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SALMON, WILDLIFE, AND WINE: MARINE-DERIVED NUTRIENTS IN HUMAN-DOMINATED ECOSYSTEMS OF CENTRAL CALIFORNIA

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Abstract. Pacific salmon transfer large quantities of marine-derived nutrients to adjacent forest ecosystems with profound effects on plant and wildlife production. We investigated this process for two highly modified California wine country rivers, one with (Mokelumne River) and one without (Calaveras River) consistent salmon runs. Mokelumne River Chinook salmon transported biomass and N comparable to Pacific Northwest salmon streams. Calaveras River levels were much less. Scavenger numbers correlated with salmon carcass counts over time on the Mokelumne River but not the Calaveras River. Likewise, salmon carcasses were consumed significantly faster on the Mokelumne River. Native riparian vegetation as well as cultivated wine grapes adjacent to Mokelumne River spawning sites received 18–25% of foliar N from marine sources, significantly higher than vegetation along the Calaveras River. These data suggest that robust salmon runs continue to provide important ecological services with high economic value, even in impaired watersheds. Loss of Pacific salmon can not only negatively affect stream and riparian ecosystem function, but also affect local economies where agriculture and salmon streams coexist.

Key words: Calavaras River; Chinook salmon; marine isotope; Mokelumne River; nitrogen; nutrient transfer; riparian ecosystem; vineyards.

Introduction

Because of their large populations and body sizes, Pacific salmon (*Oncorhynchus* spp.) are a major food source for terrestrial and aquatic organisms associated with spawning streams, from bears (*Ursus* spp) to bacteria (Willson et al. 1998, Cederholm et al. 1999, Hilderbrand et al. 1999*b*). Pacific salmon spend most of their life cycles as top predators in the nutrient-rich North Pacific Ocean, where they incorporate carbon, nitrogen, phosphorus, and other micronutrients into their body tissues. These tissues provide an important nutrient and energy subsidy to oligotrophic streams where the salmon spawn and eventually die (Willson and Halupka 1995, Wipfli et al. 1998). Spawning salmon release nutrients into streams through normal metabolic processes, release of gametes, consumption of salmon flesh by predators and scavengers, and decay of carcasses.

Recently, the use of stable isotopes to trace trophic pathways has revealed that marine-derived nutrients from Pacific salmon are transferred not only into aquatic ecosystems, but into adjacent terrestrial ecosystems (Chaloner et al. 2002, Helfield and Naiman 2002, Bilby et al. 2003). The large difference in heavy isotope (e.g., ^{15}N and ^{13}C) composition of salmon tissue relative to freshwater or terrestrial values has been used to estimate the proportion of salmon-derived N or C in animal tissues, invertebrates, biofilms, and plant communities (Gende et al. 2002). For instance, the ratio of the heavier element ^{15}N to its lighter, more abundant isotope ^{14}N is higher in sea water than in fresh water. Similar high ratios occur in marine organisms and in salmon which prey on marine organisms during their time at sea. Thus, ecosystem subsidies provided by spawning salmon are marked by the distinct isotopic "signature" of the marine environment. Therefore stable isotope analysis provides a means for tracing marine elements from spawning salmon through the trophic systems of the streams they use, as well as those of adjacent terrestrial systems. Marine-derived nitrogen (MDN) has been found in riparian vegetation tissue far from river banks (Ben-David et al. 1998). Observations of MDN signatures in bird guano (Hocking and Reimchen 2002), adult aquatic insects, and terrestrial vertebrate scat and urine (Hilderbrand et al. 1999*a*) suggest a pathway of nutrient transport from salmon tissue to terrestrial systems beyond simple transport through root systems of trees (Naiman et al. 2002).

Salmon carcasses play an important role in the behavior and ecology of many terrestrial consumers (Hansen 1987, Ben-David 1997, Hilderbrand et al. 1999*b*). Densities of many vertebrates increase around streams in which salmon are spawning as they move in from surrounding areas to feed on the salmon (Gende et al. 2002). This can have a profound effect on salmon

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nutrient dispersal. Terrestrial scavengers may move 58% to 90% of all salmon biomass to land, sometimes hundreds of meters from the stream (Reimchen 2000), providing a transport mechanism for as much as 85% of MDN uptake of riparian foliage within 0.5 km of the spawning channel (Hilderbrand et al. 1999*a*).

The salmon subsidy results in an increase in the abundance and growth rates of aquatic invertebrates and fish (Wipfli et al. 2003) and riparian tree production (Helfield and Naiman 2001). Salmon-derived nutrients are also part of a positive feedback loop that benefits salmon populations. These nutrients cause aquatic and terrestrial insect populations to increase, resulting in faster growth and higher survival rates in juvenile salmon (Larkin and Slaney 1997). The complexity of stream habitat, important for both juvenile and spawning salmon, also increases when large, salmon-fertilized trees fall into the water.

In light of this overwhelming evidence of salmon importance over many scales of ecological function, there have been calls for managers to take into account the role of salmon nutrients in aquatic and terrestrial ecosystems (e.g., Larkin and Slaney 1997). However, these processes have mainly been studied in pristine systems of Washington, British Columbia, and Alaska. In this paper, we document their importance to human-dominated ecosystems in central California.

