the LFC. Conversely, with the exception of prickly sculpin, most other native fishes were either equally common in the LFC or more abundant downstream in the HFC. For example, 90% of Sacramento pikeminnow were captured in the HFC at the Live Oak RST, and in seining, 68% of total Sacramento pikeminnow catch occurred in the HFC. Both sampling programs found that alien fish species were more abundant in the HFC.

Canonical correspondence analysis was conducted separately on the LFC and the HFC in order to compare and contrast the effects of a fairly stable flow and temperature regime of the LFC to the more variable HFC. Manual selection of environmental factors within the LFC data identified water temperature, river kilometer, and year as highly significant (P = 0.001), and season (P = 0.01) and flow (P = 0.03) as significant to observed fish assemblages. The first two CCA axes explained 17% of the variation within the species data (Table 4). Both year and flow contributed to axis 1, while season contributed to axis 2. Water temperature and river kilometer were important gradients for both axes. The LFC CCA biplot displays a separation of salmonids from other fish categories (Figure 3a). Chinook and steelhead were negatively associated with flow and positively associated with river kilometer and year. In addition, Chinook salmon was negatively associated with water temperature and season. All other fish categories, excluding Sacramento sucker, had a positive relationship with flow and a negative relationship with river kilometer and year. Tule perch had the highest weighted average for water temperature and season.

Manual selection of environmental factors within the HFC data identified water temperature, river kilometer, year, and season as highly significant (P = 0.001) to observed fish assemblages. The first two CCA axes explained 17.5% of the variation within the species data (Table 4). Season, water temperature, and year contributed to axis 1 and river kilometer contributed to axis 2. The HFC CCA biplot displays a separation of fishes into cold and warmwater assemblages (Figure 3b). The coldwater assemblage was made up of Chinook salmon, steelhead, sculpin, and wakasagi. In addition to a negative correlation with water temperature, these fishes had a negative correlation with season. Chinook salmon exhibited a strong positive relationship to year, and wakasagi and sculpin to river kilometer. The warmwater assemblage was made up of native and introduced cyprinids, tule perch, centrarchids, Sacramento sucker, and western mosquitofish. These fish categories had a positive relationship with water temperature and season and

TABLE 4. Results of canonical correspondence analysis relating fish categories to environmental variables sampled in the low flow channel and the high flow channel of the lower Feather River from January 1997 to August 2001.

Low flow channel	Axis 1	Axis 2	Total inertia
Eigenvalues	0.205	0.090	1.728
Species-environment correlations	0.723	0.646	
Cumulative percentage of variance explained			
Species	11.9	17.0	
Species-environment relation	57.4	82.5	
High flow channel	**Axis 1**	**Axis 2**	**Total inertia**
Eigenvalues	0.318	0.062	2.176
Species-environment correlations	0.748	0.473	
Cumulative percentage of variance explained			
Species	14.6	17.5	
Species-environment relation	74.8	89.4	

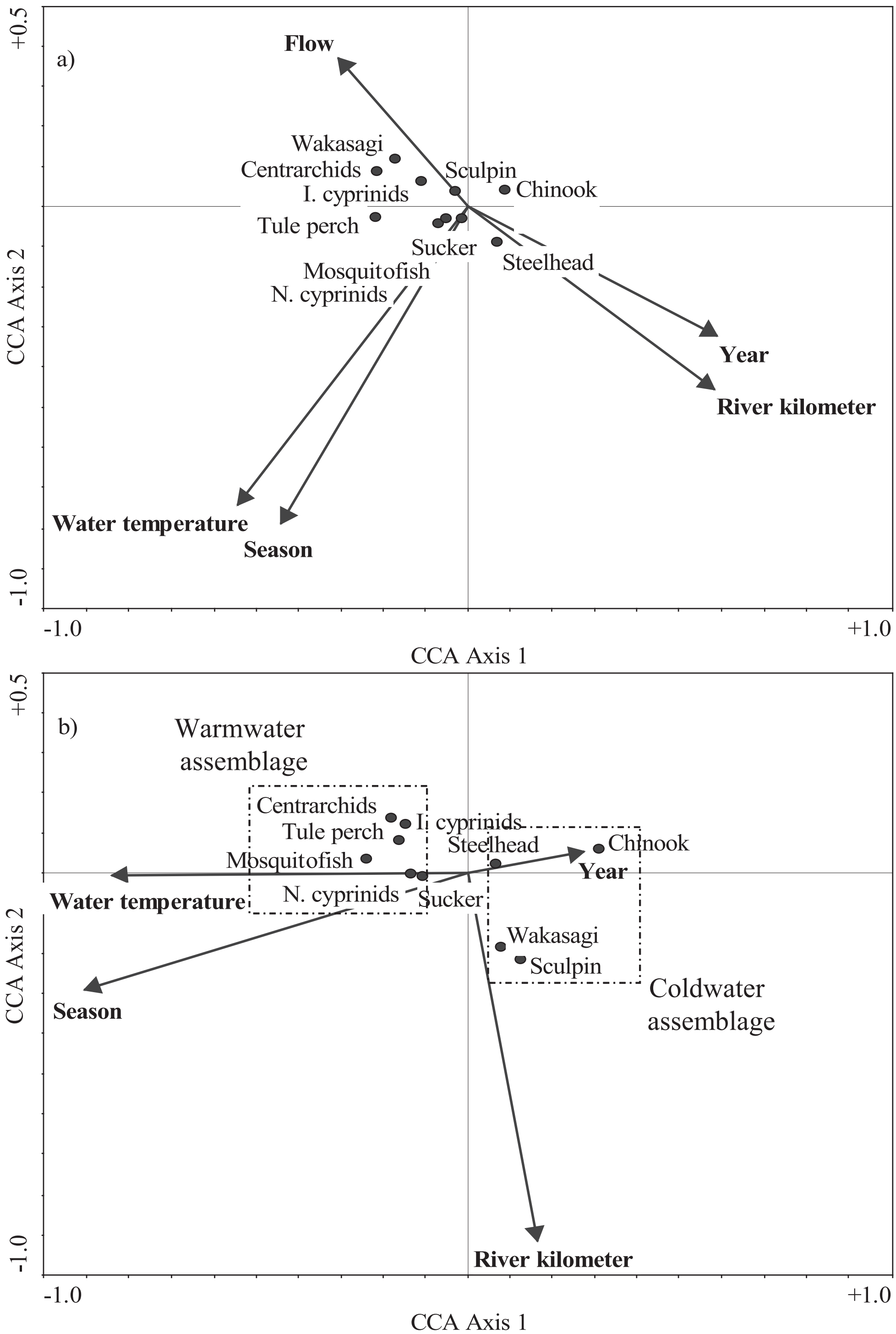

FIGURE 3. Biplot showing the results of a canonical correspondence analysis of fish categories (N. cyprinids = native cyprinids, I. cyprinids = alien cyprinids) and environmental variables on the first two canonical axes for (a) the low flow channel and (b) the high flow channel.

a negative relationship with river kilometer and year. Western mosquitofish had the highest weighted averages for water temperature and season. Centrarchids and introduced cyprinids had the lowest for river kilometer.

Salmonid emigration

In seine sampling, Chinook salmon catch was highest from January to March (Figure 4). Catch typically declined in April, and by July, juvenile Chinook salmon catch was very low. In 1999, however, catch remained high later in the year (Figure 4). When catch was highest, most fish were small (30–50 mm). Mean fish size and variability of fish size began to increase in April, with the largest fish caught in July and August.

