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Interactive effects of introduced Pacific salmon and brown trout on native brook trout: an experimental and modeling approach

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Abstract: Pacific salmon (*Oncoryhnchus* spp.) and brown trout (*Salmo trutta*) are introduced species stocked in the Laurentian Great Lakes. In their native range, salmon deliver material that enhances growth, alters isotopic ratios, and increases contaminant burdens of resident fish. However, whether salmon subsidies mediate interactions between competing species is unknown. Here, we employed a mesocosm experiment and a simulation model to determine if salmon tissue consumption influences brook trout (*Salvelinus fontinalis*) growth, isotopic ratios, and mercury concentrations and whether these were modified by brown trout. Our results indicate that brook trout growth did not increase with provision of salmon tissue and was not reduced by brown trout. However, brook trout exhibited isotopic enrichment and increased mercury concentrations, suggesting dietary intake of salmon tissue. Because salmon eggs have a higher energy density and lower mercury concentration compared with salmon tissue, our simulation model suggests that consumption of salmon eggs rather than tissue can increase growth while reducing mercury accumulation. Overall, our results suggest that the role of introduced Pacific salmon is dependent on both food quantity and quality along with diet contaminant concentrations.

Résumé : Les saumons du Pacifique (*Oncoryhnchus* spp.) et la truite brune (*Salmo trutta*) sont des espèces introduites faisant l'objet d'un empoissonnement dans les Grands Lacs laurentiens. Dans leur aire de répartition naturelle, les saumons apportent des matières qui accélèrent la croissance, modifient les rapports isotopiques et accroissent les charges de contaminants des poissons résidents. Il n'est toutefois pas établi si les apports des saumons modulent ou non les interactions d'espèces concurrentes. Nous avons employé une expérience en mésocosme et un modèle de simulation pour déterminer si la consommation de tissus de saumon influence la croissance, les rapports isotopiques et les concentrations de mercure des ombles de fontaine (*Salvelinus fontinalis*) et si les truites brunes modifient ces paramètres. Nos résultats indiquent que la croissance des ombles de fontaine n'a pas augmenté avec l'apport de tissus de saumon et n'a pas été réduite par les truites brunes. Les ombles de fontaine présentaient toutefois un enrichissement isotopique et des concentrations de mercure accrues, ce qui indiquerait un apport alimentaire de tissus de saumon. Parce que les œufs de saumon ont une plus grande densité énergétique et de plus faibles concentrations de mercure que les tissus de saumon, notre modèle de simulation donne à penser que la consommation d'œufs plutôt que de tissus de saumon peut accroître la croissance tout en réduisant l'accumulation de mercure. En général, nos résultats indiqueraient que le rôle des saumons du Pacifique introduits dépend de la quantité et de la qualité des aliments, ainsi que des concentrations de contaminants dans les aliments. [Traduit par la Rédaction]

Introduction

The introduction of species outside their native range is an ecological problem of global importance (Gozlan et al. 2010). While most focus is on harmful invasions, intentional species introductions can bring economic benefits while also resulting in ecological impacts that are complex and difficult to predict (Horan and Lupi 2010). Salmonid fishes have been widely introduced because of their economic and recreational value (Korsu et al. 2009), but their impacts on native fish have been considerable (Baxter et al. 2004; Yard et al. 2011). Moreover, anthropogenic factors, such as pollution, can interact with non-native species introductions to influence populations of native species (Kolar and Lodge 2002; Gozlan et al. 2010). The Laurentian Great Lakes are a nexus for interactions between native species and environmental change, having an extensive legacy of industrial pollution along with decades of species introductions (Allan et al. 2013).

Numerous fish species have been intentionally introduced to the Great Lakes. Non-native Pacific salmon (*Oncoryhnchus* spp.) have been stocked for over five decades, while European brown trout (*Salmo trutta*) have been established in tributaries for over a century (Crawford 2001). In the Great Lakes, salmon are potadromous and semelparous, accumulating nutrients and contaminants in the lakes and then transferring resource subsidies, in the form of excretory products, carcasses, and eggs, to tributaries during spawning migrations and subsequent death in tributaries

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(Cederholm et al. 1999; Crawford 2001). Pacific salmon were initially introduced to control invasive alewife and quickly became an economically valuable component of lake and tributary-based recreational fisheries (Dettmers et al. 2012). Several studies have assessed the effects of non-native salmon in the Great Lakes (Crawford 2001; Tsehaye et al. 2014), but comparatively little is known about their effects in tributaries (but see Ivan et al. 2011; Janetski et al. 2011, 2014). In addition, previous studies have documented the decline of native brook trout (*Salvelinus fontinalis*) as a result of competitive and predatory interactions with introduced brown trout (Fausch and White 1981; Waters 1999), but it is unclear how salmon spawning may alter this relationship. The ecological influence of spawning salmon on stream ecosystems may reflect the environmental context. The importance of salmon resource subsidies (cf. Polis et al. 2004) can reflect spawner biomass, background nutrient levels, and stream sediment size (Janetski et al. 2009, 2014). Spawner biomass determines the amount of nutrients delivered and the disturbance imparted to the stream by redd construction; in turn, background nutrients regulate the enrichment response, and sediment size determines susceptibility to disturbance (Janetski et al. 2009). Nutrients supplied by salmon can increase stream productivity (e.g., Wipfli et al. 2003), while disturbance can increase or decrease the availability of invertebrates for resident fish consumption (e.g., Scheuerell et al. 2007). In addition, stream-resident fish readily consume salmon tissue and eggs (Moore et al. 2008; Scheuerell et al. 2007), increasing their growth rates (Bilby et al. 1998; Wipfli et al. 2003) and altering their isotopic composition (Chaloner et al. 2002; Reisinger et al. 2013). Consequently, different mechanisms may explain the resident fish response to spawning salmon across a gradient of biological, physical, and chemical characteristics (Janetski et al. 2009) that vary between native and introduced ranges (Janetski et al. 2011, 2014).

In tributaries of the Great Lakes, our knowledge of the influence of spawning salmon on stream-resident fish is limited. Previous research has shown that stream-resident fish in Great Lakes tributaries readily consume salmon eggs (Ivan et al. 2011; Johnson et al. 2016), but no experimental evidence exists to establish if consumption of salmon material confers a growth benefit. Similarly, stable isotopes have been used to track movement of salmon-derived material in the native range of salmon (cf. Bilby et al. 1998; Chaloner et al. 2002), but seldom in the Great Lakes (but see Schuldt and Hershey 1995).

Previous research has also shown that the body burden of persistent organic pollutants in stream-resident fish is determined by the contaminant flux supplied by spawning salmon (Janetski et al. 2012; Gerig et al. 2016). However, whether salmon spawners biotransport heavy metals, such as mercury (Hg), is uncertain. Despite these uncertainties, recent studies suggest that common environmental contaminants, such as Hg, could be used as an ecological tracer to establish pathways by which salmon-derived resources are incorporated into stream food webs and how species compete for and utilize those resources (Ramos and González-Solís 2012; Gerig et al. 2016).