The rivers of California's Central Valley historically supported runs of 1–3 million salmon per year. Chinook salmon (*Oncorhynchus tschawytscha*) were the most abundant anadromous salmon in these streams, but four other species, to a much lesser extent, were also present (Yoshiyama et al. 1998, 2000). Presumably, nutrients derived from salmon were once very important to the regional aquatic and riparian ecosystems. Today, less than 28% of historical Chinook salmon spawning habitat is available because of dams and diversions although around 200 000 salmon still enter these rivers and their hatcheries each year (Yoshiyama et al. 2000, 2001). Up to 80% of adult fish may be harvested by sport and commercial fisheries, generating as much as $50 million annually to California's economy (Leet et al. 2001). The ecosystems of which these fish are part, however, have been dramatically changed. An estimated 60–96% of the approximately 400 000 ha of riparian forest has been transformed into agricultural production and urban development (Shelton 1987, Noss et al. 1995). This includes 163 412 ha of grape vineyards producing 2 292 505 metric tons of grapes and eventually over 1.7 billion liters of wine annually (California Department of Food and Agriculture 1998). While there is great interest in salmon restoration in California, no connection has been made to the likely historic importance of salmon for delivering marine nutrients to inland California ecosystems. Likewise, the potential importance of even depleted runs as a source of nutrients for both natural and agricultural systems has been ignored. This is compounded by the fact that hatcheries may produce 20–77% of all California ocean harvest but export large portions of salmon runs to rendering facilities (California Department of Fish and Game 2001).

To assess the importance of salmon to central California ecosystems, we (1) estimated the amount of nutrients (i.e., N and C) carried into the Central Valley by salmon and how this compares to values from more pristine settings in the Pacific Northwest; (2) surveyed salmon scavengers and predators in two adjacent streams, one with a robust salmon run and one without; and (3) compared salmon-derived N ratios in both natural riparian vegetation and riparian vineyards above and below non-passable dams on these two rivers. Our goal was to see if pathways for salmon-derived materials still functioned in highly modified salmon stream ecosystems.

STUDY SYSTEMS

The Mokelumne and Calavaras rivers flow out of the Central Sierra Nevada and enter the San Francisco Estuary between Sacramento (38°31′ N, 121°30′ W) and Stockton (37°57′ N, 121°19′ W). The area has a Mediterranean climate with precipitation occurring mainly between December and March. The Mokelumne River watershed covers an area of approximately 1620 km^2 extending from the Central Valley (50 m elevation) to the crest of the Sierra Nevada (3300 m) The river has 16 major impoundments with the lowermost being Camanche reservoir (531 387 061 m^3). Camanche outflow has lows near 4.25 m^3/s, peaks never exceeding 200 m^3/s, and average daily flow (for the period 1964–2000) of 22.6 m^3/s (minimum, 0.7 m^3/s; maximum 162.8 m^3/s; Pasternack et al. 2004). The lower Mokelumne River (LMR) is the only reach still accessible to anadromous fish and ranges in elevation from approximately 28 m at Camanche Dam (38°13′30″ N, 121°01′30″ W) to sea level at Thornton (Fig. 1). The LMR watershed consists of 213 km^2 of which about 51% is in vineyards; 31% is in dairy/grazing, and 9% is in orchards (San Joaquin County Resource Conservation District 2002), although the area is also becoming increasingly suburbanized. Riverbanks are characterized by 50–100 m sections of broken concrete and stone riprap with a thin ribbon of Fremont cottonwood (*Populus fremonti*), valley oak (*Quercus lobata*), willow (*Salix* spp.), and some white alder (*Alnus rhombifolia*). Numerous nonnative trees and shrubs are also common.

Chinook salmon and steelhead populations have been supplemented since 1964 by Mokelumne River Fish Hatchery (MRFH) production (Fig. 1). The annual LMR fall-run Chinook salmon migration begins in September, peaks in November, and tapers off in December and early January. Spawning generally occurs shortly after migration, primarily in late October through January, mainly in the 16-km reach below Camanche Dam (rkm 102.2 [river kilometer]), which was historically the downstream limit of salmon spawning. Average annual escapement was 3300 fish in the 19 years

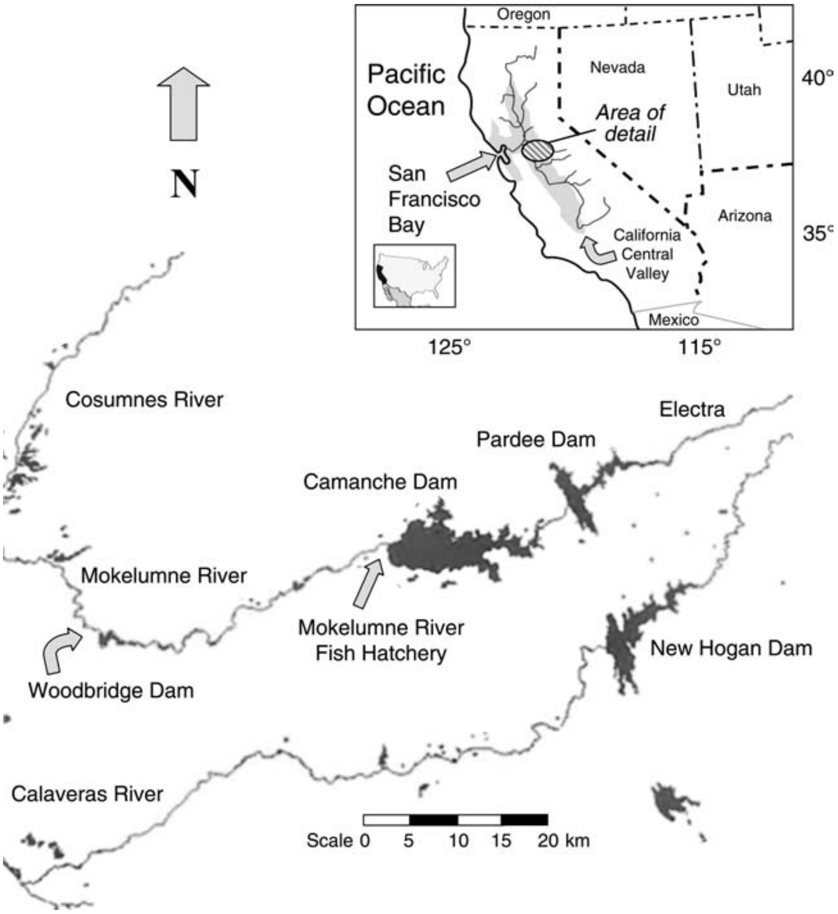

FIG. 1. The Mokelumne and Calaveras rivers in relationship to the western United States, and the California Central Valley and its major rivers (inset). The two study areas are the ~16 km reach below Camanche Dam and the ~5 km reach below New Hogan Dam.

prior to Camanche Dam construction, a period when instream gravel mining was widespread; recent escapement has ranged from 410 fish in 1991 to over 10 000 fish in 1997 (Merz and Setka 2004).

