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SEASONAL FEEDING HABITS, GROWTH, AND MOVEMENT OF STEELHEAD TROUT IN THE LOWER MOKELUMNE RIVER, CALIFORNIA

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I examined the stomach contents of 179 steelhead, *Oncorhynchus mykiss*, and sub-dermally tagged 267 steelhead that were sampled seasonally from the lower Mokelumne River, in 1998 and 1999. Post-yearling (1+) steelhead fed primarily on hydropsychid larvae, chironomid pupae, zooplankton (primarily daphniids), and baetid subimago and nymphs. Although steelhead supplemented their diets with small terrestrial mammals, crayfish, and several species of fish ($\geq$20mm TL), the estimated mean prey item size ingested was less than 5 mm. Mean prey size did not change relative to fish lifestage or fork length in either year. However average number of prey items per stomach increased with fork length of fish. Steelhead occasionally ingested benthic organisms dislodged from feeding and spawning activities of other salmonids. Small mats of filamentous algae were also consumed throughout the year, presumably for the zooplankton and early instar insects entrained in the material. Overall, the index of fullness for steelhead was less during the 1999 season than in 1998. This decrease may be attributed to cooler water temperatures. Steelhead grew 0.32 mm/day on average (min: 0.04; max: 0.92). Sub-adult steelhead were more mobile than adult fish and were re-captured up to 2.5 km from original tagging sites.

INTRODUCTION

North American steelhead, *Oncorhynchus mykiss*, populations have experienced significant reductions in the past century. Estimated spawners in the Central Valley of California have declined from over 40,000 fish in the mid-1950s to less than 10,000 by the early 1990s (Hallock et al. 1961, Hallock 1991, McEwan and Jackson 1996). Concerns over the fate of Central Valley steelhead required the National Marine Fisheries Service to list this population as threatened under the Endangered Species Act in 1998.

During the last 40 years, field studies have enhanced our basic knowledge of life history and ecological requirements of steelhead. Food availability, feeding rates, and prey selection are important considerations in restoration and management of these fish and general steelhead diet information is well documented in the literature (Shapolov and Taft 1954, Johnson and Ringler 1980, Johnson 1985, Bilby et al. 1998). Sasaki (1966), and Merz and Vanicek (1996) have described diets of sub-yearling steelhead in two Central Valley rivers. However, steelhead may spend several years in river systems before migrating to the ocean and are known to feed when returning to fresh water (Hallock et al. 1961). Currently, there is little information regarding diets, growth, or movement of age 1+ steelhead residing in anadromous streams of the Central Valley.

This report documents seasonal diet variations, growth, and movement of age 1+ steelhead in a regulated Central Valley stream, the lower Mokelumne River (LMR), during two different water years.

STUDY AREA

The Mokelumne River is a modified system that drains approximately 1,624 km^2 of the central Sierra Nevada. The LMR is approximately 54 km of regulated river between Camanche Dam, the downstream-most non-passable barrier to anadromous fish, and its confluence with the Sacramento-San Joaquin Delta. The study area, between Camanche Dam and Lake Lodi (Fig. 1), is characterized by alternating bar complex and flatwater habitats, and is above tidal influence, with a gradient of approximately 0.17 m/km. The drainage consists of 87 km^2 of mostly agricultural and urbanized land. Several small streams and storm drains enter the lower river.

At least 35 fish species occur in the LMR (Merz 2001). The most abundant native species, in addition to steelhead trout, are chinook salmon, *O. tschawytscha*, prickly sculpin, *Cottus asper*, and Sacramento sucker, *Catostomus occidentalis*. Abundant non-native fish include western mosquitofish, *Gambusia affinis*, largemouth bass,

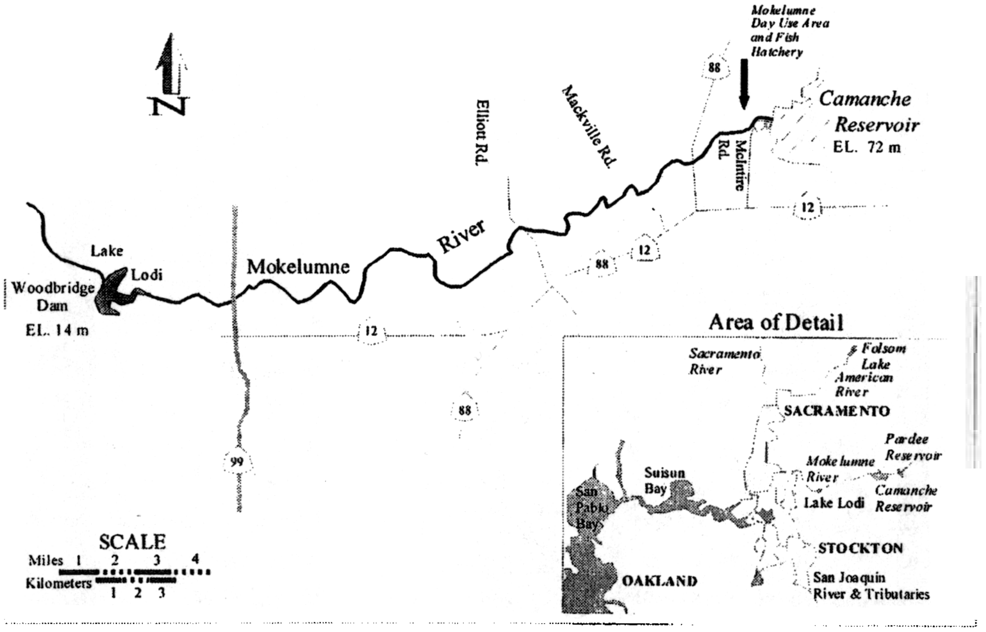

Figure 1. The lower Mokelumne River between Camanche Dam and Woodbridge Dam, San Joaquin County, California. The three reaches of river designated for this study are indicated.

