



An ecosystem model for evaluating the effects of introduced Pacific salmon on contaminant burdens of stream-resident fish



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ABSTRACT

In the Laurentian Great Lakes, introduced Pacific salmon (*Oncorhynchus* spp.) can transport persistent organic pollutants and heavy metals to tributaries during their annual spawning migrations. To evaluate contaminant biotransport by spawning Pacific salmon, we developed a mass-balance ecosystem model for a Lake Huron tributary using Ecopath with Ecosim (EwE) and Ecotracer. Within EwE and Ecotracer, we developed scenarios that reflected a range of salmon biomass inputs and different trophic pathways to predict polychlorinated biphenyls (PCB) and mercury (Hg) burdens of Brown Trout, Brook Trout, and Mottled Sculpin. Our model accurately predicted PCB concentrations in stream-resident fish across a range of salmon spawner densities. However, we were unable to similarly predict Hg concentrations of stream-resident fish. Our modeling results suggest that salmon inputs specifically control PCB concentrations in stream-resident fish whereas Hg concentrations are more strongly influenced by diffuse background sources. Our model highlights how species-specific differences in diet and growth, along with trophic pathways, can influence the magnitude of contaminant impacts by spawning salmon. Insights from our study suggest that an EwE approach could be used to evaluate other legacy and emerging bioaccumulative contaminants in a variety of ecosystems.

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1. Introduction

Contamination of aquatic ecosystems is a concern for both environmental and human health. Some contaminants of concern include persistent organic pollutants (POPs), such as polychlorinated biphenyls (PCBs), along with heavy metals, such as mercury (Hg) (Murphy et al., 2012; USEPA, 2004). Once widely used in industry but now largely banned, PCBs persist in the environment because of their stability and resistance to degradation (Blais, 2005). Unlike PCBs, Hg is naturally occurring but concentrations in the environment are increasing from combustion of fossil fuels (IJC, 2015; USEPA, 2004). Collectively, POPs and heavy metals are responsible for most consumption advisories globally (USEPA, 2004). Numerous studies have assessed the movement, fate, and ecological effects of POPs and mercury in aquatic ecosystems (e.g., Blais, 2005; Makay and Fraser, 2000). However, a more recent focus of research has been on the ability of migrating organisms to transport contaminants across ecosystem boundaries (e.g., Blais et al., 2007; Kallenborn and Blais, 2015).

Pacific salmon are an ideal study organism for contaminant biotransport (Blais et al., 2007). Salmon migrate between ocean or lake environments to streams and rivers (i.e., are anadromous or potamodromous) and die after a single spawning event (i.e., are semelparous). During spawning, salmon deliver large quantities of carcass and gametic tissue (Schindler et al., 2003) that can be contaminated with POPs and Hg (Baker et al., 2009; Gregory-Eaves et al., 2007). Despite this contamination, salmon material (e.g., carcass and eggs) represents a high-quality food resource readily consumed by invertebrate and vertebrate consumers (Chaloner et al., 2002; Scheuerell et al., 2007). For example, stream-resident fish directly consume salmon carcass and eggs material, or indirectly acquire salmon energy by consuming invertebrates that have fed upon salmon carcasses. Thus, multiple trophic pathways exist for salmon-derived nutrients and contaminants to be incorporated and moved through stream food webs (Janetski et al., 2012; Merna, 1986). Several studies have linked Pacific salmon spawner presence to elevated POP concentrations in stream-resident fish and wildlife in their native range (Christensen et al., 2005; Gregory-Eaves et al., 2007). However, less is known about Hg biotransport (but see Baker et al., 2009) and the ecological role of spawning salmon outside of their native range, including in the Laurentian Great Lakes (but see Gerig et al., 2016a,b; Janetski et al., 2012).

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The Great Lakes and their tributaries provide a unique setting to study contaminant biotransport by Pacific salmon. Salmon were introduced into the Great Lakes in the 1950s to control invasive alewife populations, and have since become an important component of the Great Lakes recreational fishery (Dettmers et al., 2012). Moreover, salmon have established populations throughout the Great Lakes by ‘naturalizing’ to many tributaries, and are also stocked from state resource agency hatcheries (Dettmers et al., 2012). Consequently, managers are concerned about factors that might compromise the economic value of salmon, such as their contaminant burden (Murphy et al., 2012). Furthermore, the legacy of industrial pollution of the Great Lakes has resulted in high concentrations of POPs and Hg in many areas (Murphy et al., 2012). Hence, migratory species such as salmon that move between lake and stream environments, while readily accumulating contaminants, represent a potential link for transferring contaminants between ecosystems. While transfer of salmon-derived POPs to stream biota has been documented in the Great Lakes (e.g., Gerig et al., 2016a,b; Janetski et al., 2012), little is known about the factors regulating species-specific patterns of bioaccumulation, or the trophic pathways by which salmon increase the contaminant concentrations of stream-resident fish. In addition, no information is available at present on the influence of salmon spawning on Hg concentrations. Given these uncertainties, ecosystem-based modeling approaches may be useful for evaluating and predicting the influence of spawning salmon on contaminants in stream-resident fish.

Ecosystem models integrate multiple sources of information to provide predictions on factors influencing complex food web dynamics (Christensen and Walters, 2004; Colleter et al., 2015). For example, Ecopath with Ecosim (EwE, www.ecopath.org; Christensen and Walters, 2004; Colleter et al., 2015) is a quantitative ecosystem-modeling platform that uses a mass balance framework to dynamically model energy flow in a food web over time. Within EwE, the sub-routine Ecotracer can be coupled to Ecosim to model dynamic changes in contaminant concentrations in a food web (Christensen and Walters, 2004). As diet is the primary pathway of contaminant transfer to upper trophic level organisms in aquatic ecosystems (Trudel and Rasmussen, 2006), such models can elucidate the trophic pathways by which PCBs and Hg bioaccumulate (Arnot and Gobas, 2004; Booth and Zeller, 2005).