The Calaveras River is a rain-dominated system with an estimated 1217-km^2 watershed. The one large dam on the river, New Hogan (rkm 68), is located at 137 m above mean sea level and is the upper extent of anadromous salmonid habitat. Flows below the dam (built circa 1964) have been modified with an average release of 6.21 m^3/s and peak of 476 m^3/s. Peak flows typically occur during the summer (late April through September) with dry channel presently occurring in less than 2% of years. Riparian vegetation is mostly Fremont cottonwood, box elder (*Acer negundo*), California buckeye (*Aesculus californica*), and several willow species (*Salix* spp.). Riparian lands are influenced by several large housing developments. Cattle grazing and a variety of crops, including wine grapes, occur throughout this region.

Very little is known about the fishes of the Calaveras River and historical salmonid records are limited. Chinook salmon runs reportedly occurred on an irregular basis although size and timing of runs is unclear (Reynolds et al. 1993 as cited in Yoshiyama et al. 2001). In the period of 1972–1984, an unusual run numbering 100-1000 fish spawned in late winter and spring in the reach just below New Hogan Dam. At the time of this study, regular adult spawning surveys were not conducted on the river but probably fewer than 100 individuals immigrated to potential spawning grounds each year (T. Kennedy, *personal communication*).

METHODS

Adult salmon, carcass, and redd enumeration

Mokelumne River.—Migrating adult Chinook salmon were enumerated via underwater video camera and adult salmon traps located at the Woodbridge Irrigation District Dam in Lodi, California (Merz and Merz 2004, Workman 2004). Annual Mokelumne River carcass and redd surveys are described in Workman (2004) and Merz and Setka (2004). Briefly, surveys were conducted weekly between 1 October 2003 and 12 January 2004 along the 16-km reach, including all available spawning habitat below Camanche Dam. Three surveyors boated and walked downstream searching for salmon carcasses and signs of redd construction. Carcasses were enumerated. Redd locations were recorded using a hand-held Global Positioning System (GPS) unit (Trimble Pro XR; Trimble Navigation Limited, Sunnyvale, California, USA) and a laser range finder (Atlanta Advantage; Laser Atlanta, Norcross Georgia, USA). Location of each redd was downloaded from the GPS unit into an ArcView (ESRI, Redlands, California, USA) coverage. Spawning densities (no. redd/m^2 spawning habitat) were then calculated for spawning areas adjacent to vegetation sampling locations to compare against those reported in the literature.

Tissue collection and analysis

We performed tissue analysis on (a) one ocean-returned, hatchery-origin adult female Chinook salmon captured by an angler in the Mokelumne River; (b) three ocean-returned adult males captured by anglers in the Mokelumne River; (c) one ocean-caught male Chinook salmon of unknown origin; (d) four post-spawned Chinook salmon (2 male; 2 female) collected from the Mokelumne River Fish Hatchery; and (e) 26 Chinook salmon eggs recovered from one spawning bed on the LMR. Approximately 1 gram (wet weight) of white muscle was extracted from the dorsal region of each salmon carcass. Fish muscle and whole eggs were dried at 80°C for 48 h, ground into fine powder using mortar and pestle, and packed into 4 × 6 mm tin capsules. We performed stable N isotope analysis using a continuous flow Europa Hydra 20/20 isotope ratio mass spectrometer at the University of California, Davis, Stable Isotope Facility. Stable isotopes are expressed in delta notation, defined as parts per thousand (‰) deviation from a standard material, and are calculated as

$$\delta^{15}\mathrm{N} = ([R_{\mathrm{sample}}/R_{\mathrm{standard}}] - 1 \times 1000$$

where $R = {}^{15}\mathrm{N}/{}^{14}\mathrm{N}$, and the standard material is atmospheric N. The typical ratio for atmospheric N is therefore $\delta^{15}\mathrm{N}_{\mathrm{standard}} = 0$.

To estimate salmon biomass transported to the Mokelumne River, we multiplied the average weight of an adult Chinook salmon by the number of fish counted at Woodbridge Dam annually. Average mass for adult California Chinook salmon is about 10 kg (Laird and Needham 1988, Moyle 2002). To estimate the amount of N and C transported to the Mokelumne and Calaveras rivers by spawning Chinook salmon we used the formula

$$\mathrm{transport} = \mathrm{nut}\% \;\times \mathrm{SW} \times \mathrm{SP}$$

where nut% is the average percentage of C or N in each tissue sample, SW is the average weight of Mokelumne River Chinook salmon, and SP is salmon escapement to the Mokelumne or Calaveras rivers.

We estimated %MDN from observed δ^{15}N values using the methods described by Helfield and Naiman (2002) using a two-source mixing model that calculates MDN percentages as

$$\%\ \mathrm{MDN} = ([\mathrm{SAM} - \mathrm{TEM}]/[\mathrm{MEM} - \mathrm{TEM}]) \times 100$$

where %MDN is the percentage of MDN in a given sample, SAM is the mean foliar δ^{15}N of each species at spawning sites, TEM is the mean δ^{15}N of conspecific foliage at reference sites, and MEM is the mean δ^{15}N of Chinook salmon tissue samples.

