BOTTOM-UP NUTRIENT AND TOP-DOWN FISH IMPACTS ON INSECT-MEDIATED MERCURY FLUX FROM AQUATIC ECOSYSTEMS

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Abstract—Methyl mercury (MeHg) is one of the most hazardous contaminants in the environment, adversely affecting the health of wildlife and humans. Recent studies have demonstrated that aquatic insects biotransport MeHg and other contaminants to terrestrial consumers, but the factors that regulate the flux of MeHg out of aquatic ecosystems via emergent insects have not been studied. The authors used experimental mesocosms to test the hypothesis that insect emergence and the associated flux of MeHg from aquatic to terrestrial ecosystems is affected by both bottom-up nutrient effects and top-down fish consumer effects. In the present study, nutrient addition led to an increase in MeHg flux primarily by enhancing the biomass of emerging insects whose tissues were contaminated with MeHg, whereas fish decreased MeHg flux primarily by reducing the biomass of emerging insects. Furthermore, the authors found that these factors are interdependent such that the effects of nutrients are more pronounced when fish are absent, and the effects of fish are more pronounced when nutrient concentrations are high. The present study is the first to demonstrate that the flux of MeHg from aquatic to terrestrial ecosystems is strongly enhanced by bottom-up nutrient effects and diminished by top-down consumer effects. Environ. Toxicol. Chem. 2013;32:612–618. © 2012 SETAC

INTRODUCTION

Methyl mercury (MeHg) is one of the most hazardous contaminants in the environment, adversely affecting the health of wildlife and humans [1,2]. Emergent aquatic insects transport MeHg to nearby terrestrial habitats, potentially exposing terrestrial consumers to aquatic pollutants [3,4], the so called darkside of cross-system subsidies [5]. The flux of MeHg from aquatic environments to terrestrial environments is especially significant because MeHg is not normally produced in terrestrial ecosystems. The conversion of inorganic Hg, the non-bioaccumulative form of Hg most commonly found in the environment, to MeHg, the highly bioaccumulative and toxic methylated form of Hg, is a microbially-mediated process that occurs primarily in aquatic systems [6–8]. Therefore, MeHg is typically only incorporated into terrestrial food chains if it is transferred from aquatic environments. Because Hg concentrations are now elevated above baseline levels in all aquatic ecosystems due to widespread anthropogenic emissions and a dynamic global atmospheric cycle [6], it is important to understand the factors that control the emergence of aquatic insects and the movement of MeHg out of aquatic systems. Recent studies have demonstrated that aquatic insects biotransport MeHg and other contaminants to terrestrial consumers [e.g., 3,5,9], but the factors that regulate the flux of MeHg out of aquatic ecosystems via emergent insects have not been studied.

Based on ecological theory, both bottom-up resource availability and top-down predation effects can alter insect emergence and the associated fluxes of MeHg from aquatic ecosystems. The bottom-up effects of nutrients potentially influence the flux of MeHg from aquatic systems by regulating productivity and emergent insect biomass [10–12]. Nutrients may also alter the flux of MeHg by affecting the concentrations of MeHg of insects as has been shown for other consumers [13–16]. The top-down influence of predation by fish could affect MeHg flux by reducing the biomass and altering the taxonomic composition of larval and emergent insects [11,12,17–19]. In the present study, we used experimental mesocosms to test the hypothesis that nutrient addition and the presence of predatory fish will influence the flux of MeHg out of aquatic ecosystems via emerging insects. How these bottom-up nutrient and top-down fish effects interact to impact MeHg flux from aquatic systems has not previously been studied.

METHODS

Experimental design

The present study was conducted in 24 mesocosms (white fiberglass tanks, 0.6 m^2 surface area, 550 L) at the Texas Christian University (TCU) Mesocosm Facility, Fort Worth, Texas, USA. We used a 2×2 factorial design in which two levels of nutrient addition (presence or absence of phosphorus [P] and nitrogen [N] additions) were cross-classified with two levels of fish presence (presence or absence of carnivorous green sunfish [Centrachidae: *Lepomis cyanellus*]). The four treatment combinations were assigned randomly to mesocosms with each treatment combination replicated six times. No replicates were lost during the experiment.