Rotary screw trap sampling yielded results similar to seining. At both Live Oak (Figure 5) and Thermalito (Figure 6), catch was highest from January to March. January, February, and March accounted for an average of 91% and 97% of the total annual Chinook salmon catch at Live Oak and Thermalito, respectively. Catches declined rapidly at both traps starting in April each year, with the two traps averaging less than 1% of the annual catch for April–June. While late season catch was generally low, the Live Oak RST caught more fish later in the season than did the Thermalito RST. Length-frequency distributions were similar between Thermalito (Figure 5) and Live Oak (Figure 6). Chinook salmon ranged in size from 20 to 114 mm at Thermalito and from 28 to 220 mm at Live Oak. Weekly mean fork length ranged from 30 to 87 mm at Thermalito and from 31 to 82 mm at Live Oak. Similar to seining data, mean fork length at each RST changed little until late April, then steadily increased until the end of trapping. However, as fish became larger and more variable in size, catch declined.

Some differences in catch size and life stage were evident between RSTs. Of the Chinook salmon trapped at Thermalito and Live Oak, 97% and 81% were less than 50 mm, respectively. Also, though 98% of Chinook salmon caught at Thermalito were categorized as parr, only 83% of those caught at Live Oak were categorized as parr. In addition, Chinook salmon of an intermediate life stage comprised 2% of the catch at Thermalito and 13% of the catch at Live Oak. Only 0.2% and 1.3% of the fish caught at Thermalito and Live Oak, respectively, were categorized as smolts.

Steelhead catch was generally low in seine sampling, making it difficult to discern trends in emigration timing. In 1999, relative abundance appeared to peak in July, but no clear trend was evident in 2000 or 2001 (Figure 7). Like juvenile Chinook salmon, steelhead captured early in the year tended to be small (young of year). A few larger juveniles appeared in July–September. Periodic, high variability in steelhead fork length demonstrates that some older and larger (probably age-1) steelhead were present throughout the study period.

Steelhead catch in RSTs differed markedly between Live Oak and Thermalito. The Live Oak RST captured very few steelhead (Figure 8). None were captured in 1999, and only 21 and 14 were captured in 2000 and 2001, respectively (Table 3). Steelhead catch was always higher at the Thermalito RST. This was especially true in 2001, when the Thermalito catch accounted for 82% of the total steelhead captured over the 3-year period. At Thermalito, the timing of steelhead catch differed somewhat between years (Figure 9). In 1999, catch was highest in the weeks of 13 and 16 April and the first week of May. In 2000, catch peaked in April, and in 2001, it peaked in March and the first two weeks of April. In all 3 years, catch dropped precipitously from April to June (Figure 9). Steelhead were small (25 mm) and showed little size variability during their peak abundance in RST sampling. As with seining, only a few larger steelhead were seen during RST sampling, typically during spring and winter (Figures 8 and 9).

During the 3 years of RST sampling, river flows were generally 20 m^3/s year-round in the LFC with the exception of one event in February/March 1999 (Figure 2). Flows in the HFC ranged from a low of 30 m^3/s in April 2001 to a high of 708 m^3/s in February 1999 (Figure 2). Chinook salmon fry passage at the Thermalito RST varied through time, but regression analysis found that emigration timing was poorly explained by environmental variables. In 1998–1999, flow, water temperature, and Secchi depth showed no relationship to Chi-

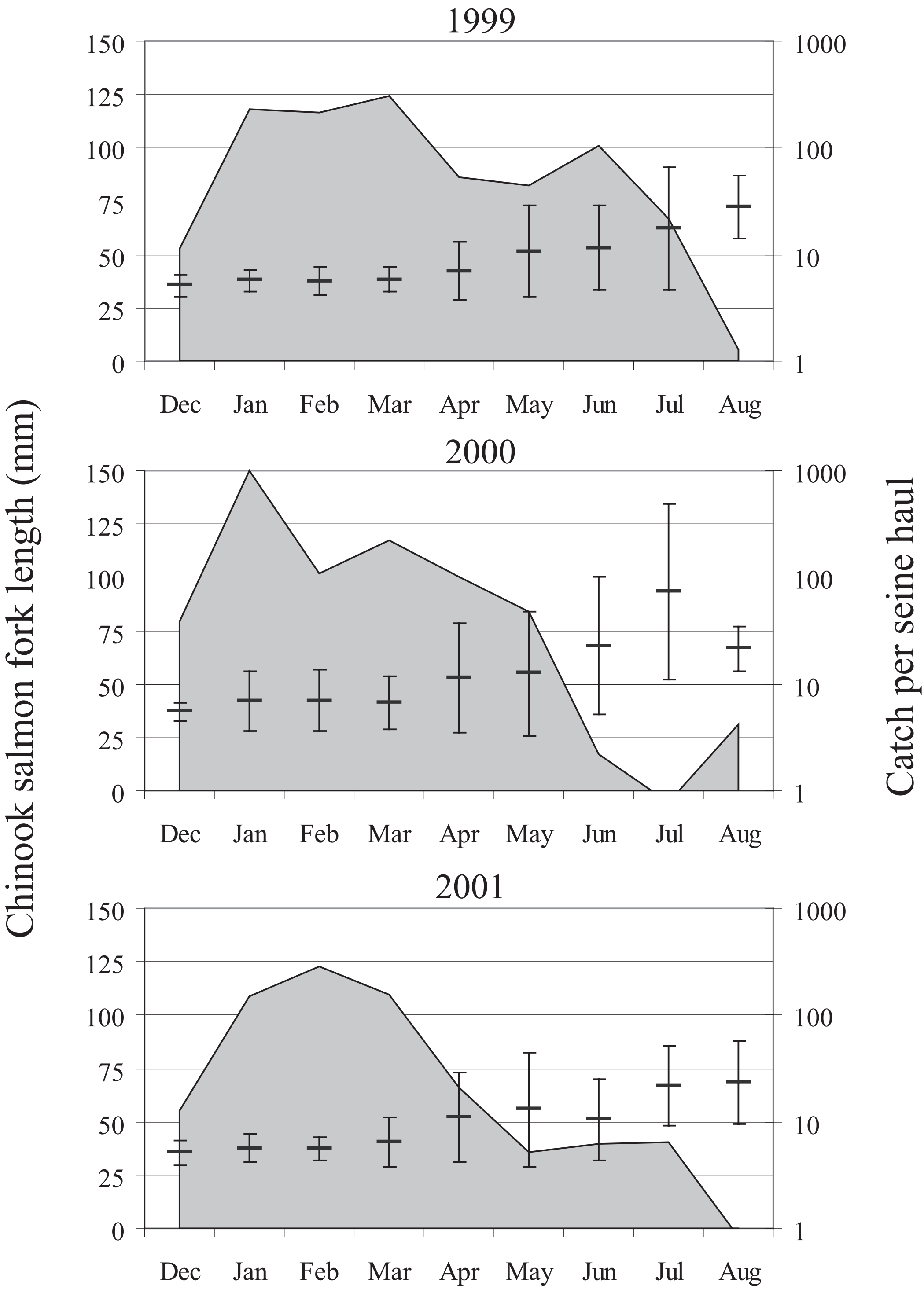

FIGURE 4. Fork lengths of Chinook salmon seined in the lower Feather River in 1999–2001. On the primary *y*-axis, the dash represents mean length and vertical lines indicate ± 2 SD. The secondary *y*-axis indicates catch per unit effort in logarithmic scale.

