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[Article]

Growth and Methylmercury Accumulation in Juvenile Chinook Salmon in the Sacramento River and Its Floodplain, the Yolo Bypass

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Abstract.—The literature indicates a strong correlation between inundation of previously oxidized soils, as can occur on a floodplain, and increased microbial methylation of mercury. There is special concern over the potential for increased methylmercury levels in the Yolo Bypass, a 24,000-ha floodplain for California's Sacramento River and its tributaries. The objective of our first study component was to compare methylmercury accumulation between juvenile Chinook salmon *Oncorhynchus tshawytscha* in the Yolo Bypass and those in the Sacramento River during a winter 2005 flood event. For each location, we tested accumulation in two groups of hatchery Chinook salmon juveniles: (1) free-ranging, coded-wire-tagged fish that were released into the floodplain and river and recaptured by downstream sampling and (2) fish that were reared in enclosures at fixed locations in both the river and floodplain. We found that free-ranging juvenile Chinook salmon in the floodplain accumulated 3.2% more methylmercury per day than did free-ranging fish in the river. However, fish in the floodplain grew 0.7% more per day than fish in the river. Variance in growth and in methylmercury content was significantly higher in the free-ranging fish than in the enclosure-reared fish, suggesting suboptimal rearing conditions in the enclosures. In a second study component, we analyzed methylmercury levels of free-ranging Chinook salmon released in the Yolo Bypass during hydrologically variable years (2001–2003 and 2005); the objective was to determine whether interannual differences in the primary source of floodwater to the Yolo Bypass were associated with different patterns of mercury accumulation in Yolo Bypass Chinook salmon. Fish in the Yolo Bypass showed different patterns of methylmercury accumulation in 2001, 2002, 2003, and 2005. Methylmercury accumulated linearly with time in years when Cache Creek provided the primary source of flood flow but followed a quadratic pattern in years when flood flow was dominated by the Sacramento River.

There is a tremendous interest in the potential for wetland and floodplain restoration in many of North America's developed lowland river systems as a means of supporting the recovery of native floodplain-adapted fish species. A growing body of research points to the importance of the flood pulse and river–floodplain connectivity for a variety of aquatic species at multiple trophic levels (Junk et al. 1989; Sommer et al. 2001). For resident biota in intermittent streams, the benefits of large flow fluctuations appear to outweigh the costs associated with a variable environment (Spranza and Stanley 2000). For fish specifically, elevated or flood-level flows can play an essential role in growth, survival, and ecology (Shiemer 2000; Sommer et al. 2001a, 2004, 2005). In northern California's San Francisco Estuary, high-flow years are known to increase populations of several species (Jassby et al. 1995), and river flow has been correlated with escapement of adult Chinook salmon *Oncorhynchus tshawytscha* in the San Joaquin River basin (Speed 1993).

The Sacramento River, one of the dominant present and historic tributaries to the San Francisco Estuary, currently supports fall, late-fall, winter, and spring Chinook salmon runs. These native populations have suffered the adverse effects of factors ranging from habitat loss and species introductions to water diversions (Bennett and Moyle 1996; Yoshiyama et al. 2000) and contaminants (Saiki et al. 1995). As a

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result, Sacramento River winter-run and spring-run Chinook salmon are protected under the U.S. Endangered Species Act.

The typical life history pattern for fall-run Chinook salmon is for fry to migrate from the tributaries during winter and spring (December–May) to the estuary (Brandes and McLain 2001). Chinook salmon rearing areas are known to include channel and off-channel backwater, wetland, and floodplain habitats in natal and nonnatal streams and associated estuaries (Bjornn 1971; Kjelsen et al. 1982; Levy and Northcote 1982; Swales et al. 1986; Swales and Levings 1989; Healey 1991; Shreffler et al. 1992; Sommer et al. 2005). In the San Francisco Estuary system, juvenile Chinook salmon have evolved to benefit from the productivity of the flood pulse through enhanced growth and improved survival (Kjelsen et al. 1982; Sommer et al. 2001). Specifically, research in the Yolo Bypass, the primary floodplain for the Sacramento River and for several other San Francisco Estuary tributaries, indicates that fall-run Chinook salmon reared in the Yolo Bypass floodplain experience more rapid development and a larger size at out-migration than those reared in the Sacramento River (Sommer et al. 2001a, 2001b). Among the specific mechanisms thought to drive the improved rearing conditions for Chinook salmon associated with flood flow are increased habitat availability, migration cues, reduced predation rates, increased food supply, favorable temperature, and increased feeding success (Bennett and Moyle 1996; Sommer et al. 2001a, 2004b, 2005; Kimmerer 2002).

Of growing concern for scientists and policy makers working to restore and manage wetland and floodplain habitats is the increased production of methylmercury in anaerobic sediments (Callister and Winfrey 1986; Blum et al. 2001). Methylmercury poses a threat to aquatic and riparian biota because it is a neurotoxin that bioaccumulates and biomagnifies in the aquatic food web (Davis et al. 2003). Methylmercury is an organomercurial formed through oxidized mercury combining with carbon. In this readily absorbed form, methylmercury has been shown to cause pathological damage and altered behavior in Atlantic salmon *Salmo salar* (Berntssen et al. 2003). Additionally, methylmercury poses a significant health risk for humans consuming fish with high mercury residues (Clarkson 1990; Renzoni et al. 1998; Mozaffarian and Rimm 2006).

Research on the aquatic cycling of mercury suggests that the inundation of floodplains and wetlands and the associated hydrologic, geomorphic, and biochemical processes play a key role in mobilization and transport of mercury. Total mercury concentrations have been correlated with total suspended sediment and periods of runoff from high flows in multiple river systems (Balogh et al. 2003). It has been shown that total mercury concentrations in sediments can vary between channel beds, banks, and wetlands and may be highest in wetlands (Blum et al. 2001). Research on California's Sacramento River found that mercury loading was positively correlated with discharge (Roth et al. 2001). In California's Carson River, flood-generated bank erosion and overbank deposition onto the floodplain are known to be extremely important mechanisms for the cycling of mercury (Carroll et al. 2004). Furthermore, although flood-level flows have the potential to mobilize and transport mercury-laden sediments, those sediments may not be washed out of the system or even travel far. Instead, they may be deposited onto the floodplain only short distances downstream (Heaven et al. 2000), leaving them susceptible to remobilization with the next large flood event.