Experimental setup

In May 2010, we filled mesocosms with a bottom layer of sediment and overlying water (Table 1). Each mesocosm received 4 L of a 50:50 mixture of commercial sand and sediment collected from several shallow ponds at the Lyndon B. Johnson National Grassland (LBJNG; near Decatur, Texas,

Table 1. Timeline showing dates of experimental setup and sampling

Date in 2010	Day of experiment	Event
May 19	1	Mesocosms filled with water and sediment.
July 8	51	Water samples collected to assess initial conditions.
July 9	52	Fish added to tanks.
July 10	53	First day of nutrient additions; nutrient additions were made every other day until the end of the experiment.
July 22	65	First water samples collected post-nutrient addition. Water samples were collected twice a month until the end of the experiment.
August 28	102	First day of emergence trapping; emergent insects were collected on 20 d during a 24-d period. Emergent insects were not collected on 4 d due to heavy rain events.
September 20	125	Final day of emergence trapping.
September 24–26	129–131	Fish removed from mesocosms; experiment ends.

USA). Prior studies have shown that the pond communities at LBJNG are contaminated with atmospheric Hg [17,20], and we used the sediment as a source of Hg. Mesocosms were filled with water pumped from the epilimnion of a shallow (2.5 m maximum depth), eutrophic pond adjacent to the mesocosm facility. Pond water was filtered through a coarse plastic screen that allowed plankton to enter the mesocosms but prevented the introduction of fish. To ensure each mesocosm received similar plankton communities, pond water was first pumped into a large holding tank, where it was mixed before being transferred to the mesocosms. After the tanks were filled, we observed flying midges and dragonflies ovipositing in the tanks. Populations of macrophytes (mostly *Chara* sp.) developed in all tanks after germinating from LBJNG sediments. Throughout the course of the experiment, water levels were maintained in the mesocosms using aged tap water.

Five weeks after adding water and sediments to the mesocosms, three juvenile green sunfish (average [± standard error] weight and total length = 1.08 ± 0.04 g and 4.0 ± 0.1 cm, respectively) were added to each tank in the fish addition treatments to achieve an average tank biomass of 3.2 ± 0.1 g per tank. Average weight and length of stocked fish were not significantly different between treatments (analysis of variance [ANOVA], $F_{1,10} = 0.23$, $p = 0.64$ and $F_{1,10} = 0.31$, $p = 0.59$ for weight and total length, respectively). Green sunfish were selected for this experiment because they are invertivorous [21] and commonly found in warm-water fish communities throughout North America [22]. The stocking biomass used in the experiment is similar to the average biomass of centrachids in Texas reservoirs [23]. Tanks were monitored daily, and in the first four days after stocking, three tanks each had one fish suffer a mortality. These fish were removed and replaced with a similarly-sized fish. At the end of the experiment, tanks were drained and fish were removed and weighed. All but one fish in one of the nutrient addition replicates were recovered at the end of the experiment. Fish in both treatment combinations grew over the course of the experiment such that the average tank biomass increased by $124.1 \pm 25.7\%$ and $50.6 \pm 5.4\%$ in the with- and without-nutrient–addition treatments, respectively.

Nutrient addition began one day after fish stocking. Mesocosms in nutrient-addition treatments received $10 \,\mu g/L$ phosphorus and $30 \,\mu g/L$ nitrogen as KH_2PO_4 and NH_4Cl, respectively, dissolved in 50-mL deionized water every other day. Tanks in the no nutrient-addition treatments received control additions of 50-mL deionized water every other day. The nutrient addition regimen was chosen because it was sufficient to produce eutrophic conditions in a previous mesocosm experiment [24].

Emergence trapping of aquatic insects began five weeks after fish were added and nutrient additions started. Tent-shaped emergence traps covered the entire surface of the mesocosm and were composed of PVC frames floating on polyethylene foam covered with nylon mesh (mesh size = 2.84 ± 0.05 mm). Emergent insects were collected on 20 d over a 24-d period. Insects were not collected on four dates during the 24-d period because of heavy rains, which greatly reduced insect emergence and compromised sample integrity. Insects were collected from traps in the early morning and frozen at $-20°C$.