Terrestrial scavenger surveys

Mokelumne River.—Fourteen Chinook salmon carcasses were obtained from the Mokelumne River Fish Hatchery (MRFH). Carcasses were measured (fork length) and sexed, and spawning stage (pre-spawn or post-spawn) was noted. Twelve carcasses were staked to the ground and two were laid on the ground between 10 November 2003 and 5 January 2004. All carcasses were stationed within 3 m of the riverbed along the ~16 rkm (river kilometer) spawning reach. Stealthcam MC2-G 35mm infrared motion detector scouting cameras (Stealth Cam, Bedford, Texas, USA) were used at all sites. Cameras were programmed to shoot one picture every 15 min beginning when motion was detected, and were not removed until carcasses were skeletonized.

During salmon carcass and redd surveys, three surveyors enumerated identifiable Turkey Vultures (*Cathartes aura*), a common carcass scavenger, to assess the relationship between carcass numbers and scavenger densities. Crews used a drift boat or canoe to float downstream from the base of Camanche Dam approximately 16 rkm, the extent of major spawning habitat. Weekly counts of vultures were made over approximately 8 h during regular salmon carcass and redd surveys.

Calaveras River.—The Calavaras River was studied in the year following the Mokelumne River studies after we realized that our study would be improved if we compared a stream with low salmon use with the Mokelumne. Thirteen adult Chinook salmon carcasses were obtained from the Mokelumne River Fish Hatchery and physical data noted. Between 15 November 2004 and 15 January 2005, individual carcasses were laid out along the riparian area of the Calaveras River approximately 2.5–5 km downstream of New Hogan Reservoir, following the methods described above. During weekly camera operation, one to two surveyors walked a 3-km trail along the river bank, enumerating identifiable Turkey Vultures and searching for signs of salmon spawning (redds and carcasses). Camera settings and operation were the same for both rivers.

Vegetation sample collection and analysis

To evaluate the effects of salmon-derived nutrients on native riparian vegetation and riparian vineyard production, we divided the Mokelumne and Calaveras watersheds into spawning sites (i.e., sites adjacent to reaches accessible to spawning salmon) and reference

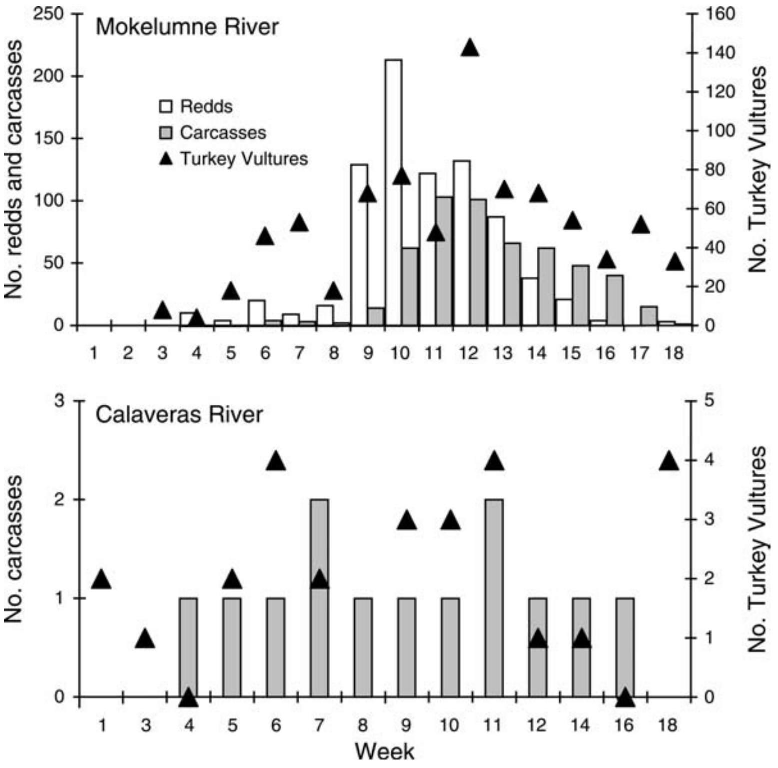

FIG. 2. Observations of fall-run Chinook salmon redds, post-spawn carcasses, and Turkey Vultures during surveys of the lower Mokelumne River (1 October 2003 through 12 January 2004) and the Calaveras River (1 October 2004 through 15 January 2005). In the Calaveras River, all carcasses were placed for study. Values are the total number observed for each study length per week (see *Methods*).

sites (sites adjacent to reaches not accessible to spawning salmon above Camanche and New Hogan dams). Field sampling occurred between April and May in 2003 and 2005. We set up four transects, extending 50 m from the river bank in one reference and one spawning site in each watershed. Because alders fix N, we avoided transects where they constituted more than 50% of the trees observed (Bilby et al. 2003); in sample areas they were a small percentage (<5%) of the shrubs and trees. We collected samples every 5 m along each transect ($n = 80$). Foliar samples were taken from the nearest *Salix exigua* (trunk diameter of 5–6 cm) with canopy in direct sunlight and nearest *Populus fremontii* (trunk diameter of 15–30 cm; $n = 80$). Each watershed had two vineyard sites accessible to spawners and two reference vineyards. All sample vineyards were located within 25 m of either river channel and were watered directly from the channel. Foliage and stem samples were taken from approximately every fourth plant (vine stems between 5 and 8 cm) of *Vitis vinifera* along the closest vineyard row to the river channel at each site ($n = 72$).

Foliage samples were dried at 80°C for 48 h, ground into fine powder using mortar and pestle, and packed into 4 × 6 mm tin capsules. We measured stable isotope ratios ($^{15}N:^{14}N$) with a continuous flow Europa Hydra 20/20 isotope ratio mass spectrometer at the University of California, Davis, Stable Isotope Facility. Stable isotopes were analyzed as they were for salmon.

RESULTS

Between 15 August 2003, and 15 January 2004, 10 240 adult Chinook salmon were counted passing Woodbridge Irrigation District Dam with 8117 of these entering the Mokelumne River Fish Hatchery (Fig. 1). An unknown number of hatchery carcasses (<1000) were returned to the river. A total of 501 naturally occurring Chinook salmon carcasses were counted during the carcass survey with a peak of 103 observed during week 11 (24–28 November 2003; Fig. 2); 808 Chinook salmon redds were counted with a peak of 203 observed during week 10 (16–23 November 2003).