The objective of our study was to utilize an ecosystem model to determine the extent to which salmon-mediated contaminant biotransport determines the PCB and Hg burdens of stream-resident fish in Great Lakes streams. To achieve this objective, we first parameterized an Ecopath food web model using data from empirical and literature sources. Second, we evaluated a baseline scenario using Ecosim and Ecotracer, which reflects how a typical salmon run can influence stream-resident fish PCB and Hg concentrations over time. Third, we expanded the baseline scenario to evaluate how variation in salmon run size (i.e., spawner biomass) influenced contaminant concentrations in stream-resident fish. Results from the biomass scenarios were validated via comparison with observed fish contaminant loads in Great Lakes tributaries receiving salmon spawners. Finally, we developed a set of scenarios to determine how direct and indirect trophic pathways might influence the magnitude of salmon contaminant transfer to stream-resident fish.

2. Materials and methods

2.1. Study site

Our model system was Hunt Creek, a second-order tributary stream to Lake Huron located in the northeastern portion of Michigan’s lower peninsula. The stream has stable flows, and is similar to

other cold water streams in the Upper Great Lakes (Grossman et al., 2012; Wills et al., 2006). Located within the Michigan Department of Natural Resources Hunt Creek Fisheries Research Station, the stream has never received salmon spawners nor experienced significant fishing pressure, and thus represents a largely undisturbed system from which to build our base model. The fish community of Hunt Creek consists of Brown Trout (*Salmon trutta*), Brook Trout (*Salvelinus fontinalis*), Mottled Sculpin (*Cottus bairdi*), and Redside Dace (*Clinostomus elongatus*). Brown and Brook Trout are both drift feeders and top predators in stream communities, and occupy a similar functional role within the stream community (Zimmerman and Vondracek, 2007). Mottled Sculpin and Redside Dace are both important forage fish, but Mottled Sculpin are primarily benthic feeders while Redside Dace are water column feeders (Zimmerman and Vondracek, 2007).

2.2. Ecopath model

We first parameterized a balanced Ecopath model that was representative of the Hunt Creek ecosystem using both empirical and literature sources (Appendix A Supplementary material). Ecopath uses a series of linear equations to describe biomass interactions between trophic levels, and gives a static, mass-balanced representation of food web structure in Hunt Creek at steady-state. For each functional group i :

$$BA_i = B_i * (P/B)_i * EE_i - \sum (B_j * (Q/B)_j * DC_{ij}) - Y_i - E_i \quad (1)$$

where BA_i is biomass accumulation of group i ; B_i is the biomass of group i ; P/B_i is the production to biomass ratio of group i ; EE_i is ecotrophic efficiency (proportion of production that is used within the system); Q/B_j is the consumption to biomass ratio of predator j ; DC_{ij} is the proportion of group i in the diet of predator j ; Y_i is fishery yield; and E_i is net emigration. Both Y_i and E_i were assumed to be 0. Our model of the Hunt Creek food web consisted of 16 functional groups, including periphyton, microorganisms, invertebrates, Brown Trout, Brook Trout, Mottled Sculpin, Redside Dace, and a detritus component partitioned into non-salmon and salmon material (Fig. 1, Table A1). Salmon material was partitioned into salmon eggs, which are released during spawning, and salmon carcasses, which enter the detrital pool upon salmon death (Table A1). Salmon egg biomass was based upon empirically collected biometric data where we assumed a gonadosomatic index of 0.2 (Gerig, unpublished data and Groot and Margolis, 1991). We also assumed that 50% of the spawners were female. The invertebrate functional group was further divided into five functional feeding groups: grazers, collector-filterers, collector-gatherers, shredders, and predators (cf. Cummins, 1973). Brook and Brown Trout were sub-divided into juvenile and adult age-classes within the model.

Once all initial values were entered, we balanced the model to ensure that the assumption of mass-balance was met. We did so by ensuring that all EE_i values were less than or equal to 1.0. If one or more EE_i values were greater than 1.0, this indicated that more of a resource is used than is available and parameters must be adjusted in order to balance energy flow in the ecosystem (cf. Christensen and Walters, 2004). In open systems like streams, resources are constantly in flux due to flowing water and input of external material, and the assumption of mass-balance may not be supported at all times (Meyer and Poepperl, 2004). However, in our study we assumed that fluxes into the study area generally equaled fluxes out of the study area; this assumption is consistent with other applications of EwE to streams (Meyer and Poepperl, 2004; Warren et al., 2014). Food web parameter values are reported in Table A2, and final diet compositions are provided in Table A3. In this simulation, we assumed that adult fish consumed salmon eggs while juvenile fish and invertebrates consumed salmon carcasses. We did not

