Contaminants in linked aquatic–terrestrial ecosystems: Predicting effects of aquatic pollution on adult aquatic insects and terrestrial insectivores

Johanna M. Kraus[1,2]

[1]US Geological Survey, Columbia Environmental Research Center, 4200 New Haven Road Columbia, Missouri 65201 USA

Abstract: Organisms that move across ecosystem boundaries connect food webs in apparently disparate locations. As part of their life cycle, aquatic insects transition from aquatic larvae to terrestrial adults, thereby linking freshwater ecosystem processes and terrestrial insectivore dynamics. These linkages are strongly affected by contamination of freshwater ecosystems, which can reduce production of adult aquatic insects (i.e., emergence), increase contaminant concentrations in adult insect tissues, and alter contaminant flux to terrestrial ecosystems. Despite the potential impact of contaminants on adult aquatic insects, little is known about predicting these effects. Here, I develop a heuristic model based on contaminant properties and ecotoxicological principles to predict the effects of various classes of aquatic contaminants on adult aquatic insects and discuss implications for terrestrial insectivores living near contaminated freshwaters. The main finding is that contaminant classes vary greatly in how their biologically-mediated effects on aquatic insects affect terrestrial insectivores. Highly bioaccumulative contaminants that are well retained during metamorphosis, like polychlorinated biphenyls (PCBs), are often non-toxic to aquatic insect larvae at concentrations commonly found in the environment. Such contaminants flux from aquatic ecosystems in large quantities in the bodies of emerging adult aquatic insects and expose terrestrial insectivores to toxic levels of pollution. On the other hand, contaminants that are less bioaccumulative, excreted during metamorphosis, and more toxic to insects, like trace metals, tend to affect terrestrial insectivores by reducing production of adult aquatic insects on which they prey. Management applications of this model illustrate type and severity of risk of aquatic contaminants to consumers of adult aquatic insects.

Key words: spatial subsidies, aquatic–terrestrial linkages, food web, conceptual model, metamorphosis, insects

The fates of food webs in neighboring ecosystems are often spatially linked by movements of nutrients, resources, and predators (Polis et al. 1997, Nakano and Murakami 2001, Baxter et al. 2005, Allen and Wesner 2016). In freshwater ecosystems, aquatic insects that metamorphose from aquatic larvae to terrestrial adults play key roles as prey subsidies that move nutrients and energy from aquatic to terrestrial food webs (Jackson and Fisher 1986, Nakano and Murakami 2001, Baxter et al. 2005, Allen and Wesner 2016). Interruption or modification of the magnitude, timing, or dietary value (e.g., stoichiometry, polyunsaturated fatty acids, contaminant concentration) of emerging adult aquatic insects can reduce insectivore abundance and biomass, lower insectivore reproductive success, and increase predation pressure on alternative prey with consequences for aquatic and terrestrial food webs (Baxter et al. 2005, Rohr et al. 2006, Marcarelli et al. 2011). Contaminants, which are increasingly recognized as a global stressor of aquatic ecosystems (Lavoie et al. 2013, Morrissey et al. 2015, Bernhardt et al. 2017), strongly affect emergence production, assemblage composition, timing of adult aquatic insect emergence, concentration of contaminants in adult insect tissues,

E-mail address: [2]Jkraus@usgs.gov

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and contaminant flux from aquatic to terrestrial food webs (Fig. 1; Menzie 1980, Clements et al. 2000, Kraus et al. 2014a, Chumchal and Drenner 2015). Despite the importance of these impacts for terrestrial and aquatic insectivores (e.g., birds, bats, lizards, spiders, rodents, and fish; Walters et al. 2008, Sullivan and Rodewald 2012, Kraus et al. 2014a, Chumchal and Drenner 2015, Schiesari et al. 2018), no model currently exists for predicting effects of aquatic contaminants on adult aquatic insects.

Contaminant impacts on adult aquatic insects vary somewhat predictably both among and within contaminant classes as a function of their toxicity, propensity to bioaccumulate, and retention in tissues across metamorphosis. For example, some contaminants strongly reduce metamorphosis and emergence production (including changes in assemblage composition and timing), whereas other contaminants bioaccumulate in insect larvae and are retained in their tissues across metamorphosis to adulthood (Kraus et al. 2014b, Wesner et al. 2019). Trace metal contamination and neonicotinoid insecticides strongly reduce adult aquatic insect emergence and are implicated in the global decline in insect biomass (Hallmann et al. 2014, Kraus et al. 2014a, Morrissey et al. 2015, Cavallaro et al. 2017), thus eliminating an important prey source for many terrestrial insectivores including spiders, young waterfowl, aerial insectivorous birds, and bats (Hallmann et al. 2014, Morrissey et al. 2015). In contrast, other contaminants, such as persistent organic pollutants and organometals (and possibly algal toxins, personal care products, and pharmaceuticals), do not necessarily reduce emergence production at a site even though they also bioaccumulate in insect larvae and strongly persist in their tissues across metamorphosis (Walters et al. 2008, Tweedy et al. 2013, Moy et al. 2016, Kraus et al. 2017, Richmond et al. 2018). When these highly-contaminated adult aquatic insects fall prey to terrestrial insectivores, they become vectors of contaminant exposure and reduce insectivore reproduction, health, and juvenile success (Custer et al. 2003, Walters et al. 2010, Chumchal and Drenner 2015).