Micropterus salmoides, bluegill, *Lepomis macrochirus*, and golden shiner, *Notemigonus crysoleucas*. The LMR steelhead population is supplemented by Mokelumne River Hatchery production and fish imported from the Feather River and Nimbus hatcheries. Presently, hatchery steelhead are released only below Woodbridge Dam, a seasonal flashboard dam used to fill Lake Lodi (Fig. 1). Numerous rainbow trout, *O. mykiss*, of various origins are regularly planted in the river above Camanche Dam. California hatchery production steelhead have been adipose fin-clipped since 1997. However, hatchery rainbow trout are not clipped.

During the 1998 study period, mean daily discharge from Camanche Dam peaked at 103.9 m^3/s on 14 February and again at 101.4 m^3/s on 30 June. Flows dropped to 8.8 m^3/s on 3 September 1998 (Fig. 2). Flows during 1999 peaked at 87.8 m^3/s on 21 February and reached a minimum of 9.2 m^3/s on 7 September. Water temperatures ranged from 9.1 °C in February to 15.5 °C in November 1998 (annual mean 13.2 °C) and 9.1 °C in February to 15.3 °C in September 1999 (annual mean 12.2 °C) (Fig. 3).

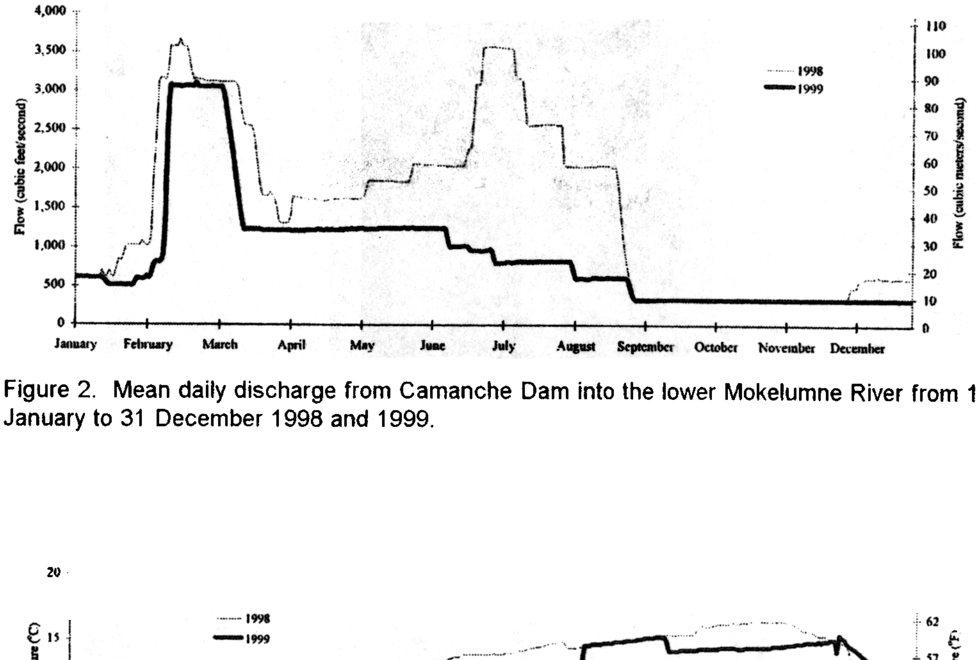

Figure 2. Mean daily discharge from Camanche Dam into the lower Mokelumne River from 1 January to 31 December 1998 and 1999.

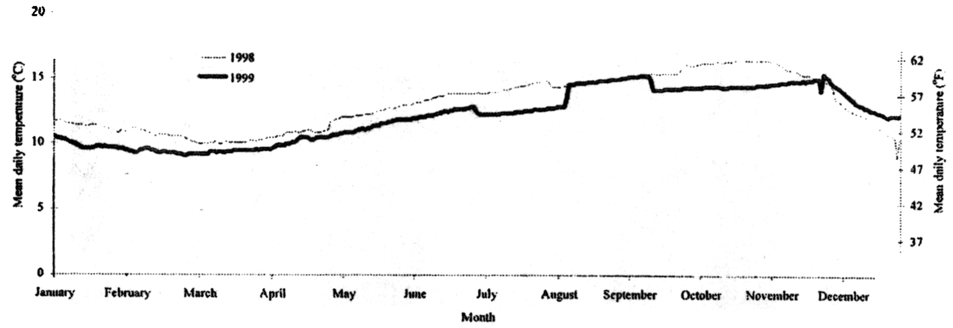

Figure 3. Lower Mokelumne River mean daily temperature measured directly below Camanche Dam from 1 January to 31 December 1998 and 1999.

METHODS AND MATERIALS

The Mokelumne River above Lake Lodi was separated into three reaches based on stream gradient and substrate characteristics (Fig. 1). Habitat types were identified and assigned to one of five habitats (modified from Bisson et al. 1981): 1) channel pools (unbroken surface, slow velocity, deep water); 2) glides (moderately shallow water with an even flow that lacked pronounced turbulence); 3) runs (rippled surface, fast velocity, shallow water); 4) riffles (stream bed substrate protruding through water surface); and 5) off channel pools (slow, deep water adjacent but contiguous to the main channel).