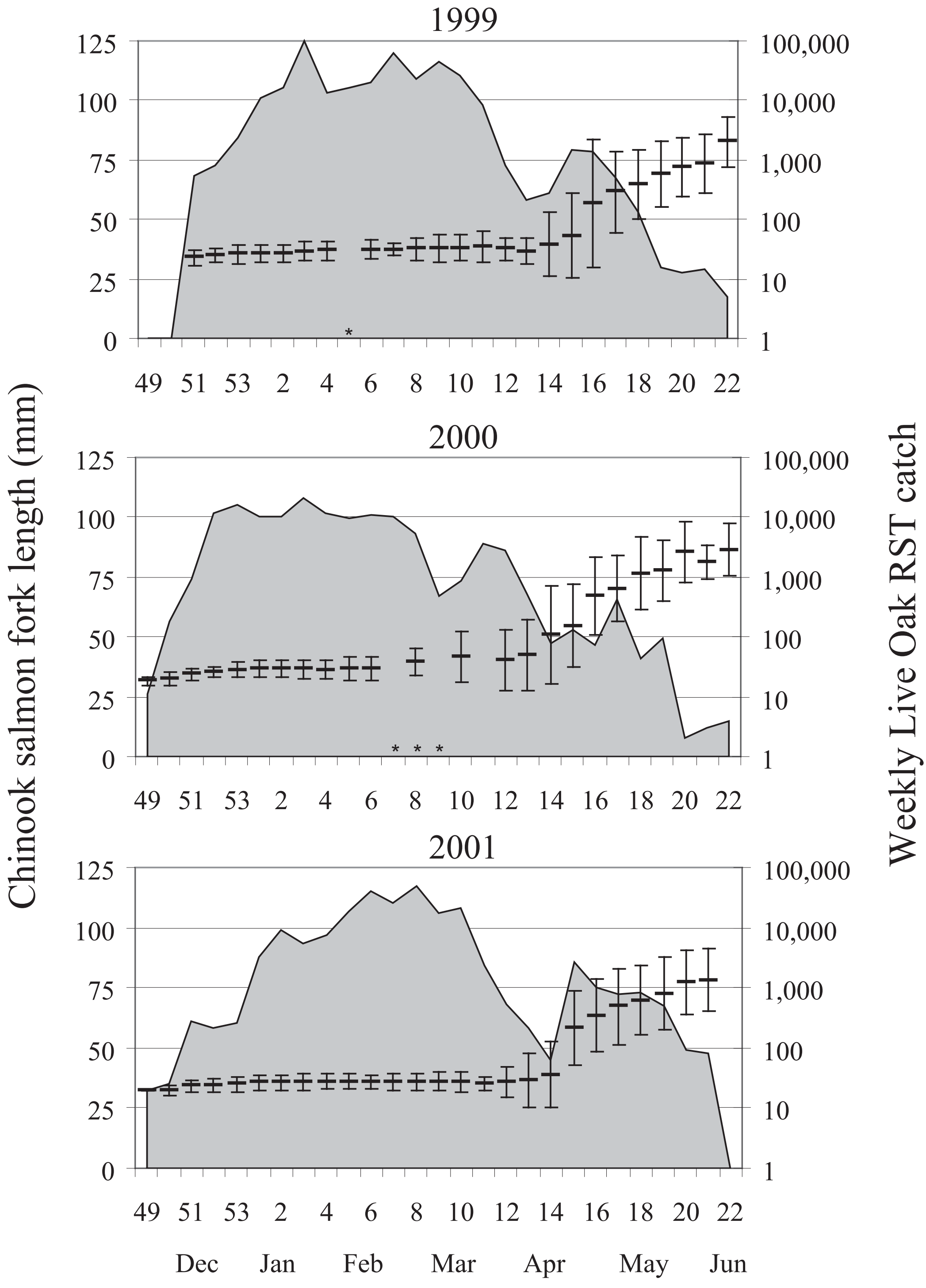

FIGURE 5. Weekly fork lengths and catch of Chinook salmon captured at the Live Oak rotary screw trap in 1999–2001. On the primary *y*-axis, the dash represents mean length and vertical lines indicate ±2 SD. The secondary *y*-axis indicates weekly catch in logarithmic scale. Asterisk denotes interpolated values.

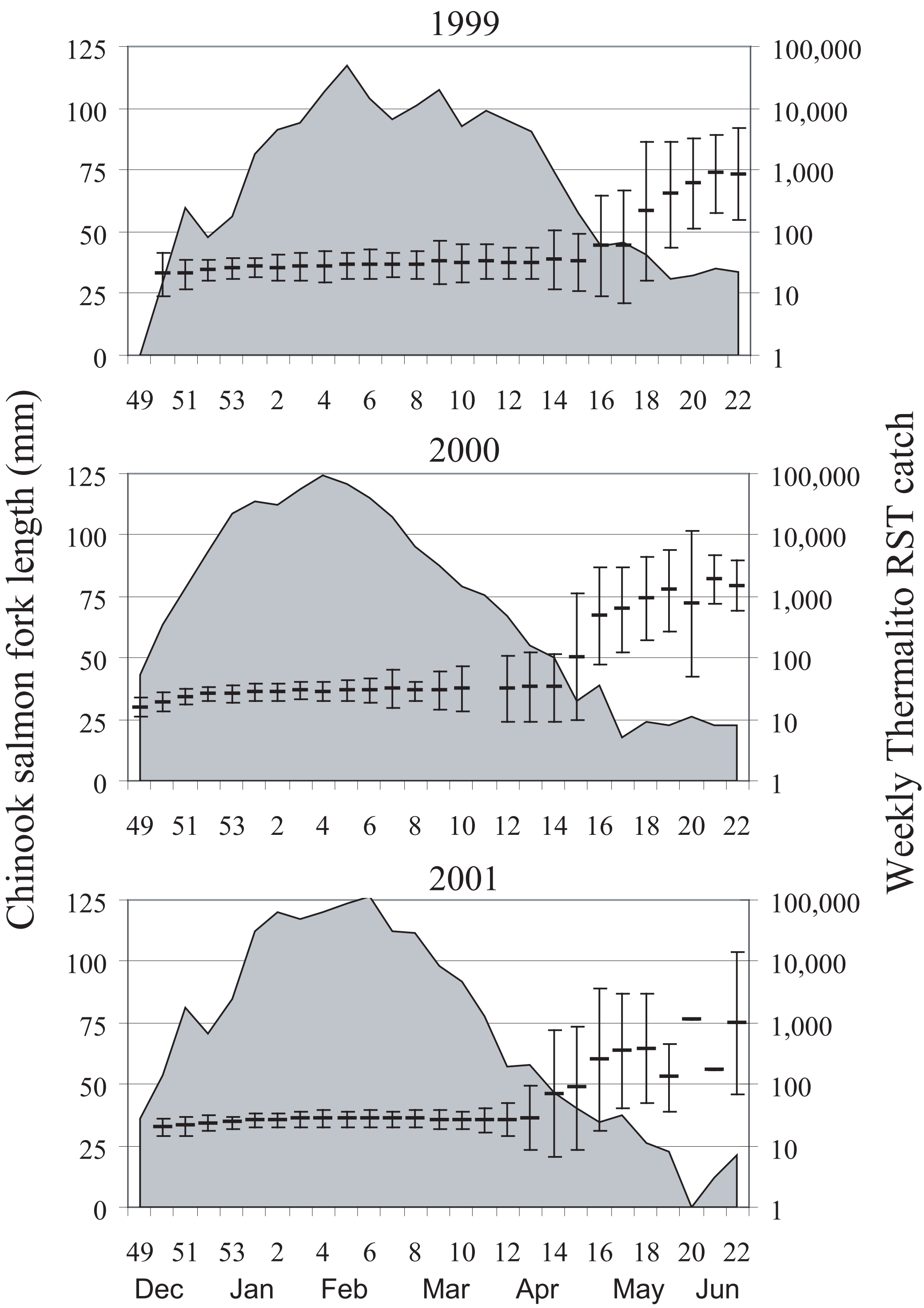

FIGURE 6. Weekly fork lengths and catch of Chinook salmon captured at the Thermalito rotary screw trap in 1999–2001. On the primary *y*-axis, the dash represents mean length and vertical lines indicate ± 2 SD. The secondary *y*-axis indicates weekly catch in logarithmic scale.