In California's Sacramento River and San Joaquin River drainages, decades of mercury mining in northern California's Coast Range and hydraulic gold mining in the Sierra Nevada resulted in thousands of metric tons of elemental mercury being dumped on the ground and into streams (Alpers et al. 2005). Recently, these tributaries to the San Francisco Estuary have been the focus of a great deal of mercury-related research (Domagalski 1998; Foe and Croyle 1999; Domagalski et al. 2004). Since the period of intensive mercury loading, both drainages have been heavily altered and impacted by levees, dams, land reclamation, and water diversions that have trapped mercury-laden sediments along channel banks and on historical floodplains. As a result, there is special concern over the potential for proposed floodplain and wetland restoration in and around the San Francisco Estuary to mobilize the mercury in those sediments, resulting in a significant increase in the system's methylmercury load (Davis et al. 2003). Concern is perhaps greatest in locations like the Yolo Bypass. This bypass receives significant inflow from Cache Creek, a river that (1) drains a section of the Coast Range that was extensively mined for mercury and (2) is recognized as a significant source of the total mercury load to the San Francisco Estuary (Domagalski et al. 2004). Additionally, hydraulic residence times are typically longer in the Yolo Bypass than in the Sacramento River and water temperatures are warmer (Sommer et al. 2001b, 2004a), which potentially invokes higher methylation rates.

The primary objective of this study was to investigate the relative impacts of floodplain (Yolo Bypass) versus river-channel (main-stem Sacramento River) rearing on growth and methylmercury accumulation in juvenile Chinook salmon. A secondary objective was to support fishery and habitat management in the San Francisco Estuary by (1) quantifying the patterns of methylmercury accumulation and the range of residues exhibited at out-migration by Chinook salmon rearing in the Yolo Bypass in comparison with fish rearing in the Sacramento River channel and (2) contextualizing those findings by contrasting them with the relative growth experienced by juvenile Chinook salmon on the floodplain and in the river.

Specifically, this study was designed to test the related hypotheses that (1) Chinook salmon reared in the Yolo Bypass floodplain will accumulate methylmercury faster than those reared in the Sacramento River and will have higher methylmercury levels at out-migration, (2) Yolo Bypass Chinook salmon will grow faster than Sacramento River fish, and (3) interannual variability in the tributaries providing the primary source of flood flows to the Yolo Bypass will affect methylmercury levels in floodplain-reared Chinook salmon. Specifically, we hypothesized that Yolo Bypass Chinook salmon will exhibit increased methylmercury accumulation rates and higher levels at out-migration in years when the bypass floods with flows originating principally from Cache Creek and west-side tributaries rather than from the Sacramento River.

Methods

The first two hypotheses were tested during winter 2005 using coded wire tag (CWT) release and recapture and in situ enclosure experimentation. To test the third hypothesis, we examined methylmercury accumulation in coded-wire-tagged, released, and recaptured Chinook salmon that reared in the Yolo Bypass during four different flood seasons (2001, 2002, 2003, and 2005). In two of these cases (2001 and 2005), the primary source of flood flow to the bypass was from Cache Creek and other west-side tributaries (Figure 1). In the other two cases (2002 and 2003), flood flows were dominated by the Sacramento River.

Study sites.—The San Francisco Estuary is a complex composed of two main regions: (1) downstream bays and (2) the Sacramento–San Joaquin Delta, a broad network of tidally influenced channels receiving inflow from the Sacramento and San Joaquin rivers (Figure 1a). Historically, the system experienced large annual snowmelt-driven flow pulses in spring. For the past several decades, however, much of this snowmelt has been stored in reservoirs for release during summer and autumn, periods of historically lower flow. As a result, the historical spring pulse at present is substantially reduced, except during large, late-season storms.

The Yolo Bypass is a 24,000-ha flood control channel that serves as the primary floodplain of the Sacramento–San Joaquin Delta (Sommer et al. 2001, 2005). The Yolo Bypass currently floods every other year on average, generally during winter and spring high-flow periods. Peak inundation on the floodplain is typically from January to March, but the bypass can flood as early as October and as late as June. The bypass receives its primary input at its north end, from Sacramento River and Feather River floodwaters conveyed over the Freemont Weir. Flows in the Sacramento River basin must exceed 2,000 m^3/s in order for water to spill into the bypass via the Fremont Weir (Sommer et al. 2001). The bypass may also receive additional waters from the American River and several smaller streams and drains on its west side, including Cache Creek, Knights Landing Ridge Cut, and Putah Creek (Figure 1a, b).

In addition to Chinook salmon, the Yolo Bypass supports a host of wildlife including over 10 native fish species, such as the federally protected delta smelt *Hypomesus transpacificus*, steelhead *O. mykiss*, and splittail *Pogonichthys macrolepidotus*, as well as over 200 bird species (Sommer et al. 2001b). The majority of the Yolo Bypass mosaic, which includes riparian, wetland, upland, and perennial pond habitats, is managed for wildlife (Sommer et al. 2005).

Free-ranging study.—Juvenile Chinook salmon from the Feather River Hatchery were tagged with CWTs and released in groups of approximately 50,000 at the north end of the Yolo Bypass during winter flood events in 2001–2003 and 2005 (Figure 1b). In 2005, about 50,000 fish with CWTs were released in the Sacramento River. Free-ranging Chinook salmon released in the Yolo Bypass were recaptured with a rotary screw trap in the lower end of the Yolo Bypass toe drain during their out-migration (Figure 1b; Sommer et al. 2004a). Recapture period in the bypass ranged from 1 to 56 d after release in 2005 and 1–80 d after release in 2001–2003. In all 4 years, the majority of recaptures were made within the first 30 d. Free-ranging Chinook salmon released into the Sacramento River in 2005 were recaptured by the U.S. Fish and Wildlife Service (USFWS) via purse seining, beach seining, and midwater trawling (Brandes and McLain 2001; Sommer et al. 2001). Recapture period in the Sacramento River ranged from 1 to 75 d after release, with the majority of recaptures also occurring within the first 30 d.