Steelhead were sampled between Lake Lodi and Camanche Dam during seasonal fish community surveys. Sampling was performed for 3 days the 1st week of January, April, August, and October 1998 and 1999. Sampling occurred between 0900 and 1500 hr with a 5.5-m electrofishing boat at representative habitats from each reach. The minimum target sample size was 13 fish per season, based on preliminary stomach samples (Hurtubia 1973). All specimens were measured in the field to the nearest 1 mm fork length (FL). Life stages of captured fish were identified and assigned to one of four stages: 1) Parr (darkly pigmented, distinct parr marks, no silver coloration, scales firmly set); 2) Silvery parr (parr marks visible but faded, intermediate degree of silvering); 3) Smolt (parr marks highly faded or absent, bright silver or nearly white coloration, scales easily shed (deciduous)); and 4) Adult (FL > 250 mm, no parr marks, well developed coloration, including dark spots above the lateral line, scales not easily shed). Stomachs of fish greater than 120 mm FL were evacuated following the methods described in Bowen (1983), Light et al. (1983), and Giles (1980). Stomach samples were immediately preserved in an 80-85% ethyl-alcohol solution, packed in ice, and transported to the laboratory for analysis. A sub-set of steelhead was marked to track movement and growth within the LMR. Liquitex brand fluorescent acrylic paints and Higgins brand non-waterproof india ink were injected with a 26-gauge needle and a 3-cc syringe using different mark locations and colors to distinguish individual fish following the methods described by Fay and Pardue (1985). Combinations of color and injection locations (base of pectoral, pelvic, and caudal fins) were used to identify marking date and capture location and fish were released on site. Tracking of marked fish was accomplished by steelhead observations during seasonal electrofishing, seining, and angler surveys and two rotary screw traps operated in the lower Mokelumne River below the Woodbridge Irrigation District Dam (WIDD) (Fig. 1).

Laboratory Analysis

Stomach contents were hand-sorted in the laboratory under a dissecting microscope and magnifying illuminator. Food items were identified to family for aquatic organisms and order for terrestrial organisms; life stages (larva, pupa, or adult) were determined. Adult Ephemeroptera, Trichoptera, Plecoptera, and Diptera were classified as terrestrial. Food items were further categorized into the following size classes: class 1 = <2 mm;

class 2 = 2-7 mm; class 3 = 8-13 mm; class 4 = 14-20 mm; class 5 = >20 mm (Baldridge[1] et al. 1987). Prey lengths were then estimated using the mean length for each size class.

Because most food items removed from fish stomachs were disarticulated or partly digested, representative samples of whole prey items from benthic, drift, and seine samples (Merz and Workman[2] 1998; Merz 1998[3]) were used to estimate dry biomass of stomach contents by oven drying selected samples of each taxon at 70 °C for 24 h to constant weight and then weighing the samples (Bowen 1983). As many of these organisms were extremely small (less than 0.0001 g), groups of 20-50 organisms of a particular taxon from each sample were dried, depending on how many could be obtained. Mean weight was calculated for the taxon, lifestage, and size class by dividing the dry weight of the group by the number of individuals. Mean weight was multiplied by numbers of the same taxon found in fish stomachs. Dry weight sums were used to estimate seasonal diet composition of steelhead trout following the methods of Johnson and Johnson (1981). Diet was pooled on a seasonal basis and analyzed by frequency of occurrence, numeric, and gravimetric (dry weight) methods (Bowen 1983). To assess the relative importance of food items, an index of relative importance (IRI) (Hyslop 1980) was calculated for each food category,

$$IRI = (\%N + \%W) \times \%O,$$

where,

%N = a food item's percentage of the total number of organisms ingested,
%W = a food item's percent of the total weight of food ingested, and
%O = a food item's percentage frequency occurrence in all stomachs that contained food.

To make dietary comparisons, IRI values of each food item were converted to percentages based on total IRIs for each season (Merz and Vanicek 1996).

An overall index of fullness (IF) for each sample season was calculated by dividing the mean weight of stomach contents for that period by mean FL of all steelhead trout examined that contained food and multiplying this value by 100 (Merz and Vanicek 1996).

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[1] Baldridge, J. E., T. K. Studley, T. P. Keagan and R. F. Franklin. 1987. Response of fish populations to altered flows project. Study Plan. Entrix, Inc., Walnut Creek, California, USA.

[2] Merz, J.E. and M.L. Workman. 1998. Lower Mokelumne River fish community survey. Report, East Bay Municipal Utility District, Fisheries and Wildlife Division, Lodi, California, USA.

[3] Merz, J. E. 1998. An evaluation of spawning gravel enhancement projects in the lower Mokelumne River, California. Report, East Bay Municipal Utility District, Fisheries and Wildlife Division, Lodi, California, USA.

Statistical Methods

A paired t-test was used to compare mean daily river flow and water temperature immediately below Camanche Reservoir between years and to compare mean indices of fullness between years (Zar 1996). Estimated mean prey size was compared to steelhead FL and sample year using the JMP linear regression model function, which performs an analysis of variance (ANOVA) (Sall et al. 2001). ANOVA was also used to compare mean number of ingested prey items and life stage and FL of steelhead. Chi-square (1-way test) was used to compare growth to lifestage of tagged fish and was also used to compare recapture location and lifestage of steelhead (Sall et al. 2001).

RESULTS

Mean daily releases from Camanche Dam were significantly higher in 1998 than 1999 (t = -16.11; df = 364; P <0.0001) (Fig. 2). Mean daily water temperatures released from Camanche Dam were significantly cooler in 1999 than 1998 (t = -21.2; df = 365, P <0.001).