To increase understanding of how aquatic contamination alters aquatic–terrestrial linkages, I use information about physicochemical characteristics and ecotoxicological effects of various contaminant classes to develop a heuristic model that predicts contaminant concentrations in aquatic insects, impacts on emergence production, and flux of contaminants to terrestrial ecosystems via adult aquatic insects. This approach complements efforts that conversely use basic ecological principles to predict ecotoxicological effects of contaminants on aquatic communities and ecosystems (Rohr et al. 2006, Halstead et al. 2014). I discuss potential impacts of model outcomes on terrestrial insectivores, as well as limitations of the model and need for future studies. Finally, I provide examples of how this model is currently being applied to inform research approaches and management strategies of freshwaters in historically mined, industrially polluted, and agricultural landscapes. Understanding how the effects of stressors like aquatic contaminants cascade across ecosystem boundaries is an important challenge for applied ecology and ecosystem management (Muehlbauer et al. 2019).

HEURISTIC MODEL

To predict the potential impacts of aquatic contaminants on emergence production, adult concentrations, and contaminant flux, I modeled the relationship between toxicity and contaminant retention during metamorphosis for various contaminant classes (Figs 2, 3). It is not possible to quantitatively model multiple contaminant classes along the same toxicity axis because different classes use different metrics of toxicity. Thus, to examine differences among classes, I qualitatively mapped the relative toxicity and contaminant retention across metamorphosis by contaminant class (Table 1, Fig. 2). To derive predictions about relative effects of individual contaminants within classes, I used least squares linear regressions to model the relationships between toxicity and retention across insect metamorphosis (i.e., the natural log ratio of adult to larval concentrations) within 3 major contaminant classes (i.e., metals, polycyclic aromatic hydrocarbons [PAHs], and polychlorinated biphenyls [PCBs]) based on published toxicity values for contaminants with known retention across metamorphosis (Fig. 3).

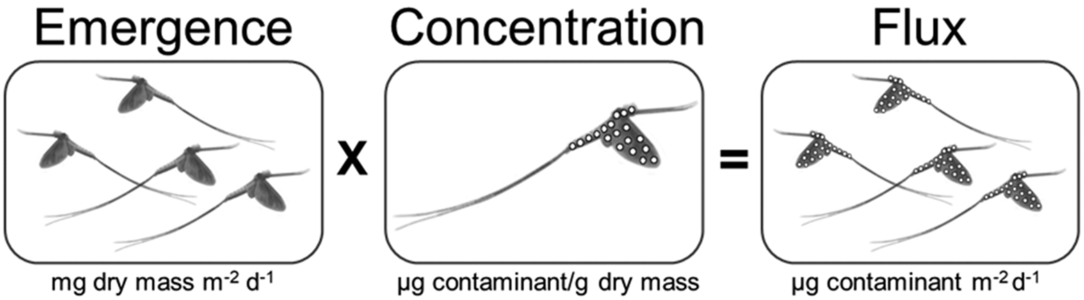

Figure 1. Flux of aquatic contaminants to the terrestrial ecosystem by adult aquatic insects as a function of emergence production and contaminant concentration within adult insect bodies. White circles represent contaminant ions or molecules within insect bodies. Insect images are courtesy of Jeremy Monroe at Freshwaters Illustrated.

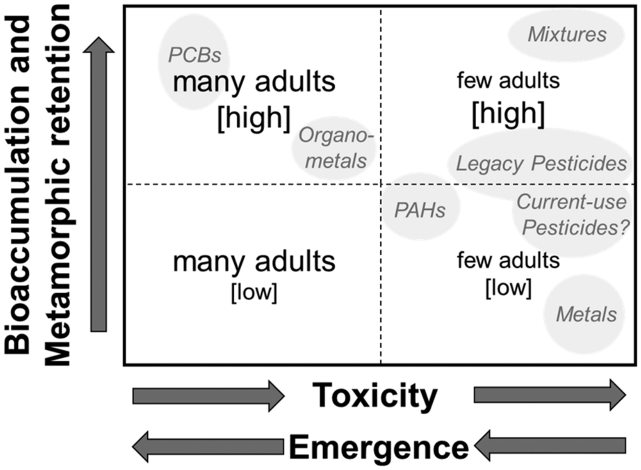

Figure 2. Heuristic Model Part I: Predicting effects on emergence of adult aquatic insects and contaminant concentrations among various classes of aquatic contaminants. As toxicity of a given compound/element increases, adult aquatic insect emergence is predicted to decrease, leading to loss of prey resources for insectivorous consumers. As persistence of the contaminant across insect metamorphosis increases, the likelihood of effects of exposure on consumers increases. Gray text shows approximate position within this framework of different classes of contaminants at environmentally relevant concentrations. 'many adults' and 'few adults' illustrate the relative biomass or abundance of emerging adult aquatic insects given the combination of toxicity and retention during metamorphosis in each quadrant of the graph. Similarly, [low] and [high] represent low concentrations and high concentrations, respectively, of contaminants in emerging adult aquatic insects in each quadrant of the graph.