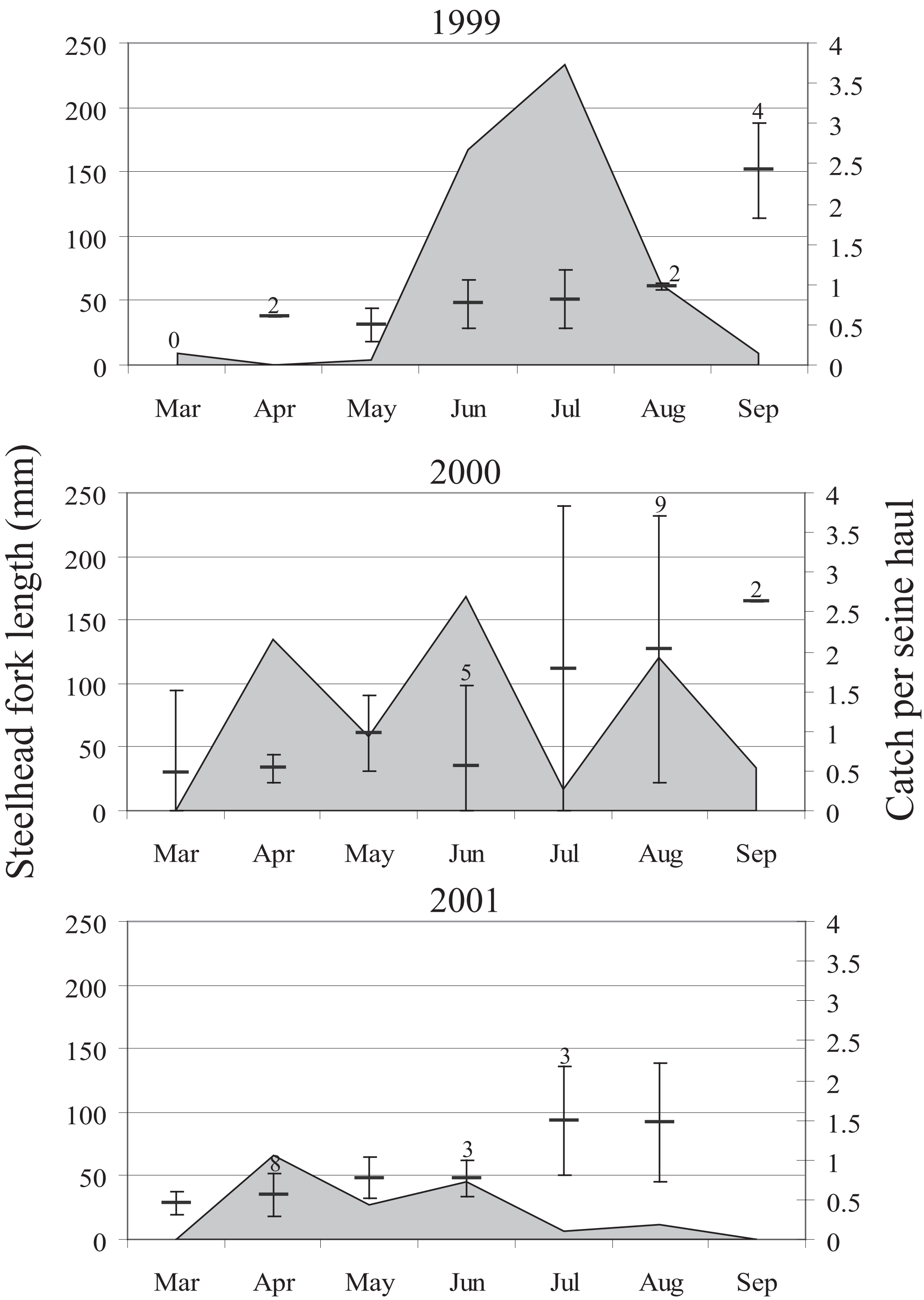

FIGURE 7. Monthly fork lengths of steelhead seined in the lower Feather River in 1999–2001. On the primary *y*-axis, the dash represents mean length and vertical lines indicate ± 2 SD. Numbers above the lines show sample sizes less than 10. The secondary *y*-axis indicates catch per unit effort. No sampling was conducted in September 2001.

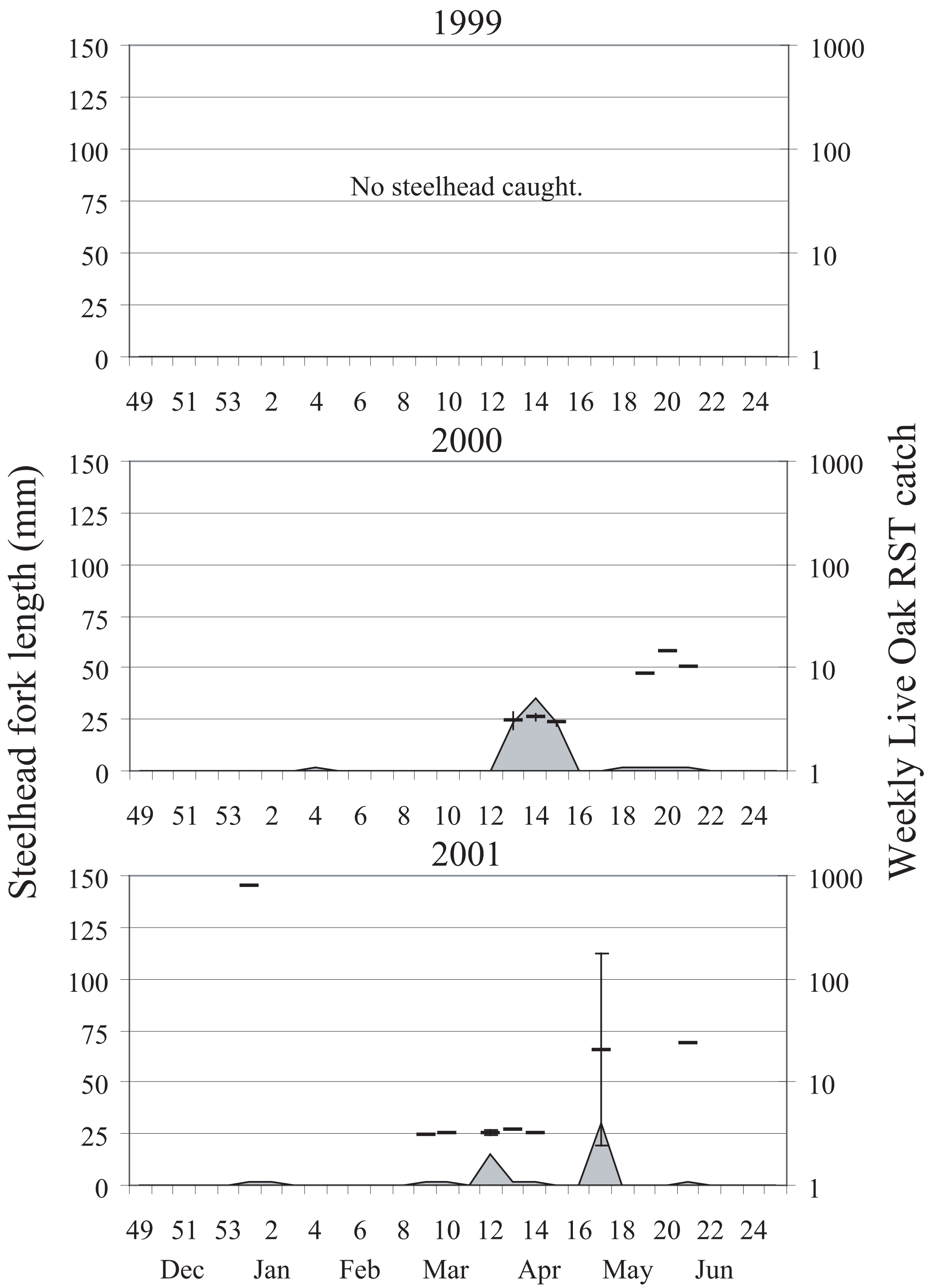

FIGURE 8. Weekly fork lengths and catch of steelhead captured at the Live Oak rotary screw trap in 1999–2001. On the primary *y*-axis, the dash represents mean length and vertical lines indicate ±2 SD. The secondary *y*-axis indicates weekly catch in logarithmic scale. No sampling was conducted July–September 2000.