The stomach contents of 179 steelhead were examined (Table 1). Adequate numbers of stomachs (minimum 13) were sampled except during the summer of 1998, when only three were sampled. Seasonal mean FL varied from 193 mm in fall to 380 mm in winter 1998 and 193 mm in fall to 252 mm in spring 1999. On the basis of length frequency groupings, most steelhead sampled appeared to be in their second (age 1+) to fourth (age 3+) year. Only two adipose fin clips were observed in 611 fish during the study period, indicating very few hatchery steelhead rear in the river above Woodbridge Dam.

Table 1. Seasonal sample size and mean fork lengths (FL) of steelhead trout from the lower Mokelumne River, 1998 and 1999.

Year		*Winter*	*Spring*	*Summer*	*Fall*
	Sample size	13	14	3	35
	Minimum FL	137	215	145	121
	Maximum FL	380	279	253	442
	Mean FL	248	238	206	193
	SD	66	25	55	83
	Sample size	62	22	14	16
	Minimum FL	118	170	92	130
	Maximum FL	435	365	332	340
	Mean FL	196	252	220	193
	SD	68	41	69	68

Composition of Diets

Steelhead trout fed on a wide variety of food items including stonefly (Plecoptera) nymphs, terrestrial ants (Hymenoptera), small fish, and mice (*Peromyscus* sp.). However, the major portions of their diets, in order of relative importance, were hydropsychid caddisfly larvae, chironomid pupae, baetid mayfly nymphs and subimago, and zooplankton (primarily daphniids). This general pattern occurred in both years (Table 2).

Seasonal diet trends of LMR steelhead (Fig. 4 and 5) show that aquatic insects were a major food item throughout all seasons, especially during 1999. Of these, trichopterans, chiefly hydropsychid larvae, were important for all seasons. In contrast, aquatic dipterans (mostly chironomid pupae) were a dominant food source only during the fall of 1998 and all seasons of 1999. Aquatic ephemeropterans (mostly baetid subimago) were a dominant food in fall 1998 and winter and fall 1999 (Fig. 4). Zooplankton provided high IRI values for steelhead trout only during winter 1998 and spring of both years (Fig. 4).

Piscivory

Although fish were found in the diets of steelhead trout throughout the study period, %IRI of prey fish was high only during the winter of 1998, when collective prey fish IRI was 39% (Fig. 4).

Fish eggs, juveniles, or adults were found in 10% of steelhead trout stomachs sampled. Sculpin were the most common fish (including eggs) observed in stomachs, followed by chinook salmon eggs and fry, and cyprinid and Sacramento sucker eggs and juveniles. Chinook salmon fry (34-39 mm FL) were found in the stomachs of steelhead trout ($\geq$147 mm FL) and had the highest %IRI value of all fish ingested. Adult prickly sculpin (43-52 mm SL) were observed in the stomachs of steelhead trout $\geq$175 mm FL, but were less common.

Feeding relative to prey size

The estimated mean prey item size ingested by steelhead trout captured was 4.78 mm (SD 1.76). The seasonal mean prey item size did not change significantly relative to fork length of the fish sampled in either year (Fig. 6).

Feeding relative to fish lifestage and size

Mean estimated prey item size did not change significantly relative to steelhead lifestage in either year ($F = 1.97$; df = 4, 130; $P = 0.100$). However, mean number of prey items was significantly related to fish size in 1998 ($F = 15.29$; df = 7; $P = 0.008$) and 1999 ($F = 18.75$; df = 11; $P = 0.001$) (Fig. 7).

Table 2. Major food items of steelhead trout in the lower Mokelumne River, 1998 and 1999, presented as percent Index of Relative Importance (IRI%) for each year.

Prey Item	*Life Stage*	*1998*	*1999*
Aquatic Invertebrates			
Ephemeroptera			
Baetidae	nymphs	2.2%	6.1%
	subimago	10.8%	4.6%
Other	nymphs	0.4%	0.6%
	subimago	0.0%	0.4%
Diptera			
Chironomidae	larvae	1.8%	2.4%
	pupae	21.3%	48.4%
	larvae	0.1%	0.5%
	pupae	0.0%	0.3%
Trichoptera			
Hydropsychidae	larvae	32.0%	20.5%
	pupae	3.7%	2.1%
	larvae	0.1%	0.5%
	pupae	0.2%	1.7%
Oligochaeta		0.8%	0.6%
Zooplankton		15.0%	4.2%
Aquatic Invertebrate Sub-total		**88.4%**	**92.8%**
Fish			
Salmonidae	eggs	0.6%	0.2%
	juveniles	0.0%	3.5%
Cottidae	eggs	1.4%	0.0%
	larvae & adults	2.2%	0.2%
Other	eggs	0.0%	0.0%
	larvae & adults	0.5%	0.1%
Unidentifiable		0.3%	0.1%
	Fish Sub-total	**5.5%**	**4.0%**
Terrestrial Arthropods		5%	2.4%
Others		4.6%	0.8%
	Grand Total	**100.0%**	**100.0%**