Before their release in 2005, a subset of the tagged Chinook salmon were weighed and measured to determine fork length (FL, mm) and weight (g). All recaptured fish were weighed and measured again at the time of recapture. All recaptures were euthanized

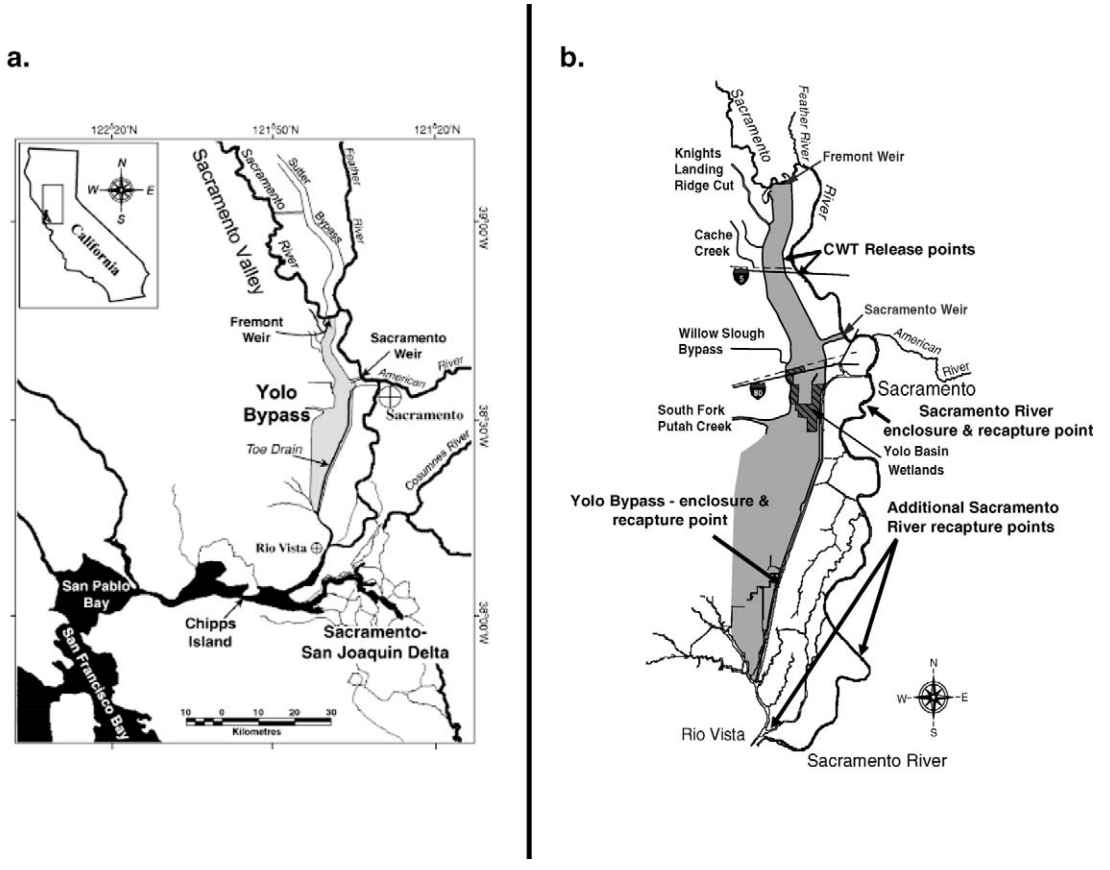

FIGURE 1.—**(a)** Map of the location of the Yolo Bypass, California, in relation to the San Francisco Estuary and its tributaries and **(b)** detail view of the Yolo Bypass, its tributaries, and the parallel section of the Sacramento River. The Chinook salmon coded wire tag (CWT) release and recapture points and enclosure rearing locations are indicated for both the Yolo Bypass and the Sacramento River.

using tricaine methanesulfonate (MS-222) and were frozen at less than -10°C until recovery of CWTs and analysis for methylmercury. Euthanasia was performed after lengths and weights were recorded.

Enclosure study.—Juvenile Chinook salmon were reared in enclosures in the Yolo Bypass and the Sacramento River for 1 month (February 11–March 13, 2005). The study was timed to correspond with a winter flood event, when both our released tagged Chinook salmon and wild Chinook salmon would be rearing and migrating through the bypass.

Eight fish enclosures were constructed from 76.2-cm segments of 35.6-cm-diameter, schedule-40 polyvinyl chloride pipe. Each pipe section was drilled to create multiple 7.6-cm holes and was lined with 6.4-mm square-mesh sleeves. The enclosures were sealed at the upstream end with an end cap and at the downstream end with a clear acrylic plate, both of which had mesh-covered holes added to allow flow and food to pass through the enclosure. Each enclosure was equipped with a 7.6-cm-diameter feeding hole in the upstream end; the feeding hole was sealed with a black rubber stopper. Once per week, Chinook salmon in both locations were fed the contents of a 1-m drift net that was set adjacent to the enclosures for a 10-min interval. Two sets of replicate enclosures (four total) were cabled to trees near the western bank at the lower end of the Yolo Bypass toe drain. An additional two sets of replicate enclosures were cabled to the dock at Sherwood Harbor on the Sacramento River (Figure 1b). Data from each set of two enclosures were pooled for analysis.

Fifteen juvenile Chinook salmon from the Feather River Hatchery were stocked in each enclosure shortly after the onset of a major flood event. We measured FL and weight before stocking and upon collection of fish over the course of the subsequent 30-d sampling period. After collection, fish were euthanized immediately and frozen at less than −20°C for methylmercury analysis.

Physical and chemical analyses.—Whole-body methylmercury concentrations were analyzed from a total of 304 juvenile Chinook salmon. Frozen samples from both the enclosure and the CWT release and recapture portion of the 2005 study (combined $N =$ 199) were analyzed by Moss Landing Marine Laboratories (Marine Pollution Studies Laboratories, Moss Landing, California) using methods described by Bloom (1989). Specifically, samples were digested in a 25% potassium hydroxide–methanol solution before analysis. An aliquot of the digestate was added to Milli-Q water and buffered to pH of 5. An ethylating agent was added to each sample to form a volatile methyl–ethylmercury derivative, which was then purged onto graphite carbon traps as a means of preconcentration and interference removal. The sample was then isothermally chromatographed, pyrolitically broken down to elemental mercury, and detected using a cold-vapor fluorescence detector (Bloom 1989).

The analysis included a subset of the fish sampled at the outset of the study to provide a value for initial methylmercury content. Additionally, 105 archived frozen recaptured fish (with CWTs) from 2001, 2002, and 2003 were analyzed for methylmercury by Battelle Marine Sciences Laboratory (Sequim, Washington) via the same protocol. Results were calculated in terms of nanograms per gram dry weight and were then converted to wet weight (reported here) for a more meaningful live weight concentration. Quality assurance–quality control (QA/QC) objectives for both sets of analyses were a 70–130% range of recovery and a relative precision of ±25%. All results met QA/QC objectives. Achieved detection limits for analysis were 2.06 ng/g (Battelle Marine Sciences Laboratory) and 2.0 ng/g (Moss Landing Marine Laboratories).