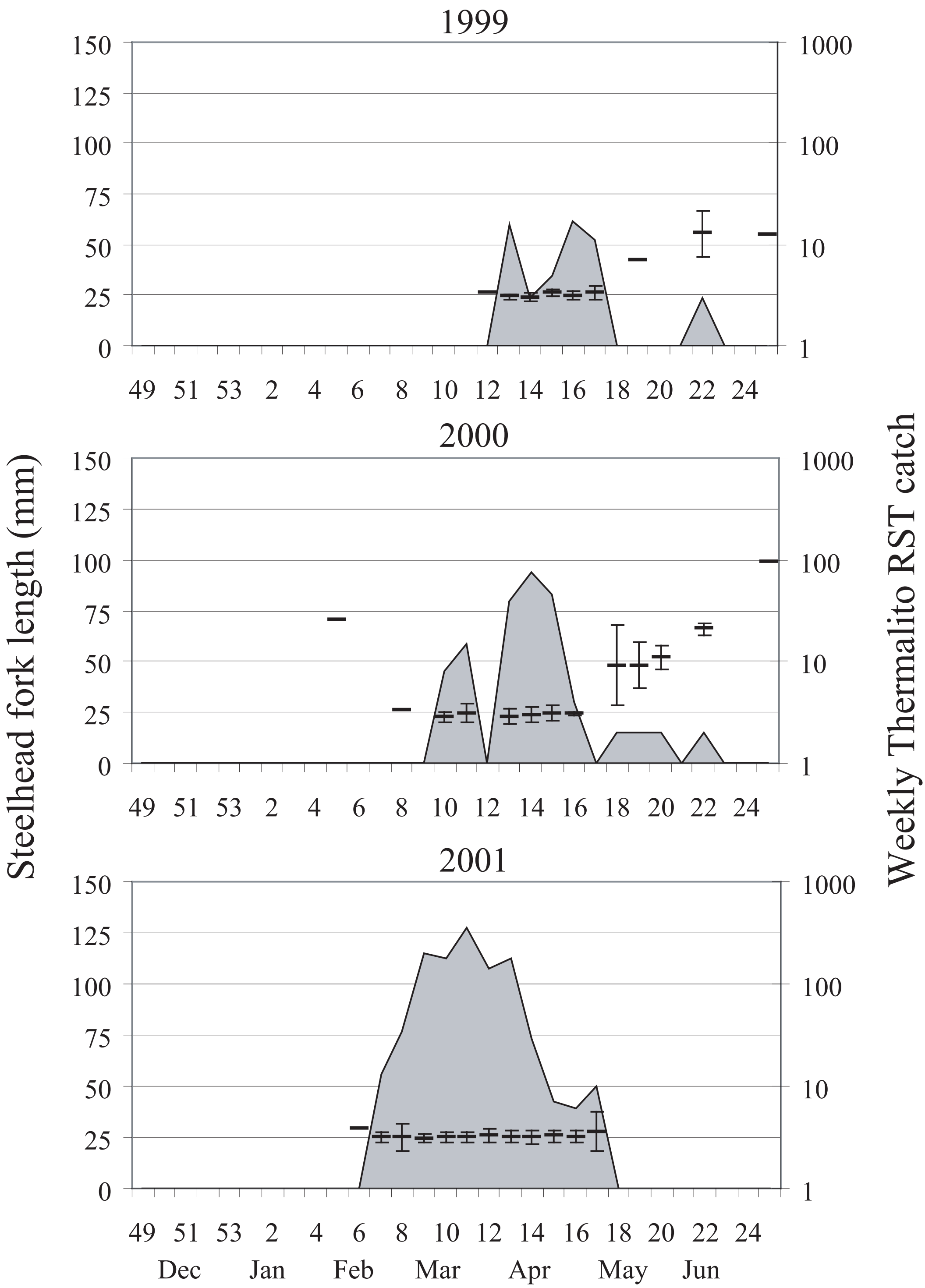

FIGURE 9. Weekly sizes and catch of steelhead captured at the Thermolito rotary screw trap, 1999–2001. On the primary *y*-axis, the dash represents mean length and vertical lines indicate ±2 SD. The secondary *y*-axis indicates weekly catch in logarithmic scale.

nook salmon emigration ($P > 0.05$). Results from the 1999–2001 analysis also failed to show a significant flow effect for either the Thermalito or Live Oak RST (Table 5). However, Chinook salmon spawn timing ($P < 0.001$) and water temperature ($P = 0.036$) were statistically significant predictors of weekly Chinook salmon catch at the Thermalito RST (Table 5). In 1999–2001, flow, water temperature, Secchi depth, and spawn timing collectively accounted for 67% of variation in Thermalito RST catch.

Similar to the Thermalito RST, 1998–1999 Live Oak RST catch did not show any significant relation to environmental variables ($P > 0.05$). In 1999–2001, the regression model explained only a moderate proportion of the observed variation in catch, 48% (Table 5). Secchi depth, the only statistically significant variable ($P = 0.007$), was negatively correlated with Live Oak Chinook salmon catch (Table 5).

Discussion

Species composition and distribution

In rivers of the western United States, natural flow regimes are thought to benefit native fishes and limit the success of alien fishes (Meffe 1984; Moyle and Williams 1990; Strange et al. 1992; Brown and Ford 2002). In California, alien fishes, such as ictalurids and centrachids, are known to proliferate in rivers exhibiting more lentic conditions and lacking strong winter/spring flood events (Marchetti and Moyle 2000; Moyle 2002). These patterns have been associated with upstream river regulation and the resulting stabilization of flow regime. Developments in stream ecology theory, along with these fish observations, have led to increasing interest in the idea of restoring rivers and, presumably, native fish populations, by allowing or imitating natural flow events (Stanford et al. 1996; Poff et al. 1997).

However, our results indicate that the lower Feather River supports relatively strong native fish populations despite a decidedly unnatural flow regime. Chinook salmon were the most prevalent species, but other native fishes with diverse life histories and habitat requirements were also common. Seining data showed that 10 of the top 15 species in rank abundance were natives, while RST data found that 11 of the top 15 fishes in rank abundance were natives. These most abundant native fishes included Sacramento sucker, steelhead, hardhead, Sacramento pikeminnow, tule perch, prickly and riffle sculpin, and Pacific lamprey. Native fishes dominated the LFC, but were also abundant throughout the

TABLE 5. Results from 1999–2001 multiple linear regression analyses of Chinook salmon catch per unit effort from Thermalito and Live Oak rotary screw traps (RST).

