

ENVIRONMENTAL STUDIES

Food web controls on mercury fluxes and fate in the Colorado River, Grand Canyon

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Mercury (Hg) biomagnification in aquatic food webs is a global concern; yet, the ways species traits and interactions mediate these fluxes remain poorly understood. Few pathways dominated Hg flux in the Colorado River despite large spatial differences in food web complexity, and fluxes were mediated by one functional trait, predation resistance. New Zealand mudsnails are predator resistant and a trophic dead end for Hg in food webs we studied. Fishes preferred blackflies, which accounted for 56 to 80% of Hg flux to fishes, even where blackflies were rare. Food web properties, i.e., match/mismatch between insect production and fish consumption, governed amounts of Hg retained in the river versus exported to land. An experimental flood redistributed Hg fluxes in the simplified tailwater food web, but not in complex downstream food webs. Recognizing that species traits, species interactions, and disturbance mediate contaminant exposure can improve risk management of linked aquatic-terrestrial ecosystems.

INTRODUCTION

Contaminants are agents of global change (1, 2); yet, their transport, storage, and fate within ecological communities remain poorly understood (3). Mercury is a global pollutant of aquatic ecosystems with far-reaching implications for wildlife and human health because its organic form, methylmercury (MeHg), is a potent neurotoxin that biomagnifies in food webs (4). Mercury occurs in food webs throughout the world, even in seemingly remote and somewhat inaccessible locations (4). A prime example is the relatively isolated Grand Canyon National Park (USA) where aquatic animals in the Colorado River accumulate Hg at levels posing risks to wildlife and humans (5). While biomagnification of Hg in food webs is well characterized (4), there are few studies examining how the traits of animals and food web interactions combine to mediate the movement of Hg and other contaminants in linked aquatic-terrestrial food webs (3). For example, predator-resistant prey may sequester Hg into “trophic dead ends” rather than being transferred to higher level predators (6). Likewise, aquatic insects with terrestrial adult stages can move Hg and other contaminants from water to land via their emergence (7, 8). These insects are important prey for many terrestrial insectivores (9, 10), so changes in their rates of emergence driven by food web interactions within the river may influence contaminant exposure and risks in linked riparian food webs (11, 12).

Revealing how community dynamics (e.g., species traits and interactions) influence wildlife exposure and the movement of contaminants in ecosystems requires greater integration of community ecology with ecotoxicology (3, 13, 14). Efforts to bridge these disciplines have been hampered because of fundamental differences in their conceptual and historical underpinnings (15). Ecotoxicologists

have emphasized changes in chemical concentrations within food webs and have addressed questions such as how do chemical properties, food web structure, and animal movements affect wildlife exposure by using models reliant on stable isotope, kinetic, or mass balance-based approaches [e.g., (4, 16, 17)]. While these approaches provide valuable information on the processes governing chemical uptake, elimination, or biomagnification, they provide little insight on the magnitude of fluxes, key pathways of contaminant movement, or species interactions governing fluxes within food webs. In contrast, food web and ecosystem scientists have worked to understand how species traits (e.g., prey vulnerability and mobility) and interactions influence the flows of energy and the mass of materials within food webs [i.e., the trophic basis of production (18)] but have rarely considered how their conceptual frameworks and approaches could address contaminant movement and wildlife exposure to toxins in the environment [but see (19)].

The Colorado River drains the arid southwestern United States and northern Mexico, providing a wide array of ecosystem services including consumptive water use by >40 million people. Where the river flows through Grand Canyon, it is one of the most intensively managed rivers in North America yet is also highly valued for its ecological (e.g., prevalence of endemic and imperiled species) and cultural significance (20). The operation of Glen Canyon Dam (GCD) on the Colorado River has altered flow, sediment, and thermal regimes in Grand Canyon, causing large spatial discontinuities in river primary productivity, species assemblages, and the flows of energy and materials in food webs (21–23). The tailwater section immediately below the dam has a simple, inefficient food web that was strongly perturbed by an experimental flood owing to large shifts in patterns of invertebrate production, Rainbow Trout production, and their consumption of invertebrates needed to support this production. Downstream food webs were more complex, efficient, and resistant to flood disturbance (22, 24). Flooding is a regular feature of most river ecosystems; yet, it is unclear how these common disturbances and their associated changes in community dynamics might alter contaminant fluxes in food webs. Here, we coupled energetic flow food webs (22) with measures of Hg concentrations in organic matter and animals (5) to estimate Hg flux and fate (how much Hg remained in the aquatic food web versus exported to

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the riparian zone via aquatic insects) in food webs before and after an experimental flood. Mercury-based food webs were constructed for six sites spanning 370 km of the Colorado River (fig. S1), and spatial and temporal variability in these food webs provides a unique opportunity to explore how differences in food webs (e.g., different animal traits, species interactions, and resistance to disturbance) influence contaminant fluxes that ultimately govern animal exposure.

RESULTS AND DISCUSSION

A few key pathways and trophic interactions mediated by species traits dominated Hg fluxes. At the base of the food web, >80% of Hg fluxes to invertebrates were via consumption of abundant amorphous detritus and diatoms (Fig. 1 and table S1). Unexpectedly, 56 to 80% of Hg fluxes to fishes were via consumption of blackflies (*Simulium* spp.; table S1), which sustained nearly one-third of total fish production, on average, although blackflies contributed only modestly to invertebrate production in any segment of the river (22, 24).