Statistical analysis.—Fish were divided into groups by fish type (i.e., free-ranging or enclosure-reared) and location (i.e., Yolo Bypass floodplain or Sacramento River). Free-ranging fish were recaptured at inconsistent intervals; the total number and frequency of recapture differed between the Yolo Bypass and the Sacramento River. Enclosure-reared fish, however, were sampled at regular intervals and numbers that were consistent between the locations. To address this difference in sampling, we elected to analyze differences in terms of change per day between each of the four location–fish-type groups for each of the three variables (length, weight, and mercury). Because samples were collected on inconsistent days and with inconsistent patterns in recapture relative to time, we chose, for each location, to include all samples from all days in our analysis.

To facilitate comparison, all values were $\log_e$ transformed because of the range and variance in values for growth variables (weight and FL), methylmercury content, and (in the case of the free-ranging fish) time of exposure before recapture. Because different methodologies were used for the enclosure-reared and free-ranging portions of our study, we elected to analyze these groups separately.

Patterns in growth and methylmercury content in 2005 were compared separately for each fish type across both locations using analysis of covariance (ANCOVA) mixed analysis (including tests for fixed effects, fit, and covariance) and residual analysis (including tests for normality, symmetry, independence, and homoscedasticity). The location × duration of residence (d) interaction was significant for each fish type. As a result, a different slope was fit to each location–fish-type combination and the interaction was significant for both fish types (test of fixed effects: $P <$ 0.0001). Because all fish in 2005 were from the same group and initially of very similar size, a common intercept was fit to both locations for each fish type. Different residual variances were also fit to each fish type.

In addition, to examine the relationship between fish type and covariance relative to per-day changes in weight, length, and methylmercury accumulation, we also performed a combined ANCOVA that included both enclosure-reared and free-ranging fish. The three-way interaction of location, fish type, and duration of residence (i.e., days of exposure) was significant, and we calculated fish-type-specific covariance for both growth variables as well as for mercury accumulation.

Methylmercury content relative to duration of residence and the overall trend in methylmercury accumulation over the sample group were also compared in free-ranging floodplain Chinook salmon from 2001 to 2003 and 2005. Comparisons were performed using ANCOVA mixed model analysis (with separate variances per year, tests for fixed effects, fit, and covariance) and residual analysis (including tests for normality, symmetry, independence, and homoscedasticity).

Results

Growth of Free-Ranging Fish

For the free-ranging Chinook salmon, the floodplain group showed greater growth per day (weight increase = 3.5% per day; FL increase = 1% per day) than the free-ranging Sacramento River group (weight increase = 2.8% per day; FL increase = 0.8% per day). All per-day growth levels were significant ($P <$ 0.0001; Table 1; Figure 2).

TABLE 1.—Weight, fork length (FL), and methylmercury (MeHg) concentration for free-ranging and enclosure-reared juvenile Chinook salmon in the Yolo Bypass floodplain and the Sacramento River, California. Enclosure-reared fish statistics are based on samples taken in equal numbers after 12 and 24 d. Change-per-day statistics were all significant at $P \leq 0.0001$.

Variable	Range	Mean (SD)	Change per day (%)
Free-ranging fish in floodplain			
Weight (g)	0.9–13.1	2.1 (2.1)	3.5
FL (mm)	49–106	62.3 (11)	1.0
MeHg (ng/g)	11.7–234	56.7 (11)	5.0
Duration of residence (d)	5–55	14.2 (10.8)	—
Free-ranging fish in river			
Weight (g)	0.5–12.7	2.4 (10.8)	2.8
FL (mm)	44–107	61 (13.2)	0.8
MeHg (ng/g)	11.3–269	41.5 (31.7)	1.8
Duration of residence (d)	1–76	21.4 (21.5)	—
Enclosure-reared fish in floodplain			
Weight (g)	0.9–2.4	1.6 (0.4)	1.3
FL (mm)	53–64	57.9 (2.8)	0.4
MeHg (ng/g)	18.4–60	32.4 (11.5)	1.4
Enclosure-reared fish in river			
Weight (g)	0.7–1.9	1.3 (0.3)	0.0
FL (mm)	50–65	56.5 (4.4)	0.4
MeHg (ng/g)	18.3–49.2	30.7 (9.6)	1.6

Growth of Enclosure-Reared Fish

Growth in weight for the enclosure-reared Chinook salmon was higher in the Yolo Bypass floodplain group (weight increase = 1.3% per day) than in the Sacramento River group. Growth in FL was similar for the river and floodplain groups (weight increase = 0.4% per day for both). All per-day growth levels were significant ($P < 0.0001$) except for weight growth in the enclosure-reared river group (Table 1; Figure 3).

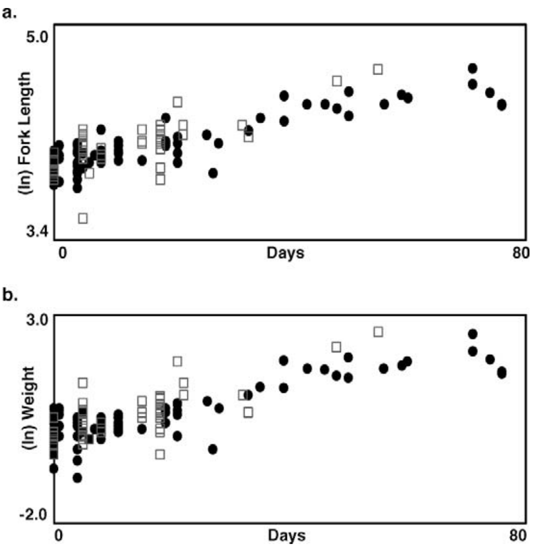

FIGURE 2.—Comparison of **(a)** fork length (mm) growth and **(b)** weight (g) growth in free-ranging juvenile Chinook salmon that were coded-wire-tagged, released, and recaptured in the Yolo Bypass (open squares) and the Sacramento River (black circles), California, during a winter flood in 2005. Fork length and weight data have been $\log_e$ transformed.

Methyl Mercury Accumulation in Free-Ranging Fish

Methylmercury accumulation was significantly higher ($P < 0.0001$) in the free-ranging floodplain Chinook salmon (increase = 5.0% per day) than in free-ranging Sacramento River fish (increase = 1.8% per day; Table 1), despite similar overall ranges in methylmercury residues in fish from the floodplain (11.7–234 ng/g) and river (11.3–269 ng/g; Figure 4).