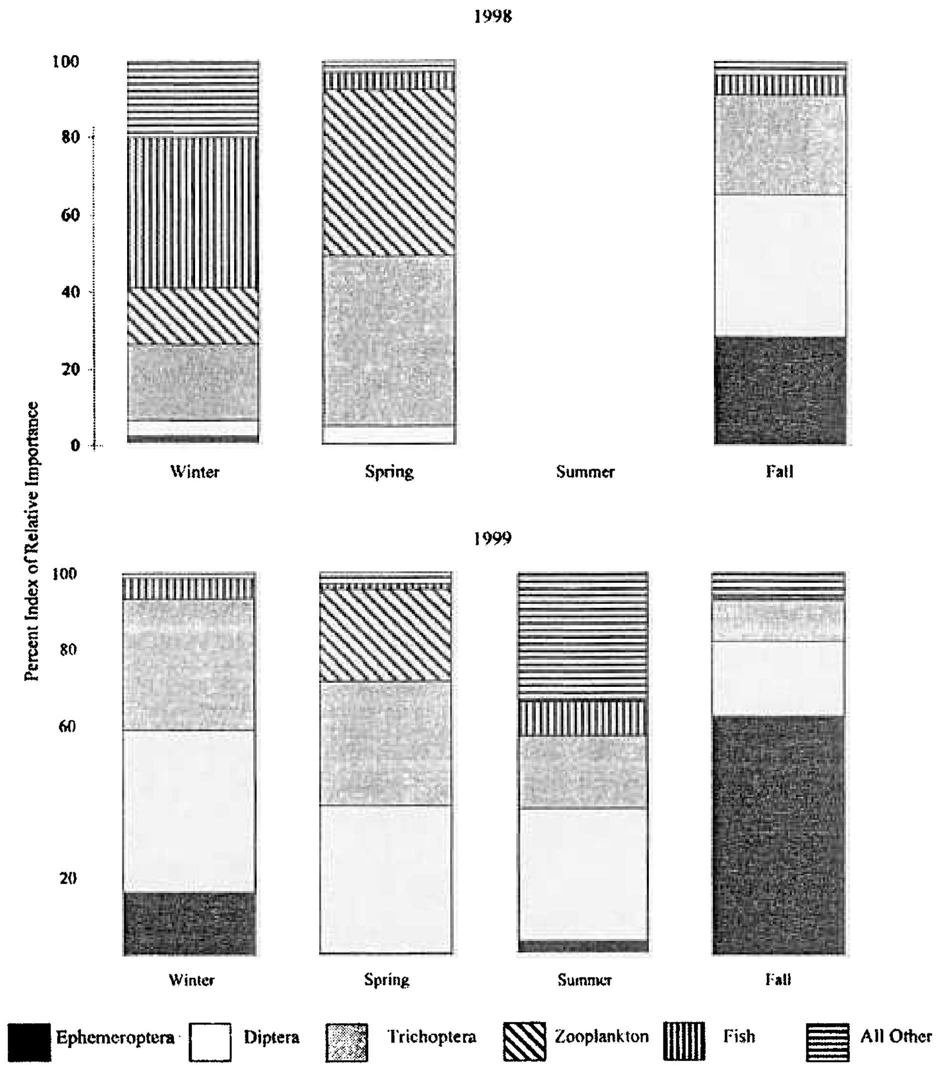

Figure 4. Major food items of steelhead in the lower Mokelumne River by season, 1998 and 1999. Food items are presented as percent Index of Relative Importance (IRI%) for each season.