Between 15 August 2004 and 15 January 2005, <100 adult Chinook salmon were estimated to have entered the Calaveras River (T. Kennedy, *personal communication*). No redds or carcasses were observed other than the carcasses placed for the scavenger surveys.

Salmon-derived nutrients transported to the rivers

If we use the peak and 10-yr average (1993–2004) of Chinook salmon in the LMR (11 904 and 8162, respectively), annual migrations bring as much as 119 040 kg, with an average of 81 620 kg, of biomass. We estimate ~562 g of N is carried into the river in each

TABLE 1. Comparison of Mokelumne and Calaveras rivers to several other published stream studies of salmon-derived N along the Pacific Northwest.

Water body	Location	Stream length (km)	Salmon species	Mean mass (kg)	Mean annual escapement	Spawning density (no. salmon/m^2)	Mean annual biomass (kg)†	Mean annual N (kg)	Riparian foliage (MDN %) (range)	Source
Mokelumne	CA	16	Chinook	10	8162	0.48	81 620 (40 819)‡	5097 (2548)‡	21 (18–25)	1
Calaveras	CA	33	Chinook	10	<100	<0.01	<1000	<57	11 (5–16)	2
Kennedy	WA	5	chum	5.6	35 000	NP	196 000	5939	22 (NP)	3
Clatse	BC	1	pink, chum	1.8, 5.6	17 000, 5000	22	58 600	1776	29 (13–49)§	4
Neekas	BC	2.1	pink, chum	1.8, 5.6	18 000, 30 000	23	200 400	6072	54 (48–65)§	4
Kadashan	AK	NP	pink	1.8	77 500	NP	139 500	4227	23 (12–32)	5
Indian	AK	NP	pink	1.8	22 600	1	40 680	1233	23 (12–32)	5
Hansen	AK	2.1	sockeye	2.6	3986	1.9	10 364	315	25 (15–33)	6
Happy	AK	6.45	sockeye	2.6	5165	0.8	13 429	408	25 (15–33)	6
Ice	AK	16.13	sockeye	2.6	8622	0.53	22 417	681	25 (15–33)	6
Lynx	AK	2.26	sockeye	2.6	2921	1.29	7595	231	25 (15–33)	6
Pick	AK	4.03	sockeye	2.6	10 776	2.67	28 018	852	25 (15–33)	6

Note: Locations are: CA, California; WA, Washington; and AK, Alaska, USA; BC, British Columbia, Canada. NP, not provided.

† Mean annual biomass of adult salmon returning to each river.

‡ Number in parenthesis is wild spawners.

§ Estimated from figures.

Sources: 1, Merz and Moyle (this study); 2, U.S. Fish and Wildlife Service and California Department of Fish and Game, unpublished data; 3, Bilby et al. (2003); 4, Mathewson et al. (2003); 5, Helfield and Naiman (2001); 6, Helfield and Naiman (2002.)

returning fish. This suggests that annual spawning migrations bring as much as 6690 kg (average 4587 kg) of MDN and 35 288 kg (average 24 195 kg) of carbon to the LMR watershed each year, similar to observations in more pristine habitats of the Pacific Northwest (Table 1). If we assume the Calaveras River has a recent annual escapement of fewer than 100 adult Chinook salmon, then fewer than 57 kg of MDN and 296 kg of marine-derived carbon enter the lower Calaveras River annually. However, extrapolating our results with estimates of past run sizes in the past two decades (Yoshiyama et al. 2001), as much as 560 kg MDN and 2960 kg of marine-derived carbon could have been carried into the Calaveras River in some years.

Terrestrial scavenger surveys

A total of 14 vertebrate species, including two domestic animals, were observed feeding on 27 Chinook salmon carcasses on the Mokelumne (284 photos) and Calaveras rivers (226 photos) (Table 2). Although up to six individual organisms (Turkey Vultures) were observed in a single photo, we observed only two

TABLE 2. Observations of vertebrate species photographed feeding on Chinook salmon carcasses on two rivers in California, USA.

Species	Mokelumne River			Calaveras River		
	No. photos†	No. individuals‡	Maximum (mean)§	No. photos†	No. individuals‡	Maximum (mean)§
Black rat	2	2	1 (1)	0	0	0
Coyote	3	4	2 (1.33)	0	0	0
Domestic cat	2	2	1 (1)	63	63‖	1 (1)
Domestic dog	2	2	1 (1)	2	2	1 (1)
Gray fox	0	0	0	15	15	1 (1)
Gray squirrel	0	0	0	2	2	1 (1)
Mule deer	3	3	1 (1)	0	0	0
Opossum	8	8	1 (1)	7	7	1 (1)
Raccoon	75	98	3 (1.31)	45	48	2 (1.07)
Raven	0	0	0	1	1	1 (1)
Redtailed Hawk	0	0	0	8	8	1 (1)
River otter	2	4	2 (2.00)	3	4	2 (1.33)
Striped skunk	2	2	1 (1)	0	0	0
Turkey Vulture	79	156	6 (1.97)	80	813	2 (1.04)

Note: Observations were 14 Chinook salmon carcasses along the lower Mokelumne River, 10 November 2003 through 7 January 2004 and 13 Chinook salmon carcasses along the Calaveras River, 12 November 2004 through 15 January 2005.

† Number of photos in which each species was observed.

‡ Total number of individuals counted for each species.

§ Maximum (mean) number of individuals observed in a single photo.

‖ Appears to be one individual.