Methyl Mercury Accumulation in Enclosure-Reared Fish

Methylmercury accumulation was similar in the enclosure-reared floodplain (increase = 1.4% per day) and river (increase = 1.6% per day) treatment groups (Table 1), although it was slightly higher in fish from river enclosures. Ranges in methylmercury residues were larger in the floodplain Chinook salmon (18.4–60 ng/g) than in the river fish (18.3–49.2 ng/g; Figure 5).

Interannual Pattern Assessment

Methylmercury accumulation in free-ranging floodplain Chinook salmon relative to duration of residence was not significantly different among the 4 years examined. Overall patterns in methylmercury accumulation, however, did differ significantly between different sampling years. In our mixed model analysis,

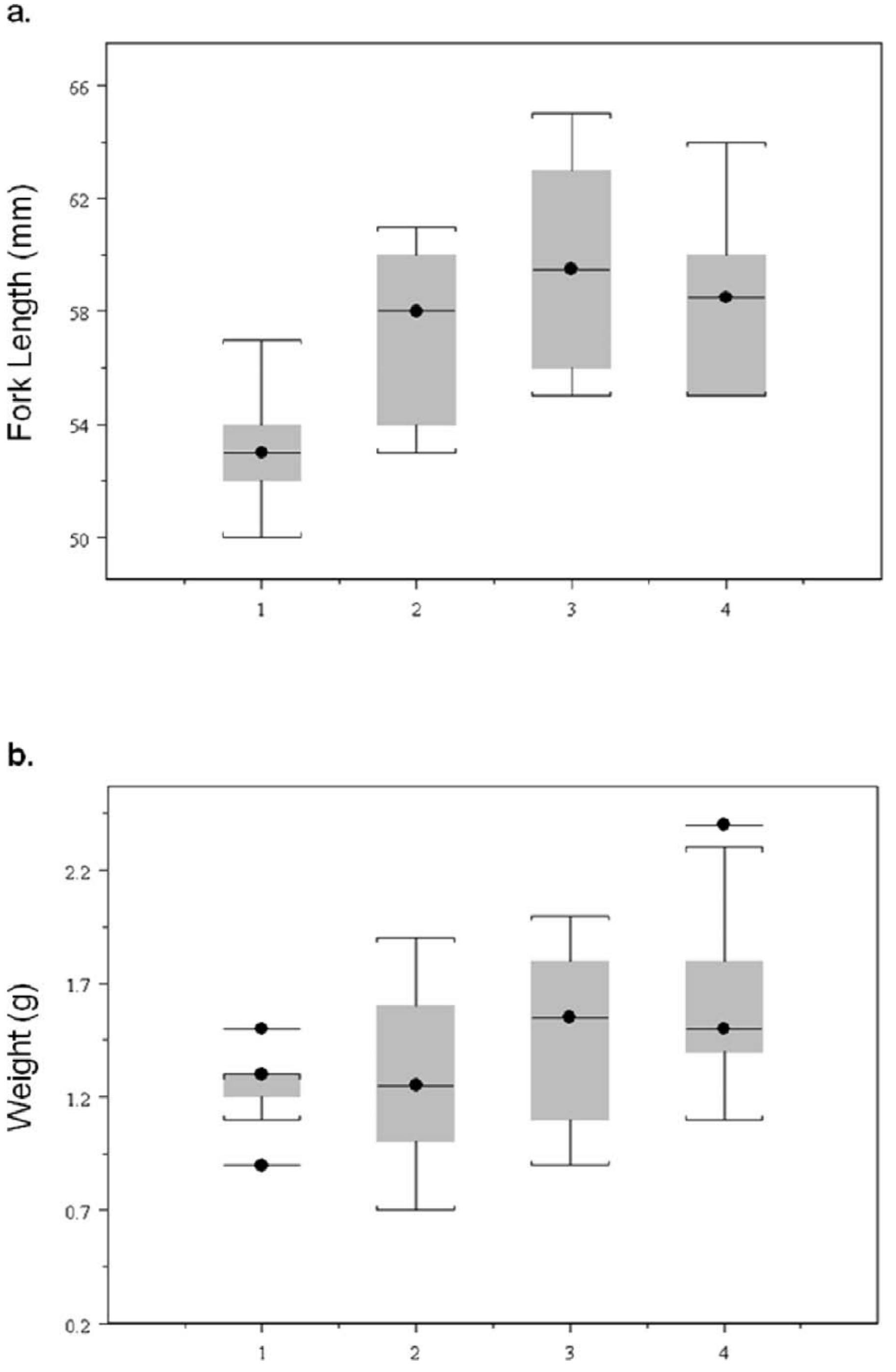

FIGURE 3.—Box plot, including sample range, median, lower and upper quartiles, and outliers, comparing **(a)** fork length (mm) growth and **(b)** weight (g) growth in enclosure-reared juvenile Chinook salmon after (1) 12 d in the Sacramento River (SR); (2) 12 d in the Yolo Bypass (YB); (3) 24 d in SR; and (4) 24 d in YB during a winter flood in 2005.

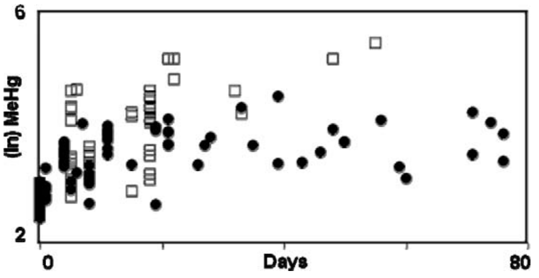

FIGURE 4.—Comparison of whole-body methylmercury concentration (ng/g; $\log_e$ transformed) in free-ranging juvenile Chinook salmon in the Yolo Bypass (open squares) and the Sacramento River (black circles), California, during a winter flood in 2005.

2001 and 2005 could be modeled using linear functions, but 2003 displayed curvature in response over time and 2002 was ambiguous. A quadratic term ([duration of residence]^2 × year) was applied to assess curvature in the response function and was significant for both 2002 and 2003 ($P < 0.0001$). The quadratic terms were not significant for 2001 ($P = 0.7776$) and 2005 ($P = 0.6717$), which was consistent with the observation of a generally linear pattern for data in those years. Additionally, separate intercepts were fit for each year because initial batches of fish (though from the same source or location) were different from year to year.

Patterns in methylmercury accumulation were different in all 4 years (Figure 6). Across all categories, 2001 and 2002 were the most similar of any 2 years. These patterns remained significant when models were fit both with a common sample period for each year (30 d) or with the complete sample periods, which varied from year to year. As a result, we chose to include all data points from each year. The model was fit with different variances for each year; variances were similar for 2001–2003 (Levene's test: $P = 0.4684$), and 2005 was the most variable of the 4 years.