Interactions between introduced and native fish species are complex (Korsu et al. 2009) and can be modulated by resource subsidies (Baxter et al. 2007). In their native range, spawning salmon alter diets of co-occurring rainbow trout (*Oncorhynchus mykiss*) and Arctic grayling (*Thymallus arcticus*), positively influencing the growth of both species (Scheuerell et al. 2007). Rainbow trout growth increased from direct consumption of salmon carcasses and eggs, while grayling growth increased from consumption of invertebrates dislodged by spawning salmon (Scheuerell et al. 2007). In contrast, introduced rainbow trout negatively impacted the growth of native Dolly Varden (*Salvelinus malma*) through competitive interactions by disrupting their access to terrestrial invertebrate prey (Baxter et al. 2007). In Great Lakes tributaries, the presence of spawning salmon could either confer bioenergetic benefits for both brook and brown trout or result in increased competition for resources (cf. Fausch and White 1986; Ivan et al. 2011).

Our objective was to evaluate the consequences of interactions between non-native and native fish species, in the context of a novel resource subsidy. For this study, we first conducted a mesocosm experiment to determine the effects of a new resource, salmon tissue, on native brook trout and whether those effects are modulated by the presence of introduced brown trout. We hypothesized that brook trout with access to salmon material would exhibit (*i*) higher growth, due to consumption of high-quality salmon tissue; (*ii*) altered isotopic ratios, reflecting incorporation of isotopically enriched salmon tissue; and (*iii*) increased Hg concentrations, resulting from consumption of Hg-laden salmon tissue. We further expected that brook trout growth rates, isotopic ratios, and Hg concentrations would be lower in the presence of brown trout because interspecific competition would reduce the consumption of salmon tissue. We then developed a coupled bioenergetics–bioaccumulation model to determine specifically how diet composition, energy density, and Hg content of diet items could interact to influence brook trout growth and Hg accumulation observed in our experiment.

Methods

Mesocosm

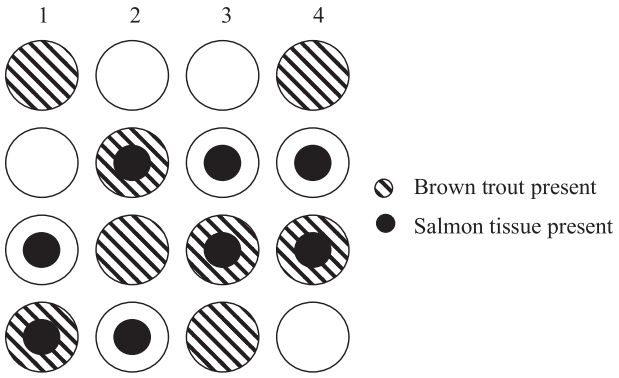
Experimental setup

We conducted a mesocosm experiment from 11 June to 26 July 2014 at the Hunt Creek Fisheries Research Station in Lewiston, Michigan (see Grossman et al. 2012 for detailed site information on Hunt Creek). Experimental mesocosms consisted of 16 flow-through polyurethane tanks (1.0 m diameter, 0.5 m height). Tanks were supplied with gravity-fed water from an artesian well, which was then split from a main water supply pipe to four secondary spouts. Each secondary spout supplied water to four tanks. At each secondary spout, an inline filter removed flocculent iron. Each mesocosm was aerated continuously with air stones to ensure an adequate supply of oxygen. During the experiment, mean ± SD water temperature (10.9 ± 1.8 °C) and oxygen (9.8 ± 0.7 mg·L^{-1}) was measured twice daily.

Young-of-the-year (age-0) brook trout and brown trout were obtained from Marquette and Oden State Fish Hatcheries, Michigan Department of Natural Resources, 1 week prior to the start of the experiment. Hatchery fish were fed a maintenance ration of bloodworms prior to the start of the experiment, and five brook trout and five brown trout were sacrificed to determine initial stable isotope values and Hg concentrations. At the start of the experiment, fish were divided into three size classes (small: 50–59 mm; medium: 60–69 mm; and large: ≥70 mm), and initial individual length (mm) and mass (g) measured. Each fish received a unique fin clip to assess individual growth over the experiment. During the experiment, fish length and mass were measured weekly, while mesocosm tanks were checked daily for mortalities. The mortality rate during the experiment was low (<15%) and similar to other published studies (cf. Wipfli et al. 2003). If a mortality occurred, it was replaced with a fish of the same species of similar length and mass to maintain experimental conditions. Prior to analysis, we censored our data to only include fish that had been in the experiment for more than 35 days to ensure that replacement fish did not bias our inference. At the end of the experiment, all experimental fish were euthanized and then stored frozen at –20 °C for later stable isotope and Hg analyses.

Brook trout were subjected to four treatments (Fig. 1): (1) salmon tissue absent and brown trout absent; (2) salmon tissue present and brown trout absent; (3) salmon tissue absent and brown trout present; and (4) salmon tissue present and brown trout present. The experiment was fully crossed, with four replicates (i.e., tanks) of each treatment. For treatments without brown trout, two

Fig. 1. Mesocosm experimental design, which consisted of 16 flow-through tanks, with four randomized treatments per block (1–4). Brook trout were present in all tanks.



brook trout from each size class were placed into tanks. For treatments with brown trout, one brook trout and one brown trout from each size class were placed into tanks. Regardless of treatment, each tank held six fish to maintain equal densities and total biomass. For treatments without salmon tissue, tanks received 5.0 g of chironomid midge larvae (*Chironomus plumosus*) twice daily. For treatments with salmon tissue, tanks received 2.5 g of chironomids and 2.5 g of salmon tissue twice daily. Thus, each tank received the same wet mass of food, and any uneaten food was removed daily. Salmon tissue used in the experiment was fall run Chinook salmon (*Oncorhynchus tshawytscha*) collected from the Little Manistee River (Michigan) weir by the Michigan Department of Natural Resources during fall 2013. Prior to the experiment, salmon were homogenized whole, excluding head and gametes, and stored frozen. Salmon tissue was used as a food source to simulate carcass tissue that is putatively available for consumption during natural salmon runs (cf. Cederholm et al. 1999; Wipfli et al. 2003). Note that salmon eggs were not provided to salmon treatments due to availability, but were included as a diet item in subsequent model simulations due to previous studies demonstrating resident fish consumption of salmon eggs (Ivan et al. 2011). Data for salmon eggs used in the model were obtained from freshly spawned Chinook salmon from the Little Manistee River. Chironomid midge larvae were obtained from JEHM Co. (www.jehmco.com). Chironomid larvae were chosen as an alternative food item because they are often found in the diet of trout in tributaries of the Great Lakes (Wills et al. 2006).