Water sampling and chemical analysis

To assess initial conditions, water samples were collected 50 d after filling the tanks. Prior to adding the fish and nutrients, there were no differences in water chemistry between tanks (ANOVA; all p values ≥ 0.22). Beginning on July 22, two weeks after nutrient additions began and fish were stocked, water samples were collected every other week throughout the experiment. This resulted in four sets of samples that were analyzed for total phosphorus (TP), total nitrogen (TN), and chlorophyll a (Chl a). Total phosphorus and TN were determined from unfiltered water samples. Total phosphorus was measured on a Cary UV-Vis spectrophotometer as PO_3^{-4}, after digestion with potassium persulfate, using the molybdenum blue method [25]. Total nitrogen samples were digested with alkaline potassium persulfate and analyzed as NO– on a Varian Cary 50 UV-Vis spectrophotometer using second derivative UV spectroscopy [26]. Chlorophyll a was used as a surrogate for phytoplankton biomass, and samples were filtered onto 0.45 μm microcellulose filters, frozen, extracted with HPLC-grade acetone, and measured using a Turner Designs Trilogy fluorometer.

Identifying emergent insects and estimating biomass

Insect samples collected during the experiment were pooled for each tank. Two taxa of insects, non-biting midges (Chironomindae) and dragonflies (Odonata: Anisoptera), dominated emergence from the mesocosms and were therefore the focus of the present study. Midges collected during the experiment were divided into two size classes: large (defined as individuals ≥ 4.0 mm total length) and small (<4.0 mm total length). From each tank, ten small and ten large individuals were identified to subfamily. Most (99.4%) large midges were members of the herbivorous subfamilies Chironominae and Orthocladiinae, with 0.6% belonging to the predatory subfamily Tanypodinae. Relative to large midges, a larger percentage of small midges belonged to the predatory subfamily Tanypodinae (6.4%) with the remaining 94.6% belonging to the herbivorous subfamilies Chironominae and Orthocladiinae. All dragonflies belonged to the family Libellulidae. Pooled samples were dried at $60°C$ and weighed. Mean emergence was determined by averaging emergence from all tanks within a treatment combination.

Hg analysis

Prior to Hg analysis, invertebrate samples were homogenized to a fine powder using a clean mortar and pestle or ball-mill grinder. Small and large midges were analyzed in composite samples, whereas the dragonflies were analyzed individually. All small and large midges and a subset of dragonfly samples ($n = 5$) from different treatment combinations were analyzed for MeHg and inorganic Hg at the Dartmouth College Trace Element Analysis Core Lab, Hanover, Delaware, USA, using a MERX automated MeHg system (Brooks Rand) interfaced with an Agilent 7500c inductively coupled plasma–mass spectrometry [27,28]. Remaining dragonfly samples were analyzed for total Hg (MeHg + inorganic Hg) in the Aquatic Ecology Lab at TCU with a Direct Hg Analyzer (DMA-80; Milestone). Certified reference materials (TCU: National Research Council Canada, DORM-3 and MESS-3; Dartmouth: National Institute of Standards and Technology, Mussel 2976) analyzed using both techniques were within certified ranges. The MeHg concentrations in dragonfly samples were estimated from total Hg concentrations based on the average percentage of MeHg determined in a subset of dragonflies (average % MeHg = $78.5 \pm 4.8\%$). We estimated flux of Hg leaving a mesocosm in each taxa over the course of the experiment by multiplying the total emergent biomass of each taxa by the concentration of MeHg in their tissues.

Statistical analysis

Statistical analysis was performed with SPSS (Version 19). We used a two-way analysis of variance to examine both the main and interaction effects of nutrient additions and fish presence on response variables. Main effects are the independent impact of each factor (nutrient addition or fish presence), while interaction effects are the amount of measured variation in the response variables due to the interdependence between nutrient addition and fish presence. When the interaction term was not significant, it was removed from the model. When a nutrient × fish interaction effect was detected, we tested for simple effects. The analysis of simple effects allowed us to determine if the effects of a treatment factor differed in the presence and absence of the other factor. In the presence of fish, dragonfly emergence was completely suppressed (see *Results*), resulting in an emergence biomass and MeHg flux from all replicates with fish of 0 g and ng, respectively, and making it inappropriate to determine the effect of fish and nutrients on these dependent variables using the two-way ANOVA approach described above. In these cases, we tested for an effect of fish on all treatment combinations using the non-parametric Mann-Whitney U test and tested for an effect of nutrients after removing treatment combinations that contained fish (i.e., those in which all replicates had a value of 0) using a one-way ANOVA. We used a one-way univariate ANOVA to compare average MeHg concentrations among taxa. Some variables were ln-transformed to meet the assumption of homogeneity of variance. For a given dependent variable, if data was between zero and one we multiplied by 100 and then added one if any replicates contained zeros prior to ln-transformation. We present untransformed data in all figures and indicate which variables were transformed prior to analysis in the Supplemental Data (Table S1). Statistical significance for all analyses was inferred at $p < 0.05$.