In the simple tailwater food web, most of the Hg accumulated in diatoms and amorphous detritus flowed to non-native New Zealand mudsnails (*Potamopyrgus antipodarum*) and introduced amphipods (*Gammarus lacustris*; Fig. 1A). New Zealand mudsnails were hyper-abundant (reaching densities of up to 200,000 m⁻²) (22, 25) and accounted for 41% (61 $\mu\text{g m}^{-2} \text{ year}^{-1}$) of total Hg fluxes to invertebrates in the tailwaters (Fig. 2). Trout ate little of the annual mudsnail and amphipod production, so these invertebrates were a trophic dead end [sensu (6)] for Hg transfer. Combined Hg flux to mudsnails and amphipods was 121 $\mu\text{g m}^{-2} \text{ year}^{-1}$, but only a small fraction (1.02 $\mu\text{g m}^{-2} \text{ year}^{-1}$) of that Hg was subsequently transferred to Rainbow Trout via consumption [table S1 and (26)]. The dominant flux of Hg to trout was from the comparatively rare black-

flies (Fig. 1A), which accounted for 76% of the total dietary trout intake of Hg. Blackflies themselves only accounted for 1% of the total flow of Hg from organic matter to invertebrates in the pre-flood tailwater (table S2), further emphasizing the importance of this multilevel Hg pathway within the broader food web.

Mercury fluxes in the more complex downstream food webs (sites 2 to 6) greatly differed from those at the tailwater site. Total fluxes of Hg from organic matter to invertebrates were much lower at downstream sites (mean Hg flux of 2 $\mu\text{g m}^{-2} \text{ year}^{-1}$; Figs. 1, C and D, middle, and 2). An exception was site 2 where Hg fluxes to invertebrates were ~10 \times higher than the other downstream sites owing to high blackfly production and their consumption of Hg-contaminated organic matter (Fig. 2). Fish assemblages were more diverse at downstream sites than in the tailwater with ~9 dominant species (Fig. 1) and consumed nearly all of the available invertebrate production (22). Because the fish consumed nearly all invertebrate production, they also consumed all the Hg provisioned in tissues within the invertebrate community. Thus, total Hg fluxes to all invertebrates and the total Hg fluxes to all fishes were roughly equivalent (Figs. 1, middle and 2, overlapping or nearly overlapping 95% confidence intervals (CIs). Site 2 was again the exception to this pattern because blackfly production far exceeded the amount consumed by fishes, resulting in total fluxes of Hg from organic matter to invertebrates (mean, 29 $\mu\text{g m}^{-2} \text{ year}^{-1}$) that were 10 \times higher than fluxes from invertebrates to fishes (mean, 3 $\mu\text{g m}^{-2} \text{ year}^{-1}$; Fig. 2). At downstream sites, populations of New Zealand mudsnails were much smaller, and the lack of this predator-resistant taxon resulted in much more efficient Hg transfer from invertebrates to fishes.

Flooding strongly affected Hg flux at the tailwater site but had little effect on downstream sites (Fig. 1B). Flooding removed biomass and associated contaminants of non-native amphipods and mudsnails; mudsnail production declined by 81% because of the flood disturbance (24). In contrast, the flood stimulated blackfly

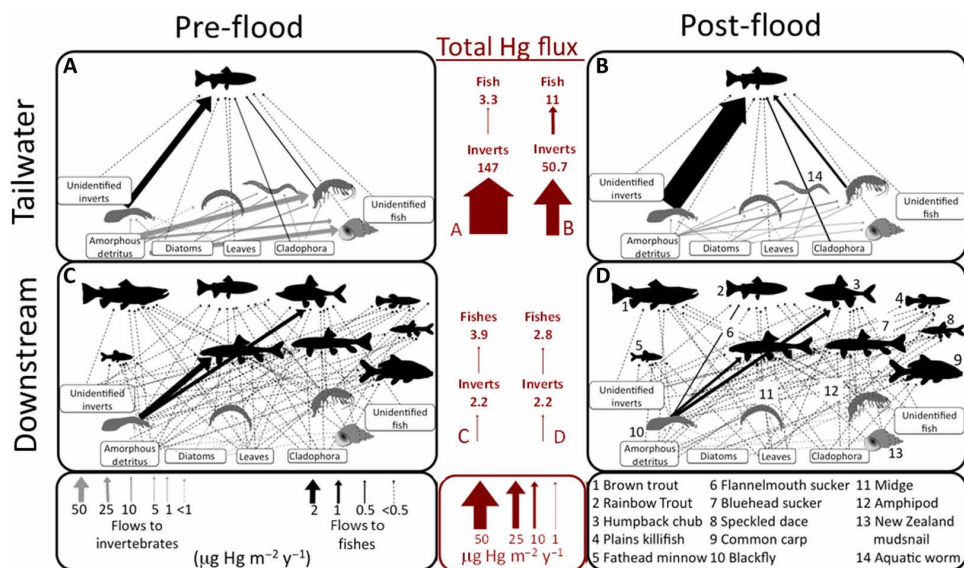


Fig. 1. Mercury food web fluxes over space and time. Hg fluxes in Colorado River food webs at the tailwater (A and B) and a representative (C and D) downstream site (site 3) before and after an experimental flood in the Grand Canyon. (Note scale differences in fluxes to invertebrates versus fishes). Arrows represent estimated total annual flows of Hg to consumers based upon their consumption rates and Hg concentrations of various diet items. Total Hg flux to invertebrates and fishes for each food web are summed in the center panel (red arrows) and labeled A to D to correspond with the detailed food web panels. Native fishes face left; non-native fishes face right. Numbers in (B) and (D) refer to animal key at bottom right (see table S3).