Stable isotope analyses

Stable carbon and nitrogen isotope ratios were measured for whole fish homogenized tissue and diet sources (chironomids, provisioned salmon tissue, nonprovisioned salmon eggs) using an Elemental Analyzer (Costech, Valencia, USA) coupled to a Delta Plus Isotope Ratio Mass Spectrometer (Thermo Scientific, Waltham, USA) located in the Center for Environmental Science and Technology at the University of Notre Dame. Prior to analysis, all samples were oven-dried at 60 °C, homogenized into a fine powder, and stored at –20 °C. Data were included in subsequent analyses if the standard deviation of the acetanilide standard was <0.2‰ (cf. Chaloner et al. 2002). The standard deviations for acetanilide standards were 0.08‰ and 0.06‰ for N and C, respectively. Stable isotope ratios of N ($\delta^{15}N$) and C ($\delta^{13}C$) were expressed as

$$(1) \qquad \delta^{15}N \text{ or } \delta^{13}C = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where R is the ratio of ^{15}N to ^{14}N or ^{13}C to ^{12}C. All $\delta^{13}C$ values were lipid-corrected using individual C:N ratios (cf. Post et al. 2007).

Hg analyses

Total Hg concentrations of brook and brown trout and diet sources (chironomids, provisioned salmon tissue, nonprovisioned salmon eggs) were determined using a Direct Mercury Analyzer 80 (DMA-80, Milestone S.r.l., Sorisole, Italy), also located at the Center for Environmental Science and Technology. All samples were prepared for Hg analysis in the same manner as for stable isotope analyses. Prior to analysis, 0.02 g of homogenized sample was weighed into ashed nickel boats, placed into the DMA-80, and analyzed via fixed wavelength atomic absorption spectrophotometry (cf. Abma et al. 2015). The DMA-80 was calibrated using standard reference materials (National Research Council of Canada, DORM-4, 410 ± 55 ng Hg·g^{-1}) and all results were expressed in parts per billion (ng·g^{-1}) wet mass. Standard reference materials, instrument and method blanks, duplicates, and matrix spikes were incorporated into each run to ensure data quality. Percent recovery from DORM-4 standard was 99.2% ± 2.2% (n = 11), and the detection limit was 0.141 ng·g^{-1}.

Statistical analyses

We used a randomized block analysis of variance (rb ANOVA) with a split plot design (α = 0.05; Zar 2010) to analyze the experimental results. Our main treatment factors were (*i*) salmon tissue (presence or absence) and (*ii*) brown trout (presence or absence). Size class (small, medium, large) was considered a subtreatment across blocks (cf. Wipfli et al. 2003). We interpreted a significant interaction between salmon tissue and brown trout treatments as evidence that the presence of brown trout mediated the response of brook trout to salmon tissue. All treatments were randomly assigned within each block, each of which was fed by a different output spout from the same water source. Response variables were growth rate (change in length or mass over the experimental period; mm·day^{-1} or g·day^{-1}), stable isotope ratio ($\delta^{15}N$ and $\delta^{13}C$, ‰), and total Hg concentration (ng·g^{-1}). We also used an analysis of covariance (ANCOVA) (α = 0.05; Zar 2010) to assess if variation in growth rate with respect to mass was related to variation in isotope ratios and total Hg among treatments. Assumptions of ANOVA and ANCOVA were assessed visually using Q–Q and plots of residuals. All statistical analyses were performed using the R software platform (https://cran.r-project.org/).

We used two different yet complementary approaches to link the consumption of salmon tissue to variation in brook trout Hg concentrations. First, we used ANCOVA to establish if $\delta^{13}C$ was related to Hg concentration (ng·g^{-1}) among treatments. Second, for fish from salmon treatments, we estimated the extent of salmon consumption using a Bayesian stable isotope-mixing model (MixSiar in R version 3.0.2; Stock and Semmens 2015). This model estimated how variation in the dietary contribution of salmon mediated Hg accumulation among individual brook trout. This model directly accounts for uncertainty in diet isotope ratios and trophic discrimination factors (e.g., standard deviation, SD). Tissue discrimination factors used were 3.4 (SD = 1.0) for $\delta^{15}N$ and 1.0 (SD = 0.5) for $\delta^{13}C$ (cf. Reisinger et al. 2013). The model was fit using an iterative Markov chain Monte Carlo fitting routine. Chain length was set to 100 000 with a burn-in of 50 000 and residual-only error structure (cf. Stock and Semmens 2015).

Simulation modeling

Bioenergetics model

To better understand the coupling of fish growth and contaminant burden, we used a simulation model to assess how energy density and Hg concentration of diet items could explain brook trout growth and Hg accumulation. To do so, we modified a time dynamic bioenergetics model (cf. Hanson et al. 1997; Rashleigh and Grossman 2005) and parameterized it using species-specific physiological parameters (Hartman and Cox 2008) for brook trout. Through this energetics-based approach, consumed energy is first allocated to catabolic processes and then to waste losses; remain-

Table 1. Stable isotope ratio, mercury concentration, and sample size of brook and brown trout at the end of the mesocosm experiment.

Species	Treatment	$\delta^{15}N$	$\delta^{13}C$	Mercury ($ng \cdot g^{-1}$)	Sample size
Brook trout	Initial pre-experiment	11.3±0.1	–19.3±0.2	24.3±1.7	5
	No salmon, BNT absent	9.1±1.1	–20.1±0.3	18.1±3.0	25
	Salmon, BNT absent	10.9±0.6	–20.8±0.5	159.1±57.2	27
	No salmon, BNT present	9.2±1.0	–20.1±0.3	17.8±5.4	13
	Salmon, BNT present	10.5±0.4	–20.9±0.3	162.5±39.2	12
Brown trout	Initial pre-experiment	11.6±0.2	–19.5±0.1	31.8±3	5
	No salmon, BNT present	9.43±1.0	–19.8±0.1	24.1±2.8	13
	Salmon, BNT present	10.3±1.0	–20.2±0.3	87.6±34.2	13

Note: Initial stable isotope ratio and mercury concentration for fish used in the experiment are also reported. Mercury concentration is reported as $ng \cdot g^{-1}$ wet mass. Values are reported as mean ± standard deviation.

Table 2. Stable isotope ratio, mercury concentration, and energy density of diet items fed to brook and brown trout in the mesocosm experiment and used to parameterize the bioenergetics–bioaccumulation model.

Diet item	$\delta^{15}N$	$\delta^{13}C$	Mercury ($ng \cdot g^{-1}$)	Energy density ($J \cdot g^{-1}$)	Sample size
Chironomids	4.6±3.1	–20.7±3.8	17.1±25.3	4265.7±515.2	5
Salmon tissue	11.8±0.3	–23.2±0.6	193.7±25.9	4806.4±457.0	5
Salmon eggs	—	—	14.6±5.8	6548.6±119.8	5
Hatchery feed	7.5±0.2	–20.2±0.1	—	—	5

Note: Isotope values of hatchery feed is also included for reference. Energy density ($J \cdot g^{-1}$ wet mass) was determined by bomb calorimetry, and mercury concentration ($ng \cdot g^{-1}$ wet mass) was determined using atomic absorption spectrophotometry. Values are reported as mean ± standard deviation.