RESULTS

Adding nutrients altered the primary producer biomass and water chemistry of mesocosms. Nutrient addition significantly enhanced concentrations of Chl *a*, TP, and TN (Fig. 1a–c; Supplemental Data, Table S1). Fish significantly enhanced concentrations of TP, and we detected a significant nutrient × fish interaction effect on TP (Fig. 1b; Supplemental Data, Table S1). Analysis of simple effects indicated that nutrient addition significantly increased TP in both fish and fishless treatments, but fish only significantly increased TP in mesocosms receiving nutrient additions (Supplemental Data, Table S2).

As predicted, nutrient addition and fish had strong and opposing effects on insect emergence. Nutrient addition significantly enhanced the emergent biomass of small and large midges and dragonflies, whereas the presence of fish significantly reduced emergence of these taxa (Fig. 2a–c; Supplemental Data, Table S1). In fact, fish eliminated all dragonfly emergence. We also detected a significant nutrient × fish interaction effect on large midge emergence. Analysis of simple effects indicated that nutrient addition significantly enhanced large midge emergence only when fish were absent, whereas fish significantly reduced large midge emergence under both low- and high-nutrient conditions (Fig. 2b; Supplemental Data, Table S2).

Concentrations of MeHg in emergent insects were not significantly affected by nutrient addition or fish, except in the case of small midges whose MeHg concentrations were enhanced by nutrient addition (Figs. 3a–c, Supplemental Data, Table S1). Although there were limited effects of the nutrient and fish treatments on MeHg concentrations, we observed differences in MeHg concentrations among small midges, large midges, and dragonflies (ANOVA, $F_{2,53} = 69.6$; $p < 0.001$). The MeHg concentrations of small midges, which were composed of a relatively high proportion of predatory taxa, were three times greater in MeHg concentration than large midges, which were composed almost exclusively of herbivorous taxa (Fisher's least significant difference [LSD]; $p = 0.01$; Fig. 3a,b). The MeHg concentrations in predatory dragonflies emerging from tanks were significantly greater than that of small and large midges (Fisher's LSD; $p < 0.001$).

Nutrient addition and fish had strong effects on the emergence-mediated flux of MeHg out of the mesocosms. Nutrient addition significantly increased the flux of MeHg from mesocosms in both small and large midges (Fig. 4a,b; Supplemental Data, Table S1). In contrast, fish significantly reduced the MeHg flux from mesocosms in small and large midges and dragonflies (Fig. 4a–c; Supplemental Data, Table S1). We also detected a significant nutrient × fish interaction effect on the flux of MeHg in large midges. Analysis of simple effects indicated that nutrient addition significantly enhanced flux of MeHg in large midges only when fish were absent, and that fish significantly reduced the flux of MeHg in large midges under both low- and high-nutrient conditions (Fig. 4b; Supplemental Data, Table S2).