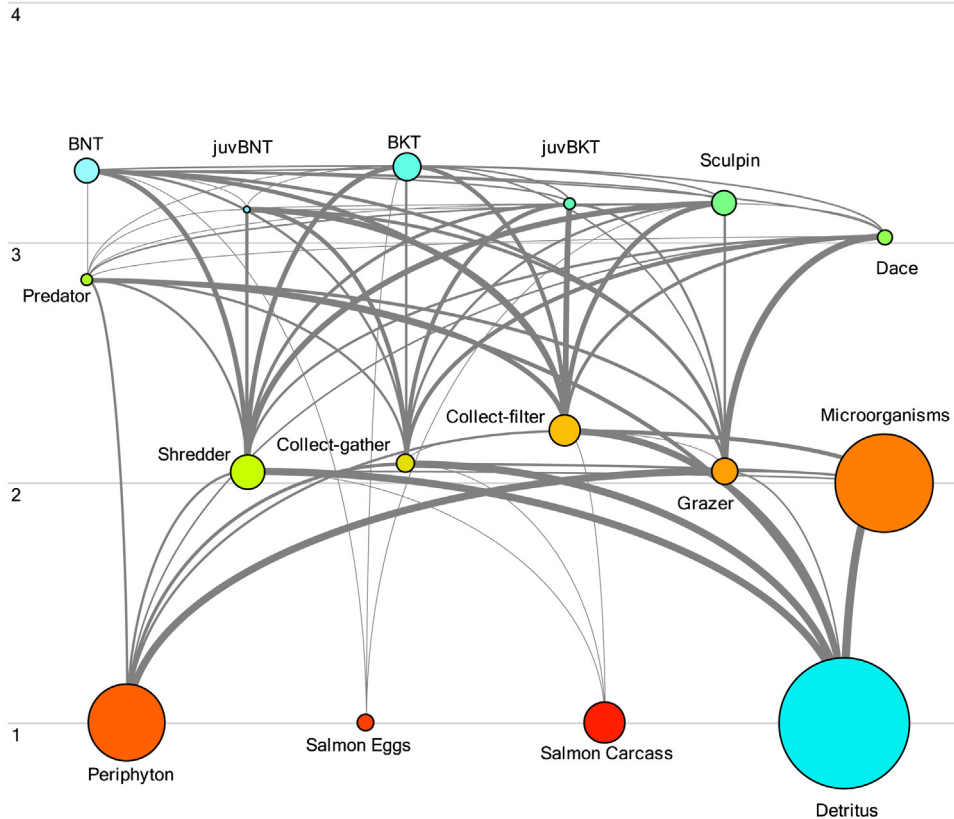


Fig. 1. Conceptual food web diagram for Hunt Creek, Michigan, USA. Nodes represent functional groups with size proportional to the standing biomass. Lines represent feeding connections with thickness proportional to the biomass flow between trophic levels. Trophic level is given on the left-hand side of the diagram. Species abbreviations include: Brown Trout (BNT); Brook Trout (BKT); Mottled Sculpin (Sculpin); Redside Dace (Dace); and juvenile (juv). Invertebrate functional groups occupy the second level of the food web.

conduct a formal sensitivity analyses, as per Ecopath convention (Christensen and Walters 2004). However, we followed a number of pre-model fitting diagnostics to ensure stable model performance (after Heymans et al., 2016).

2.3. Ecosim simulation

Once the Ecopath model was balanced, we utilized Ecosim to simulate the seasonal influx of salmon spawners to Great Lakes streams. Ecosim uses systems of differential equations to model fluxes between biomass pools to evaluate how changes in ecological processes influence trophic structure (Christensen and Walters, 2004). The Ecosim equation for each food web functional group is:

$$dB_i/dt = g_i * \sum (C_{ji}) - \sum (C_{ij}) + I_i - (M_i + F_i + e_i) * B_i \quad (2)$$

where g_i is growth efficiency; $\sum (C_{ji})$ is the rate of consumption of all prey j by group i ; $\sum (C_{ij})$ is the rate of consumption of group i by all predators j ; I_i is the immigration rate; M_i is the mortality not attributable to other functional groups; F_i is the fishing mortality rate; e_i is emigration rate; and B_i is biomass. In our models, I_i , F_i , and e_i are equal to 0. All consumption terms are density-dependent, which allows consumer diets to vary from their initial values as a function of changing prey biomasses (Christensen and Walters, 2004).

We simulated salmon spawning by applying a continuous forcing function to the salmon carcass and egg functional groups, to represent the seasonal availability of eggs and carcasses from salmon spawning. Salmon egg and carcass biomass was held at zero and unavailable for consumption for 10 monthly time steps (to simulate absence of salmon spawners) and then biomass of salmon

carcass and eggs were introduced for the remaining two months. In the second monthly time step, salmon biomass was divided by half to represent the short-term availability of salmon material in Great Lakes streams during the months of October and November (cf. Janetski et al., 2012; Johnson et al., 2016). We ran model simulations over 30 years (i.e., yearly time steps for 30 model iterations) with yearly fall salmon runs. This run length allowed sufficient time for all functional groups to reach steady-state for all scenarios (cf. Christensen and Walters, 2004; Warren et al., 2014).

Change in food web structure elicited by salmon spawning depends on the degree of salmon resource use by individual functional groups via direct and indirect trophic interactions that change dynamically through time. For all model runs, we assumed that bottom-up stimulation of primary productivity during salmon spawning did not occur. Previous studies have demonstrated that Great Lakes streams have higher background nutrient concentrations and are more susceptible to sediment disturbance, which minimize the potential enrichment effect of salmon observed in native ranges (Collins et al., 2011; Janetski et al., 2014).

2.4. Ecotracer simulation

We used the Ecotracer routine associated with EWE to model the flow of salmon-derived contaminants through the food web over time. Ecotracer runs in parallel to Ecosim by calculating changes in contaminant concentrations as the biomass equations are solved through time. Within Ecotracer, a contaminant is partitioned between water and the biomass of functional groups at any moment (Christensen and Walters, 2004). The concentration of a contaminant in a given functional group is expressed as a function of gains from direct uptake from water and uptake from food

sources versus losses due to instantaneous loss rates, unassimilated food, and mortality (Christensen and Walters, 2004).

The Ecotracer equation for each group is:

$$\begin{aligned} dC_i/dt = & \sum (C_j * GC_i * Q_{ij}/B_j) + (u_i * B_i * C_o) + (c_i * I_i) \\ & - \sum (C_i * Q_{ij}/B_i) - (C_i * MO_i) + (1 - GC_i) \\ & * (S_j * C_j * Q_{ji}/B_j) - (e_i * C_i) - (d_i * C_i) \end{aligned} \quad (3)$$

where C_j is concentration in food j ; GC_i is the proportion of food assimilated by type i organisms; Q_{ji} is the biomass flow rate from j to i (estimated in Ecopath as $B_i * (Q/B)_i * DC_{ij}$); B_j is the food j biomass; u_i is a parameter representing uptake per biomass per time per unit environmental concentration; C_o is the contaminant concentration of water; c_i is the contaminant concentration per unit biomass in immigrating biomass; I_i is the biomass of group immigrants; Q_{ij} is the biomass flow rate from i to j ; MO_i is the non-predation death for type i ; e_i is the emigration rate; and d_i is the metabolism of the contaminant in group i . We simplified the above equation by assuming that immigration and emigration were zero. In addition, we assumed that direct contaminant uptake from water was zero, given that the majority of a fishes' contaminant burden comes from dietary sources (cf. Trudel and Rasmussen, 2006). In addition, metabolic transformation of contaminants, such as PCBs and Hg, occur at slow rates and were assumed to be zero in our model (cf. Trudel and Rasmussen, 2006). These reasonable simplifications allowed us to focus on the role of salmon in stream-resident fish contaminant bioaccumulation.