Among contaminant classes, metals and current-use pesticides are generally more toxic to aquatic insects, less bioaccumulative, and less retained across metamorphosis than PCBs and lipophilic organics (Table 1, Fig. 2; Kenaga 1982, Hare 1992, Kraus et al. 2014b). Trace metals, PAHs, and some current-use pesticides increase mortality and reduce adult emergence of aquatic insects but are not highly bioaccumulative nor in most cases well retained during insect metamorphosis (Table 1, Fig. 2, lower right panel). Organometals and metalloids (e.g., methylmercury and selenomethionine) and lipophilic organic contaminants like PCBs are not highly toxic to aquatic insects at concentrations commonly found in the environment but accumulate in relatively high concentrations in larval insects and are well transferred across metamorphosis (Table 1, Fig. 2, upper left panel). Finally, bioaccumulative legacy pesticides like dichlorodiphenyltrichloroethane (DDT) and some contaminant mixtures may reduce emergence of adult aquatic insects while increasing contaminant concentrations in surviving adults (Table 1, Fig. 2, upper right panel).

Within contaminant classes, metal retention across metamorphosis is positively related to both toxicity and metal softness (i.e., greater tendency to form covalent bonds; Fig. 3A; McCloskey et al. 1996, Kinraide 2009, Li et al. 2012, Wu et al. 2012, Kraus et al. 2014b). Thus, softer metals may more readily lower emergence production and increase adult aquatic insect tissue concentrations (McCloskey et al. 1996, Kinraide 2009, Li et al. 2012, Wu et al. 2012) than harder metals. Organic compounds vary markedly in terms of their predicted impacts on emergence production and adult insect tissue concentrations. For non-polar organic contaminants with intermediate lipophilicity (i.e., fat solubility; log of the octenol-water partitioning coefficient [log Kow] = 5 – 7), retention across metamorphosis initially increases with increased toxicity, then levels out for compounds with log Kow of ~6 (Fig. 3B; Schultz et al. 1990, Li et al. 2012, Kraus et al. 2014b, Fu et al. 2015). For more hydrophilic non-polar organic compounds (log Kow < 5), retention across metamorphosis decreases with increased toxicity (Fig. 3B; Schultz et al. 1990, Kraus et al. 2014b, Fu et al. 2015). For highly bioaccumulative organic contaminants (log Kow ~7) like PCBs and tetrachlorodibenzodioxins, relative toxicity within these classes is not necessarily correlated with retention (Kraus et al. 2014b) and has more to do with congener structure (Fig. 3C; Van den Berg et al. 1998, 2006). Thus, to (grossly) generalize for organic contaminants, hydrophilic compounds are more likely to reduce emergence and have lower contaminant concentrations in adult insect tissues, contaminants with intermediate lipophilicity tend to reduce emergence and have higher tissue concentrations, and lipophilic compounds do not affect emergence but tend to have higher concentrations in adult aquatic insect tissues.

IMPLICATIONS FOR TERRESTRIAL INSECTIVORES

Placing contaminants within the heuristic model proposed here allows us to generate predictions about where and how they may affect terrestrial insectivores (e.g., spiders, birds, bats, and lizards) via their effects on aquatic insect emergence, contaminant concentrations within aquatic insect tissues, and contaminant fluxes conveyed by adult aquatic insects. Contaminants that are lost during insect metamorphosis but lead to high mortality of aquatic insects at concentrations commonly found in the environment (either at the adult stage or earlier; Wesner et al. 2019) have the potential to cause a loss of food or prey resource problem for insectivores of adult aquatic insects (Fig. 2, bottom right panel). In these cases, loss of prey resources is more likely to drive effects of aquatic contaminants on insectivores than eating contaminated prey (e.g., Kraus et al. 2014a). For example, secondary production and emergence severely decrease in trace metal-polluted streams (Clements et al. 2000, Kraus et al. 2014a), whereas trace metals are heavily lost during metamorphosis (e.g., 39–94% of body burdens; Kraus et al. 2014b). As a result, riparian spider biomass has been reported to be related to changes in aquatic emergence production but not tissue metal concentrations or flux (Paetzold et al. 2011, Kraus