ing energy is allocated to growth (Hanson et al. 1997; Rashleigh and Grossman 2005). This individual-based bioenergetics model was defined as follows:

$$(2) \qquad dM/dt = (C - Eg - Ex) \cdot ED_p - (ACT \cdot R + SDA) \cdot J_{O2}/ED_{bkt}$$

where dM/dt is the organism's change in mass over time; C is consumption; Eg is egestion; Ex is excretion; ED_p is the energy density of the prey; ACT is the activity rate multiplier; R is respiration; SDA is specific dynamic action; J_{O2} is the oxycalorific coefficient; and ED_{bkt} is the energy density of the brook trout (cf. Hanson et al. 1997). Model inputs include empirically derived daily mean water temperatures, diet proportions, diet energy density, and brook trout energy density. Water temperature values reflected those obtained from the mesocosm study. Energy density ($J \cdot g^{-1}$ wet mass) for salmon tissue, chironomids, salmon eggs, and brook trout were measured empirically using a bomb calorimeter (cf. Glover et al. 2010; Parr Instrument Co., Moline, Illinois, USA; Tables 1 and 2). Following convention, the model was fit to observed weekly growth data for brook trout using a maximum likelihood approach to determine what proportion of maximum consumption realized (P) best fit the observed data. The parameter P was determined from brook trout growth data that were pooled across treatments. The value of P was determined to be 0.53 and was used for all model scenarios (see below for scenario description; also see online Supplementary material Fig. S1[1]).

Bioaccumulation model

Brook trout growth predictions were coupled to a dynamic bioaccumulation model based on the model of Arnot and Gobas (2004). The model was defined as follows:

$$(3) \qquad dM/dt = \left[M_{bkt} \cdot \left(k_D \sum w_i C_{D,i}\right)\right] - (k_e) \cdot M_{Hg}$$

where dM/dt is the change in the mass of the contaminant in the brook trout over time; M_{bkt} is the mass of the brook trout obtained from the bioenergetics model; k_D is the uptake efficiency of the contaminant; $\Sigma w_i C_{D,i}$ is the product of diet proportion and contaminant concentration of a given diet item; k_e is the elimination rate; and M_{Hg} is the mass of the contaminant in the brook trout (cf. Arnot and Gobas 2004). Diet Hg concentrations used in the model were measured empirically (Table 2). Our bioaccumulation model differs from the work of Arnot and Gobas (2004) in that the model components dealing with contaminant uptake via the gills and metabolic transformations were removed (Trudel and Rasmussen 2006). In addition, we used a fixed rate of Hg loss based upon previous research (Trudel and Rasmussen 1997; Madenjian et al. 2012). Given that greater than 99% of contaminant uptake in fish comes from diet, and the duration of our simulation was only 50 days, these simplifying assumptions were deemed reasonable (Trudel and Rasmussen 2006). Brook trout growth and Hg accumulation was modeled across five scenarios related to variability in diet: (1) 100% chironomids; (2) 50:50 chironomids:salmon tissue; (3) 100% salmon tissue; (4) 50:50 chironomids:salmon eggs; and (5) 100% salmon eggs. For each scenario, the simulation lasted 50 days to mimic the duration of the mesocosm experiment. Starting mass of brook trout for the simulation was 2.5 g, which approximated the median mass of individuals at the beginning of the experiment. All modeling was conducted using the deSolve package in R (https://cran.r-project.org/web/packages/deSolve/index.html).

Results

Mesocosm experiment

During our 7-week experiment, brook trout exhibited positive growth rates, increasing in length and mass irrespective of treatment. Overall, brook trout grew at a mean rate of 0.4 mm (SD = 0.1 mm, range = –0.1–0.6 mm) and 0.07 g (SD = 0.03 g, range = 0.01–

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2016-0502.

0.16 g) per day. Contrary to our hypothesis, brook trout growth with respect to length or mass was not influenced by the provision of salmon tissue (length ANOVA, $F_{[1,68]} = 0.35$, $p = 0.55$; mass ANOVA, $F_{[1,68]} = 0.15$, $p = 0.69$; Fig. 2A) or the presence of brown trout (length ANOVA, $F_{[1,68]} = 0.001$, $p = 0.98$; mass ANOVA, $F_{[1,68]} = 0.06$, $p = 0.79$; Fig. 2B). However, large fish were found to grow at higher rates with respect to mass but not length (length ANOVA, $F_{[2,68]} = 2.9$, $p = 0.06$; mass ANOVA, $F_{[2,68]} = 6.72$, $p = 0.002$; Fig. S2A[1]). Consistent with our hypothesis, brook trout isotopic ratios differed in the presence of salmon tissue ($\delta^{15}N$ ANOVA, $F_{[1,68]} = 81.2$, $p < 0.001$; $\delta^{13}C$ ANOVA, $F_{[1,68]} = 15.1$, $p < 0.001$), but this result was not affected by the presence of brown trout ($\delta^{15}N$ ANOVA, $F_{[1,68]} = 1.01$, $p = 0.31$; $\delta^{13}C$ ANOVA, $F_{[1,68]} = 0.21$, $p = 0.64$). In treatments with salmon tissue, brook trout were significantly enriched in $\delta^{15}N$, which was 20% higher relative to non-salmon treatments (Fig. 2C; Table 1), and significantly depleted in $\delta^{13}C$, which was 3% lower relative to non-salmon treatments (Fig. 2D; Table 1). Large fish were found to have higher $\delta^{15}N$ but lower $\delta^{13}C$ relative to fish from medium and small size classes ($\delta^{15}N$ ANOVA, $F_{[2,68]} = 4.5$, $p = 0.010$; Fig. S2B[1]; $\delta^{13}C$ ANOVA, $F_{[2,68]} = 5.1$, $p = 0.008$; Fig. S2C[1]). Consistent with our hypothesis, brook trout Hg concentrations were higher in salmon treatments (Hg ANOVA, $F_{[1,68]} = 164.75$, $p < 0.001$), but once again this result was not affected by brown trout (Hg ANOVA, $F_{[1,68]} = 1.2$, $p = 0.28$). We observed no size response in Hg concentration (Hg ANOVA, $F_{[2,68]} = 2.4$, $p = 0.09$). Overall, brook trout Hg concentrations exhibited a ninefold increase in salmon relative to non-salmon treatments (Fig. 2E).

Given the variability in growth among treatments for brook trout, we explored how growth rate with respect to mass was related to isotopic composition and total Hg concentration. We found a significant relationship between brook trout growth rate and $\delta^{15}N$ (ANCOVA, $F_{[1,64]} = 7.8$, $p < 0.001$), with treatments provisioned with salmon tissue having higher $\delta^{15}N$ relative to non-salmon treatments (ANCOVA, $F_{[1,64]} = 72.0$, $p < 0.001$). However, this relationship was not influenced by brown trout (ANCOVA, $F_{[1,64]} = 1.2$, $p = 0.27$; Fig. 3A). Similarly, brook trout growth rate was related to $\delta^{13}C$ (ANCOVA, $F_{[1,64]} = 9.3$, $p = 0.003$; Fig. 3B), with treatments provisioned with salmon having lower $\delta^{13}C$ relative to non-salmon treatments (ANCOVA, $F_{[1,64]} = 80.7$, $p < 0.001$). This relationship was not influenced by brown trout (ANCOVA, $F_{[1,64]} = 0.42$, $p = 0.52$; Fig. 3B). No interactions were observed between growth rate and salmon, indicating that provision of salmon was not driving growth rates ($\delta^{15}N$ ANCOVA, $F_{[1,64]} = 0.16$, $p = 0.69$; $\delta^{13}C$ ANCOVA, $F_{[1,64]} = 0.62$, $p = 0.43$).