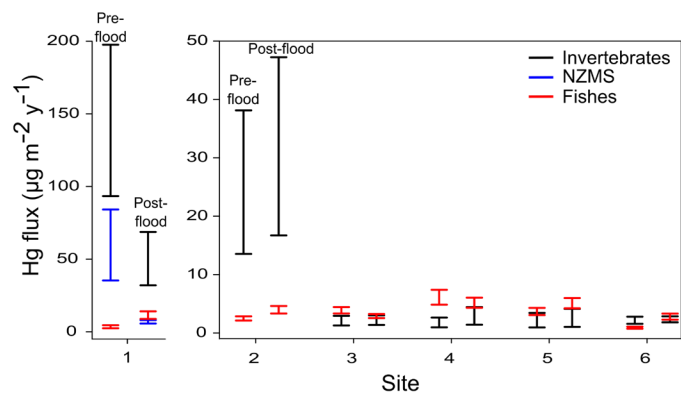


Fig. 2. Total Hg fluxes to invertebrates and fishes. Total fluxes of Hg to invertebrates, New Zealand mudsnail (NZMS), and fishes before and after an experimental flood. Fluxes at site 1 are graphed on a separate scale. Bars represent 95% bootstrapped CIs. Flux to NZMS at sites other than site 1 was negligible (not shown).

production by sixfold. The result of these gains and losses in species production resulted in a net decline in the total Hg flux from organic matter to invertebrates from 147 to $51 \mu\text{g m}^{-2} \text{year}^{-1}$ after the flood (Fig. 1, middle). At the same time, Hg fluxes to trout increased threefold because the flood stimulated the production of Hg-rich blackflies, driving higher rates of consumption by a larger post-flood Rainbow Trout population (24). This increase in blackfly production was presumably due to benthic scouring during the flood that could have improved habitat quality for blackflies and improved conditions for growth of early successional stages of epilithic algae (i.e., diatoms) that are of high nutritional value (24). In contrast, downstream food webs were more stable and resistant to flood disturbance (22); consequently, flood effects on Hg fluxes in these food webs were minor (Figs. 1 and 2).

Blackflies have flying adults that can play a role in transferring Hg from the river to the land. Hence, we investigated three possible fates of Hg in larval blackflies: (i) consumed by fishes, (ii) excreted and recycled to the river during metamorphosis, or (iii) exported to riparian food webs via adult emergence (Fig. 3). Fishes consumed most blackfly-derived Hg across all sites, although the magnitude of fluxes changed with the flood. For example, Hg flux from blackflies to fish at the tailwater increased $3.6\times$ after the flood (from 320 to $1150 \mu\text{g m}^{-1}$ of river per year, Fig. 3A); yet, the fate of Hg (i.e., consumed by fishes) was unchanged because trout ate nearly all blackfly production during both time periods (blackfly consumption was 88 and 94% before and after the flood, respectively, Fig. 3B). This observation is consistent with many investigations showing that fishes can consume large proportions of aquatic insect secondary production [e.g., (27, 28)] with negative consequences for insect emergence (29). In contrast, blackflies at site 2 exported substantial Hg to the riparian zone via adult emergence ($880 \mu\text{g m}^{-1}$ of river per year, Fig. 3A). There was greater blackfly emergence at site 2 and hence greater export of Hg to the riparian zone compared to other sites because blackfly production at this site greatly exceeded fish consumption. Only 10 to 14% of blackfly Hg at site 2 went to fish; the remainder was excreted during metamorphosis or transported to land in adult blackflies (Fig. 3B). The fate of Hg in blackflies at downstream sites was intermediate of those from sites 1 and 2. Because fishes ate most blackfly production, only a small amount (0 to $115 \mu\text{g m}^{-1}$) was exported to the riparian zone by adults, and flood effects on this Hg fate were minimal.

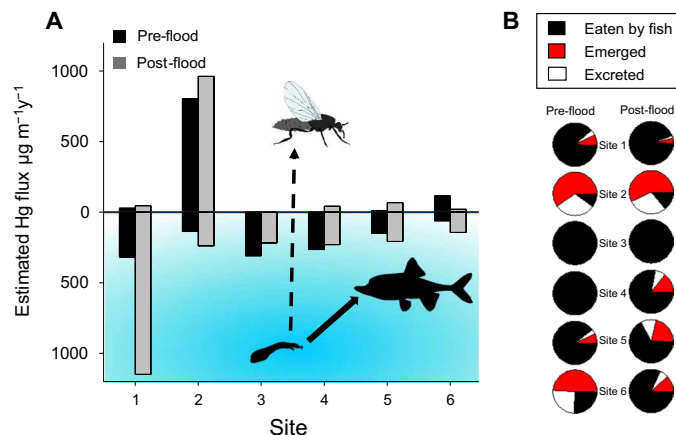


Fig. 3. Fate of Hg in coupled food webs. (A) Amount of Hg in blackfly larvae (in $\mu\text{g m}^{-1}$ of river per year) that is consumed by fishes (below the x axis, solid arrow) or is exported from the river via adult emergence (above the x axis, dashed arrow). (B) Proportion of Hg in blackfly larvae that is consumed by fishes, retained in adult blackflies, or excreted during metamorphosis.

