

# Ecological Factors Controlling Insect-Mediated Methyl Mercury Flux from Aquatic to Terrestrial Ecosystems: Lessons Learned from Mesocosm and Pond Experiments



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*Ecological understanding must be integrated into toxicology for a better, more coherent whole.*

(Chapman 2002)

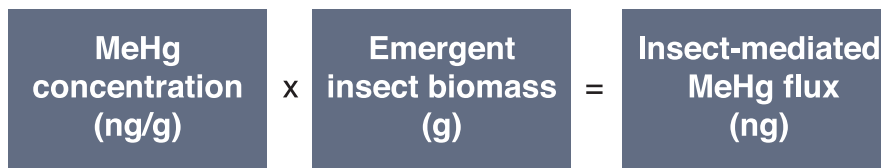
## 1 Introduction

The diets of terrestrial consumers can be subsidized by emerging adult aquatic insects that transport energy and nutrients from aquatic to terrestrial ecosystems (Polis et al. 1997; Baxter et al. 2005). However, this cross-ecosystem movement of materials by aquatic insects can have a “dark side” because emerging aquatic insects also transport bioaccumulative contaminants such as methyl mercury (MeHg) and polychlorinated biphenyls (PCBs) to terrestrial ecosystems (Walters et al. 2008; Tweedy et al. 2013). The concentration of MeHg and PCBs in emerging aquatic insects is correlated with the level of contamination of aquatic ecosystems (Cristol et al. 2008; Walters et al. 2010; Tweedy et al. 2013; Gann et al. 2015) and can be high enough to pose a health hazard to terrestrial consumers (Brasso and Cristol 2008; Walters et al. 2010; Jackson et al. 2011; Gann et al. 2015; Williams et al. 2017). Although ecological factors (such as aquatic community structure) are known to influence adult aquatic insect emergence and the cross-ecosystem transport of energy and nutrients (e.g., McCarty 1997; Davis et al. 2011; Greig et al. 2012; Wesner 2016), less is known about the ecological factors that regulate the cross-ecosystem transport of contaminants by emerging insects (Chumchal and Drenner 2015; Schiesari et al. 2018).

This chapter provides an overview of our mesocosm and pond experiments that investigated how ecological factors affect the transport of MeHg out of aquatic ecosystems by emerging insects (hereafter insect-mediated MeHg flux). In our studies, we calculated insect-mediated MeHg flux as the product of the MeHg concentrations and biomass of emerging insects (typically measured on a per area

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$$\begin{array}{|c|} \hline \text{MeHg} \\ \text{concentration} \\ \text{(ng/g)} \\ \hline \end{array} \times \begin{array}{|c|} \hline \text{Emergent} \\ \text{insect biomass} \\ \text{(g)} \\ \hline \end{array} = \begin{array}{|c|} \hline \text{Insect-mediated} \\ \text{MeHg flux} \\ \text{(ng)} \\ \hline \end{array}$$

**Fig. 1** Insect-mediated MeHg flux is calculated as the product of MeHg concentrations and biomass of emerging adult aquatic insects (typically measured on a per area basis over a fixed period of time). The resulting product represents an estimate of the absolute amount of contaminant leaving an ecosystem within the tissues of emerging insects

basis over a defined period of time; Fig. 1). Therefore, any factor that affects either the MeHg concentration or the biomass of emerging insects could influence insect-mediated MeHg flux. Multiplying MeHg concentration (ng/g) by the biomass (g) of emerging insects results in an estimate of the absolute amount of MeHg (ng) leaving the aquatic ecosystem within the tissues of emerging insects. Our experimental studies examined how four ecological factors affect aquatic insect-mediated MeHg flux: (1) fish predation and community structure, (2) nutrient levels and trophic state, (3) drying disturbance and pond permanence, and (4) seasonality of insect emergence.