The Ecotracer portion of the model was parameterized using initial contaminant concentrations for each functional group, concentrations per biomass of spawning salmon, and contaminant assimilation efficiency (Table A4). We used empirical measurements from Hunt Creek in 2013 (Gerig, unpublished data) to estimate initial concentrations of PCBs and Hg for Brown Trout, Brook Trout, and Mottled Sculpin. Salmon carcasses, salmon eggs, and invertebrates were assessed from samples collected in Great Lakes tributaries receiving salmon runs (Gerig, unpublished data). Mercury and PCBs were selected for analysis because they represent nearly 100% of consumption advisories in the GL (USEPA, 2004). In addition, PCBs and Hg are both considered contaminants that bioaccumulate but differ in their physicochemical properties that may influence their biotransport by salmon and subsequent uptake by stream-resident fish. Methods for quantification of PCBs and total Hg concentrations are described elsewhere (Gerig et al., *in review* and Janetski et al., 2012). PCB concentrations represent the sum of 89 congeners that were analytically determined via Gas Chromatography-Mass Spectrometry. Total Hg concentrations were determined analytically using a Direct Mercury Analyzer. All concentrations were expressed as parts per billion (ng/g). Similar to the biomass simulation, we applied a continuous forcing function to the salmon eggs and salmon carcass functional groups to simulate the seasonal contaminant pulse associated with salmon spawning.

2.5. Model scenarios

We developed three scenarios to investigate the nature of stream-resident fish response to Pacific salmon spawning. First, we created a baseline simulation to assess whether stream-resident fish exhibited species-specific patterns of bioaccumulation in response to salmon spawning. For this scenario, we modeled a salmon-loading rate that approximated the median salmon biomass (0.200 kg/m^2) observed in Great Lakes streams (Gerig, unpublished data).

Second, we simulated how stream-resident fish contaminant concentrations changed across a gradient of salmon biomass-loading rates. For this scenario, we ran three simulations, in which the base Ecopath model was modified to reflect, different salmon biomasses. The salmon biomasses used in this scenario reflected a range of salmon loading rates observed in Great Lakes tributaries (minimum: 0.002 kg/m^2 , median: 0.200 kg/m^2 , maximum: 0.790 kg/m^2 ; Gerig, unpublished data). We assumed that adult fish consumed salmon eggs while juvenile fish and invertebrates consumed salmon carcasses. For this scenario, we evaluated model performance by comparing predicted contaminant concentrations to empirical data collected from Great Lakes tributaries that have received runs of salmon for greater than 30 years (Gerig, unpublished data). We then fitted a logarithmic saturating function, to the simulated data to interpolate contaminant concentrations across all observed levels of salmon biomass loading. We evaluated model prediction accuracy by calculating Pearson correlation coefficients (r_p) between observations and predictions for a given biomass loading rate and mean absolute error (MAE) for each species under all baseline scenarios (Ye et al., 2015). MAE is a metric commonly used to assess how well model predictions fit empirical observations (Harvey et al., 2003; Ye et al., 2015).

Third, we simulated how different trophic pathways could influence the magnitude of salmon contaminant biotransport to stream-resident fish. We considered three trophic pathways to contamination in this scenario, which included: (1) direct egg contamination where adult stream-resident fish consume salmon eggs; (2) direct carcass contamination where juvenile and adult stream-resident fish consume carcass material; and (3) indirect contamination where invertebrates consume salmon carcass material, and adult and juvenile stream-resident fish do not consume either salmon carcass or egg material. These pathway simulations were not compared to empirical data but rather represent a theoretical approach (cf. Warren et al., 2014) useful for understanding how diet mediates stream-resident fish bioaccumulation as a result of contaminant biotransport by salmon.

3. Results

3.1. PCB accumulation

During the baseline simulation, PCB concentrations in stream-resident fish exhibited a non-linear increase in response to salmon inputs resulting in a saturating relationship (Fig. 2A). The magnitude of response to salmon contaminant inputs differed among species. Overall, Brown Trout exhibited the highest and Mottled Sculpin exhibited the lowest PCB concentrations at steady-state. Brook Trout PCB concentrations were only 0.7X lower than Brown Trout but nearly 7.0X higher than Mottled Sculpin. Brown Trout and Mottled Sculpin exhibited the largest difference in PCB concentrations at steady-state, with Brown Trout being 9.0X more contaminated than Mottled Sculpin (Fig. 2A). Overall, the time required for stream-resident fish to reach steady-state PCB concentrations varied by species; Brown Trout, Brook Trout, and Mottled Sculpin required 9 years, 5 years, and 3 years, respectively (Fig. 2A).

Stream-resident fish PCB concentrations increased with increasing input of salmon egg and carcass material (Fig. 3A–C, Table 1). Similar to the baseline simulation, stream-resident fish PCB concentrations exhibited a saturating relationship with increased salmon loading rates. For Brown Trout, PCB concentrations increased by 3.8X from the low to median loading rate and 1.2X from the median to high loading rate (Fig. 3A). For Brook Trout, PCB concentrations increased by 3.8X from the low to median loading rate and 1.2X from the median to high loading rate (Fig. 3B). For Mottled Sculpin, PCB concentrations increased by 3.0X from the

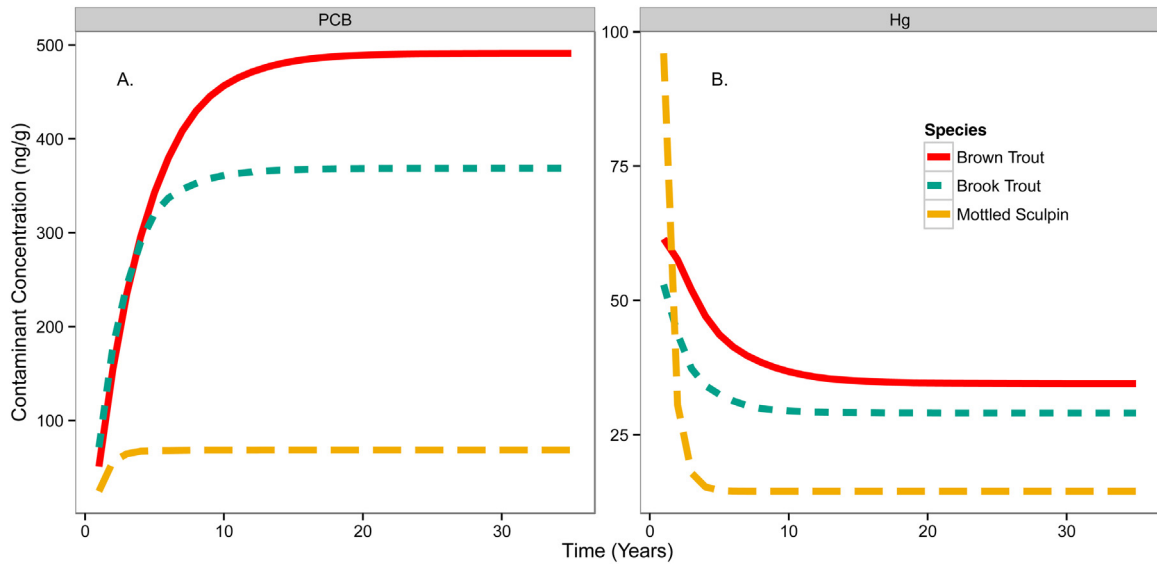


Fig. 2. Change in polychlorinated biphenyls (PCB) and mercury (Hg) concentrations for Brown Trout (solid), Brook Trout (short-dash), and Mottled Sculpin (long-dash) as a result of salmon-mediated contaminant biotransport. Simulations ran for 30 years until steady-state concentrations were reached. Simulations approximated the median biomass of a salmon run observed in Great Lakes tributaries.