Species traits, population sizes, and predator-prey interactions are well-understood mechanisms controlling community dynamics but are rarely incorporated into models of contaminant flux and fate in ecosystems (3). Differences in the traits and population sizes of mudsnails and blackflies strongly influenced the flux and fate of Hg in the Colorado River food web and thus the potential for Hg exposure for aquatic and terrestrial animals (Fig. 4). Mudsnails were highly productive in the tailwater, have a simple life history (aquatic life stage only), are sessile, and are predator resistant. As a consequence of these traits, mudsnails were a trophic dead end for Hg flux where they were abundant (Fig. 4), decoupling contaminant fluxes just as predator-resistant animals can decouple organic matter and energy flows in other food webs (6, 30–32). While the life span of mudsnails in the Colorado River is unknown, their production to biomass ratio (P:B) in the river is 3, indicating that their biomass turns over three times per year (24). This suggests a high rate of mudsnail mortality apart from predation, and the standing pool of Hg in mudsnail tissues is frequently cycled to the detrital pool. Mudsnail life history is in stark contrast with blackflies that have a complex life history, are important prey for fishes, and have adults that disperse to riparian zones. Moreover, in the Grand Canyon, blackflies have the highest Hg concentrations among aquatic invertebrates (5). They were not only the dominant Hg source for fishes but also a potential source of Hg for terrestrial insectivores such as birds, bats, lizards, and spiders.

Eagles-Smith *et al.* (33) identified hydrologic alteration and species invasions as two of the main modulators of Hg risk to wildlife and humans in an era of rapid global change, and our findings support this conclusion. Hydrologic alteration via the operation of GCD acts as a master variable controlling the invertebrate and fish assemblages and their interactions along the Colorado River. For example, the tailwater food web was highly simplified, with only one non-native fish species, Rainbow Trout, and was very inefficient at moving Hg to the top of the food web owing to large imbalances between invertebrate production and trout consumption. This imbalance was exacerbated by the extremely high production of predator-resistant, invasive New Zealand mudsnails that represented a trophic dead end with respect to the large amount of Hg they consumed.

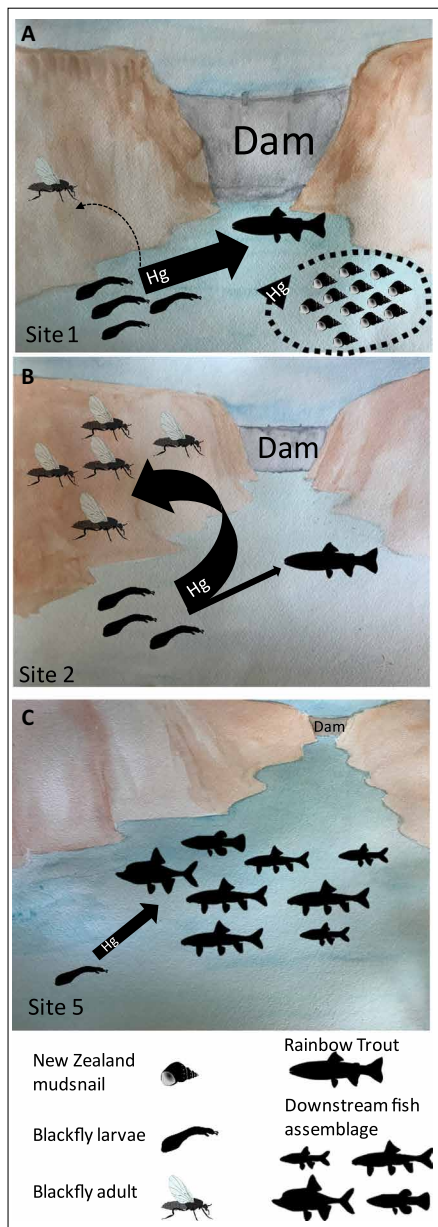


Fig. 4. Species traits and predator-prey interactions drive contaminant fate in coupled food webs. (A) Productive, predator-resistant mudsnails are a contaminant trophic dead end in the tailwater. Dashed circular arrow indicates that Hg in their tissues is recycled to the detrital pool when they die. (B and C) Differences in production of blackflies relative to fish consumption determined whether blackfly Hg remained in the aquatic food web or was exported to land by adult blackflies.

Our study encompassed an experimental flood event (34), providing a rare opportunity to assess responses of contaminant flux to this important adaptive management action. In addition, the Colorado River study system provides a particularly interesting example of how flood alteration and species invasion may interact to influence food webs and contaminant fluxes (35). Before the flood, animal production and contaminant fluxes in the tailwater were dominated by introduced and invasive taxa, including the primary consumers (i.e., mudsnails and amphipods) and vertebrate predators (i.e., Rainbow Trout). This configuration effectively dampened potential

Hg fluxes to Rainbow Trout because much of the Hg was stored and recycled by mudsnails. In this ecosystem state, production of trout, and therefore fluxes of Hg to upper trophic levels, was maintained at a relatively low level. Following the experimental flood, the food web took on a new architecture that enhanced the coupling of Hg flows to higher trophic levels. The flood increased production of favored trout prey (i.e., blackflies) that had higher Hg concentrations than other invertebrates. This, in turn, stimulated a threefold increase in Rainbow Trout production, which was largely supported by increased consumption of Hg-rich blackflies. Given our current knowledge of this food web, predicting such a response is actually within reach. This is particularly heartening given the renewed interest in modeling and managing flows in regulated rivers to support multiple ecological and societal objectives [e.g., (36, 37)].