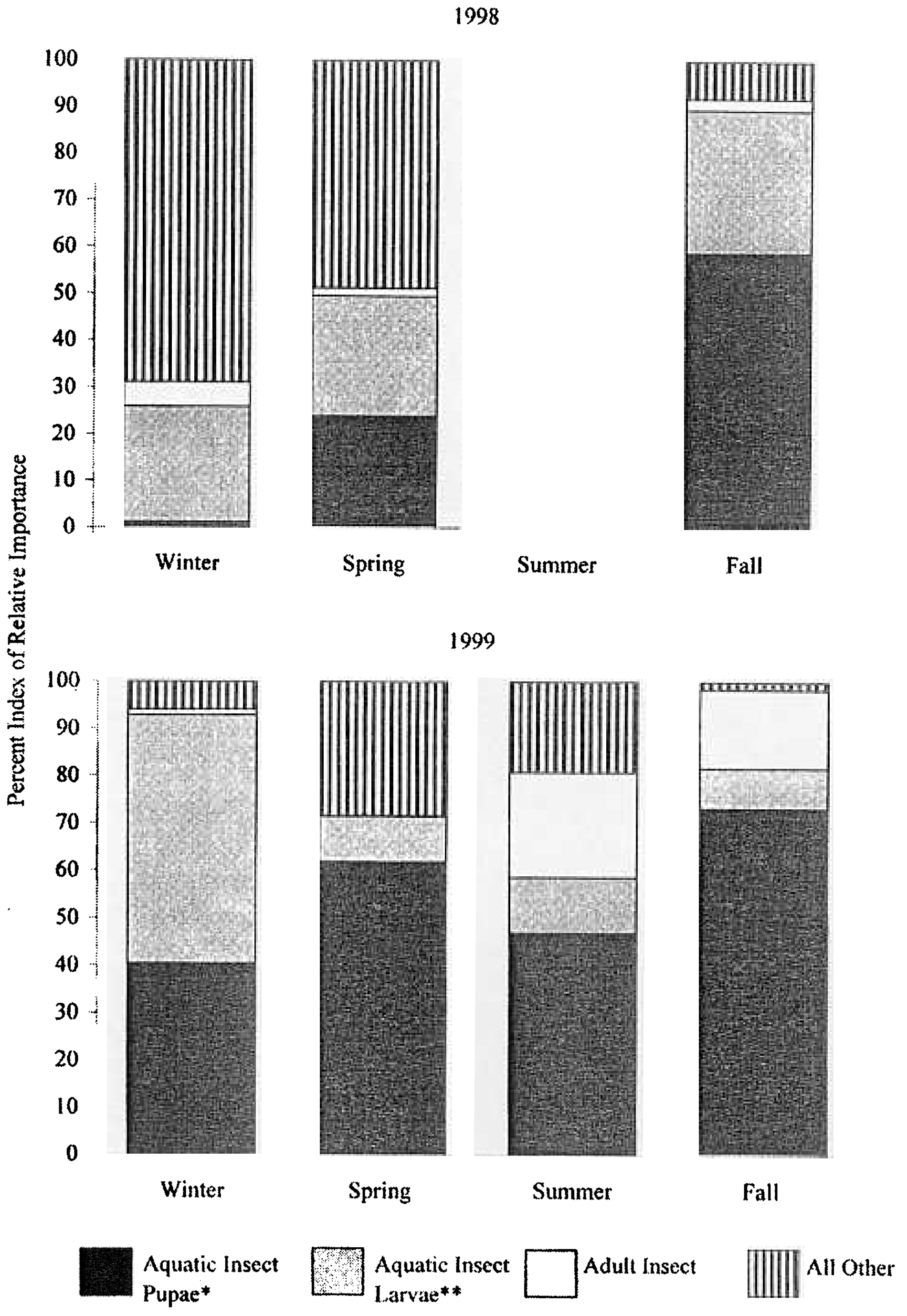

Figure 5. Life stages of organisms ingested by steelhead trout in the lower Mokelumne River by season, 1998 and 1999. Life stages are presented as percent Index of Relative Importance (IRI%) for each season.

*Pupae include Ephemeroptera subimago **Larvae include Ephemeroptera nymphs

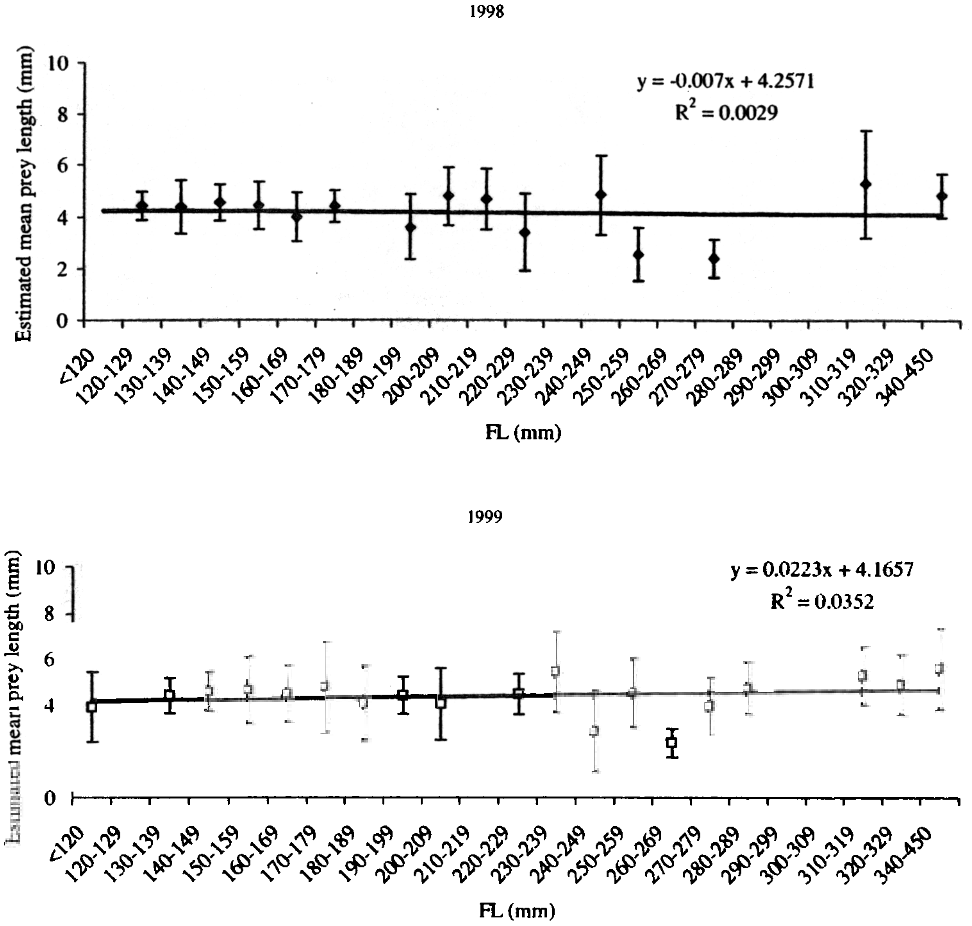

Figure 6. The relationship of Mokelumne River steelhead trout forklength (FL) and food size ingested, 1998 and 1999, as indicated by mean food item size, trend line and one standard deviation.

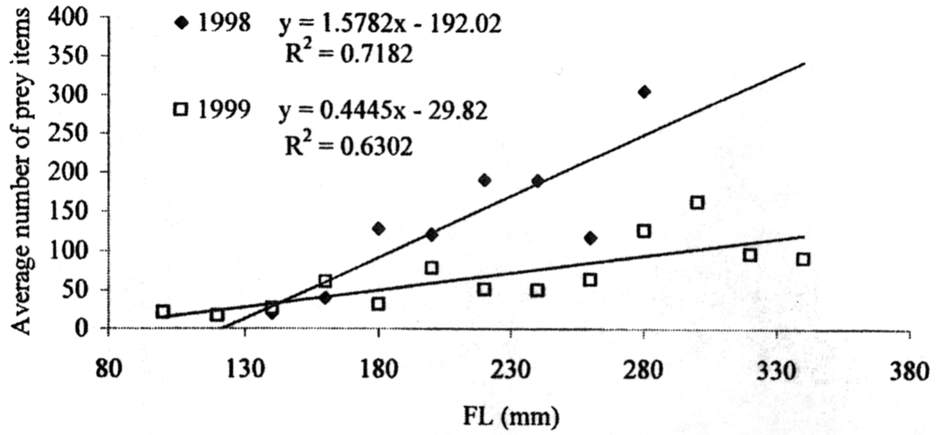

Figure 7. Average number of prey items per steelhead stomach in 1998 and 1999. Equations for simple linear regression are indicated for 1998 and 1999.