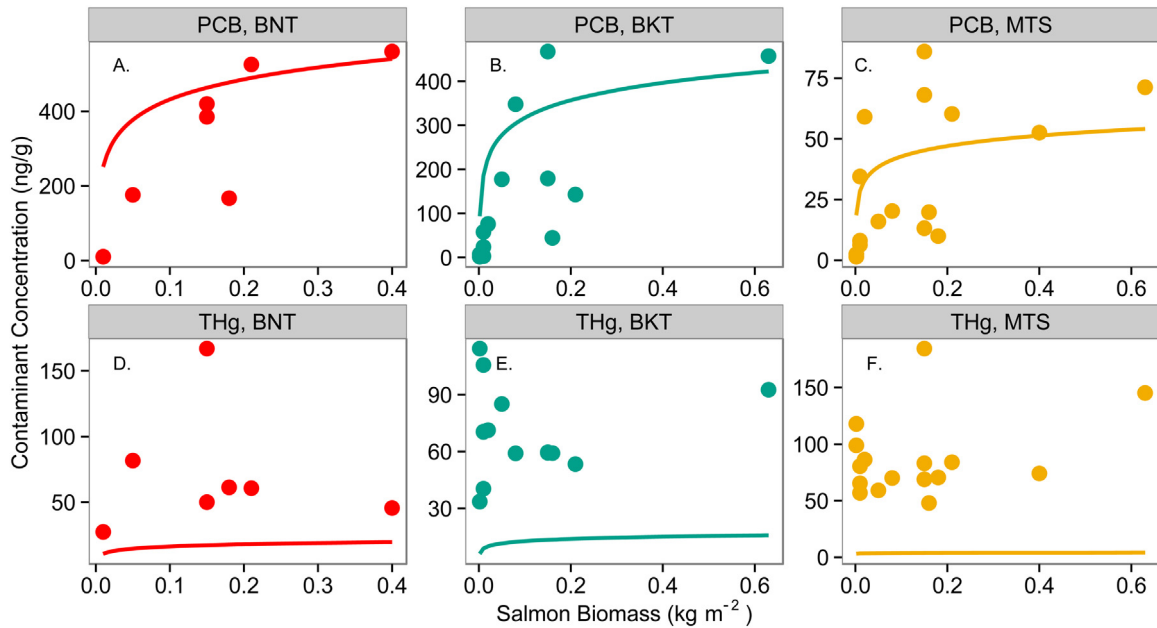


Fig. 3. Concentrations of polychlorinated biphenyls (PCB) and mercury (Hg) as a function of salmon biomass for Brown Trout (BNT), Brook Trout (BKT), and Mottled Sculpin (MTS). Ecotracer predictions are represented by curves, and individual points represent observed contaminant concentrations at a given spawner biomass in tributaries across the Great Lakes.

Table 1

Species-specific comparison of Ecotracer predictions to empirical observations for polychlorinated biphenyls (PCB) and mercury (Hg) under varying salmon spawner biomasses. Concentrations for predicted PCB and Hg represent steady-state values at the end of the simulations. MAE = mean absolute error.

Contaminant	Species	Observed range	Predicted Range	Correlation Coefficient (r_p)	p-value	MAE
PCB	Brown Trout	10–560	250–540	0.84	0.02	132
	Brook Trout	2–467	93–422	0.73	0.01	137
	Mottled Sculpin	1–86	18–54	0.59	0.02	21
Hg	Brown Trout	28–166	10–20	0.22	0.62	54
	Brook Trout	34–114	6–16	–0.08	0.77	58
	Mottled Sculpin	48–184	3–4	0.08	0.75	83

low to median loading rate but did not change from the median to high loading rate (Fig. 3C). Among scenarios, Brown Trout had the highest while Mottled Sculpin had the lowest PCB burdens.

Ecotracer was effective at predicting PCB concentrations given similarities between model estimates and observed values (Fig. 3A–C). For Brown Trout, modeled PCB concentrations varied from 250 to 540 ng/g under salmon spawner biomasses ranging from 0.01 to 0.40 g/m². Modeled Brown Trout PCB concentrations were highly correlated with observed values across spawner biomass scenarios (Fig. 3A, Table 1, $r_p = 0.84$, $p = 0.02$, MAE = ±133 ng/g). For Brook Trout, model predictions of PCB concentration varied from 93 to 422 ng/g under salmon spawner biomasses ranging from 0.002 to 0.63 g/m². Modeled Brook Trout PCB concentrations were correlated with observed values across spawner biomass scenarios (Fig. 3B, Table 1, $r_p = 0.73$, $p = 0.01$, MAE = ±137 ng/g). For Mottled Sculpin, model predictions varied from 18 to 54 ng/g under salmon spawner biomasses ranging from 0.002 to 0.630 g/m². Modeled Mottled Sculpin PCB concentrations were correlated with observed values across spawner biomass (Fig. 3C, Table 1, $r_p = 0.59$, $p = 0.02$, MAE = ±21 ng/g). Despite high overall correlations, model predictions consistently overestimated PCB concentrations at low spawner biomasses and underestimated PCB concentrations at high spawner biomasses for all species.