Beyond the broadscale drivers of Hg modulation in food webs (33), local bottom-up and top-down controls can have large effects on both the flux of contaminants within aquatic food webs and fluxes of contaminants to land. For instance, bottom-up nutrient loading can increase primary production, leading to increased secondary production of aquatic insects. These changes can enhance insect emergence production and insect-mediated contaminant flux in lotic (19) and lentic ecosystems (7, 38). Likewise, fishes can exert strong top-down controls on the size structure and emergence production of aquatic insect communities (39, 40) with cascading effects on contaminant flux. For example, Chumchal and Drenner (7) showed that the presence of fish in small ponds could influence Hg flux from water to land by consuming and suppressing the emergence of large-bodied taxa such as dragonflies and damselflies. Although the emergence of small-bodied taxa increased in response to fish presence, these gains did not offset the reduction in Hg flux incurred through the loss of large-bodied taxa (11). In our study, while productivity of invertebrates was much higher at the tailwater site than downstream sites, Hg flux to land was trivial owing to the clear preference by Rainbow Trout for blackflies in comparison to taxa that do not have a terrestrial adult life stage (i.e., mudsnails, amphipods, and aquatic worms). Substantial amounts of Hg flux from the river only occurred where blackfly production far exceeded fish consumption and was thus “released” from top-down control. Together, these results demonstrate a complex interplay among secondary production, food web structure and interactions, and the magnitude of insect-mediated contaminant flux to land.

Although organic MeHg is the form of Hg that biomagnifies and is toxic to animals, here, we measured total Hg because it includes both organic and inorganic forms. Much of the Hg entering aquatic food webs are in the inorganic form, and the proportion of total Hg that is organic varies greatly across trophic levels, generally increasing with food web trophic position as the organic form is preferentially retained in animal tissues with each trophic step (41). Since inorganic and organic Hg are to a certain extent traveling in tandem through food webs, the dominant fluxes of total Hg are highly informative to the exposure and retention of MeHg to higher trophic level organisms such as fish. Biomagnification of Hg is the primary driver of environmental exposure and associated health risk, but Hg fluxes within food webs may not necessarily determine the Hg concentrations in those consumers. For example, a large flux of Hg from blackflies to a small population of fishes could have large direct effects on those fishes and their consumers. Alternatively, if fish populations expand as a result of invertebrate productivity (as we observed for Rainbow Trout in the tailwater), then a large flux of Hg

from blackflies could effectively be “diluted” by the addition of fish biomass or by enhancing fish growth rates. In this manner, biomass accretion could effectively offset the change in Hg flux with regard to Hg concentrations in the existing population.

While quantitative food web sampling was conducted at least quarterly over 2 years, we only sampled Hg once (after the flood and at the midpoint of the food web sampling; fig. S2). By applying Hg collected at a single time point to calculate fluxes that were based on two estimates of annual animal production and consumption, we are assuming that the Hg concentrations within the food web vary little over time. Walters *et al.* (5) hypothesized that the main source of Hg in the Colorado River in the Grand Canyon was likely atmospheric deposition of Hg in the upper watershed, which would be transported to Lake Powell and subsequently released to the river via GCD. Aqueous total Hg concentrations collected at site 1 just downstream from the dam were low and relatively invariant before, during, and after our study, suggesting that the sources of Hg to the Colorado River food web are temporally stable (table S4). However, Eagles-Smith *et al.* (42) found a lack of concordance between inorganic sources of Hg and Hg accumulation in fishes in western North America. This suggests that the net production of MeHg at local scales may be more important than the sources of inorganic Hg in determining fish Hg bioaccumulation at landscape scales. This implies that any flooding effects on MeHg production at sites in Grand Canyon could potentially influence our model estimates of Hg flux before the flood. However, nominal changes in Hg concentrations over time (say 1.5 to 3 times) would have minor influence on these estimated Hg fluxes relative to the very large differences in animal production and consumption that occurred over space and time in our study.

Examining Hg fluxes in these food webs allowed us to identify the key pathways of Hg movement [i.e., the trophic basis of exposure; *sensu* (18)] and provided unique insights beyond our current understanding of the processes governing Hg biomagnification that have been gleaned over the past several decades [reviewed in (4, 33)]. Critically, differences in Hg flux and fate were not simply due to spatial variation in species composition or in Hg tissue concentrations (5). Rather, these differences were directly tied to species traits and their influence on trophic interactions. For example, Hg concentrations in blackflies did not vary significantly in space (5), so the variability in their role in contributing to Hg flux to fishes and to the riparian zone was a function of their own production and the match/mismatch between that production and blackfly consumption by fish. Moreover, blackflies are important for Hg flux to fishes because they are particularly vulnerable to fish predation (e.g., as characterized by high drift rates, small body size, and exposed feeding locations). In contrast, any among-site variability in the concentration of Hg in mudsnail tissues was immaterial to Hg flux because they are invulnerable to fish predators such as Rainbow Trout.