In contrast with $\delta^{15}N$ and $\delta^{13}C$, the relationship between brook trout growth rate and total Hg concentration displayed a significant interaction between treatments provisioned with salmon (ANCOVA, $F_{[1,64]} = 4.9$, $p = 0.03$; Fig. 3C). We observed a strong positive relationship between total Hg and growth rate in salmon treatments; faster-growing fish increased their Hg concentrations more quickly than slower-growing fish. In contrast, in treatments without salmon tissue, Hg accumulation decreased with increasing growth rates; slower-growing fish had higher Hg concentrations than faster-growing fish. Moreover, brook trout Hg levels exhibited a significant interaction with $\delta^{13}C$ ratio between salmon treatments (ANCOVA, $F_{[1,44]} = 50.4$, $p < 0.001$; Fig. 3D), suggesting that brook trout Hg content increased as they became depleted in $\delta^{13}C$. Results from the Bayesian stable isotope model also suggested that brook trout Hg concentration increased as salmon became more prevalent in their diet (Fig. S3[1]).

Contrary to our original hypothesis, the presence of brown trout did not affect brook trout growth, isotope ratios, or Hg concentration. Brook trout growth rates were higher than co-occurring brown trout, with respect to both length (ANOVA, $F_{[1,44]} = 36.9$, $p < 0.001$; Fig. 2A) and mass (ANOVA, $F_{[1,44]} = 45.5$, $p < 0.001$; Fig. 2B). Brown trout responded similarly to brook trout in the presence of salmon tissue (ANOVA, $F_{[1,44]} = 0.06$, $p = 0.80$) and were enriched in $\delta^{15}N$ (ANOVA, $F_{[1,44]} = 18.4$, $p < 0.001$; Fig. 2C). Overall, brook and brown trout from salmon treatments were more depleted in $\delta^{13}C$ compared with non-salmon treatments (ANOVA, $F_{[1,44]} = 25.9$, $p < 0.001$), but brown trout were more enriched in $\delta^{13}C$ relative to brook trout (ANOVA, $F_{[1,44]} = 39.7$, $p < 0.001$; Fig. 2D). Similar to brook trout, brown trout Hg concentrations increased in salmon treatments (ANOVA, $F_{[1,44]} = 219.4$, $p < 0.001$; Fig. 2E). However, an interaction was observed between the provision of salmon tissue and species identity (ANOVA, $F_{[1,44]} = 33.8$, $p < 0.001$), suggesting that brown trout were less contaminated with Hg than brook trout in the presence of salmon, but more contaminated with Hg in the absence of salmon (Fig. 2E).

Simulation modeling

In our bioenergetics–bioaccumulation model, diet items consumed by brook trout differed in their energy content (ANOVA, $F_{[2,12]} = 43.6$, $p < 0.001$; Table 1) and Hg concentration (ANOVA, $F_{[2,12]} = 246.2$, $p < 0.001$; Table 1). We used the empirical estimates of energy density and Hg concentration of diet items to parameterize our model. Salmon tissue has a similar energy density to chironomids (Tukey's honestly significant difference (HSD) test, $p = 0.12$), whereas salmon eggs have a higher energy density than either salmon tissue or chironomids (Tukey's HSD, $p < 0.001$). For Hg, salmon tissue was significantly higher compared with salmon eggs or invertebrates (Tukey's HSD, $p < 0.001$), whereas no difference was observed between salmon eggs and invertebrates (Tukey's HSD, $p = 0.84$).

Variation in prey energy densities had a moderate effect on brook trout growth, whereas Hg accumulation was strongly influenced by Hg concentration in food. Our model predicted that consumption of salmon tissue would result in a modest 3% increase in growth for the 50:50 chironomids:salmon tissue scenario and a 7% increase in growth for the 100% salmon tissue scenario, relative to the 100% chironomids scenario (Fig. 4A, Fig. S1[1]). By contrast, consumption of salmon eggs, which have a higher energy density than salmon tissue, resulted in a 14% increase in growth for the 50:50 chironomids:salmon egg scenario and a 26% increase in growth for the 100% salmon egg scenario, relative to the chironomids-only scenario (Fig. 4A). Overall, consumption of 100% salmon eggs resulted in a 19% increase in growth relative to the 100% salmon tissue scenario. Brook trout Hg accumulation also differed considerably depending upon the diet consumed. Our model predicted that consumption of salmon tissue would result in a 4.6-fold increase in Hg concentration for the 50:50 chironomids:salmon scenario and an eightfold increase in Hg concentrations for the 100% salmon tissue, relative to the chironomids-only scenario (Fig. 4B). In contrast, consumption of salmon eggs, which have lower Hg concentration than salmon tissue, resulted in a 3.7% decrease in Hg concentration for the 50:50 chironomids:salmon egg scenario and a 7% decrease in Hg concentration for the 100% salmon egg scenario, relative to the chironomids-only scenario (Fig. 4B). Overall, consumption of 100% salmon tissue resulted in an 8.5-fold higher Hg concentration relative to the 100% salmon egg scenario.

Discussion

Our mesocosm experiment suggested that brook trout growth and Hg accumulation were much more influenced by provision of salmon material than by the presence of brown trout. Moreover, our model demonstrated that diet can mediate both growth and Hg bioaccumulation in brook trout. Consistent with our hypothesis, we showed that consumption of salmon tissue strongly increased Hg levels in brook trout. However, contrary to our hypothesis, provision of salmon tissue did not increase growth despite assimilation, as indicated by isotopic ratios. Further, brook trout exhibited higher growth rates than co-occurring brown trout, an unexpected result based on past studies (e.g., Dewald and Wilzbach 1992; Waters 1999). Our simulation model

Fig. 2. Response of brook trout to provision of salmon tissue and presence of brown trout (BNT): (A) length growth rate (mm·day^{-1}), (B) mass growth rate (g·day^{-1}), (C) tissue δ^{15}N (‰), (D) tissue δ^{13}C (‰), and (E) total mercury concentration (ng·g^{-1}). Values reported are medians with upper and lower quartiles to illustrate variability. Light-shaded boxplots are brook trout, and dark-shaded boxplots are brown trout.