Feeding Activity

Seasonal feeding activity, as indicated by Index of Fullness (IF), suggests greatest feeding activity occurred during winter in both years (Fig. 8). Seasonal IF in 1999 was significantly less than in 1998 (*t*-ratio = -3.26; df = 3; *P* = 0.047). Index of Fullness was not significantly related to FL in either year (F = 0.0260; df = 2; 136; *P* = 0.97). However, IF for each size of fish was significantly less in 1999 (F = 9.89; df = 1, 137; *P* = 0.002). Of the 179 steelhead trout stomachs sampled, only one (0.6%) empty stomach was observed from a 380-mm FL adult male releasing milt in winter 1998.

Mats of filamentous algae were observed in 43 (24%) of the stomachs sampled. During fall 1998 and winter 1999, 18 (10%) of the stomachs sampled contained chinook salmon and steelhead trout eggs. Interestingly, bird feathers were found in 15 (8%) of the stomachs sampled. Small mammal hair (excluding one intact mouse) was found in two (1%) steelhead trout stomachs. Thirty of 288 (10%) steelhead captured by electrofishing during this study had distinct hook scars, including fishing line protruding from mouths.

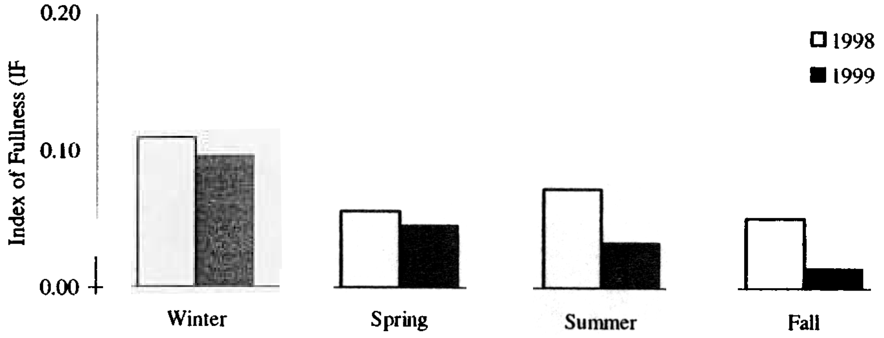

Figure 8. Seasonal feeding patterns of steelhead trout in the lower Mokelumne River, 1998-1999, as indicated by Index of Fullness (IF).

Fish Dispersal and Growth

A total of 267 steelhead was tagged during the 2-year study, including two adipose fin-clipped fish. Of these, 22 (8 %) were recaptured (Adult = 6; Smolt = 2; Silvery/parr = 9; Parr = 5) (Table 3) by electrofishing (21), seine (1) and creel surveys (1) through July 2001. No fish were re-captured by rotary screw trap nor were any adipose fin-clipped fish re-captured. Recaptured steelhead were observed anywhere from 5 to 985 days after tagging (mean = 269 days). Average fish growth was 0.32 mm/day (min = 0.04; max = 0.92). Smaller fish tended to grow more quickly than larger fish (Table 3). However, no significant difference was observed for daily growth between lifestages (F = 1.269; df = 21; *P* = 0.315). While all recaptured adult steelhead were observed at their initial tagging sites, a significant number of tagged parr, silvery/parr, and smolts

Table 3. Growth rates of tagged steelhead in the lower Mokelumne River, California.

Tagged			Recapture							
Date	FL (mm) (mm)	Lifestage*	Date	FL (mm)	Lifestage*	Growth (mm)	Total Days	Growth/day (mm)	Degree Days	Average Temperature (°C)
11/9/1998	80	P	7/20/2000	231	AD	151	985	0.15	12,497	12.7
11/10/1998	160	P	1/14/1999	163	SM	3	65	0.05	809	12.5
11/10/1998	135	P	1/19/1999	141	SP	6.5	70	0.09	858	12.3
5/14/1998	34	P	5/26/1998	45	P	11	12	0.92	169	13.0
5/14/1998	32	P	5/26/1998	42	P	10	12	0.83	169	13.0
1/21/1999	151	P	7/28/1999	236	SP	85	188	0.45	2,033	10.8
Average:	99		Average:	143			Average:	0.42		
12/16/1998	145	SP	1/19/1999	158	SP	13.5	34	0.40	357	10.5
7/27/1999	258	SP	10/23/2000	320	AD	62	455	0.14	6,093	13.4
1/20/1999	224	SP	1/23/2001	386	AD	162	368	0.44	4,545	12.4
4/27/1999	245	SP	7/27/1999	275	SP	30	93	0.32	1,098	11.8
1/14/1999	138	SP	1/19/1999	138	SP		5	0**	57	11.5
1/19/1999	161	SP	7/28/1999	197	SP	36	195	0.18	2,335	12.0
4/27/1999	240	SP	7/27/1999	299	SP	59	88	0.67	1,098	11.9
1/14/1999	140	SP	1/19/1999	140	SP		5	0**	57	9.6
5/1/2000	207	SP	7/20/2000	240	SP	33	80	0.41	1,056	13.2
Average:	195		Average:	239			Average:	0.37		
11/9/1998	277	SM	1/21/1999	310	AD	33	73	0.45	932	12.8
1/20/1999	271	SM	7/20/2000	320	SM	49	547	0.09	6,742	12.3
Average:	274		Average:	315			Average:	0.27		
11/3/1998	354	AD	11/9/1998	354	AD		7	0**	115	16.4
11/9/1998	410	AD	7/2/1999	420	AD	10	234	0.04	2,633	11.3
5/15/1997	235	AD	11/9/1998	352	AD	117	543	0.22	2,618	14.6
7/27/1999	240	AD	10/23/2000	333	AD	93	455	0.20	6,093	13.4
7/27/1999	302	AD	10/23/2000	333	AD	31	452	0.07	6,093	13.5
Average:	308			358			Average:	0.13		