Coupling ecotoxicological perspectives with ecosystem energetics reveals how contaminant flux can govern exposure to fish and terrestrial wildlife. Moreover, we provide an ecological basis for predicting contaminant fate within aquatic foods and across aquatic-riparian boundaries. This work answers recent calls to integrate ecological and ecotoxicological perspectives (3, 13, 14), and greater application of this trophic basis of exposure approach is needed to better predict the fate of contaminants in the environment and to better manage the risks of contaminant exposure in linked aquatic-terrestrial food webs.

MATERIALS AND METHODS

Details about the 2008 experimental flood

Closure of GCD in 1963 markedly altered the flow, sediment, and temperature regime of the Colorado River through Grand Canyon (43). These changes in the physical template of the river facilitated invasion by non-native species and contributed to the extirpation of native invertebrates and fishes from the Grand Canyon segment (23, 44). Sandbars were a prominent feature of the pre-dam Colorado River, but they declined in the post-dam river because Lake Powell reservoir traps 90% of the sand that was formerly supplied to the reach, and daily fluctuations in flow associated with hydropower generation further erode these habitats (45). Sandbars provide campsites that are used by the roughly 20,000 river rafters that navigate the Grand Canyon annually and create backwaters that provide rearing habitat for native Colorado River fishes (46). Starting in 1996, experimental floods were periodically released from GCD to attempt to rebuild sandbars and backwaters. These floods were timed to occur shortly after sand has been supplied to the Colorado River from tributary streams. The 2008 experimental flood that was the focus of this study occurred from 5 to 9 March and had a maximum discharge of 1210 m³/s. While this discharge was low relative to peak annual discharge under pre-dam conditions, it was considerably higher than the present day flow variation (fig. S2). Flows are regulated through hypolimnetic release during normal operations and experimental floods, so the chemical and thermal characteristics of the river exhibit relatively minor variation over time (47).

Food web sampling

We collected quantitative and qualitative samples of food web compartments at six sites along the Colorado River for 2 years (fig. S1). We sampled sites 1 and 6 monthly for estimating invertebrate biomass and production because these sites were accessible by road and they bracketed the range of longitudinal conditions. For sites 2 to 5, we conducted quarterly sampling because they were only accessible by launching 2-week river trips through the Grand Canyon. This effort was part of a larger study (22, 24) that included 3 years of annual production and consumption data that spanned July of each year to June of the next. During this larger study, resource managers initiated an experimental flood that occurred in March 2008, most of the way through our second year of flux estimates (fig. S2). Thus, the “post-flood” year in the current study of Hg flux refers to the timeframe that included an entire year after the flood. Our first year of data in the present study, which we refer to as the “pre-flood” time period, includes 3 months of data following the flood. Our decision to calculate fluxes in this way was constrained by our sampling and methodology. Thus, we do not have a clean separation between the true pre-flood and post-flood period with respect to flux data. However, this approach is rather conservative with respect to the interpretation of our results because the differences between pre- and post-flood would have been even larger if we had been able to calculate annual fluxes for all sites using the true pre- and post-dates.

We collected 18 to 20 benthic samples per season and site and sampled the predominant habitats, in proportion to their distribution at a site, using the multiple approaches. Cobble gravel bars were sampled with a Hess sampler, when depth made this feasible. Otherwise, we retrieved submerged rocks, scrubbed and collected all invertebrates from the rock surface, and measured the rock area to estimate invertebrate densities. Talus-cliff habitats were sampled with a modified vacuum pump, and depositional habitats were sampled

with a standard ponar dredge. Invertebrate diversity in the Colorado River is remarkably low owing to the operation of GCD (22–24) and was dominated by five taxa [Lumbricidae, *G. lacustris*, Chironomidae (midges), Simuliidae (blackflies), and New Zealand mudsnail (*P. antipodarum*)] during the period of this study. Fishes were sampled with various approaches, including angling, electrofishing, and seining. Further details on invertebrate and fish collection can be found in (22). In addition to quantitative samples for invertebrates and fish biomass, we also collected samples for gut content analysis. Gut contents were collected quarterly from 2006 to 2009 from 4 to 10 individuals per taxa per sampling date. Using this approach, we quantified gut contents seasonally for 2.5 years in invertebrates ($n = 960$) and fishes ($n = 1850$) (22, 48–50).

Estimates of production, production-based food webs, and consumption rates

We estimated animal secondary production and production-based food web interactions using standard approaches (18, 51); detailed methods are provided by Cross *et al.* (22). Briefly, we estimated mean (and 95% CIs) of secondary production [in g ash-free dry mass (AFDM) $m^{-2} year^{-1}$] of invertebrate taxa and fishes using multiple standard methods, including the instantaneous growth method and the size-frequency method (51), corrected for variation in temperature and turnover rates among sites. To estimate production-based food web interactions, we coupled quantitative analysis of diets with published assimilation efficiencies and secondary production estimates to quantify both the amount of production fueled by different food resources [i.e., the “trophic basis of production” (18)] and the amount of each food resource that a taxon must consume to result in the measured animal production [i.e., consumptive demand (18, 51)]. Consumptive demand is expressed as a consumption rate (the flux of diet items to consumers in units of mass per area per time). These fluxes can be used to quantify flows of energy, elements, or contaminants within food webs when the energy or elemental/chemical content is also known. Mean consumption rates (and 95% CIs) used in this study are from Cross *et al.* (22).