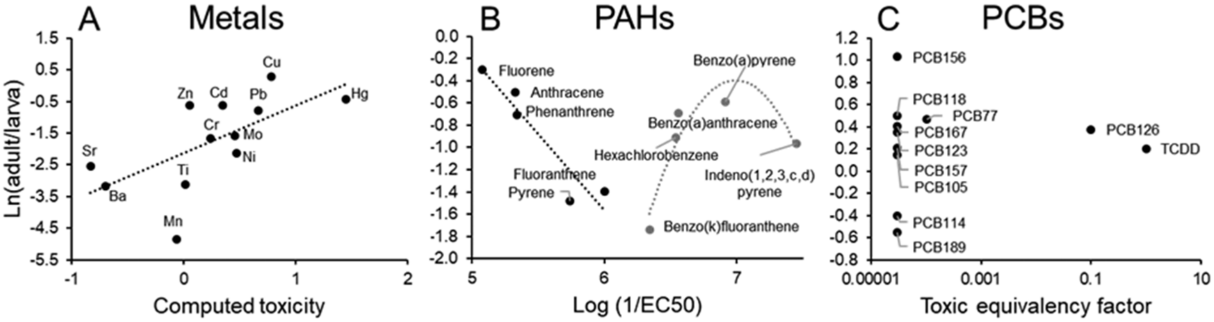

Figure 3. Heuristic Model Part II: Predicting effects of contaminants on adult aquatic insect emergence and contaminant concentration within contaminant classes. Empirical relationships between retention across insect metamorphosis (dependent variable) and different measures of toxicity (independent variable) for compounds/elements within 3 contaminant classes: metals (A), PAHs (B), and PCBs (C). Retention is measured as the natural log of the ratio of the concentrations observed in adult and larval aquatic insects (extracted from Kraus et al. 2014b). For metals, the computed toxicity scale is the predicted $\log_{10}$ of the inverse concentration of different metal ions required to reduce a variety of metrics (survival, growth, etc.) for a variety of organisms by 50% (extracted from Kinraide 2009). For PCBs, toxic equivalency factors were extracted from Van den Berg et al. (2006) for mammals, which is similar to fish and birds (Van den Berg et al. 1998). For PAHs, $\log_{10}(1/\text{EC50})$ is the $\log_{10}$ of the inverse of the baseline (non-polar) predicted concentration at which the growth rate or yield was reduced by 50% for multiple species of green algae (extracted from Fu et al. 2015). Statistically significant least squares regressions were (A) $y = 1.5x - 2.1$, $R^2 = 0.41$, (B) $y = -1.4x + 6.7$, $R^2 = 0.89$ when log Kow < 5; (black circles and dashed line) and $y = -2.8x^2 + 39.8x - 139.5$, $R^2 = 0.86$ when log Kow = 5 to 7 (gray circles and dashed line).

et al. 2014a). On the other hand, contaminants that are highly retained but not very toxic at concentrations commonly found in the environment have the potential to expose insectivores to detrimental concentrations of dietary contaminants (i.e., an exposure problem; Fig. 2, top left of panel). For example, PCBs exhibit low aquatic toxicity but high persistence in tissues. Insects lose at maximum only 17% of their PCB body burdens across metamorphosis. PCB concentrations are 1.3× higher in adult insects compared with larvae (i.e., bioamplification; Kraus et al. 2014b) because insects also lose 20 to 80% of their body mass during metamorphosis. As a result, patterns of PCB bioaccumulation in riparian spiders and modeled exposure of aerial insectivorous birds are similar to aquatic insect and sediment concentrations (e.g., Walters et al. 2010, Kraus et al. 2017, Walters et al. 2018).

Contaminants and contaminant mixtures that are both highly toxic and retentive in adult aquatic insects at concentrations commonly found in the environment could lead to a variety of outcomes depending on the relative magnitude of these processes. For example, at concentrations found in most ecosystems, the effects of methyl mercury bio accumulation are more important than its lethal toxicity to adult aquatic insects, leading to high exposure and bioaccumulation in their terrestrial consumers (Tweedy et al. 2013, Chumchal and Drenner 2015, Gann et al. 2015, M. M. Chumchal, Texas Christian University, personal communication). On the other hand, dietary exposure of terrestrial insectivores to mercury could be very low near aquatic ecosystems affected by neonicotinoid insecticides because there would be few adult aquatic insects left to eat. If there are fewer adult insect prey available, mobile aerial consumers such as song birds and bats might be less likely to be attracted to the ecological trap of mercury-laden prey, thus severing the linkage between aquatic and terrestrial exposure. Many freshwater ecosystems are simultaneously exposed to multiple contaminants, and a strength of this framework is its ability to generate hypotheses regarding what effects different contaminant mixtures will have on aquatic–terrestrial linkages.

A final strength of this heuristic model is that it can help predict how contaminant properties alter the relevance of contaminant concentration vs contaminant flux conveyed by adult aquatic insects in driving diet-mediated effects of aquatic contaminants on terrestrial insectivores. Changes in emergence production and aquatic contaminant concentrations in adult aquatic insects have well-studied implications for insectivores. However, the product of these 2 factors, contaminant flux, which is a direct measure of how much contaminant is moving from water to land in prey (Table 1, Fig. 1; Menzie 1980, Chumchal and Drenner 2015), varies in its role as a driver of consumer exposure and risk depending on contaminant class. For example, mercury flux in small-bodied adult aquatic insects emerging from ponds is positively correlated with concentrations of mercury in riparian spiders (Tweedy et al. 2013). However, this straightforward relationship between contaminant flux and consumer risk appears to occur only when contaminants both biomagnify through the food web and are well retained across metamorphosis at concentrations that do not significantly reduce adult aquatic insect emergence. For contaminants that do not biomagnify or are lost across metamorphosis, or are at concentrations that strongly reduce adult emergence, contaminant flux

Table 1. Data to inform Part I of the Heuristic Model: Relative toxicity, bioaccumulation, metamorphic retention, and contaminant flux of various contaminant classes to adult aquatic insects. Contaminant flux is predicted based on relative toxicity and mean retention of that class of contaminants across insect metamorphosis.