DISCUSSION

In the present study, we experimentally demonstrated that both bottom-up and top-down forces have the potential to affect the fluxes of a highly toxic contaminant from one ecosystem to another. We found that nutrient addition led to an increase in MeHg flux from aquatic ecosystems, primarily through enhancing the biomass of emerging insects whose tissues were contaminated with MeHg. The bottom-up effect of nutrients on the flux of resource subsidies (i.e., emerging insects) to terrestrial ecosystems has previously been demonstrated across productivity gradients in field studies [29] and in systems that have
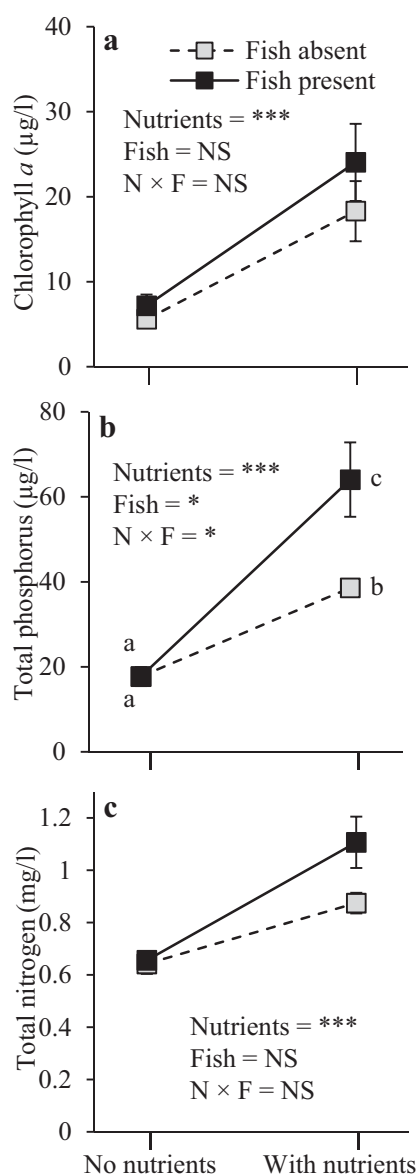
Fig. 1. Two-way interaction plots illustrating the main effects of nutrient additions (Nutrients) and fish presence (Fish) on water quality in experimental mesocosms. Water samples were collected twice a month throughout the experiment after nutrient additions began. Values represent the treatment combination average (± standard error) of four sampling dates. Non-significant (NS), *, **, and *** represent p values that were ≥ 0.05, < 0.05, < 0.01, and < 0.001, respectively. Complete statistical results are reported in Supplemental Data, Table S1. When a significant Nutrient × Fish interaction (N × F) was detected, we tested for simple main effects. Treatment combinations identified with different lowercase letters were significantly different from one another, whereas those that share a letter were not. The p values from the test of simple main effects are reported in Supplemental Data, Table S2.
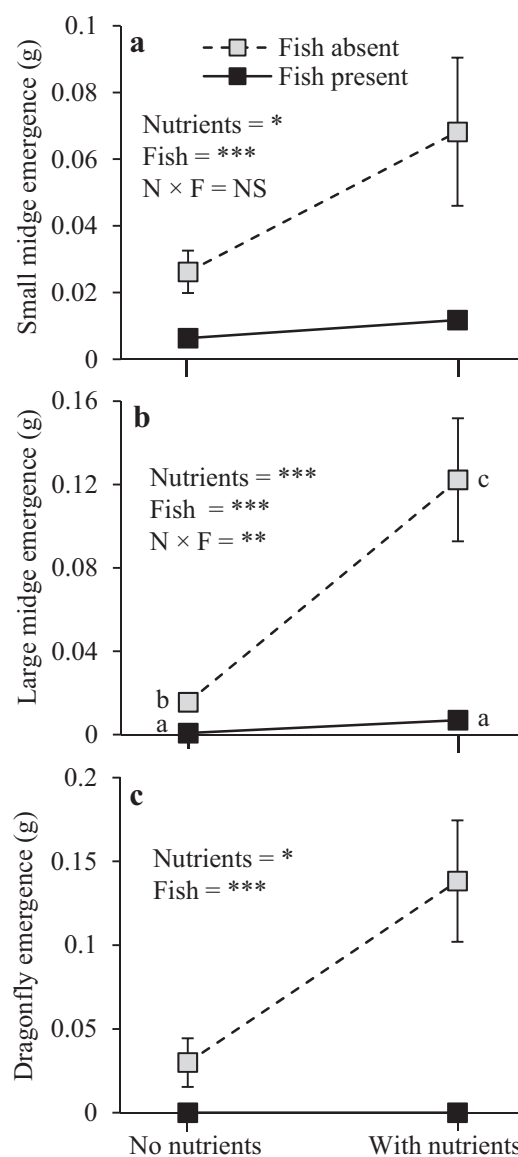

Fig. 2. Two-way interaction plots illustrating main effects of nutrient additions (Nutrients) and fish presence (Fish) on emerging insect biomass. Values represent the treatment combination average (± standard error) of insect biomass collected during 20 d. Significant/non-significant main and interaction effects (N × F), and simple effects are illustrated using symbols and lowercase letters that are described in the caption for Figure 1.

been experimentally manipulated [10–12,30]. The present study suggests that increased nutrient inputs into aquatic ecosystems increases the risk that terrestrial consumers will be exposed to greater fluxes of aquatically-derived MeHg. Indeed, many terrestrial consumers that inhabit riparian areas adjacent to aquatic ecosystems can derive a substantial portion of their food resources from emergent aquatic insects [31,32]. Our findings are particularly significant given that many surface waters are experiencing cultural eutrophication [33]. Although the effects of eutrophication on water quality have been studied extensively [33], the present study suggests that eutrophication

may impact consumers in terrestrial ecosystems (e.g., spiders and birds) by enhancing the transport of contaminants by emergent insects moving from aquatic to terrestrial environments.