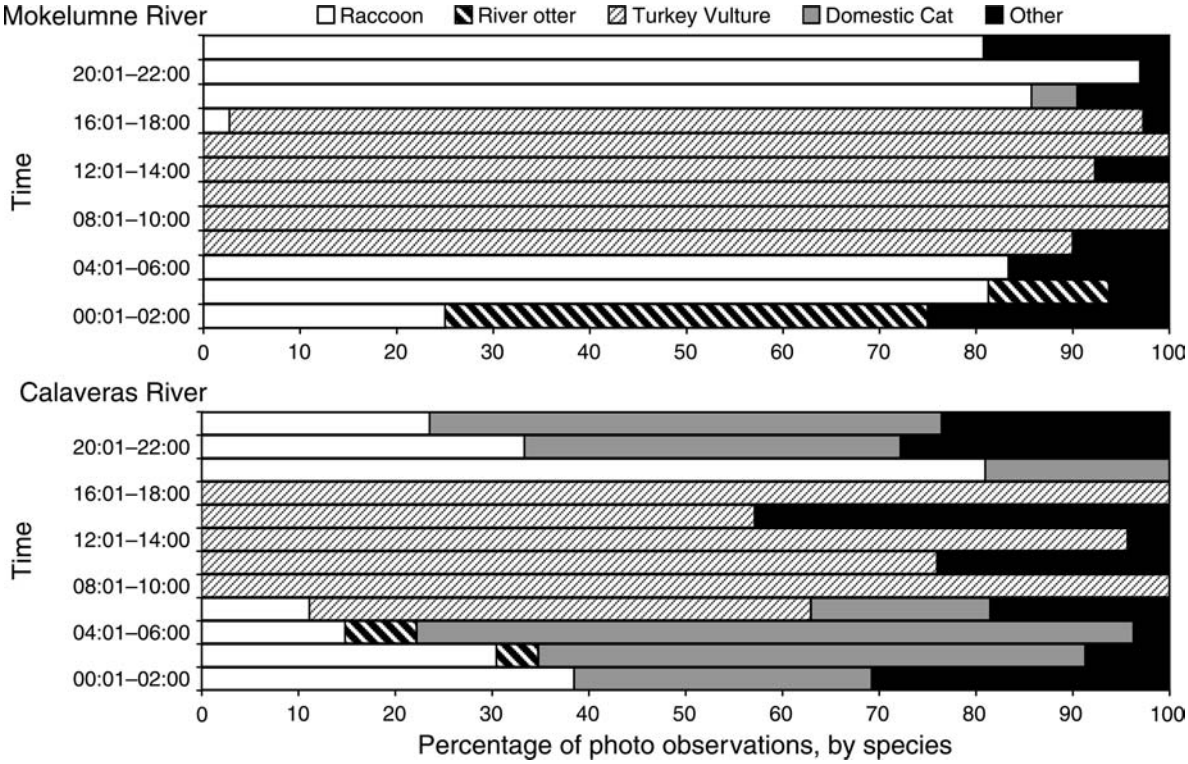

FIG. 3. Diurnal observations of scavengers observed in photos taken at Chinook salmon carcass stations along the Mokelumne and Calaveras rivers.

incidences of more than one species pursuing a single carcass (opossum and domestic cat; domestic dog and coyote).

Turkey Vultures and raccoons were the most common frequenters of salmon carcasses on the Mokelumne River, while Turkey Vultures and a domestic cat were most common on the Calaveras River. A distinct diurnal pattern was observed on both rivers (Fig. 3). Specifically, Turkey Vultures were the dominant day-feeder on salmon carcasses. During the nocturnal period, raccoons were the dominant species, although domestic cats (in most cases a single individual) were common on the Calaveras River.

Chinook salmon carcasses were consumed in as little as 12 h and as long as 189 h (mean 72.8 h). Carcasses were consumed significantly faster on the Mokelumne River (53.7 ± 43.9 h [mean ± SD]) than the Calaveras River (95.0 ± 59.7 h) ($F = 4.4436$, df = 1, 25, $P = 0.0448$). Carcass length had no significant effect on consumption rates ($F = 0.6504$, df = 1,25, $P = 0.4273$). Sex of carcasses had no significant effect on consumption time ($F = 0.4131$, df = 1, 25, $P = 0.5260$). Spawning had no significant effect on consumption rate of male carcasses ($F = 0.6132$, df = 1, 10, $P = 0.4517$). However, carcasses of unspawned females (eggs still intact) were consumed significantly faster than post-spawning female and male carcasses (2 d compared to 3.5 d; $F = 6.1911$, df =1, 13, $P = 0.0261$).

Turkey Vultures were common along the LMR, observed individually and in roosts of as many as 39 individuals. The rise and fall in vulture numbers correlated with the rise and fall of salmon carcasses observed on the LMR ($r^2 = 0.52$, $F = 14.6$, df = 1, 13, $P = 0.0019$; Fig. 1). On the Calaveras River, Turkey Vultures were less common. The highest concentration was three individuals. No natural salmon carcasses were observed on the Calaveras River and no significant correlation between Turkey Vulture numbers and placed salmon carcasses was observed ($r^2 = 0.001$, $F = 0.1155$, df = 1, 12, $P = 0.7399$).