Contaminant classes	Compound/element examples	Relative toxicity		Relative bioaccumulation		Metamorphic retention[†]		Contaminant flux
		Level	Cite	Level	Cite	Mean (SE)	Cite	Predicted
Trace metals	Ba, Cd, Cr, Cu, Hg, Mn, Mo, Ni, Pb, Sr, Ti, Zn	High	Kenaga 1982, McCloskey et al. 1996, Kinraide 2009	Low/Med	Hare 1992	−1.81 (0.37)	Kraus et al. 2014b	Low
Organometals	MeHg, Se-met	Low	Chumchal and Drenner 2015	High	Chumchal and Drenner 2015	−0.28 (0.24)	Kraus et al. 2014b	High
PCBs	Various congeners	Low	Kenaga 1982, Van den Burg 2006	High	Walters et al. 2016	0.13 (0.10)	Kraus et al. 2014b	High
PAHs	Fluorene, pyrene, hexachlorobenzene, indeno(1, 2, 3, c, d)-pyrene	High	Fu et al. 2015	Low	Fu et al. 2015, Walters et al. 2016	−0.88 (0.19)	Kraus et al. 2014b	Low
Current-use pesticides	Neonicotinoids, bifenthrin, atrazine	High	Morrissey et al. 2015	Low	Hladik et al. 2015	0.28 (0.56)	Table S1[‡]	Low/Med
Legacy pesticides	DDT degradates, hexachlorobenzene	High	Kenaga 1982	Med/High	Grier 1982, Walters et al. 2016	−0.47 (0.35)	Kraus et al. 2014b	Med

[†] Natural log of adult divided by larval concentrations

[‡] Data provided in the supplemental materials, Table S1. Represents transfer from larvae with low tissue concentrations.

can be uncorrelated with consumer risk. For example, in a study of insect emergence from metal-contaminated streams in the central Rocky Mountains, flux of the trace metals Zn, Cu, and Cd via adult aquatic insects was highest from low-metal streams (Kraus et al. 2014a). However, riparian insectivores of adult aquatic insects were unaffected by metal flux from low metal streams. Instead, consumers were more affected by loss of prey near high-metal streams. Spider densities across a gradient of stream metal concentrations were unrelated to contaminant concentration or flux but were positively correlated with dipteran emergence (Kraus et al. 2014a).

MODEL ASSUMPTIONS AND DATA GAPS

The purpose of a heuristic model is to provide a baseline set of predictions as a practical, albeit simplistic, starting point for solving a problem. The current model assumes that the physicochemical properties of contaminants and their known ecotoxicological effects on aquatic insects at concentrations commonly found in the environment are the main drivers of 1) adult aquatic insect production, contaminant concentration, and flux from contaminated freshwater ecosystems and 2) effects on insectivorous consumers of these insects. Deviations from model predictions point to situations where these simplifying assumptions do not hold and other factors may be equally or more important in driving the effects of aquatic contaminants on adult aquatic insects and their insectivores. For example, in circumstances where the contaminants themselves are not the major driver of insect production, other factors besides exposure drive contaminant flux from aquatic to terrestrial food webs. Tweedy et al. (2013) observed that in mercury contaminated ponds, nutrient enrichment (a bottom-up ecological process) and presence of fish (a top-down ecological process), and not mercury concentrations, largely drive aquatic insect emergence and, thus, patterns of mercury flux and uptake by riparian spiders. In other circumstances, such as comparisons across geologically and topographically complex landscapes, variation in water chemistry and species characteristics (e.g., contaminant concentration, organic matter, pH, water hardness, timing of exposure, species identity and genetic adaptation; Clements et al. 2016), rather than contaminant concentrations alone, drive toxicity and bioaccumulation of contaminants. In these cases, measurements of local conditions are key to site-specific predictions.

Landscape, food-web, consumer, and prey characteristics can also be affected by contaminants and will influence how contaminant impacts on aquatic insects play out for their consumers. Factors such as habitat loss and alteration, aquatic and terrestrial diversity, trophic structure, prey preferences and ability to capture insects, consumer mobility, prey size and behavior, and timing of emergence are all common potential modifiers of insectivore responses to aquatic contaminants (Baxter et al. 2005, Sullivan and Rodewald 2012, Sullivan and Manning 2019). For example, assemblages in metal-contaminated streams have relatively few metal-sensitive mayflies but more true flies (dipterans) and metal-bioaccumulating stoneflies (Clements et al. 2000, Kraus et al. 2014a). Riparian spiders like long-jawed orb weavers (Tetragnathidae) can eat mayflies and dipterans, but stoneflies tend to be too large-bodied to capture. Thus, even if stoneflies contribute to the emergence production and metal flux from a stream, they are unlikely to affect riparian tetragnathid biomass. Consumer mobility can also strongly affect insectivore responses to changes in adult aquatic insect emergence. For example, diminished resources, regardless of prey contaminant concentrations, are likely to have larger effects on specialist consumer populations with small foraging ranges than contaminant exposure (e.g., Power et al. 2004). However, for generalist, higher-order and highly-mobile consumers, like birds and bats, loss of aquatic insect resources from 1 local source would not be expected to affect populations as much as exposure from eating contaminated prey (e.g., Custer et al. 1998). More research is needed to flesh out the role of these factors in driving the effects of aquatic contaminants on adult aquatic insects and insectivorous consumers.