We did not find a consistent nutrient addition effect on MeHg concentrations in emerging insects. The MeHg concentration of large midges and dragonflies were not affected by nutrient additions, whereas MeHg concentrations in small midges were enhanced by nutrient additions. In several large field surveys, the concentration of MeHg in biota has been inversely correlated with various measures of trophic state and primary production [13,34–37]. Somatic growth dilution and algal bloom dilution are two possible mechanisms that explain the observed inverse relationship, both of which have been demonstrated in controlled experiments [14,38,39]. However, several examples in the literature have shown that nutrient concentrations are positively correlated
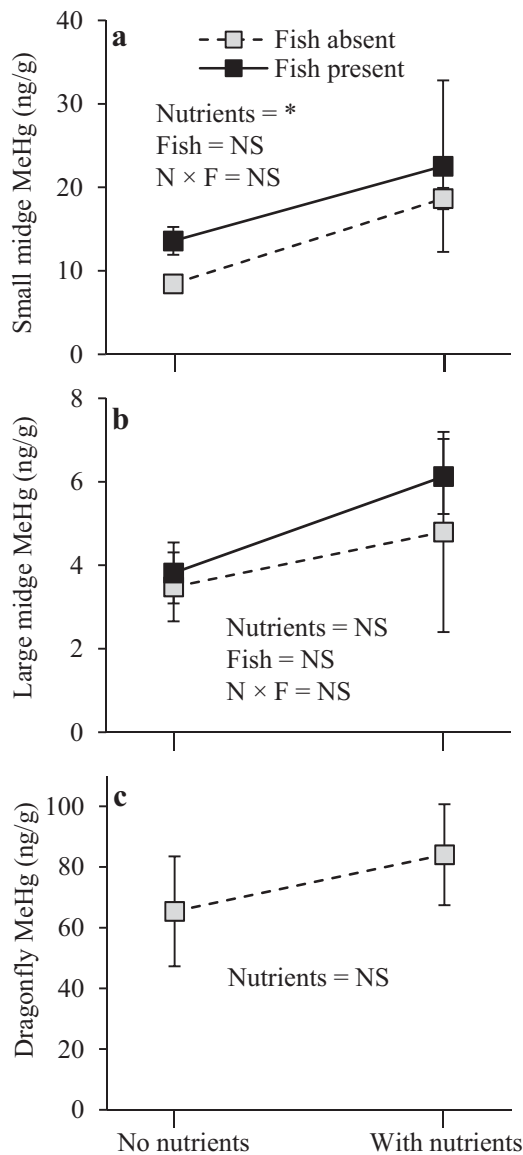
Fig. 3. Two-way interaction plots illustrating main effects of nutrient additions (Nutrients) and fish presence (Fish) on emerging insect MeHg concentration. Values represent the treatment combination average (± standard error). The MeHg concentrations were not determined in dragonflies from tanks with fish, because fish completely eliminated dragonfly emergence. Significant/non-significant main and interaction effects (N × F) and simple effects are illustrated using symbols and lowercase letters that are described in the caption for Figure 1.
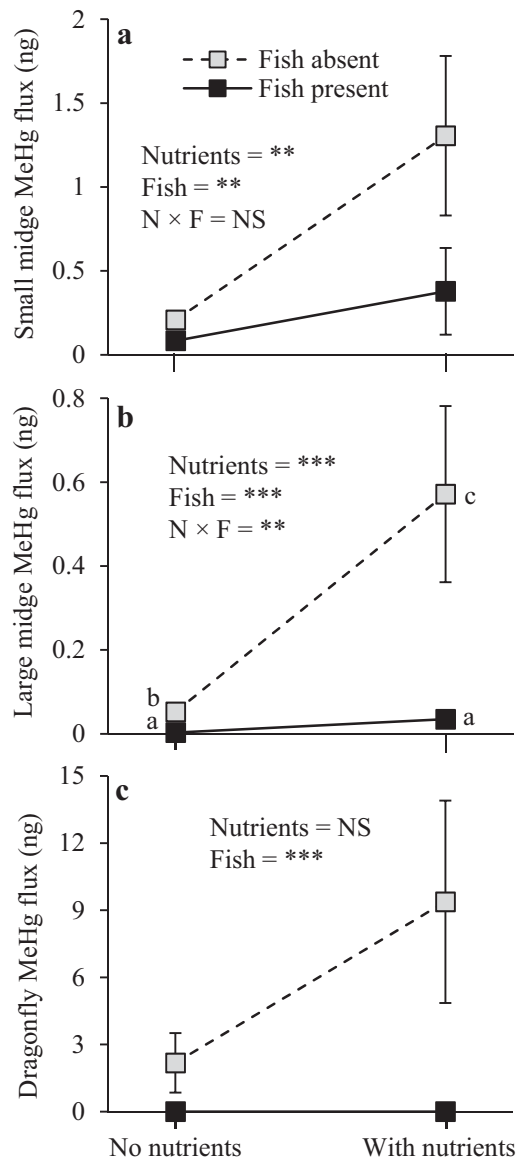
Fig. 4. Two-way interaction plots illustrating main effects of nutrient additions (Nutrients) and fish presence (Fish) on emerging insect MeHg flux. Values represent the treatment combination average (± standard error). Significant/non-significant main and interaction effects (N × F) and simple effects are illustrated using symbols and lowercase letters that are described in the caption for Figure 1.