Covariance across Fish Types

Covariance was significantly higher in free-ranging Chinook salmon than in enclosure-reared fish across both weight (free-ranging: covariance = 0.136; enclosure-reared: covariance = 0.05734; $P < 0.0001$) and FL (free-ranging: covariance = 0.01072; enclosure-reared: covariance = 0.00348; $P < 0.0001$) growth variables. Similarly, for methylmercury accumulation, a significantly higher covariance ($P < 0.0001$) was observed in free-ranging fish (0.2883) than in enclosure-reared fish (0.09215).

Discussion

Our hypotheses for this study were that (1) Chinook salmon reared in the Yolo Bypass floodplain would accumulate methylmercury faster than fish reared in the Sacramento River and would have higher methylmercury levels at out-migration, (2) Yolo Bypass Chinook

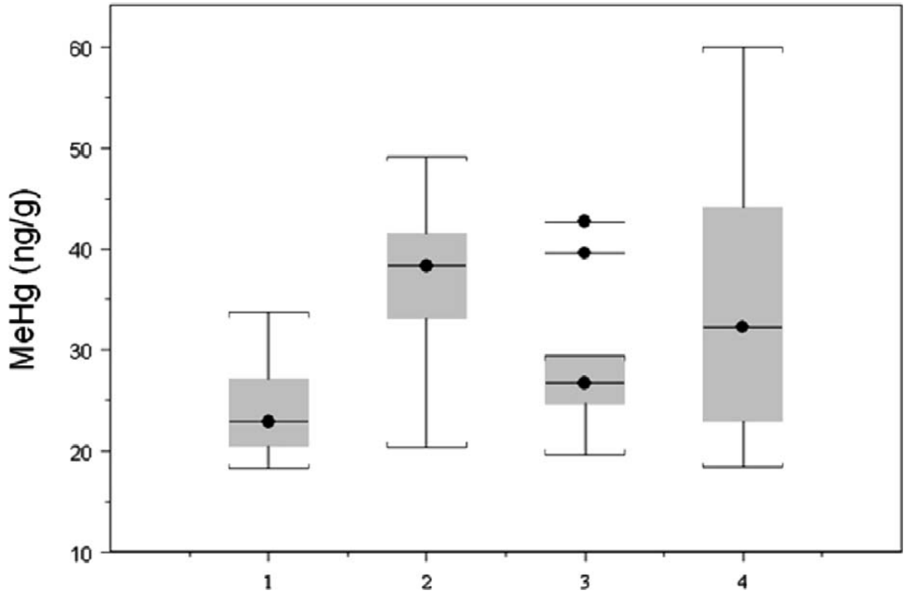

FIGURE 5.—Box plot, including sample range, median, lower and upper quartiles, and outliers, comparing whole-body methylmercury concentration (ng/g) in enclosure-reared juvenile Chinook salmon after (1) 12 d in the Sacramento River (SR); (2) 12 d in the Yolo Bypass (YB); (3) 24 d in SR; and (4) 24 d in YB during a winter flood event in 2005.

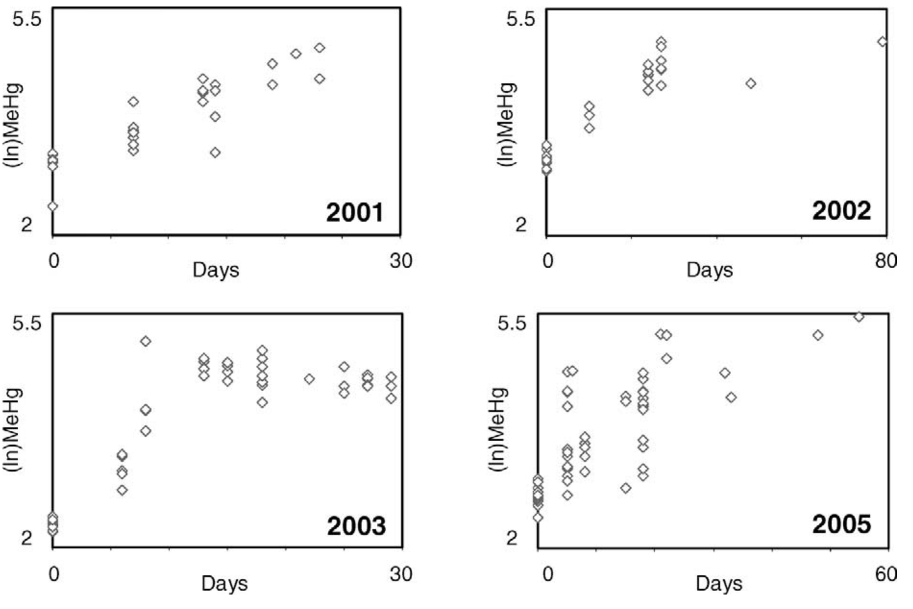

FIGURE 6.—Whole-body methylmercury concentrations (ng/g; $\log_e$ transformed) in free-ranging juvenile Chinook salmon released and recaptured in the Yolo Bypass, California, during winter floods in 2001, 2002, 2003, and 2005.

salmon would grow faster than Sacramento River fish, and (3) interannual variations in origin of Yolo Bypass floodwaters would affect methylmercury levels in floodplain-reared Chinook salmon. Specifically, we expected that Yolo Bypass Chinook salmon would exhibit increased methylmercury accumulation and higher levels at out-migration in years when the Yolo Bypass flooded with flows principally from Cache Creek and west-side tributaries. Findings from the growth and methylmercury accumulation portions of the study supported hypotheses 1 and 2, indicating improved growth for juvenile Chinook salmon rearing on floodplains and also reflecting the potential for increased mercury uptake on floodplains. Our findings from the interannual comparison portion of the study did not, however, support hypothesis 3, that methylmercury levels would be higher in years when flood flow originated principally from Cache Creek. Instead, these findings indicated a more complex set of relationships between patterns in methylmercury accumulation and source of flood flow and raised questions about the specific roles of downstream aqueous methylmercury transport, on-site methylmercury production, foraging patterns in the two habitats, and differing prey mercury levels as potential drivers of those relationships.