Thermalito RST				
Effect	Coefficient	SE	*t*	*P*
Flow	–1.619	2.684	–0.60	0.550
Temperature	–24.103	11.025	–2.19	0.036
Secchi	11.454	23.947	0.48	0.635
Adult spawn timing	0.024	0.004	5.35	0.000
				Adjusted $R^2 = 0.674$

Live Oak RST				
Effect	Coefficient	SE	*t*	*P*
Flow	–0.005	0.005	–0.91	0.371
Temperature	–6.067	3.441	–1.76	0.087
Secchi	–69.141	24.174	–2.86	0.007
Adult spawn timing	0.001	0.003	0.52	0.606
				Adjusted $R^2 = 0.488$

rest of the study area. Although aliens occurred frequently in the HFC, they did not dominate the downstream portion of the Feather River. This finding is in contrast to other studies on regulated rivers that have found that alien fishes become increasingly dominant in downstream reaches (Marchetti and Moyle 2000; Ford and Brown 2001).

The most numerous alien species observed in our sampling was wakasagi. Wakasagi are not considered a riverine species (Moyle 2002), and their abundance in the lower Feather River may partially be due to wash downs from Lake Oroville. The extent to which wash downs from Lake Oroville and the Thermalito Complex have influenced observed abundance patterns of this and other species in the lower Feather River is unclear. Since the lower Feather River seemingly provides many suitable habitats for black basses and other centrarchids, it is unlikely that wash downs would be necessary to support populations observed in our study. However, upstream reservoirs have undoubtedly contributed to past and any ongoing colonization of the Feather River by alien species.

Flows in the LFC are stable year-round. In the HFC, flow regime is not stable, but would not be characterized as natural. In sampling years 1998–1999 and 1999–2000, higher flows occurred in the HFC during winter and again, to a lesser extent, during summer. In 2000–2001, flows were relatively low all year, with slight flow increases occurring in late summer. During all three sampling years, neither seining nor RST sampling revealed changes in relative abundance of native or alien fishes that might be expected if natural spring flow pulses were critical drivers of species abundance in the lower Feather River. Additional years of relative abundance data, such as that analyzed by Brown and Ford (2002), would make it possible to statistically explore interannual relationships between flow and fish abundance. It is also important to note that this study was conducted during a relatively wet hydrologic period. Were the same studies conducted after a series of drought years, different results might be obtained. In addition, comparison with historic data from before the construction of Oroville Dam would be extremely helpful in interpreting long-term effects of river regulation. Unfortunately, past studies on the Feather River (e.g., Warner 1955) largely focused on Chinook salmon and provided no quantitative information related to resident fishes.

River regulation is often broadly depicted as beneficial to alien species and harmful to natives (e.g., Moyle and Williams 1990). However, native or alien status, in itself, has little to do with how we should expect populations of a given fish species to be affected by dams or other habitat conditions. Members of native and alien fish assemblages in California share many similar requirements for successful life history. Smallmouth bass, for example, widely recognized as an alien species negatively impacting native fish populations, are common in many rivers throughout California (Brown and Moyle 1993; Dill and Cordone 1997; Moyle 2002), both regulated and unregulated. Smallmouth bass are widespread because they are well suited to California stream environments and face minimal competition from native species. Similarly, warm, turbid, and lentic conditions are favorable to some alien fishes (e.g., bluegill sunfish, largemouth bass, and ictalurids), but are also the preferred habitat of many native fishes (hitch, Sacramento blackfish).

Earlier spawn timing is the primary mechanism by which native fishes are thought to benefit from natural, spring flood events (Moyle 2002), and several studies have described a relationship between spring flows and subsequent recruitment of spring-spawning natives (Marchetti and Moyle 2000; Brown and Ford 2002). However, with such studies, it is often difficult to discern whether there is a commensurate decrease in the abundance of alien species or whether alien abundance has declined only relative to the large recruitment class of some native fishes. In California's unregulated rivers, spring run-off typically occurs over several months (Mount 1995), but most late spawning or bottom nesting alien species should be capable of spawning successfully after flows recede and where conditions are otherwise suitable (e.g., backwaters). Whether natural flow regimes actually reduce abundance of alien fishes, as opposed to just enhancing the reproductive success of natives, is a topic worthy of further study.

Water temperature appears to be an extremely important factor regulating species composition in the lower Feather River. The CCA suggested that water temperature explains a large percentage of variation in species occurrence and abundance. This was evident in the HFC CCA, in which coldwater and warmwater assemblages clearly differentiate. The LFC CCA further indicated the importance of cooler water to Chinook salmon. Coldwater temperatures, which are strongly correlated with season and proximity to the dam, may be an important factor in providing suitable conditions for native fishes and in preventing domination by alien species. The LFC seems to provide a thermal refuge for many native species that alien fishes have been unable to colonize successfully. The benefits of this cooler water may extend even below Thermalito Outlet and into the HFC. In a study of larval fish in Putah Creek, California, Marchetti and Moyle (2000) also found that cool, flowing water below an impoundment provided better spawning habitat for native fishes. A larval study currently being conducted may provide some insight into these issues.

Besides increased temperature, the warmwater assemblage was associated with later seasons and downstream locations. This assemblage is more characteristic of the lower portions of the river (HFC). The river below the Thermalito outlet is appreciably warmer during the summer and is enriched with planktonic organisms flushed out of the shallow and mesotrophic Thermalito Complex bays. Generally, native fishes such as tule perch, hardhead, hitch, Sacramento sucker, and Sacramento pikeminnow are abundant below the Thermalito Outlet and appear to be successfully coexisting with alien centrarchids and cyprinids, as well as native anadromous salmonids.

Our interpretations of flow effects on fish assemblage composition in the Feather River were aided by the disparity in flow regime between the LFC and HFC. The CCA suggests that flow variation does not influence assemblage structure in the HFC, but has a key role in structuring fishes in the LFC. It is likely that fishes in the HFC are adapted to flow variation and are not affected to the same extent as fish that reside in the normally stable LFC. While wakasagi and centrarchids are generally associated with slower waters, they had the strongest correlation to increased flow. Wakasagi may have been more abundant during high-flow situations due to washouts entering the system from Lake Oroville through the Fish Barrier Dam. Centrarchid numbers may have increased by the same mechanism. Alternatively, higher flows in the LFC may have muted the temperature discontinuity between the LFC and HFC, which could have facilitated centrarchid colonization and spawning.

The degree to which flows are impaired in a given river (relative to normal, non-drought, nondiverted conditions) may have a large effect on the assemblage of fishes observed and on the response of that assemblage to changes in flow regime. Rivers that have very low spring and summer flows, due either to regulation, diversions, or natural drought conditions, will be more susceptible to invasion by lentic, warmwater, and stress-tolerant alien fish species. Water temperature can be a critical variable mediating interactions between fish species with some overlap in thermal preference (Baltz et al. 1982; Reeves et al. 1987). Cool water temperatures typical of regulated rivers with higher base flows may offer competitive advantages to some native species over alien species with a preference for warmer temperatures. This mechanism would explain the near complete domination of alien species in extreme habitats of the Central Valley, agricultural drains, and severely dewatered river channels (May and Brown 2002). Native fishes living in impaired flow environments can be expected to respond dramatically to increased flows, which enhance native spawning success and perhaps reduce the abundance of alien fishes. In contrast, regulated rivers with consistent, moderate base flows and typically cool water temperatures may already host healthy native fish populations and will therefore show little measurable response to high spring flow events when they occur.