with MeHg concentrations in biota [15,16,40–43]. The hypothesized mechanism for the observed positive relationship between MeHg concentration and productivity is the stimulation of MeHg production by microbial communities. Given the equivocal nature of the relationship between nutrient enrichment and MeHg in biota, an important question for future research is this: Under what conditions do nutrient inputs lead to reduced or enhanced MeHg concentrations in biota? The question is significant in particular to the issue of cross-system transport of MeHg, because MeHg flux out of aquatic ecosystems is the product of both MeHg concentration in biota and the amount of emergent insect biomass. Therefore, a nutrient-induced increase or decrease in MeHg concentration in emerging insects could enhance or reduce MeHg flux, respectively.

The present study also found that the presence of invertivorous fish had strong top-down impacts on insect emergence and thus MeHg flux. This has important implications because humans have dramatically altered fish communities directly through purposefully stocking and accidentally introducing native and non-native fish species [44] and overfishing [45] and indirectly through enhanced frequency of drought and associated drying of small water bodies as a result of anthropogenic climate change [46]. Anthropogenic alterations of fish communities directly affect aquatic communities and aquatic ecosystem function but may also indirectly impact terrestrial ecosystems by altering aquatic subsidies [47]. The present study suggests that anthropogenic activities that enhance fish biomass might result in reduced contaminant fluxes, wheras activities

that reduce fish biomass or eliminate fish communities could amplify the flux of these contaminants.

CONCLUSIONS

The field of ecology now recognizes that virtually all ecosystems interact with their surrounding landscapes and can exhibit substantial exchanges of organisms, organic matter, and nutrients [48]. Traditionally, ecologists and ecotoxicologists have focused on the movement of organic matter and contaminants from terrestrial to aquatic ecosystems [e.g. 49]. Researchers now recognize, however, that emerging aquatic insects can provide substantial and important spatial subsidies of carbon, nutrients, and contaminants to recipient terrestrial food webs [e.g. 9,50,51]. The present study is the first to demonstrate experimentally that the flux of MeHg from aquatic to terrestrial ecosystems is enhanced strongly by bottom-up nutrient effects and diminished by top-down consumer effects. Furthermore, we found that these factors are interdependent such that the effects of nutrients are more pronounced when fish are absent, and the effects of fish are more pronounced when nutrients concentrations are high. The present study also suggests that eutrophication and altering fish communities, two globally ubiquitous anthropogenic impacts, have the potential to alter the flux of MeHg out of aquatic systems into terrestrial environments.

SUPPLEMENTAL DATA

Tables S1-S2. (44 KB DOC).

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