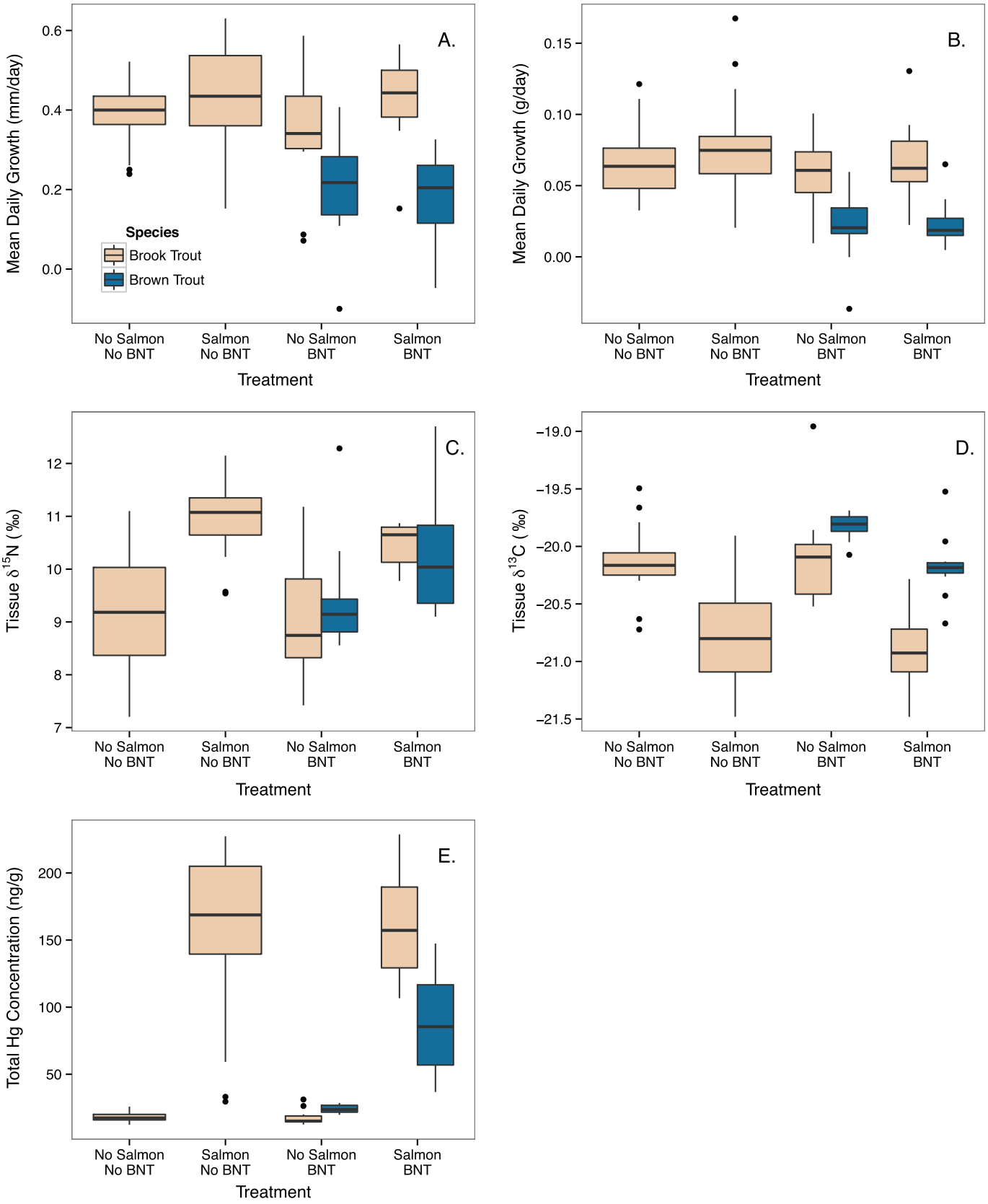
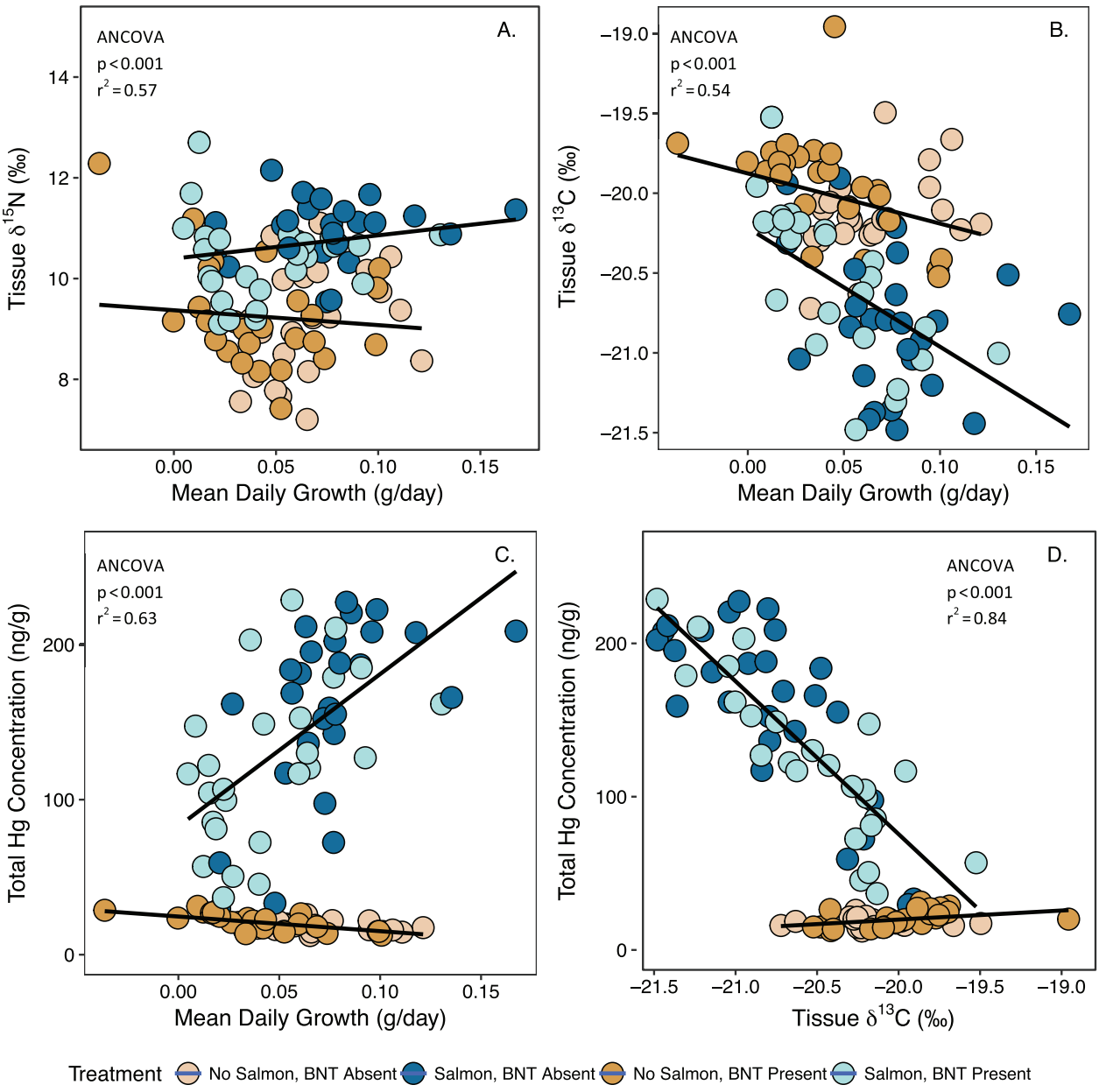


Fig. 3. Relationship between brook trout (A) mass growth rate (g·day^{-1}) and tissue δ^{15}N (‰), (B) mass growth rate (g·day^{-1}) and tissue δ^{13}C (‰), (C) mass growth rate (g·day^{-1}) and total mercury concentration (ng·g^{-1}), and (D) tissue δ^{13}C (‰) and total mercury concentration (ng·g^{-1}) among treatments. Regression line represents line of best fit for salmon and non-salmon treatments. BNT = brown trout. *p* value and r^2 statistic are from overall ANCOVA model. [Colour online.]