This conceptual model may not be universal, but we believe it is consistent with our findings on the Feather River and those from at least some other California river systems (Marchetti and Moyle 2000; Brown and Ford

2002; May and Brown 2002). We also agree with others (Marchetti and Moyle 2000; May and Brown 2002; Brown and Ford 2002) that flow manipulation provides a potentially powerful tool for restoration of rivers and enhancement of some fish populations. However, our findings suggest that natural flow regime may be a less effective fish restoration tool on rivers that already have moderate, year-round flows and cool water temperatures. Even on rivers with severely impaired flows, increased base flows and reduced water temperatures should be given equal consideration in the context of the adaptive management approach recommended by Marchetti and Moyle (2000) and Brown and Ford (2002).

Salmonid emigration

Emigration patterns for Chinook salmon in the Feather River were similar throughout the period of study in that they appear to emigrate very early and at small sizes. Furthermore, most downstream migrants were classified as presmolts. The percentage of Chinook salmon that was clearly smolt or intermediate between parr and smolt was less than 2% at Thermalito and 15% at Live Oak. Most were smaller than 50 mm (97% at Thermalito and 81% at Live Oak). The high percentages of presmolt fish and fish smaller than 50 mm indicate that most Chinook salmon smolt downstream of Live Oak. The end of emigration in all 3 years was similar to that found in previous studies (CDWR 1999). Painter et al. (1977) found that in 1968–1975, emigration typically occurred only through the end of June. Similarly, Warner (1955) found that prior to Oroville Dam, emigration ended near the beginning of June. Although we believe that most Chinook salmon emigrate past Live Oak by early April, many remain in the river later in the year. Snorkel surveys (Cavallo et al. 2003) have confirmed that thousands of juvenile Chinook salmon probably continue to rear in the Feather River throughout the spring, with as many as several thousand fish persisting through the summer, mostly in the LFC.

The early downstream migration of juvenile Chinook salmon is consistent with findings from other Central Valley rivers. Snider and Titus (1995), for example, reported that most juvenile Chinook salmon had left the nearby American River by mid-May. Healey (1991) reported that a large downstream movement of Chinook salmon fry immediately after emergence is typical of many populations. He further reported that, "the downstream migration of stream- and ocean-type Chinook fry, when spawning grounds are well upstream, is probably a dispersal mechanism that helps distribute fry among the suitable rearing habitats."

There are a number of other possible explanations for the early out-migration of juvenile Chinook salmon. Warmer water temperatures experienced during incubation and rearing period is an explanation given by some authors (Williams 2001; Connor et al. 2002). Warmer waters might cause fry to develop and emerge earlier, perhaps sooner than the river is capable of supporting them. Chinook salmon might also emigrate early to avoid high temperatures on the Sacramento Valley floor in the spring and summer.

The early downstream migration of juvenile Chinook salmon rearing below Central Valley terminal dams may reflect an adaptation to local conditions or simply a lack of quality habitat and available food base in the winter/early spring. Analysis of Feather River invertebrate occurrence and abundance in conjunction with stomach contents of juvenile Chinook salmon suggests that food supply may be poor (Esteban 2002). Historically, Chinook salmon may have emerged a month later and exploited the spring and summer food web. Fyke traps operated on the American River in 1945–1947 suggest that Chinook salmon now emigrate earlier in the season (Snider et al. 1998). However, Painter et al. (1977), sampling between 1968 and 1973 on the Feather River, found emigration patterns very similar to those observed in our current studies.

Early emigration may also be related to the large numbers of Chinook salmon produced in many Central Valley rivers. The Feather River, like the American and Sacramento rivers, hosts very large Chinook salmon spawning runs. These adult Chinook salmon populations are supplemented heavily by hatchery production. Juvenile Chinook salmon produced by large spawning populations may be subject to intense competition for food, such that density-dependent downstream dispersal occurs en masse. Unwin (1986) found that the bulk migration of Chinook salmon fry in Glenariffe stream, New Zealand was most likely a result of competition for rearing habitat.

One of the goals for most RST sampling programs, which are now common throughout Central Valley rivers, is to determine environmental factors that cue downstream migration of juvenile Chinook salmon (USFWS 2000). Seasonal high-flow events were thought to be particularly important in cueing and aiding downstream migration. However, our RST sampling on the Feather River suggests that cues from flow, turbidity, and water temperature are not necessary to trigger downstream migration of juvenile Chinook salmon. At the Live Oak RST, Secchi depth showed the strongest statistical relationship, even though the model explained only a moderate portion of the overall variation. It is unclear whether decreased water clarity encourages downstream migration or simply lowers trap avoidance for Chinook salmon migrating independently of turbidity. In general, Chinook salmon do not appear to be waiting for an environmental cue to trigger emigration.

In the Feather River, the best correlate for emigration timing may be the timing of adult Chinook salmon spawning. The regression model for the Thermalito RST shows that peaks in emigration correspond fairly well with peaks in escapement. Furthermore, average fork length changed little between mid-December and late March each year. The rapid increase in fork length at both traps between the end of March and the end of the sampling season implies that some Chinook salmon use the upper river as a nursery area in the spring. Environmental cues for emigration may be more important for Chinook salmon rearing in the river for an extended period.

Fish remaining in the river for several months grow larger and may have an advantage during emigration. They may be more adept at avoiding predators, finding food, and may be more physically prepared to smolt. Flain (1982) reported that Chinook salmon juveniles that reared in freshwater for several months to a year comprised 76% of the adult angler catch in the Rakaia River, although they comprised only 5% of the juvenile population. It is possible that a similar pattern of prolonged stream residence is successful on the Feather River and other Central Valley streams where summer environmental conditions are suitable. Currently, otolith microstructure from spawning adult Chinook salmon collected in the Feather River are being chemically analyzed (Ingram and Weber 1999). The juvenile phase of these otoliths should elucidate which life history strategies make the largest contribution to Feather River Chinook salmon spawning populations.

Conclusions

We found that the composition, distribution, abundance, and emigration of fishes in the lower Feather River was influenced by environment conditions, but did not fit many previously described patterns with regard to the importance of natural flow regime. Despite regulated flows, strong populations of native fishes were found in both LFC and HFC areas, while alien fishes tended to be found in relatively low numbers in the HFC area. Variations in flow had much more of an affect on fishes in the LFC than in the HFC. Conversely, in the HFC, the affects of temperature were much more dramatic in the formation of coldwater and warmwater fish assemblages. Flow regime also did not appear to significantly influence Chinook salmon emigration timing. These results have potential implications for developing fishery and river management strategies. Our results suggest that on regulated rivers, increased base flows and cooler water temperatures may be more important to the persistence of native fishes than previously recognized. Base flow and temperature management should be given careful consideration, along with natural flow regime concepts, as policy makers develop restoration strategies for regulated rivers.

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References

Baltz, D. M., and P. B. Moyle. 1993. Invasion resistance to introduced species by a native assemblage of California stream fishes. Ecological Applications 3:246–255.

Baltz, D. M., P. B. Moyle, and N. J. Knight. 1982. Competitive interactions between benthic stream fishes, riffle sculpin, *Cottus gulosus*, and speckled dace, *Rhinichthys osculus*. Canadian Journal of Fisheries and Aquatic Sciences 39:1502–1511.

Brown, L. R. 2000. Fish communities and their association with environmental variables, lower San Joaquin River drainage, California. Environmental Biology of Fishes 57:251–269.

Brown, L. R., and T. Ford. 2002. Effects of flow on the fish communities of a regulated California river: implications for managing native fishes. River Research and Applications 18:331–342.

Brown, L. R., and P. B. Moyle. 1993. Distribution, ecology and status of the fishes of the San Joaquin River drainage, California. California Fish and Game 79:96–114.

Cavallo, B. J., R. Kurth, J. Kindopp, and A. Seesholtz. 2003. Distribution and habitat use of steelhead and other fishes in the lower Feather River, 1999–2001. Unpublished manuscript available from the California Department of Water Resources, Sacramento, California.