Growth and Mercury Accumulation in Two Habitats

In 2005, free-ranging Chinook salmon rearing in the Yolo Bypass exhibited higher apparent growth rates than those rearing in the Sacramento River across both of the growth variables we measured (weight and FL). These findings reinforced earlier research of Sommer et al. (2001b), who demonstrated improved growth in floodplain-reared juvenile Chinook salmon. Previous research has also established a positive correlation between improved growth for juvenile Chinook salmon and timing of migration, as well as increased survival and rate of return (Beckman et al. 1998, 1999). The correlation between size and survival has also been demonstrated for juvenile masu salmon *O. masou*, Atlantic salmon, and coho salmon *O. kisutch* (Kazutaka et al. 2003; Kallio-Nyberg et al. 2004; Ebersole et al. 2006). From this standpoint, our findings also suggest the potential for improved survival among juvenile Chinook salmon rearing in the Yolo Bypass relative to those rearing in the Sacramento River.

The free-ranging Chinook salmon also accumulated methylmercury faster in the Yolo Bypass than in the Sacramento River, and fish from the Yolo Bypass generally showed higher methylmercury levels per weight at out-migration than did fish from the Sacramento River. The implications of these findings, however, should be interpreted in the context of life stage. The young fall-run Chinook salmon that pass through Yolo Bypass will grow approximately three orders of magnitude over the course of their lives (3–6 years). With this in mind, unless methylmercury accumulation affects short- or long-term growth, the observed levels of methylmercury bioaccumulation occurring in these juveniles during their 1–12-week floodplain rearing phase would ultimately represent insignificant concentrations in the tissues of adult fish.

It should be noted that our enclosure-reared Chinook salmon did not exhibit the same level of growth or mercury accumulation observed in the free-ranging group. Like the free-ranging fish, enclosure-reared fish experienced improved growth in the floodplain relative to the Sacramento River. Overall, however, the enclosure-reared Chinook salmon grew poorly on the floodplain and in the river, with free-ranging floodplain fish experiencing greater than twice the growth of enclosure-reared floodplain fish. The poor growth observed in the enclosure-reared fish from both habitats may have resulted from cage design, fish density, prey availability, or prey diversity, as has been demonstrated in other river-dwelling salmonid species (Zimmerman and Vondracek 2006). This potential explanation is supported by the observation of limited growth in enclosures despite available prey being supplemented with weekly feedings of drift invertebrates in both the Yolo Bypass and Sacramento River locations.

Variance in both growth and methylmercury accumulation was significantly higher for free-ranging fish than for the enclosure-reared fish. This may reflect increased variability in environmental conditions, prey availability, or ecological interactions experienced by the free-ranging fish, which were able to utilize a diverse habitat spanning many miles, relative to fish reared in a fixed location within that habitat. This difference points to the potential for environmental variability to influence patterns in growth, development, and methylmercury accumulation at both individual and population levels in river and floodplain habitats; the need for research methods that can capture that variability is also indicated.

Annual Patterns in Mercury Uptake

Yolo Bypass Chinook salmon exhibited differing annual patterns in methylmercury uptake in each of the 4 years studied. In 2001 and 2005, the principal source of floodwater was Cache Creek, which had consistently high mercury levels due to historical mining activity (Domagalski 2001; Domagalski et al. 2004), and methylmercury accumulation among floodplain-reared fish exhibited a linear trend, continuing to increase with duration of residence. Conversely, in 2002 and 2003, when the relative contribution of flood flows from Cache Creek was significantly lower because of large inputs from the Sacramento River and other tributaries with less mercury, the fish exhibited a quadratic pattern of methylmercury accumulation. In these years, methylmercury accumulation initially increased with duration of residence but then leveled off in fish that remained in the system longer. These findings may provide clues about some of the mechanisms underlying increased mercury uptake on the floodplain. River stage measurements at the Fremont Weir, the point where flood waters from the Sacramento River enter the Yolo Bypass at high flows, confirm that peak river stages during the study periods (January–March) were below crest stage (10.2 m) in 2001 (9.2 m) and 2005 (9.8 m) but exceeded crest stage in 2002 (10.7 m) and 2003 (10.6 m; California Department of Water Resources 2005). The observed linear increases in methylmercury uptake in 2001 and 2005 may indicate that in years when flood flows are dominated by inflow from Cache Creek and other west-side tributaries (as opposed to the Sacramento River), increased loading of inorganic mercury transported in suspended sediments, conservatively transported methylmercury in flood flows, or both factors might be increasing methylmercury levels in floodplain Chinook salmon. Investigations of mercury sources and patterns of aqueous mercury accumulation in relation to streamflow in the Cache Creek watershed indicate that downstream transport of mercury-laden materials would probably increase substantially during heavy rains (Suchanek et al. 2003) like those large enough to trigger flooding in the Yolo Bypass. With this in mind, Yolo Bypass floods dominated by Cache Creek inflow may—relative to Sacramento River-dominated events—contain elevated mercury levels, both as a function of the flows coming primarily from Cache Creek and as a result of elevated downstream transport. Nutrient and contaminant concentrations in the Yolo Bypass have been shown to closely resemble those of the Sacramento River during periods when the river is contributing the primary flood flow; likewise, concentrations in the bypass resemble those of Cache Creek and other smaller tributaries once Sacramento River contributions have ceased (Schemel et al. 2002). In addition, tributary flood inputs into the Yolo Bypass are known to form hydrologic bands once on the floodplain, resisting mixing during all but the lowest flow events (Sommer et al. 2008). Tributary band width is not proportional to amount of flow (Sommer et al. 2008). Instead, the westernmost bands, which include Cache Creek, may spread out over a larger relative area as a function of the west to east slope of the bypass and the consequently shallower area in which the western bands disperse (Sommer et al. 2008). During events when the Sacramento River band is not present, the Cache Creek band has the potential to extend out even further, spanning an even greater area of the floodplain (Sommer et al. 2008). Potentially compounding the possibility of elevated mercury from

Cache Creek, these relatively smaller-magnitude but more widely dispersed flows may more rapidly achieve the anoxic conditions favorable to methylation. Despite investigations into this relationship by state fishery and water quality managers, significant uncertainties remain concerning mercury loading behavior, mercury transport, and relationships between total mercury loading and methylmercury formation (Labiosa et al. 2005).