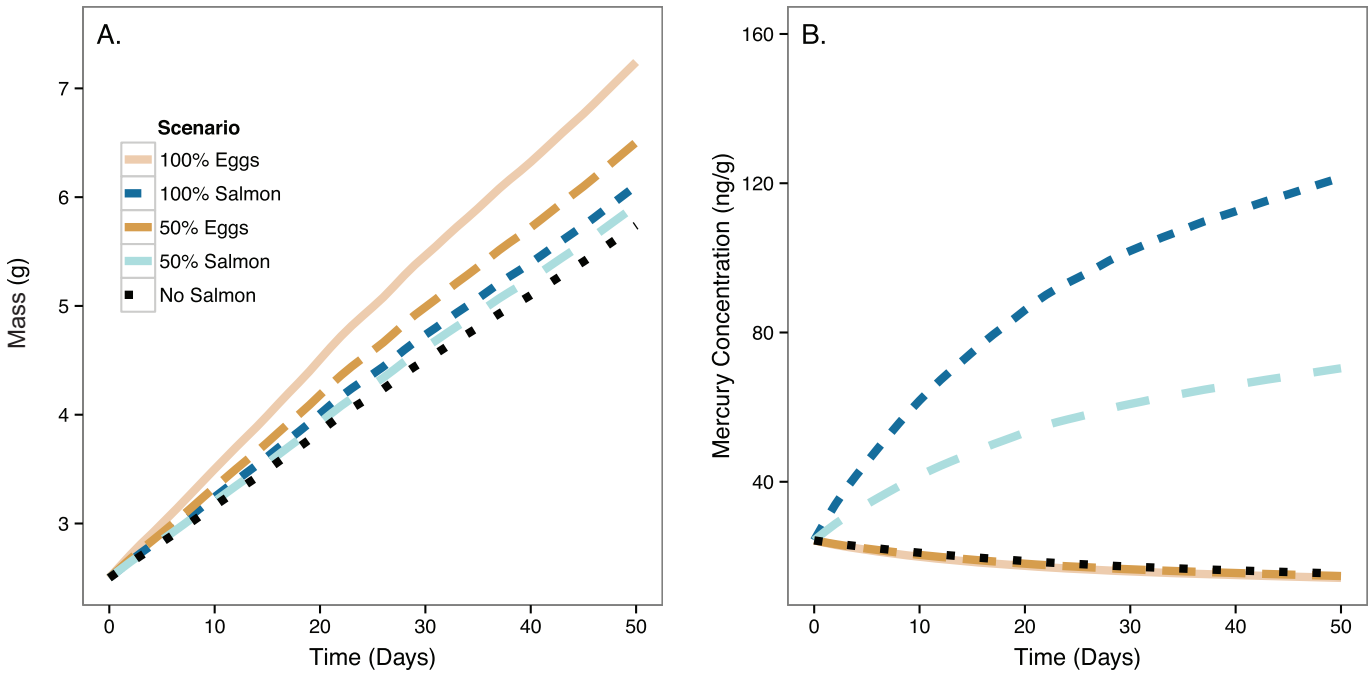
complemented our mesocosm experiment by elucidating the role of diet in regulating growth and Hg accumulation. Specifically, our model suggests that consumption of salmon eggs rather than salmon tissue moderately increases growth while reducing Hg accumulation in brook trout. Taken together, our experiment and model highlight that the bioenergetic influence of introduced salmon on brook trout is dependent on the type and amount of salmon tissue consumed.

Role of introduced salmon as a resource subsidy

Salmon material has been shown to stimulate productivity, including the growth of resident fish. For example, a meta-analysis found that the presence of salmon spawners increased resident fish growth, and this relationship was strongly driven by spawner biomass (Janetski et al. 2009). The positive response of resident fish has been attributed to direct ingestion of salmon material (Moore et al. 2008), increased invertebrate production (Chaloner and Wipfli 2002), or increased invertebrate drift (Scheuerell et al. 2007). However, the primacy of these trophic pathways remains uncertain (Janetski et al. 2009).

In our mesocosm experiment, we showed that brook trout exhibited equivalent growth rates among treatments regardless of whether they were or were not provisioned with salmon tissue. Thus, consumption of salmon material did not elicit strong subsidy effects (cf. Harvey and Wilzbach 2010). However, in salmon treatments, ANCOVA revealed that brook trout growth rate was positively correlated with Hg concentration and that δ^{13}C was negatively correlated to Hg concentrations, while salmon dietary proportion was positively related to Hg levels. These findings indicate that brook trout with increased reliance on salmon tissue had concomitant increases in both growth rate and Hg concentra-

Fig. 4. Modeled change in brook trout (A) mass and (B) total mercury concentrations over a 50-day simulation under five scenarios reflecting different diet sources and proportions. [Colour online.]



tions. These observations suggest that the response of brook trout to a novel resource subsidy is dependent on their ability to increase their rate of consumption and energy intake when resource availability is high (Moore et al. 2008). Thus, the response of resident fish to salmon subsidies may be most pronounced when background resource availability is low relative to the flux of material delivered (Flecker et al. 2010; Marcarelli et al. 2011). Therefore, locations with low in situ food availability may experience the largest benefits from salmon resources by alleviating nutritional limitation (Wipfli and Baxter 2010).

Diet quality may also mediate the growth response of organisms provisioned with a resource subsidy. The putative subsidy effect is strongest when resource quality differs among diet items and high-quality diet items are selected for in greater proportion than their availability (Marcarelli et al. 2011; Polis et al. 2004). Empirically, we demonstrated that salmon eggs are more energetically dense than salmon tissue or aquatic invertebrates, which resulted in enhanced growth in our model. This finding is similar to previous empirical studies, where resident fish growth increased as a result of consumption of salmon eggs (Moore et al. 2008; Scheuerell et al. 2007). In contrast, we did not observe growth differences in salmon treatments within our mesocosm experiment. Similarly, the addition of salmon carcasses without eggs did not increase growth of resident fish in a carcass addition experiment (Harvey and Wilzbach 2010). This suggests that resource quantity may interact with resource quality to magnify the effects of salmon subsidies on resident fish. Future research should validate our experimental results in natural streams receiving salmon spawners throughout the introduced range of salmon in the Great Lakes.