PCB concentrations varied considerably depending on the trophic pathway to contamination. Direct consumption of salmon eggs resulted in elevated PCB concentrations in Brown Trout, Brook Trout, and Mottled Sculpin of 450, 332, and 45 ng/g, respectively (Fig. 4A). In contrast, direct consumption of carcass material and indirect consumption of contaminated invertebrates resulted in markedly lower PCB accumulation in stream-resident fish (Fig. 4A). Direct consumption of salmon carcasses resulted in PCB concentrations for Brown Trout, Brook Trout, and Mottled Sculpin of 21, 16, and 7 ng/g. In contrast, consumption of contaminated invertebrates resulted in PCB concentrations for Brown Trout, Brook Trout, and Mottled Sculpin of 40, 36, and 22 ng/g, respectively. Direct consumption of salmon eggs by Brown Trout, Brook Trout, and Mottled Sculpin resulted in a 20X, 20X, and 6X increase in PCB concentrations, respectively, compared to direct consumption of carcass material (Fig. 4A). Similarly, direct consumption of salmon eggs by Brown Trout, Brook Trout, and Mottled Sculpin resulted in an 11X, 9X, and 2X increase in PCB concentrations, respectively, compared to indirect consumption of contaminated invertebrates (Fig. 4A).

3.2. Hg accumulation

In contrast to PCBs, Hg concentrations of stream-resident fish in our baseline simulation decreased over time until reaching steady-state concentrations, which were 8X lower than initial concentrations (Fig. 2B). All stream-resident fish exhibited declines in Hg over the duration of the simulation, but the magnitude of response differed among species. Similar to PCB simulations, Brown Trout had the highest and Mottled Sculpin had the lowest Hg concentrations. Brook Trout Hg concentrations were 0.7X lower than Brown Trout but nearly 4.0X higher than Mottled Sculpin. Brown Trout and Mottled Sculpin exhibited the largest difference in Hg concentrations at steady-state, with Brown Trout being 4.5X more contaminated than Mottled Sculpin (Fig. 2A).

Increasing the input of salmon egg and carcass material led to small increases in stream-resident fish Hg concentrations (Fig. 3D–F, Table 1). Similar to the baseline simulation, the rate of increase in Hg concentrations displayed a saturating relationship with increased salmon loading rates. For Brown Trout, Hg concentrations increased by 2.5X from the low to median loading rate, by 1.1X from the median to high loading rate, and 3.0X from the low to high loading rate (Fig. 3D). For Brook Trout, Hg concentrations

increased by 2.3X from the low to median loading rate and by 1.1X from the median to high loading rate (Fig. 3E). For Mottled Sculpin, Hg concentrations increased by 1.3X from the low to median loading rate but did not change from the median to high loading rate (Fig. 3F). Similar to the previous scenario, Brown Trout were the most contaminated with Hg while Mottled Sculpin were the least contaminated.

Ecotracer did not effectively predict observed Hg concentrations from empirically collected data (Fig. 3D–F, Table 1). In all simulations, input of mercury by salmon spawning led to decreases in Hg concentration over the course of the simulation for all species. As a result, our model did not yield reasonable estimates of Hg concentrations. Correlations between observed and predicted values were low ($r_p < 0.25$ for all species; Fig. 3D–F, Table 1), and mean average error for all species was high (MAE > 50 ng/g), especially given low predicted Hg concentration values. At steady-state, Brown Trout concentrations ranged from 11 to 20 ng/g under salmon spawner biomasses from 0.01 to 0.40 g/m², Brook Trout Hg concentrations ranged from 6 to 16 ng/g under salmon spawner biomasses from 0.002 to 0.630 g/m², and Mottled Sculpin concentrations ranged from 3 to 4 ng/g under salmon spawner biomasses from 0.002 to 0.630 g/m² (Fig. 3, Table 1). All predicted concentrations fell well below empirical values.

Mercury concentrations were similar among different trophic pathways to contamination. Direct consumption of salmon eggs resulted in Hg concentrations in Brown Trout, Brook Trout, and Mottled Sculpin of 11, 9, and 2 ng/g, respectively (Fig. 4B). Direct consumption of salmon carcasses resulted in Hg concentrations for Brown Trout, Brook Trout, and Mottled Sculpin of 12, 9, and 4 ng/g. Consumption of contaminated invertebrates resulted in Hg concentrations for Brown Trout, Brook Trout, and Mottled Sculpin of 22, 20, and 13 ng/g. All modeled concentrations under all Hg scenarios fell well below empirically observed Hg concentrations, suggesting that factors other than salmon regulated Hg accumulation in stream-resident fish.

4. Discussion

4.1. Implications for understanding contaminant biotransport

In this study, we developed and tested the first ecosystem model to predict the contaminant burden of stream-resident fish in response to salmon-mediated contaminant biotransport. Our contaminant biotransport model predicted with reasonable certainty the observed PCB concentrations in stream-resident fish, but not observed Hg burdens. The outcome of our modeling suggests that in tributaries of the Upper Great Lakes, salmon spawners have a stronger influence on stream-resident fish PCB than Hg burdens. Furthermore, our model suggests that salmon spawners are the main source of PCBs to stream-resident fish, while other environmental sources, such as sediment or atmospheric deposition, are much smaller (cf. Blais 2005; Hornbuckle et al., 2006). These results are consistent with previous empirical studies in the Great Lakes (Gerig et al., 2016a,b; Janetski et al., 2012) and native range (Ewald et al., 1998; Gregory-Eaves et al., 2007), which have found spawning salmon to be a key factor influencing PCB contaminant loads in stream-resident fish.

Our model predicted that the PCB concentration of stream-resident fish was dependent on the spawner biomass present in the system. Our model predicted an asymptotic relationship whereby stream-resident fish PCB concentrations increased rapidly at low salmon spawner biomasses but eventually reached an asymptote with higher salmon loadings. Prior studies have demonstrated a similar, saturating relationship between increasing spawner biomass and uptake of salmon-derived nutrients (Chaloner et al.,