Connor, W. P., H. L. Burge, and R. Waitt. 2002. Juvenile life history of wild fall Chinook salmon in the Snake and Clearwater rivers. North American Journal of Fisheries Management 22:703–712.

Dill, W. A., and A. J. Cordone. 1997. History and status of introduced fishes in California, 1871–1996. California Department of Fish and Game, Fish Bulletin 178, Sacramento, California.

CDWR (California Department of Water Resources). 1999. Feather River Chinook salmon emigration survey, December 1997-June 1998. California Department of Water Resources, Sacramento, California.

CDWR (California Department of Water Resources). 2002. Emigration of juvenile Chinook salmon in the Feather River, 1998–2001. California Department of Water Resources, Sacramento, California.

Esteban, E. M. 2002. Salmonid prey selection: evaluating a food availability model in northern California with young-of-the-year Chinook salmon (*Onchorynchus tshawytscha*) and steelhead trout (*Onchorynchus mykiss*). Master's thesis. California State University, Chico.

Flain, M. 1982. Quinnat salmon runs, 1965–78, in the Glenariffe Stream, Rakaia River, New Zealand. New Zealand Ministry of Agriculture and Fisheries, Fisheries Research Division, Occasional Publication No. 28, Wellington.

Ford, T., and L. R. Brown. 2001. Distribution and abundance of Chinook salmon and resident fishes of the lower Tuolumne River, California. Pages 253–304 *in* R. L. Brown, editor. Contributions to the biology of Central Valley salmonids. Volume 2. California Department of Fish and Game, Fish Bulletin 179, Sacramento, California.

Healey, M. C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). Pages 311–393 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Ingram, B. L., and P. K. Weber. 1999. Salmon origin in California's Sacramento-San Joaquin river system as determined by otolith strontium isotopic composition. Geology 27:851–854.

Li, H. W., C. B. Schreck, C. E. Bond, and E. Rexstad. 1987. Factors influencing changes in fish assemblages of Pacific Northwest streams. Pages 193–202 *in* W. J. Matthews and D. C. Heins, editors. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Ligon, F. K., W. E. Dietrich, and W. J. Trush. 1995. Downstream ecological effects of dams: a geomorphic perspective. Bioscience 45:183–192.

Marchetti, M. P., and P. B. Moyle. 2000. Spatial and temporal ecology of native and introduced fish larvae in lower Putah Creek, California. Environmental Biology of Fishes 58:75–87.

May, J. T., and L. R. Brown. 2002. Fish communities of the Sacramento River basin: implications for conservation of native fishes in the Central Valley, California. Environmental Biology of Fishes 63:373–388.

Meffe, G. K. 1984. Effects of abiotic disturbance on coexistence of predator-prey fish species. Ecology 65:1525–1534.

Minckley, W. L., and G. K. Meffe. 1987. Differential selection by flooding in stream-fish communities of the arid American southwest. Pages 93–104 *in* W. J. Matthews and D. C. Heins, editors. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Mount, J. F. 1995. California rivers and Ssreams: the conflict between fluvial process and land use. University of California Press, Berkeley.

Moyle, P. B. 2002. Inland fishes of California. Revised

and expanded. University of California Press, Berkeley.
Moyle, P. B., and J. E. Williams. 1990. Biodiversity loss in the temperate zone: decline of the native fish fauna of California. Conservation Biology 4:275–284.
NMFS (National Marine Fisheries Service). 1999. Endangered species act status of west coast salmon and steelhead: Chinook salmon. Available at http://www.nwr.noaa.gov/1salmon/ salmesa/pubs/ 1pgr. pdf. Accessed on 28 May 2003.
Painter, R. E., L. H. Wixom, and S. N. Taylor. 1977. An evaluation of fish populations and fisheries in the post-Oroville project Feather River. California Department of Fish and Game, Anadromous Fisheries Branch, Prepared for the California Department of Water Resources, Sacramento, California.
Poff, N. L., and seven coauthors. 1997. The natural flow regime: a paradigm for river conservation and restoration. Bioscience 47:769–784.
Reeves, G. H., F. H. Everest, and J. D. Hall. 1987. Interactions between the redside shiner (*Richardsonius balteatus*) and the steelhead trout (*Salmo gaidneri*) in western Oregon: the influence of water temperature. Canadian Journal of Fisheries and Aquatic Sciences 44:1603–1613.
Snider, W. M., and R. G. Titus. 1995. Lower American River emigration survey, November 1993 - July 1994. California Department of Fish and Game, Environmental Services Division, Sacramento, California.
Snider, B., R. G. Titus, and B. A. Payne. 1998. Lower American River emigration survey. October 1995 - September 1996. California Department of Fish and Game, Environmental Services Division, Sacramento, California.
Sommer, T. R., M. L. Nobriga, W. C. Harrell, W. Batham, and W. J. Kimmerer. 2001. Floodplain rearing of juvenile Chinook salmon: evidence of enhanced growth and survival. Canadian Journal of Fisheries and Aquatic Sciences 58:325–333.
Stanford, J. A., and six coauthors. 1996. A general protocol for restoration of regulated rivers. Regulated Rivers: Research and Management 12:391–413.
Stevens, D. E., M. A. Kjelson, and P. L. Brandes. 1984. An evaluation of the relationship between survival of Chinook salmon smolts and river flow in the Sacramento-San Joaquin Delta. Appendix A *in* Survival and productivity of juvenile Chinook salmon in the Sacramento-San Joaquin Estuary. 1984 Annual Progress Report. U.S. Fish and Wildlife Service, Fisheries Assistance Office, Stockton, California.
Strange, E. M., P. B. Moyle, and T. C. Foin. 1992. Interactions between stochastic and deterministic processes in stream fish community assembly. Environmental Biology of Fishes 36:1–15.
ter Braak, C. J. F., and P. F. M. Verdonschot. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquatic Sciences 57:153–187.
ter Braak, C. J. F., and P. Smilauer. 1998. CANOCO reference manual and user's guide to CANOCO for Windows: software for canonical community ordination (version 4). Microcomputer Power, Ithaca, New York.
Unwin, M. J. 1986. Stream residence time, size characteristics, and migration patterns of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) from a tributary of the Rakaia River, New Zealand. New Zealand Journal of Marine and Freshwater Research 20:231–252.
USFWS (U. S. Fish and Wildlife Service). 2000. Comprehensive assessment and monitoring program (CAMP). Annual Report 1999. U.S. Department of the Interior, Central Valley Project Improvement Act, Sacramento, California.
Ward, J. V., and J. A. Stanford. 1983. The serial discontinuity concept of lotic ecosystems. Pages 29–42 *in* T. D. Fontaine and S. M. Bartell, editors. Dynamics of lotic ecosystems. Ann Arbor Science, Ann Arbor, Michigan.
Warner, G. H. 1955. Studies on the downstream migration of young salmon in the Feather River. California Department of Fish and Game, Sacramento, California.
Williams, J. G. 2001. Chinook salmon in the lower American River, California's largest urban river. Pages 1–38 *in* R. L. Brown, editor. Contributions to the biology of Central Valley salmonids. Volume II. California Department of Fish and Game, Fish bulletin 179, Sacramento, California.
Yoshiyama, R. M., E. R. Gerstung, F. W. Fisher, and P. B Moyle. 2001. Historical and present distribution of Chinook salmon in the Central Valley drainage of California. Pages 71–176 *in* R. L. Brown, editor. Contributions to the biology of Central Valley salmonids, volume I. California Department of Fish and Game, Fish bulletin 179, Sacramento, California.