## 2 Mercury Cycle

Methyl mercury is a toxic, biomagnifying contaminant of global significance (Chen and Driscoll 2018). Elemental and inorganic forms of mercury (Hg) are emitted to the atmosphere from industrial activities and can circulate around the globe before being deposited on the earth's surface, resulting in elevated concentrations of Hg in remote environments (Chen and Driscoll 2018). In aquatic ecosystems, the inorganic forms of Hg that are typically deposited from the atmosphere are converted by anaerobic bacteria to toxic MeHg (Chen and Driscoll 2018), which bioaccumulates in organisms at the base of the food web (i.e., algae) (Miles et al. 2001; Pickhardt and Fisher 2007). Consumers are exposed to MeHg through their diet (Hall et al. 1997; Tsui and Wang 2004; Pickhardt et al. 2006), and MeHg biomagnifies as it is transferred through the food web, reaching elevated concentrations in organisms with high trophic positions (Lavoie et al. 2013) such as predatory insects and fish. Terrestrial consumers can be exposed to MeHg by consuming emerging aquatic insects or by consuming spiders that feed on aquatic insects (Gann et al. 2015; Chumchal et al. 2017). Methyl mercury concentrations in terrestrial spiders that consume adult aquatic insects are correlated with insect-mediated MeHg flux (Tweedy et al. 2013).

### 3 Effects of Ecological Factors on Aquatic Insect-Mediated MeHg Flux

#### 3.1 Fish Predation and Community Structure

Freshwater fish are top predators and important consumers of aquatic insects (Wesner 2016). Most large-bodied insectivorous fish in lentic freshwater ecosystems, such as bass and sunfish (Centrarchidae), locate their prey visually and are size-selective predators, preferentially feeding on large and vulnerable prey items, such as dragonflies and damselflies (Odonata) (Mittelbach 1988). Because fish predation reduces the population density of larval insects that are capable of emerging from ponds as adults, we hypothesized that fish presence could reduce insect-mediated MeHg flux from aquatic ecosystems (Henderson et al. 2012).

We tested the hypothesis that fish predation reduces insect-mediated MeHg flux in experimental ponds located near Fort Worth, Texas, USA (Fig. 2a, b), with and without centrarchids: largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*) (Tweedy et al. 2013). We used floating emergence traps to collect five taxa of emerging adult aquatic insects over a 6-week period during May and June 2011: dragonflies (Odonata:Anisoptera), damselflies (Odonata:Zygoptera), predatory chironomids (Chironomidae:Tanytopodinae), microcaddisflies (Trichoptera:Hydroptilidae), and herbivorous chironomids (Chironomidae:Chironominae and Orthocladinae) (Fig. 2c). We calculated MeHg flux for each of the five insect taxa separately as well as the sum (aggregate) of the MeHg flux from all five insect taxa. Because our experimental ponds varied in baseline levels of MeHg contamination, we used MeHg concentrations in herbivorous chironomids as a proxy for baseline MeHg contamination of the food web.

Both the level of MeHg contamination and the presence of fish had effects on insect-mediated MeHg flux. Methyl mercury flux from each insect taxon (Figs. 3a–d) except microcaddisflies (Fig. 3e) was positively and significantly related to MeHg concentrations in herbivorous chironomids (baseline contamination of the food web). Methyl mercury flux from large taxa (dragonflies and damselflies) was reduced in ponds with fish (Fig. 3a, b). The MeHg flux from small taxa (herbivorous and predatory chironomids and microcaddisflies) was not significantly affected by fish presence (Fig. 3c–e). Aggregate MeHg flux was positively and significantly related to MeHg concentrations in herbivorous chironomids (a proxy for baseline MeHg contamination of the food web) and was significantly lower in ponds with fish (Fig. 3f).