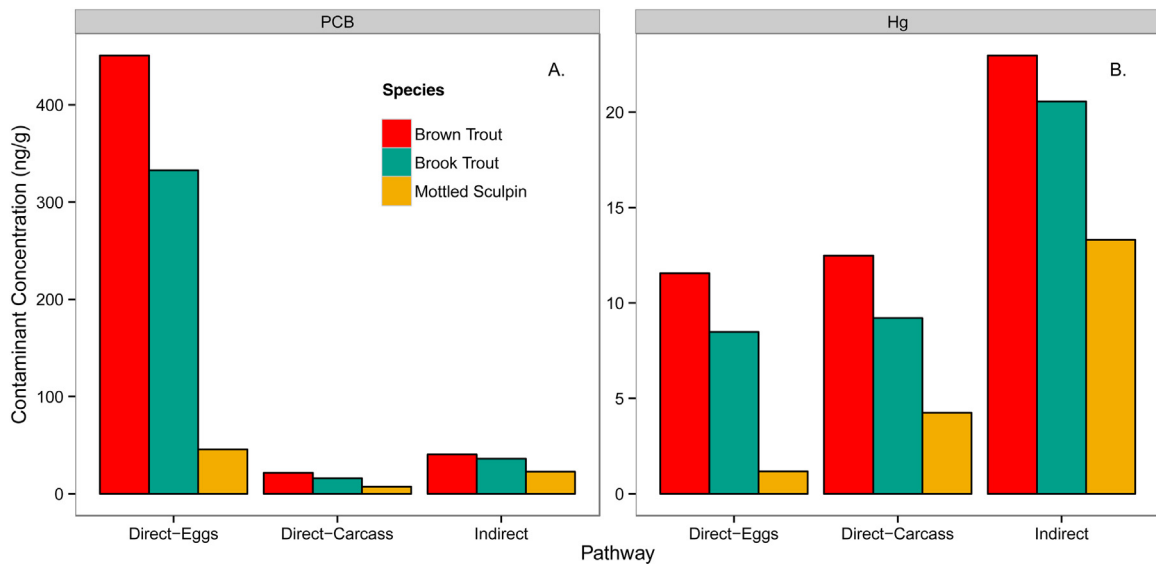


Fig. 4. Comparison of three different trophic pathways to contamination for Brown Trout, Brook Trout, and Mottled Sculpin resulting from salmon biotransport of polychlorinated biphenyls (PCB; A.) and Hg (mercury; B.). Pathways to contamination included direct consumption of eggs but no carcass consumption (Direct-Eggs); direct consumption of carcasses but no egg consumption (Direct-Carcass); and indirect consumption of contaminated invertebrates but no carcass or egg consumption (Indirect). Concentrations for PCB and Hg represent steady state values at the end of the simulations.

2002), or PCB congener patterns (Gerig et al., 2016a,b). These results suggest that rate-limiting factors (e.g., nutrient mineralization, phase partitioning between media) may control the rate of uptake of salmon-derived contaminants by stream-resident fish, ultimately establishing new steady-state concentrations (cf. Arnot and Gobas, 2004; Mackay and Fraser, 2000).

Our model predicted the range of observed PCB concentrations with a high degree of accuracy. However, the model overestimated PCB concentrations at low spawner biomasses and underestimated PCB concentrations at high spawner biomasses. Therefore, the model may overestimate the degree of dietary switching that occurs when salmon material (e.g., eggs) is available at low spawner biomasses (cf. Christensen and Walters, 2004). Further, when salmon resources are abundant, our model may have been parameterized conservatively and underestimated the extent dietary switching between salmon eggs and other prey types. Overall, our deterministic model likely did not account for the full range of variation in consumer diets, which likely contributes to this discrepancy (Gerig et al., 2016a,b). In the future, an individual-based model that accounts for variability in stream-resident fish diets across a range of spawning biomasses could be used to explore this important source of variation (cf. Moore et al., 2008).

Our model did not accurately predict observed Hg concentrations in stream-resident fish across any scenarios. For all species in our baseline simulation, Hg concentrations decreased over time to a lower, non-zero steady-state. Similarly, for our biomass scenarios, no predicted Hg concentrations fell within the range of observed values. The inability of our model to accurately predict Hg concentrations suggests that stream-resident fish bioaccumulation is controlled by Hg sources other than salmon. Prior studies have found that watershed size, primary production rate, pH, proportion of watershed in forested and wetland land cover types, and proximity to contaminated sediments influence Hg bioaccumulation (Tsui et al., 2009; Ward et al., 2010). Within our model, we ignored background sources of Hg to explicitly consider the role of salmon as a vector of Hg in tributaries of the Upper Great Lakes. However, future model refinements focused on Hg bioaccumulation should consider alternate sources of Hg.

No previous study in the Great Lakes has quantified the impact of salmon spawning on the Hg burdens of stream-resident fish.

However, in a Lake Ontario stream, spawning salmon increased Hg concentrations in water and invertebrates, with the highest Hg concentrations found in aquatic invertebrates feeding directly on salmon carcasses (Sarica et al., 2004). In contrast, within the native range of Pacific salmon, resident fish where salmon spawn have lower mercury burdens than those in areas inaccessible to salmon (Baker et al., 2009). Similarly, Lake Trout residing in streams with anadromous Arctic Charr have lower mercury concentrations than in streams lacking Charr (Swanson et al., 2010). These differences among studies may reflect differential partitioning of PCBs and Hg between salmon egg and carcass tissues, and contrasts in dietary composition among species. Mercury binds to cysteine protein in muscle tissue (Kuwabara et al., 2007), while PCBs are fat-soluble and accumulate in lipid-rich tissues, such as fish eggs (Harmelin-Vivien et al., 2012). Thus, direct consumption of eggs could lead to increased PCB accumulation based upon differences in contaminant partitioning among tissues. Further, in our model, consumption of invertebrates feeding on salmon carcasses resulted in the largest increases in Hg contamination, suggesting that indirect pathways may be most important to Hg accumulation. However, because predicted mercury concentrations from these scenarios were 2–4X lower than observed concentrations, we suspect that the flux of Hg from background sources exceeds that supplied by salmon, and largely determines species-specific rates of bioaccumulation (cf. Baker et al., 2009).

Our model revealed species-specific differences in the rate of bioaccumulation for both PCBs and Hg. For all baseline simulations, Brook and Brown Trout contaminant characteristics started similarly, but Brown Trout finished all simulations with higher contaminant concentrations. By contrast, Mottled Sculpin consistently showed the lowest contaminant concentrations. Modeled species-specific differences in PCB and Hg accumulation are similar to published empirical results (Merna, 1986; Janetski et al., 2012; Swanson et al., 2003), which suggest that diet, growth, and trophic structure drives this pattern (Clements et al., 2012). In our model, both Brook Trout and Brown Trout are drift feeders, and their diet composition was similar (Zimmerman and Vondracek, 2007). In addition, stream-resident fish readily consume salmon eggs in large quantities when available (Ivan et al., 2011; Johnson et al., 2016), which are considered an important route for contami-

nant exposure in our model. In contrast to Brook and Brown Trout, Mottled Sculpin are benthic foragers that consume smaller numbers of salmon eggs as a function of gape limitation and habitat use (Merna, 1986; Stauffer, 1971).