RESEARCH AND MANAGEMENT APPLICATIONS

Regionally, fate and transport models, as well as empirical trend and assessment measurements, can provide information at multiple scales about contaminant distribution across the landscape (MacLeod et al. 2001, Kolpin et al. 2002). Building on these frameworks, the model presented here can be used to predict whether aquatic-dependent insectivores in a particular region are likely to suffer from prey resource depletion or contaminant exposure. These predictions can be used to shape experimental design and support efficient allocation of resources for research designed to inform management decisions. For example, the Mineral Belt of the United States Rocky Mountains is a highly-mineralized and historically-mined region. We predicted based on the information used in this model that the metals mobilized into the streams of this region would accumulate in larvae but not be retained across metamorphosis to terrestrial adults (Hare 1992, Kraus et al. 2014b, Wesner et al. 2019). However, aqueous concentrations were great enough in some streams to cause high mortality in adult aquatic insects (Kraus et al. 2014b), potentially making reduced food availability a major problem for consumers (Custer et al. 2003, Paetzold et al. 2011, Kraus et al. 2014a). Because of the predictions driven by the model presented here, we featured ecological measures of emergence production heavily in the experimental design of these studies, which allowed accurate assessment of the ecotoxicological effects of trace metals on emergence and riparian spiders in these regions (Paetzold et al. 2011, Kraus et al. 2014a). In contrast, methylmercury uptake by riparian spiders are driven by both concentrations of mercury in adult aquatic insect prey and their emergence production (i.e., mercury flux; Tweedy et al. 2013, Chumchal and Drenner 2015), which required measurement of both emergence and tissue concentrations for these studies.

Understanding the effects of aquatic pollution on aquatic–terrestrial linkages is of interest to regulatory agencies and local stakeholders. For example, adult aquatic insect mediated-PCB flux to terrestrial insectivores near the Great Lakes and other industrially polluted water bodies is being used as a measure of remedy effectiveness (e.g., sediment dredging; Custer et al. 1998, Walters et al. 2010, Kraus et al. 2017, Walters et al. 2018, Muehlbauer et al. 2019). Effects of current-use pesticides on the emergence and contamination of adult aquatic insects in wetlands critical to waterfowl production are being used in decision-making by the Canadian government and are of interest to the United States Fish and Wildlife Service (Table S1; Ballingall 2018, Cavallaro et al. 2017). Thus, by predicting and identifying problems due to the disruption and contamination of aquatic–terrestrial linkages, conceptual and quantitative models, such as the one presented here, can help prioritize research directions and decisions regarding natural resource management.

The genesis of the field of ecotoxicology (Truhaut 1977) and the publication of Silent Spring (Carson 1962) alerted the public to how exposure to contaminants can cascade through food webs and ecosystems, such as occurred between DDT and a massive reproductive crash in bald eagles (Grier 1982). Also highlighted in this early work, although not as appreciated, are the cascading problems of aquatic contamination on ecological disruptions, extinctions, and population/community declines across ecosystem boundaries caused by prey resource losses (Carson 1962, Rohr et al. 2006, Bernhardt et al. 2017, Ballingall 2018, Schiesari et al. 2018). Predicting under what conditions each (or both) of these effects occur informs the range of possible outcomes for insectivorous consumers and the approaches needed to measure those outcomes in food webs (e.g., measure concentrations for exposure problems and ecological metrics for food loss). Ultimately, this heuristic model for predicting how aquatic contaminants affect adult aquatic insects will help streamline decision making about what are often cryptic and non-intuitive effects of contaminant stressors at the land-water interface.

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LITERATURE CITED

Allen, D. C., and J. S. Wesner. 2016. Synthesis: Comparing effects of resource and consumer fluxes into recipient food webs using meta-analysis. Ecology 97:594–604.

Ballingall, A. 2018. Ottawa to phase out pesticides linked to bee deaths. The Star, Toronto, Canada. (Available from: https://www.thestar.com/news/canada/2018/08/14/ottawa-to-phase-out-pesticides-linked-to-bee-deaths.html)

Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: Reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50:201–220.

Bernhardt, E. S., E. J. Rosi, and M. O. Gessner. 2017. Synthetic chemicals as agents of global change. Frontiers in Ecology and the Environment 15:84–90.

Carson, R. 1962. Silent spring. Houghton Mifflin, Boston, Massachusetts.

Cavallaro, M. C., C. A. Morrissey, J. V. Headley, K. M. Peru, and L. Liber. 2017. Comparative chronic toxicity of imidacloprid, clothianidin, and thiamethoxam to *Chironomus dilutus* and estimation of toxic equivalency factors. Environmental Toxicology and Chemistry 36:372–382.

Chumchal, M. M., and R. W. Drenner. 2015. An environmental problem hidden in plain sight? Small human-made ponds, emergent insects, and mercury contamination of biota in the Great Plains. Environmental Toxicology and Chemistry 34:1197–1205.

Clements, W. H., D. M. Carlisle, J. M. Lazorchak, and P. C. Johnson. 2000. Heavy metals structure benthic communities in Colorado mountain streams. Ecological Applications 10:626–638.

Clements, W. H., D. R. Kashian, P. M. Kiffney, and R. E. Zuellig. 2016. Perspectives on the context-dependency of stream community responses to contaminants. Freshwater Biology 61: 2162–2170.