The calculation of these consumption rates explicitly recognizes that different food types are of different nutritional quality and are therefore assimilated at different rates. For invertebrate taxa, we used the following assimilation efficiencies based on literature values: 0.3 for diatoms, 0.1 for amorphous detritus, 0.1 for leaf litter, 0.3 for filamentous algae, 0.1 for macrophytes, 0.7 for fungi, and 0.7 for animal material (52). To calculate consumption rates for fishes, we used a range of assimilation efficiencies based on literature values for the study taxa [see appendix B in (22)]. Moreover, not all assimilated food is incorporated into new biomass; the fraction that goes toward new tissue is referred to as net production efficiency (NPE). For all invertebrate taxa, we used an NPE of 0.5 (18). NPE can vary significantly over a fish’s lifetime due to ontogenetic differences, so we applied a body size NPE relationship for fishes derived from bioenergetic models (50). The key output from the trophic basis of production calculations by Cross *et al.* (22) needed to estimate the Hg flux in this study is the consumption rate (g AFDM $m^{-2} year^{-1}$ with 95% CI) of all the resources by all the consumers in the food web. In addition to the mean annual consumption rates of food items calculated at the scale of individual invertebrate taxa and fishes, we also calculated the consumption rates and 95% CI of the consumption rates at the scale of the entire invertebrate assemblage and fish assemblages at each site. Consumption rates were all multiplied by

1.25 to convert these rates of consumption to g dry mass $m^{-2} year^{-1}$. Data on consumption rates (at the scale of taxa and assemblages) are available from Walters *et al.* (26).

Measuring Hg concentrations in resources and consumers

Detailed methods for sample collection, total Hg analysis, and quality assurance/quality control are provided by Walters *et al.* (5). Briefly, sample collection occurred from 12 to 28 June 2008 (fig. S2), approximately 3 months after the experimental flood. Sources of organic matter included fine benthic organic matter (FBOM), seston (suspended organic matter), epilithon (benthic biofilm), attached algae (*Cladophora* sp.), and epiphyton (diatoms attached to *Cladophora*). Macroinvertebrate assemblages near site 1 were dominated by non-native species including Lumbricidae, *G. lacustris*, Chironomidae, Simuliidae (blackflies), and New Zealand mudsnail (*P. antipodarum*), transitioning to assemblages dominated by blackflies and chironomids at downstream sites. We collected six fish species that are relatively common in Grand Canyon, and all of which rely primarily on macroinvertebrates for prey. These included native Bluehead Sucker (*Catostomus discobolus*), Flannelmouth Sucker (*Catostomus latipinnis*), and Speckled Dace (*Rhinichthys osculus*) and non-native Common Carp (*Cyprinus carpio*), Fathead Minnow (*Pimephales promelas*), and Rainbow Trout (*Oncorhynchus mykiss*).

Where possible, four replicate samples of each organic matter type and consumer per site were collected for Hg analyses. Samples were analyzed for the total Hg using cold vapor atomic fluorescence (CVAF; Tekran Model 2600 CVAF spectrometer) following Environmental Protection Agency Method 7474. Quality control was maintained by analysis of method blanks and repeated runs of an internal standard of known concentration. Mercury concentrations were reported as microgram per gram wet mass. We converted that to microgram per gram dry mass by assuming a 75% moisture content of organic matter and consumer tissues.

Calculating Hg flux

To calculate the flux of Hg in these food webs, we combined estimates of site-based consumption of resources by consumers in $g m^{-2} year^{-1}$ (see above) with the mean concentration of Hg in each resource using Eq. 1

$$Hg Flux_{i,j} = [Hg]_i \cdot C_{i,j} \quad (1)$$

where [Hg] is the mean concentration of Hg (in $\mu g g^{-1}$ dry mass), i is the resource (e.g., diatoms, attached algae, etc.), j is the consumer (e.g., blackflies, Rainbow Trout, etc.), and $C_{i,j}$ is the mean annual rate of consumption of resource i by consumer j (in $g m^{-2} year^{-1}$). This provides a quantitative flux of Hg to a consumer in $\mu g m^2 year^{-1}$ via its consumption of a given food item. For example, if the concentration of Hg is high in a given food resource, but very little of this food resource is eaten, then the flux will be low. In contrast, even if a food resource has a relatively low Hg concentration, but it is the preferred food resource of a given consumer, then the flux of Hg to that consumer will be high.

One critical aspect of calculating flux was to pair very fine grained, detailed gut content data with comparatively coarse sampling of food web compartments, particularly organic matter, for Hg analysis. For instance, a large fraction of some invertebrate diets was categorized as “amorphous detritus,” which was not sampled directly in the field for Hg analysis. Moreover, the methods used for identifying invertebrate