From an energetics standpoint, the leveling off of methylmercury content near the time of out-migration in Chinook salmon remaining on the floodplain longer, as we observed in 2002 and 2003, is consistent with a pattern of growth dilution. A growth dilution hypothesis would suggest that as growth increases, ingested methylmercury is diluted into a larger mass. Thus, methylmercury concentration decreases with increased growth efficiency (Trudel and Rasmussen 2006). Patterns of growth dilution in mercury uptake have been demonstrated in multiple cases (Essington and Houser 2003; Simoneau et al. 2005). In a comparison of yellow perch *Perca flavescens* in enriched versus nonenriched lake systems, Essington and Houser (2003) found that growth dilution accounted for 30–40% of the significantly (50%) lower mercury concentrations in the much larger fish (four times larger) of the enriched system. Findings by Sommer et al. (2001a, 2005) and our findings for 2001–2003 and 2005 demonstrate increased growth with increased duration of residence for Chinook salmon rearing in the Yolo Bypass. Specifically, fish that remained in the bypass longer than about 15–20 d were generally of larger size than those that out-migrated earlier. Patterns we observed in 2001 and 2005, however, are not consistent with growth dilution. This is evident in the linear patterns of accumulation measured in those years and is reinforced by our finding that across all 4 years, patterns of accumulation remained consistent when the model was rerun using only a 30-d period. Possible explanations for the differing annual patterns in methylmercury accumulation include an increase in prey concentration, a reduction in activity, or both, which may result in decreased methylmercury accumulation via increased growth efficiency in years with larger flood flows from the Sacramento River.

The linear patterns of accumulation in 2001 and 2005 (assuming relatively consistent growth efficiency across all 4 years) may be explained by a relative increase in the methylmercury levels of floodplain prey in those years. Juvenile Chinook salmon rearing in the Yolo Bypass are thought to feed primarily on drift invertebrates, with chironomids (pupae and adults) serving as a primary food source (Sommer et al. 2001a). Given their predominantly benthic aquatic life history, methylmercury levels in Yolo Bypass chironomids may be a function of both local methylation rates in their home sediments and larger-scale variation in methylmercury transported conservatively in flood flows. Slotton et al. (2004) found that aqueous methylmercury concentration was strongly correlated with methylmercury concentrations of aquatic insects and small fish in the Cache Creek watershed. However, the specific form of the relationship between aqueous methylmercury and biotic methylmercury and the bioaccumulation factor varied between sites, suggesting the strong influence of site-specific effects on biotic methylmercury levels (Slotton et al. 2004). Similarly, inorganic mercury transported in flood flows would probably be only indirectly related to biotic methylmercury levels (through deposition of mercury-laden sediment that could then methylate), with local methylation rates still contributing significantly to chironomid mercury levels.

Perhaps more likely than flood flow-mediated increases in prey mercury levels through transport of aqueous mercury are the increased local methylation in the Yolo Bypass, the increased rates of bioaccumulation, or both as precipitated by the smaller Cache Creek floods. This might occur as a function of the generally smaller discharge and velocity of flood flows from Cache Creek relative to those from the Sacramento River, resulting in relatively warmer temperatures on the floodplain. Temperature data for the 3-month period (January–March) during which our 2005 study occurred confirm higher mean temperatures in the Yolo Bypass (14.2°C, SD = 2.1°C) than in the Sacramento River (11.2°C, SD = 1.7°C; Chris Foe, California Regional Water Quality Control Board, unpublished data). Altered temperatures could, in turn, result in higher biotic methylmercury levels, either through increased methylation rates or increased methylmercury bioaccumulation, which studies have demonstrated may vary with temperature (Maury-Brachet et al. 1990; Odin et al. 1994).

Study Limitations and Opportunities for Future Research

Our initial hypothesis—that Chinook salmon juveniles rearing in the Yolo Bypass would accumulate more methylmercury than those rearing in the Sacramento River main channel—did not account for whether this would occur as a function of increased rates of methylation on the floodplain, inflow from the mercury-laden waters of Cache Creek, a combination of these, or any of the other suite of potential interacting environmental, bioenergetic, and ecological drivers of methylmercury uptake. Additional research in these areas might include (1) exploring the bioenergetics of growth and mercury uptake in the two habitats, (2) quantifying local trends in methylation in the Sacramento River, the Yolo Bypass, and the bypass's west-side tributaries, and (3) estimating the relative contributions of aqueous methylmercury transported from upstream and local methylation to the total aqueous methylmercury load in the Yolo Bypass during floods with different sources of flow.

The free-ranging floodplain Chinook salmon accumulated methylmercury at a higher rate and had higher levels at out-migration than free-ranging fish in the river, giving rise to the question about the risks to salmon posed by methylmercury at the levels we measured. In a nonspecies-specific study exploring mercury content thresholds for sublethal effects on growth, reproduction, development, and behavior, Beckvar et al. (2005) found that a whole-body tissue threshold-effect level of 200 ng/g wet weight was protective of both juvenile and adult fish. Only 2 of the 199 individuals from our 2005 study surpassed the threshold proposed by Beckvar et al. (2005) and only by a narrow margin (234 ng/g for one free-ranging floodplain fish; 269 ng/g for one free-ranging river fish). The nonspecies-specific nature of the study by Beckvar et al. (2005) and the limitations of the available toxicology studies upon which it is based invite a more in-depth analysis of sublethal effects of different levels of methylmercury exposure for juvenile Chinook salmon. Based on this type of analysis, the risks in terms of behavioral toxicity of measured methylmercury levels in river and floodplain habitats could be contrasted with other habitat-specific drivers of survival, such as foraging efficiency and predator avoidance.

Also important in the cost–benefit analysis of floodplain rearing are the relative potential impacts of more rapid growth versus increased methylmercury uptake (at the levels we found) on survival at the individual, cohort, and population levels. Additionally, our design for the interannual portion of our study did not account for the specific mechanisms driving the differing interannual patterns in methylmercury uptake. Findings from all portions of the study suggest that capturing the variability of an individual Chinook salmon's foraging behavior in a habitat matrix as diverse as a floodplain may be difficult using in situ enclosure experimentation exclusively. With that in mind, coupling in situ enclosure and release and recapture methodologies can be a useful approach.

Conclusions

Findings from this study affirm that Chinook salmon juveniles in the Sacramento River drainage benefit from floodplain rearing by experiencing greater growth rates than river-rearing fish (weight increase was higher by 0.7% per day; FL increase was higher by 0.2% per day). In addition, this study quantifies the negative effects of floodplain rearing for juvenile Chinook salmon in terms of methylmercury accumulation, which was greater than that of Chinook salmon rearing in the river (increase in methylmercury concentration was higher by 3.2% per day). Additionally, although not conclusive as to the specific process yielding the variable interannual patterns in methylmercury accumulation we observed (2001–2003 and 2005), our comparison of those patterns suggests that the source of flood flow may strongly affect methylmercury accumulation in Chinook salmon rearing in the Yolo Bypass. We hope that these findings and the potential for similar dynamics in other migratory, floodplain-adapted species will invite additional research in this area.

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