Custer, C. M., T. W. Custer, P. D. Allen, K. L. Stromborg, and M. J. Melancon. 1998. Reproduction and environmental contamination in tree swallows nesting in the Fox River drainage and Green Bay, Wisconsin, USA. Environmental Toxicology and Chemistry 17:1786–1798.

Custer, C. M., T. W. Custer, P. M. Dummer, and K. L. Munney. 2003. Exposure and effects of chemical contaminants on tree swallows nesting along the Housatonic River, Berkshire County, Massachusetts, USA, 1998–2000. Environmental Toxicology and Chemistry 22:1605–1621.

Fu, L., J. J. Li, Y. Wang, X. H. Wang, Y. Wen, W. C. Qin, L. M. Su, and Y. H. Zhao. 2015. Evaluation of toxicity data to green algae and relationship with hydrophobicity. Chemosphere 120:16–22.

Gann, G. L., C. H. Powell, M. M. Chumchal, and R. W. Drenner. 2015. Hg-contaminated terrestrial spiders pose a potential risk to songbirds at Caddo Lake (Texas/Louisiana, USA). Environmental Toxicology and Chemistry 34:303–306.

Grier, J. W. 1982. Ban of DDT and subsequent recovery of reproduction in bald eagles. Science 218:1232–1235.

Hallmann, C. A., R. P. Foppen, C. A. van Turnhout, H. de Kroon, and E. Jongejans. 2014. Declines in insectivorous birds are associated with high neonicotinoid concentrations. Nature 511: 341.

Halstead, N. T., T. A. McMahon, S. A. Johnson, T. R. Raffel, J. M. Romansic, P. W. Crumrine, and J. R. Rohr. 2014. Community ecology theory predicts the effects of agrochemical mixtures on aquatic biodiversity and ecosystem properties. Ecology Letters 17:932–941.

Hare, L. 1992. Aquatic insects and trace metals: Bioavailability, bioaccumulation, and toxicity. Critical Reviews in Toxicology 22:327–369.

Hladik, M. L., M. Vandever, and K. L. Smalling. 2015. Exposure of native bees foraging in an agricultural landscape to current-use pesticides. Science of the Total Environment 542:469–477.

Jackson, J. K., and S. G. Fisher. 1986. Secondary production, emergence and export of aquatic insects from a Sonoran Desert stream. Ecology 67:629–638.

Kenaga, E. E. 1982. Predictability of chronic toxicity from acute toxicity of chemicals in fish and aquatic invertebrates. Environmental Toxicology and Chemistry 1:347–358.

Kinraide, T. B. 2009. Improved scales for metal ion softness and toxicity. Environmental Toxicology and Chemistry 28:525–533.

Kolpin, D. W., E. T. Furlong, M. T. Meyer, E. M. Thurman, S. D. Zaugg, L. B. Barber, and H. T. Buxton. 2002. Pharmaceuticals, hormones, and other organic wastewater contaminants in US streams, 1999–2000: A national reconnaissance. Environmental Science & Technology 36:1202–1211.

Kraus, J. M., P. P. Gibson, D. M. Walters, and M. A. Mills. 2017. Riparian spiders as sentinels of polychlorinated biphenyl contamination across heterogeneous aquatic ecosystems. Environmental Toxicology and Chemistry 36:1278–1286.

Kraus, J. M., T. S. Schmidt, D. M. Walters, R. B. Wanty, R. E. Zuellig, and R. E. Wolf. 2014a. Cross-ecosystem impacts of stream pollution reduce resource and contaminant flux to riparian food webs. Ecological Applications 24:235–243.

Kraus, J. M., D. M. Walters, J. S. Wesner, C. A. Stricker, T. S. Schmidt, and R. E. Zuellig. 2014b. Metamorphosis alters contaminants and chemical tracers in insects: Implications for food webs. Environmental Science and Technology 48:10957–10965.

Lavoie, R. A., T. D. Jardine, M. M. Chumchal, K. A. Kidd, and L. M. Campbell. 2013. Biomagnification of mercury in aquatic food webs: A worldwide meta-analysis. Environmental Science & Technology 47:13385–13394.

Li, Y., X. L. Li, X. Y. Du, M. Wang, J. Xin, Y. Hu, and Y. Wang. 2012. Using the QICAR model to correlate metal ion characteristics with toxicity order numbers. Human and Ecological Risk Assessment: An International Journal 18:1255–1270.

MacLeod, M., D. G. Woodfine, D. Mackay, T. McKone, D. Bennett, and R. Maddalena. 2001. BETR North America: A regionally segmented multimedia contaminant fate model for North America. Environmental Science and Pollution Research 8:156.

Marcarelli, A. M., C. V. Baxter, M. M. Mineau, and R. O. Hall. 2011. Quantity and quality: Unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. Ecology 92:1215–1225.

McCloskey, J. T., M. C. Newman, and S. B. Clark. 1996. Predicting the relative toxicity of metal ions using ion characteristics: Microtox® bioluminescence assay. Environmental Toxicology and Chemistry: An International Journal 15:1730–1737.

Menzie, C. A. 1980. Potential significance of insects in the removal of contaminants from aquatic systems. Water, Air, and Soil Pollution 13:473–479.

Morrissey, C. A., P. Mineau, J. H. Devries, F. Sanchez-Bayo, M. Liess, M. C. Cavallaro, and K. Liber. 2015. Neonicotinoid contamination of global surface waters and associated risk to aquatic invertebrates: A review. Environment International 74:291–303.