diet composition were different from fish diet analysis. Invertebrate diets were analyzed with fine-scale microscopy such that categories included amorphous detritus and diatoms (48). Fish diets were identified using more coarse identifications [see (49, 50)]. Therefore, on a few occasions, we used different media measured for Hg concentration to characterize Hg concentrations in diet items invertebrates and fishes (26). For invertebrates, (i) diatom concentrations were equal to the mean of Hg concentrations measured in epilithon and epiphyton at each site; (ii) amorphous detritus concentration was calculated as the mean of Hg concentrations measured in seston, epilithon, and FBOM at each site; and (iii) leaves were the concentrations of Hg measured FBOM. For filamentous algae and macrophytes, we used the concentration of Hg measured in *Cladophora* and hereafter refer to both of these categories as *Cladophora*. For fishes, all Hg concentrations for specific invertebrate taxa were used (e.g., blackflies, midges, etc.). For resources, we used the following: (i) Amorphous detritus was the average Hg concentrations measured in FBOM and seston at each site (i.e., none of these fishes are grazers, so we did not include epilithon concentrations in this calculation as we did for invertebrates); (ii) *Cladophora* was the Hg concentrations measured in *Cladophora*; (iii) unspecified aquatic invertebrates in fish diets were the mean of Hg concentrations measured in all aquatic invertebrates at that site; (iv) “fish” in fish diets were the mean of Hg concentrations measured in all fish at that site; and (v) leaves in fish diets were the Hg concentrations in FBOM. Some fish diets contained unidentified material, human food (e.g., vegetable scraps likely from campers that use the river for washing dishes), and terrestrial insects, but these resources were so minimal they were not included in Hg flux calculations.

While quantitative food web sampling was conducted at least quarterly over 2 years, we only sampled Hg once (after the flood and at the midpoint of the food web sampling; fig. S2). By applying Hg collected at a single time point to calculate fluxes that were based on two estimates of annual animal production and consumption, we are assuming the Hg concentrations within the food web vary little over time. Aqueous total Hg concentrations collected at site 1 were low and relatively invariant before, during, and after our study, suggesting that the sources of Hg to the Colorado River food web are temporally stable (table S4). In addition, small changes in Hg concentrations over time (say 1.5×) would have minor influence on Hg fluxes relative to the very large differences in animal production and consumption that occurred over space and time in this study.

Calculating fate of Hg in blackflies

We investigated three possible fates of Hg accumulated in larval blackflies: (i) consumed by fishes, (ii) excreted and recycled to riverine food webs during metamorphosis, or (iii) exported to riparian food webs via adult emergence. Invertebrate predators are largely absent in this system, so fish are the primary consumers of larval blackflies. In the first two cases, the fate of Hg accumulated in blackflies was to remain in the aquatic system; in the latter case, the fate of Hg was to move to the riparian zone, where it could potentially enter terrestrial food webs. We calculated the flux of blackfly Hg to fishes using the same approach as above (i.e., fish consumption of blackflies multiplied by blackfly Hg concentration in $\mu\text{g m}^{-2} \text{ year}^{-1}$, see Eq. 1). We then estimated the emergence of blackflies as the difference between the secondary production of blackflies (in $\text{g m}^{-2} \text{ year}^{-1}$) and fish consumption of blackflies (in $\text{g m}^{-2} \text{ year}^{-1}$). Emergence can also be estimated via established linear relationships with secondary production

of insect taxa (51, 53) as has been done to calculate emergence fluxes of Hg by others (19). An important source of uncertainty in that approach is variation in consumption by fishes, which can account for a large proportion of insect production (27, 28) and regulate rates of emergence (29). Because we had measured blackfly consumption by fishes across sites and time periods and found it highly variable (22), we expected that calculating their emergence via the difference approach would yield the most accurate estimates. The biomass of blackflies emerged was then estimated by Eq. 2

$$E_b = P_b - C_{b,f} \quad (2)$$

where E_b is the emergence rate of blackflies (in $\text{g m}^{-2} \text{ year}^{-1}$), P_b is the rate of secondary production of blackflies ($\text{g m}^{-2} \text{ year}^{-1}$), and $C_{b,f}$ is the rate of consumption of blackflies by fishes (in $\text{g m}^{-2} \text{ year}^{-1}$).

To calculate the flux of Hg via blackflies to riparian zone, we used Eq. 3

$$\text{Hg Flux}_{b,rz} = E_b \cdot [\text{Hg}]_b \cdot M_{l,a} \quad (3)$$

where E_b is blackfly emergence ($\text{g m}^{-2} \text{ year}^{-1}$), $[\text{Hg}]_b$ is the concentration of Hg in blackflies ($\mu\text{g g}^{-1}$), and $M_{l,a}$ is the fraction of Hg transferred from larvae to adults during metamorphosis [for insects, this is typically 0.66; (54)]. Fluxes are in dry mass units. We rescaled the areal units from $\text{g m}^{-2} \text{ year}^{-1}$ to μg of Hg per linear meter of river per year ($\text{g m}^{-1} \text{ year}^{-1}$) to better reflect the way in which riparian predators will likely respond to prey availability (55, 56). Hg flux of $\text{g m}^{-1} \text{ year}^{-1}$ represents the total retention or output of blackfly-associated Hg for a 1-m-long segment of river, and this flux could vary greatly if it was measured in a narrow or wide part of the river. Average river width for each sampling site was calculated using a geographic information system, (GIS) by measuring river width every 0.1 km throughout a sampling site and then averaging these 15 to 30 individual width measurements (number of individual width measurements varied depending on the length of the sampling reach).

SUPPLEMENTARY MATERIAL

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/6/20/eaaz4880/DC1>

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consumers, total Hg fluxes to invertebrates and fishes, and the fate of Hg associated with blackflies. Additional data related to this paper may be requested from the authors.

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