Insights from experiment–model integration

Bioenergetics modeling can provide a mechanistic understanding of how fish growth impacts population dynamics, ecosystem function, and contaminant accumulation within aquatic food webs (Madenjian et al. 2000). Integrating experiments with bioenergetic models can allow for greater inference by exploring potential causal mechanisms driving observed patterns. For example, Madenjian et al. (1994) used a bioenergetics–bioaccumulation model to explain variation in the PCB concentrations of Lake Michigan salmonines as a function of diet, consumption rate, and growth efficiency. Chemical tracers are particularly effective in fish for understanding energy flow and food web dynamics because more than 99% of their contaminant burden is obtained from dietary sources (Trudel and Rasmussen 2006).

Our study has important implications for the role of salmon tissue and egg consumption in brook trout growth and Hg accumulation. First, our study demonstrated that when dietary resources have different Hg concentrations and are consumed in different proportions, Hg is an effective tracer for incorporation of salmon-derived material. Previously, Hg has been shown to elucidate trophic level, food sources, and interecosystem habitat use (Ramos and González-Solís 2012), while in the Great Lakes, Hg was an effective tracer of salmon consumption in aquatic invertebrates (Sarica et al. 2004). Second, our model demonstrated that diet composition can mediate both growth and Hg bioaccumulation. In particular, modeled consumption of salmon eggs resulted in increased growth (cf. Scheuerell et al. 2007) and reduced Hg accumulation (cf. Cyr et al. 2016). Third, certain individual brook trout in the mesocosm experiment grew to sizes larger than predicted under any of our modeled scenarios. One explanation for this finding is that brook trout with high growth rates had larger than average consumption rates irrespective of treatment (e.g., salmon or no salmon). Fourth, we found that across treatments, fish from the large size class exhibited higher growth rates and $\delta^{15}N$ ratios than fish from small or medium size classes. Dominance hierarchies have been observed within stream salmonid populations, where larger fish increase in mass more rapidly than smaller fish (Wipfli et al. 2003). Thus, large fish are able to exert competitive dominance and thereby maximize foraging efficiency (Ahrens et al. 2012). When taken together, our results suggest that fish growth in response to salmon is controlled by the interactions between resource quantity and quality, along with individual factors including fish size and behavior that regulate foraging opportunities and energy acquisition.

Implications for contaminant accumulation and biotransport

Variation in the diet and energy intake of individual fish may also have implications for contaminant bioaccumulation and biotransport (Gerig et al. 2016). Our study showed that Hg burden, while primarily controlled by diet, can be influenced by growth. Somatic growth dilution occurs when organisms dilute a contaminant into a larger body mass; the growth dilution hypothesis holds that the faster an individual grows, the more the contaminant burden is diluted by increasing body mass (Trudel and Rasmussen 2006). In our mesocosm, we found that faster-growing brook trout in non-salmon treatments exhibited lower Hg concentrations, conforming to the growth dilution hypothesis. In contrast, we observed that faster-growing brook trout provisioned with salmon had higher Hg concentrations than slower-growing individuals, opposite to the predictions of the growth dilution hypothesis (Trudel and Rasmussen 2006). This suggests that consumption of a highly contaminated food source can override the influence of growth efficiency and dilution (Madenjian et al. 1994; Trudel and Rasmussen 2006). Additionally, we found with our model that brook trout Hg accumulation was slightly lower in fish that consumed salmon eggs compared with chironomids, despite these diet items having similar Hg content. This suggests that consumption of energy-dense salmon eggs resulted in increased growth, thereby diluting the Hg burden in brook trout. However, consumption of eggs may lead to potential trade-offs in bioaccumulation with other pollutants, such as PCBs, which accumulate in lipid-rich tissues.

Pacific salmon deliver contaminants to ecosystems that often lack direct point sources of pollution (Blais et al. 2007). Previous research, in both the native (Gregory-Eaves et al. 2007) and nonnative (Janetski et al. 2012; Gerig et al. 2016) range of salmon, has shown that organisms that reside where salmon spawn exhibit higher body burdens of persistent organic pollutants. Moreover, the magnitude of uptake is linked to the flux of pollutants supplied by salmon (Gregory-Eaves et al. 2007; Janetski et al. 2012). Our study demonstrates that consumption of salmon tissue increases the Hg load in brook and brown trout. At present, no study has assessed salmon-mediated Hg transport to resident fish in the Great Lakes. However, a previous study found that spawning salmon increased Hg concentrations in aquatic invertebrates by more than 10 times as a result of carcass consumption (Sarica et al. 2004). We expect that resident fish will be similarly impacted if they consume substantial quantities of salmon tissue. However, whether spawning salmon provide enough Hg to induce behavioral or physiological effects will depend upon the flux of Hg supplied by salmon and the degree to which resident fish consume salmon tissue over food from other sources (Kraus et al. 2014; Scheuhammer et al. 2007). Dietary exposure to mercury can result in behavioral changes in fish when tissue concentrations exceed 200 parts per billion (Beckvar et al. 2005), which is within the upper range of tissue concentrations observed in this study. Further research is needed to quantify the impact of salmon-mediated Hg transport in natural streams, especially on the stream-resident fish community.

Interactions between brook and brown trout

Contrary to our expectation, we found no evidence that brown trout adversely affected brook trout growth or altered their use of introduced salmon tissue. In fact, brook trout grew faster than brown trout when held together. These results are surprising given that introduced brown trout have been implicated in the decline of native brook trout in North America (Fausch and White 1981; Waters 1999). Several potential explanations exist. First, the mesocosms may have been saturated with food, thereby reducing interspecific competition for resources (Korsu et al. 2009). Second, competition between brook and brown trout varies with size and age; therefore, in our mesocosm juvenile brook trout may outcompete brown trout due to aggressive foraging behavior (Fausch and White 1986). Third, the negative influence of brown trout on brook trout may be most apparent in natural systems where multiple age-classes of trout co-occur; brown trout grow larger and live longer than brook trout, and thus older brown trout may detrimentally impact smaller brook trout through direct predation and competition for optimal foraging locations (Waters 1999). These interactions may explain the observed decline in brook trout populations in portions of their native range (Hudy et al. 2008). Last, mesocosm water temperatures of ~10 °C may have favored growth of brook trout, which prefer cooler water temperatures than brown trout, although water temperatures in the mesocosms were intentionally within the suitable feeding range for both species (Dewald and Wilzbach 1992). In total, the unexpected response of brook trout that we observed highlights the need for evaluation of competitive mechanisms across varying conditions, using both controlled laboratory and natural experiments (Pine et al. 2009).

Our mesocosm study demonstrated that provision of salmon resources did not modulate interactions between brook and brown trout, but that consumption of salmon tissue by both species increased Hg accumulation. Our simulation model suggested that consumption of salmon eggs increases growth and limits Hg accumulation, but trade-offs in bioaccumulation of other pollutants may exist. Therefore, by coupling a controlled mesocosm experiment with a simulation model, we were able to demonstrate that the influence of salmon resources on resident fish is dependent on the quantity and quality of food in the diet, contaminant allocation to salmon tissues, and individual fish characteristics. Overall, this study highlights the complex nature of interactions between salmon and resident fish, which have important implications for fisheries management in the Great Lakes and elsewhere.

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