Moy, N. J., J. Dodson, S. J. Tassone, P. A. Bukaveckas, and L. P. Bulluck. 2016. Biotransport of algal toxins to riparian food webs. Environmental Science and Technology 50:10007–10014.

Muehlbauer, J. D., C. A. Lupoli, and J. M. Kraus. 2019. Aquatic-terrestrial linkages provide novel opportunities for freshwater ecologists to engage stakeholders and inform riparian management. Freshwater Science 38:946–952.

Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences 98: 166–170.

Paetzold, A., M. Smith, P. H. Warren, and L. Maltby. 2011. Environmental impact propagated by cross-system subsidy: Chronic stream pollution controls riparian spider populations. Ecology 92:1711–1716.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward and integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28:289–316.

Power, M. E., W. E. Rainey, M. S. Parker, J. L. Sabo, A. Smyth, S. Khandwala, J. C. Finlay, F. C. McNeely, K. Marsee, and C. Anderson. 2004. River-to-watershed subsidies in an old-growth conifer forest. Pages 217–240 *in* G. A. Polis, M. E. Power, and G. R. Huxel (editors). Food webs at the landscape level. The University of Chicago Press, Chicago, Illinois.

Richmond, E. K., E. J. Rosi-Marshall, D. M. Walters, J. Fick, T. Brodin, A. Sundelin, and M. R. Grace. 2018. A diverse suite of pharmaceuticals contaminates stream and riparian food webs. Nature Communications 9:1–9.

Rohr, J. R., J. L. Kerby, and A. Sih. 2006. Community ecology as a framework for predicting contaminant effects. Trends in Ecology and Evolution 21:606–613.

Schiesari, L., M. A. Leibold, and G. A. Burton Jr. 2018. Metacommunities, metaecosystems and the environmental fate of chemical contaminants. Journal of Applied Ecology 55:1553–1563.

Schultz, T. W., N. L. Wyatt, and D. T. Lin. 1990. Structure-toxicity relationships for nonpolar narcotics: A comparison of data from the *Tetrahymena*, *Photobacterium* and *Pimephales* systems. Bulletin of Environmental Contamination and Toxicology 44:67–72.

Sullivan, S. M. P., and D. W. P. Manning. 2019. Aquatic–terrestrial linkages as complex systems: Insights and advances using network models. Freshwater Science. 38:936–945.

Sullivan, S. M. P., and A. D. Rodewald. 2012. The energetic pathways that move contaminants from aquatic to terrestrial environments. Environmental Toxicology and Chemistry 31:1175–1183.

Truhaut, R. 1977. Ecotoxicology: Objectives, principles and perspectives. Ecotoxicology and Environmental Safety 1:151–173.

Tweedy, B. N., R. W. Drenner, M. M. Chumchal, and J. H. Kennedy. 2013. Effects of fish on emergent insect-mediated flux of methyl mercury across a gradient of contamination. Environmental Science & Technology 47:1614–1619.

Van den Berg, M., L. Birnbaum, A. T. Bosveld, B. Brunström, P. Cook, M. Feeley, J. P. Giesy, A. Hanberg, R. Hasegawa, S. W. Kennedy, and T. Kubiak. 1998. Toxic equivalency factors

(TEFs) for PCBs, PCDDs, PCDFs for humans and wildlife. Environmental Health Perspectives 106:775.

Van den Berg, M., L. S. Birnbaum, M. Denison, M. De Vito, W. Farland, M. Feeley, H. Fiedler, H. Hakansson, A. Hanberg, L. Haws, and M. Rose. 2006. The 2005 World Health Organization reevaluation of human and mammalian toxic equivalency factors for dioxins and dioxin-like compounds. Toxicological Sciences 93:223–241.

Walters, D. M., K. M. Fritz, and R. R. Otter. 2008. The dark side of subsidies: Adult stream insects export organic contaminants to riparian predators. Ecological Applications 18:1835–1841.

Walters, D. M., T. D. Jardine, B. S. Cade, K. A. Kidd, D. C. G. Muir, and P. Leipzig-Scott. 2016. Trophic magnification of organic chemicals: A global synthesis. Environmental Science & Technology 50:4650−4658.

Walters, D. M., M. A. Mills, K. M. Fritz, and D. F. Raikow. 2010. Spider-mediated flux of PCBs from contaminated sediments to terrestrial ecosystems and potential risks to arachnivorous birds. Environmental Science & Technology 44:2849–2856.

Walters, D. M., R. R. Otter, J. M. Kraus, and M. A. Mills. 2018. Riparian spiders indicate the magnitude and sources of polychlorinated biphenyl (PCB) contamination at a large contaminated sediment site. Environmental Toxicology and Chemistry 37:2467–2474.

Wesner, J. 2019. Using stage structured food webs to assess the effects of contaminants and predators on aquatic–terrestrial linkages. Freshwater Science. 38:928–935.

Wu, F., Y. Mu, H. Chang, X. Zhao, J. P. Giesy, and K. B. Wu. 2012. Predicting water quality criteria for protecting aquatic life from physicochemical properties of metals or metalloids. Environmental Science & Technology 47:446–453.