MDN enrichment of riparian vegetation

Foliar $\delta^{15}N$ of Fremont cottonwood was significantly higher at spawning sites than reference sites on the Mokelumne ($F = 59.9271$, df = 1, 15, $P < 0.0001$) and Calaveras ($F = 59.9271$, df = 1, 15, $P < 0.0001$) rivers and significantly higher on Mokelumne River spawning sites than those on the Calaveras River (Fig. 4). Foliar $\delta^{15}N$ of sandbar willow was significantly higher at spawning sites relative to reference sites on the Mokelumne River ($F = 20.6758$, df = 1, 27, $P = 0.0001$) but not the Calaveras River ($F = 0.9775$, df = 7, $P = 0.3610$). Foliar $\delta^{15}N$ of wine grapes was significantly higher at spawning sites relative to reference sites on the Mokelumne ($F = 40.1806$, df = 1, 38, $P < 0.0001$) and Calaveras ($F = 5.4066$, df = 1, 19, $P =$

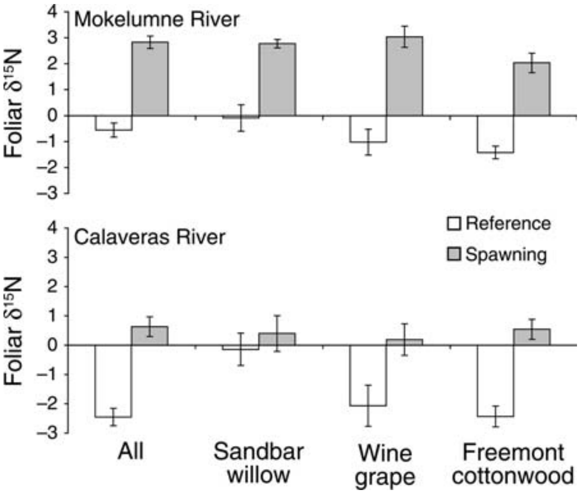

FIG. 4. Foliar δ^{15}N of riparian vegetation at spawning and reference sites along the Mokelumne and Calaveras rivers. Data are means ± SE.

0.0313) rivers and significantly higher on Mokelumne River spawning sites than those on the Calaveras River. We estimate that Mokelumne River riparian vegetation, including cultivated wine grapes, adjacent to spawning sites, derived 18–25% of N from a marine source (Table 1), similar to other studies (Fig. 5). Calaveras River estimates of 5–16% were significantly less ($F = 26.33$, df $= 1, 33$, $P < 0.0001$). Analysis of variation indicates a significant relationship between percent MDN in riparian foliage and estimated mean annual N per stream area within several Pacific Coast streams ($F = 18.78$, df $= 1, 5$, $P = 0.0075$).

DISCUSSION

Our study shows that salmon can subsidize ecosystems even in highly altered rivers that flow through agricultural areas. Significant amounts of marine-derived nutrients were detected in riparian foliage, including vineyards, along a regulated river that supports a robust salmon run. As in more pristine systems, salmon carcasses served as food for a wide variety of vertebrates and attracted large numbers of some species. We observed 14 terrestrial vertebrate species, including "herbivores" such as mule deer (*Odocoileus hemionus*) and western gray squirrels (*Sciurus griseus*), feeding directly on salmon carcasses. Similarly, Jauquet et al (2003) observed 18 terrestrial vertebrates directly consuming salmon carcasses or eggs in a forested watershed in Washington. Although the LMR drainage has lost large vertebrate scavengers, such as bears (*Ursus* spp.), wolves (*Canis lupis*), and to a great extent, bald eagles (*Haliaeetus leucocephalus*), domestic animals, such as cats (*Felis domesticus*) and dogs (*Canis domesticus*) and commensal animals, such as Turkey Vultures, opossums, and raccoons, may function in a similar manner. These animals and invertebrate scavengers, presumably transport nutrients to adjacent agricultural fields, including vineyards. The distinct differences in carcass consumption rates and scavenger numbers (mainly Turkey Vultures) between the Mokelumne and Calaveras rivers suggest that the nutrient transport system observed in more pristine systems continues to function in highly modified systems if the salmon runs also continue. However, once runs reach an unknown lower threshold, this transport mechanism may suffer, possibly because attraction cues, such as spawning activity and carcass concentrations, are insufficient to attract scavengers. Carcass quality may also affect this mechanism, as is illustrated by the faster consumption rates for unspawned females.

If we use the 10-yr average Mokelumne River escapement and data provided by Gresh et al. (2000), the Mokelumne River currently supports ~4% of California's adult Chinook salmon escapement. Gresh et al. (2000) used the findings of Larkin and Slaney (1997) to estimate that salmon carcasses have 3.03% N content, resulting in an estimate that salmon currently contribute 43 000 kg of N annually to California ecosystems. It is important to note that Larkin and Slaney (1997) used an average N content for all Pacific salmon species. However, species such as sockeye (*O. nerka*) have different dietary requirements than those of Chinook salmon (Groot and Margolis 1991). Trophic level can have a significant effect on the distribution of N isotopes in animals (DeNiro and Epstein 1981). Nitrogen content of Mokelumne River Chinook salmon tissue from our samples averaged 5.62% (SD = 0.90). If we use the peak estimate of 600 000 California Central Valley Chinook salmon escapement for the year 2001, and our average N estimate, California runs may actually contribute as much as 6000 metric tons of biomass, 1800 metric tons of C, and 337 metric tons of N to the Central Valley annually (784% more than estimated by Gresh et al. 2000). California's state fish hatchery system currently donates most salmon bodies from spawning production to profit and nonprofit organizations via rendering facilities. For the entire state hatchery system this loss may be 230–390 metric

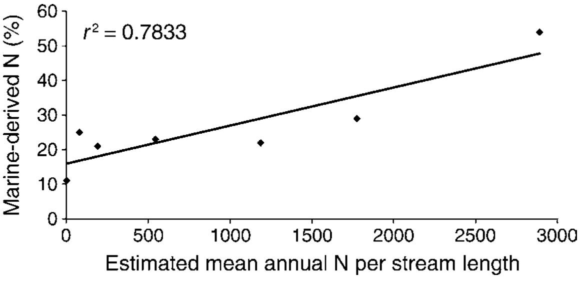

FIG. 5. The relationship between the percentage of marine-derived N (%MDN) observed in riparian foliage adjacent to spawning sites and the estimated mean annual salmon-derived N per stream length for the Pacific Northwest. Data are taken from four studies on 12 streams. Some data are pooled, depending on study methods (see Table 1).

tons of salmon (13–22 metric tons of MDN) removed from the Sacramento–San Joaquin River system annually.