*P = parr; SP = silvery parr; SM = smolt; AD = adult

**Fish recaptured 7 days or less after tagging were excluded from growth averages

were recaptured upstream and downstream of the original tagging sites (min = 0.8 km; max = 2.5 km). When comparing re-capture locations of adult and sub-adult steelhead recaptured at least 7 days after tagging, a significantly higher number of juveniles were captured at sites other than the original tagging location ($G^2 = 7.18$; df = 20, $P = 0.007$).

DISCUSSION

The diet of LMR steelhead trout was composed chiefly of immature stages of aquatic insects, similar to what has been reported in other studies (Shapovalov and Taft 1954, Johnson and Johnson 1981, Angradi and Griffith 1990, Merz and Vanicek 1996). However, due to the opportunistic feeding behavior displayed by steelhead trout (Byan and Larkin 1972, Moyle 1976, Barnhart 1986), a variety of other prey items momentarily swamped their diets, as can be seen in the consumption of salmonid eggs and juveniles in fall and winter 1998 (Fig. 4). Steelhead trout were observed actively feeding downstream and amongst spawning chinook salmon and other steelhead trout. During this time, in addition to salmonid eggs, large numbers of hydropsychid (Trichoptera) larvae and pupae were observed in sampled steelhead trout stomachs, presumably dislodged from the benthos by spawning activity.

While several aquatic insects appear to play an important role in the diets of LMR steelhead trout, it appears that these fish may rely on pupating and emerging individuals during certain periods. Specifically, Diptera pupae and Ephemeroptera nymphs undergoing transformation (subimago) provided over 50% of relative IRI for steelhead trout in fall of both years (Fig. 5). Large numbers of exoskeletons from emerging hydropsychids and heptageniids were also observed sporadically in individual trout, which were apparently keying in on these items. While IRI values were not calculated for ingested exoskeletons in this study, they may provide some caloric value for steelhead trout, further emphasizing the importance of pupating and emerging aquatic insects in the diets of these fish.

Angradi and Griffith (1990) reported that 30% of rainbow trout stomachs they sampled from the Snake River, Idaho contained filamentous algae. Similarly, 24% of steelhead stomachs sampled from the LMR contained mats of algae. Angradi and Griffith (1990) found a correlation between this phenomenon and number of Trichoptera larvae consumed. I also observed Trichoptera larvae in most (93%) of the LMR steelhead stomachs sampled that contained algae. Steelhead were observed during this study scraping the substrate with their sides and mouths, dislodging algae, which was either ingested by them or other trout close by. This behavior also occurred below spawning salmonids. Very early baetid instars and several species of zooplanton ($\leq$1 mm TL) have been reported in algal mats sampled during benthic and drift studies within this geographic area (Merz[4] 1992, Merz[5] 1998). This suggests steelhead trout may actively pursue algal material and may benefit by the concentration of relatively small prey items contained within the mats. This subject should be studied further.

Smith and Li (1982) found that in a California stream, increased fish size and water

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temperature resulted in increased standard metabolism and food demand by juvenile steelhead. Fish responded to these factors by selecting microhabitats with higher velocities, and shallower and coarser substrate to capture prey from portions of the water column substantially faster and more productive than at their resting positions. Similarly, LMR steelhead had higher IF values in 1998 than 1999 suggesting greater feeding activity during a warmer and higher flow water year (Figs. 3 and 8). While larger prey items (20 mm + TL), such as fish and crayfish occasionally appeared in the stomachs of steelhead trout, average prey size did not increase with size of fish or during the warmer water year (Fig. 6), supporting findings by Smith and Li (1982). Although this study did not specifically look at microhabitat use, adult Mokelumne River steelhead were more apt to remain in one area than juvenile fish and were observed in the same sampling sites for as much as 543 days after tagging. This is most likely due to the ability of larger fish to obtain and keep territories (Keeley and McPhail 1998; Keeley 2000).

In summary, these data suggest that while LMR steelhead trout eat a wide variety of prey items of various sizes, the majority of items ingested by several year-classes are small aquatic insects and zooplankton. Steelhead trout also ingest algal material although it is unclear whether very small prey items within the algae or the algal material itself is the purpose of this feeding behavior. River temperature influences the number, but not necessarily the size, of prey items ingested by individual fish. Mokelumne River steelhead may remain in a single habitat for up to 543 days, but this is dependent on the size and age of the fish. Further understanding of specific habitat/feeding relationships of these fish may improve restoration efforts within the Sacramento-San Joaquin System.

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