Contrasting growth rates may also influence species-specific rates of bioaccumulation in our model. In EwE, growth rate of each functional group was modeled using the production to biomass ratio (P/B), which is a measure of biomass turnover rate (Christensen and Walters, 2004). In our model, the P/B ratio was set at 0.34, 0.66, and 1.50 yr⁻¹ for Brown Trout, Brook Trout, and Mottled Sculpin, respectively (Randall and Minns, 2000). We found that higher P/B ratios resulted in lower contaminant concentrations, similar to prior studies (Trudel and Rasmussen, 2006; Ward et al., 2009). This pattern suggests that fish species that grow slower and live longer can become more contaminated from increased contaminant exposure. Thus, widely stocked Brown Trout may present a greater risk with respect to human consumption advisories because of species-specific life history characteristics (e.g., increased longevity, slow growth), which lead to higher rates of contaminant accumulation.

4.2. Management implications

Our model improves our understanding of the risks to ecosystem and human health associated with contaminant biotransport. Fish consumption advisories are widespread, with over 40% of the total U.S. stream length listed as impaired due to bioaccumulative contaminants (USEPA, 2004). However, assessments for fish consumption advisories generally do not account for biotransported contaminants (Michigan DEQ, 2014). This omission is potentially significant. For example, based on our modeled assessment, Brook and Brown Trout PCB tissue concentrations were high enough to warrant restrictive consumption advisories of no more than one meal per month based on US EPA criteria (USEPA, 2000). To begin controlling salmon biotransport, management agencies could use our model to determine appropriate salmon escapement levels into streams, which could limit contaminant transfer from salmon.

The ability of our model to predict observed PCB concentrations has important implications for future management and research of contaminant biotransport in the Great Lakes. Over 1000 contaminants have been identified in the Great Lakes, and one third of those have potentially toxic effects on aquatic biota, wildlife, and human health (Murphy et al., 2012; USEPA, 2000). Moreover, the contaminants examined in our study represent only two of twenty-two known bioaccumulative chemicals of concern (BCCs) found in the Great Lakes (USEPA, 1995). Legacy pollutants such as Mirex, Dieldrin, and Chlordane all exhibit similar physicochemical properties to PCBs, and are likely subject to biotransport by Pacific salmon (O'Toole et al., 2006; USEPA, 1995). Since these chemicals accumulate in tissues similar to PCBs, our model could be amended to predict concentrations of other contaminants by obtaining contaminant concentrations for salmon tissue, eggs, and stream-resident fish.

Our model could also be tailored to advance our understanding of ecosystem-level impacts of emerging contaminants. For instance, a global synthesis characterizing bioaccumulation potential for organic chemicals (OCs) was recently published (Walters et al., 2016). This synthesis suggests that bioaccumulation of OCs increases for compounds that are moderately hydrophobic and resistant to metabolic transformation. Our model could be integrated with this information to assess potential ecosystem impacts of emerging bioaccumulative OCs, such as perfluorooctane sulfonate, perfluorooctanoic acid, and pentachloroanisole (USEPA, 2013). This may be a particularly useful application of our model because adequately screening potential chemicals, which present regional and global risk, remains challenging (Walters et al., 2016).

In the future, researchers could use a similar model to forecast potential impacts of biotransported chemicals across a wide-array of ecosystems and potential contaminant biovectors.

The ability to trace contaminants using ecosystem simulations is also useful for understanding the dynamics of contaminant accumulation. This utility is reflected in the increased use of mass-balance food web models coupled to bioaccumulation models in contaminant tracing studies (Larsen et al., 2016; Taffi et al., 2015). However, quantitative models to evaluate contaminant biotransport are lacking in the literature (Kallenborn and Blais, 2015). Historically, direct anthropogenic loading and atmospheric transport have been considered the most important pathways when considering transport and deposition of bioaccumulative pollutants (Blais et al., 2007; Hornbuckle et al., 2006). While perhaps true globally, this approach ignores the potentially large, localized impact of migratory organisms, such as salmon and other fishes (Blais et al., 2007 and Kallenborn and Blais, 2015). While several studies have examined empirical relationships regarding contaminant biotransport in fish (Gregory-Eaves et al., 2007 and Janetski et al., 2012) and birds (Brimble et al., 2009; Michelluti et al., 2010), ours is the first study to apply an ecosystem model to contaminant biotransport.

The Ecosim with Ecosim (EwE) ecosystem-modeling platform has been applied to a diversity of systems to inform ecosystem-based management of fisheries. At present, over 1000 studies have used EwE models (Coll et al., 2015), but comparatively few have used the Ecotracer component; notable exceptions include Booth and Zeller (2005), and Larsen et al. (2016). While Ecotracer has been used to track contaminant bioaccumulation in food webs, our study is the first to directly assess the predictive ability of EwE with Ecotracer for two different contaminants, and to directly assess Pacific salmon contaminant biotransport. Despite the relatively simple parameterization, our Ecotracer model reasonably predicted the concentrations of PCBs in multiple stream-resident fish species, suggesting potential for further development and use of this approach. However, our model was unable to predict Hg concentrations in resident fish because background sources appear to be more important to bioaccumulation of Hg than salmon. If future models are augmented with background sources of contaminants, predictions could potentially be improved.

5. Conclusions

Our study represents the first use of an ecosystem simulation model to quantify contaminant biotransport by salmon spawners. We demonstrated that EwE with Ecotracer is an effective tool to predict the PCB concentration of stream-resident fish in Great Lakes tributaries exposed to contaminants biotransported by Pacific salmon. However, our model was unable to accurately predict observed patterns of Hg bioaccumulation, suggesting that salmon play a minor role in Hg accumulation dynamics in stream-resident fish. Our model also highlights how species-specific differences in diet, growth, and trophic pathway can affect the magnitude of contaminant burdens in stream-resident fish. Furthermore, insights from our study suggest that a similar EwE approach could be used to evaluate other legacy and emerging bioaccumulative contaminants. Such models could prove useful for providing managers with critical information about the role of migratory fishes and potential impacts on fish, wildlife, and humans in those systems.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2017.03.027>.

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