Despite the potential for a large nutrient subsidy by salmon to riparian systems, it is possible that a portion of elevated δ^{15}N values observed were the result of other processes (Bilby et al. 2003). Denitrification rates, for example, increase under water-saturated, low-oxygen conditions, which are common at locations immediately adjacent to streams. Channel gradient, soil types, and precipitation can also affect foliar isotopic signatures. Furthermore, non-salmon bearing watersheds may have increased foliar δ^{15}N in plants growing in valley bottoms, due to greater soil N availability and net nitrification relative to more upland sites (Garten 1993). This may partially explain the higher δ^{15}N observed below New Hogan Reservoir than above the reservoir on the Calaveras River. However, while their numbers are estimated to be very low, Chinook salmon and steelhead spawning in the lower Calaveras River may also partially explain this increased MDN signal (Bilby et al. 2003). More importantly, the significantly higher δ^{15}N levels in vegetation sampled below Camanche Dam compared to vegetation from above the dam or anywhere on the Calaveras River is best explained as the result of marine-derived N from salmon rather than from edaphic or geographic factors (Helfield and Naiman 2001).

Ben-David et al (1998) identified three pathways by which salmon-derived isotopes can be transported to the terrestrial environment. They are (1) freshets and overbank floods; (2) uptake by riparian root systems via the hyporheic zone; and (3) piscivores and scavengers. While direct uptake by root systems of riparian plants is still a likely mechanism in regulated rivers, flooding is not. On the Mokelumne River, over-bank flooding rarely occurs during the spawning season (Pasternack et al. 2004) so carcasses typically can not be carried out of the river channel. However, riparian irrigation pumps may draft water directly from the channel to agricultural fields, sometimes 15+ km away. Depending on pump filtration (i.e., sand filters and screening), there is thus potential for salmon nutrients to be transported to irrigated crops. On both the Mokelumne and Calaveras rivers, scavengers eliminated carcasses in 2–8 d. While feeding on salmon, vultures appeared to stay in the river corridor, roosting and defecating in riparian trees when not feeding. Predation on live salmon, however, was not witnessed except for an osprey (*Pandion haliaetus*) taking adult steelhead. Furthermore, we observed numerous salmon jaw bones in vineyards and remaining riparian forest, supporting scavenger transport as an important mechanism.

Management implications

Our study indicates that managing regulated rivers for salmon has benefits far beyond simply providing fish for fishermen. The marine-derived nutrients of salmon can positively affect both natural riparian systems and agricultural crops, with considerable economic benefit.

Thus, increased production and diversity of plant communities along salmonid streams has been attributed to nutrient contributions made by salmon (Helfield and Naiman 2001, Bartz 2002, Naiman et al. 2002). Bilby et al. (2003) argue that nutrients from wild salmon can even be important to riparian restoration projects, reducing the need for artificial fertilization (Hyatt et al. 2004). The dramatic reduction in California Central Valley riparian forests may make salmon-derived nutrients even more crucial to the maintenance of remnant riparian vegetation and the terrestrial and aquatic animals that rely upon it. Our Calaveras River data suggests that lack of adequate salmon numbers may even affect animal abundance and diversity, as could be seen in the slower consumption rate of imported carcasses and low Turkey Vulture numbers.

Given the known positive effects of salmon nutrients on riparian vegetation, it should not be surprising that the nutrients are also found in crops grown in fields near salmon rivers. In the Mokelumne River basin, the main riparian crop is grapes for making wine and the vines had elevated marine isotope levels. In arid regions, where irrigation is essential to agriculture, both wine grape and juice grape yield has been found to be highly responsive to N fertilizer (Ahmedullah et al. 1987, Spayd et al. 1993). During the wine-making process, N in grapes is used by yeast for synthesizing structural proteins, enzymes, nucleic acids, and pytimidine nucleotides and is essential for yeast growth (Bisson 1991, 1999, Buescher et al. 2001). Assimilable N has been shown to increase sugar fermentation and ethanol formation and N in grape juice can be increased by addition of fertilizers in the vineyard (Buescher et al. 2001). This addition can have a significant influence on wine quality (Bell et al. 1979). In the context of sustainable agricultural practices, this can be quite dramatic. We contacted three Central Valley fertilizer distributors to obtain present N fertilizer costs. Depending on dry or wet form, 32–45% N fertilizer costs US\$500.00–\$2854.91 per ton. This does not include application costs. Therefore, 600 000 salmon could be worth US\$186 000–1.06 million as N fertilizer alone. Hatcheries consequently could be removing as much as US\$68 000 in N from the Central Valley.

According to Vance (2001), production of high-quality, protein-rich food is extremely dependent upon availability of sufficient N and has become a contentious issue due to its excessive use, production costs, and the lack of readily available N fertilizer sources for extensive agriculture. Exacerbating the issue is that N fertilizer production requires 3% to 5% of U.S. annual natural gas production (Heichel 1987, Galloway et al. 1995). This fragile relationship was exemplified by fourfold natural gas price increases in 2001. Natural gas prices escalated from \$2.50 million per BTU to \$10 million per BTU, resulting in a fertilizer production cost increase from

$100 to $363 per metric ton, compromising farm profitability. This price increase vividly demonstrates that N fertilizer production is susceptible to any energy shortage or crisis. As fuel prices increase, the actual economic and ecologic value of salmon-derived nutrients will increase as well.

According to Naiman et al (2002), recognition of the contributions of marine-derived nutrients from salmon has direct implications for resource management in terms of creating effective regulations and guidelines that treat the watershed as an integrated salmon-producing system. The long-term sustainability of salmon ecosystems requires that salmon escapement be set at levels that ensure an adequate supply and distribution of marine derived nutrients. Even salmon derived from hatchery production clearly can have considerable ecologic and indirect economic value. Our findings further illustrate the complexity of interactions surrounding salmonid streams (Helfield and Naiman 2002), even where humans dominate the landscape.

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