The reduction of aggregate insect-mediated MeHg flux in the presence of fish was caused by the suppression of biomass of large taxa (dragonflies and damselflies) emerging from ponds and not alteration of MeHg concentrations within taxa (Tweedy et al. 2013). The suppression of emerging dragonflies and damselflies led to a relatively large reduction of aggregate MeHg flux because these predatory taxa have high MeHg concentrations and occur at high biomasses, thus they account for a large proportion of aggregate MeHg flux. The difference in aggregate

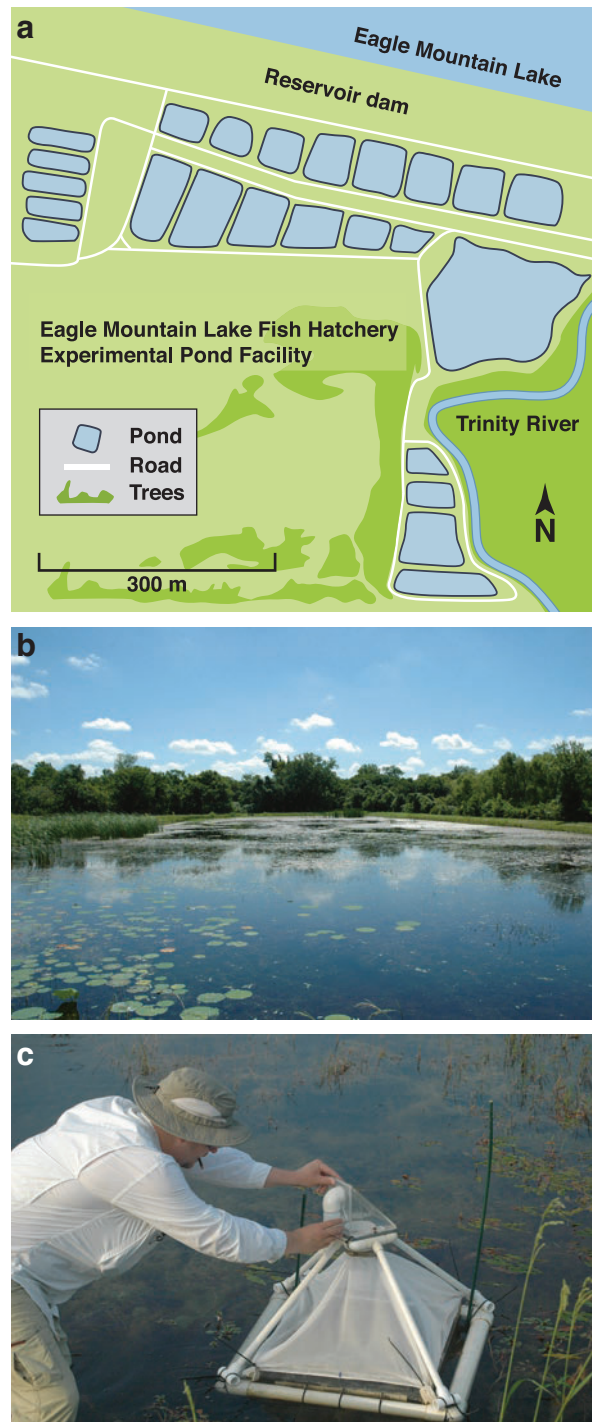
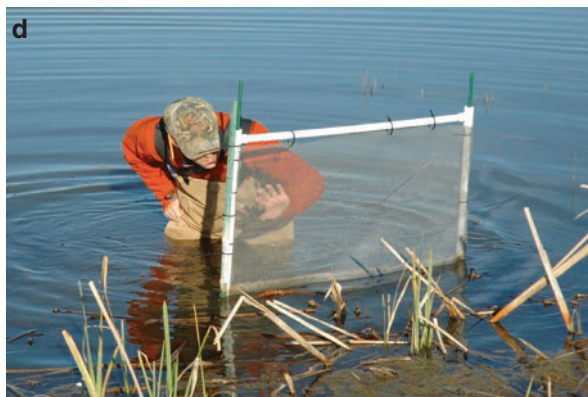


Fig. 2 (continued)

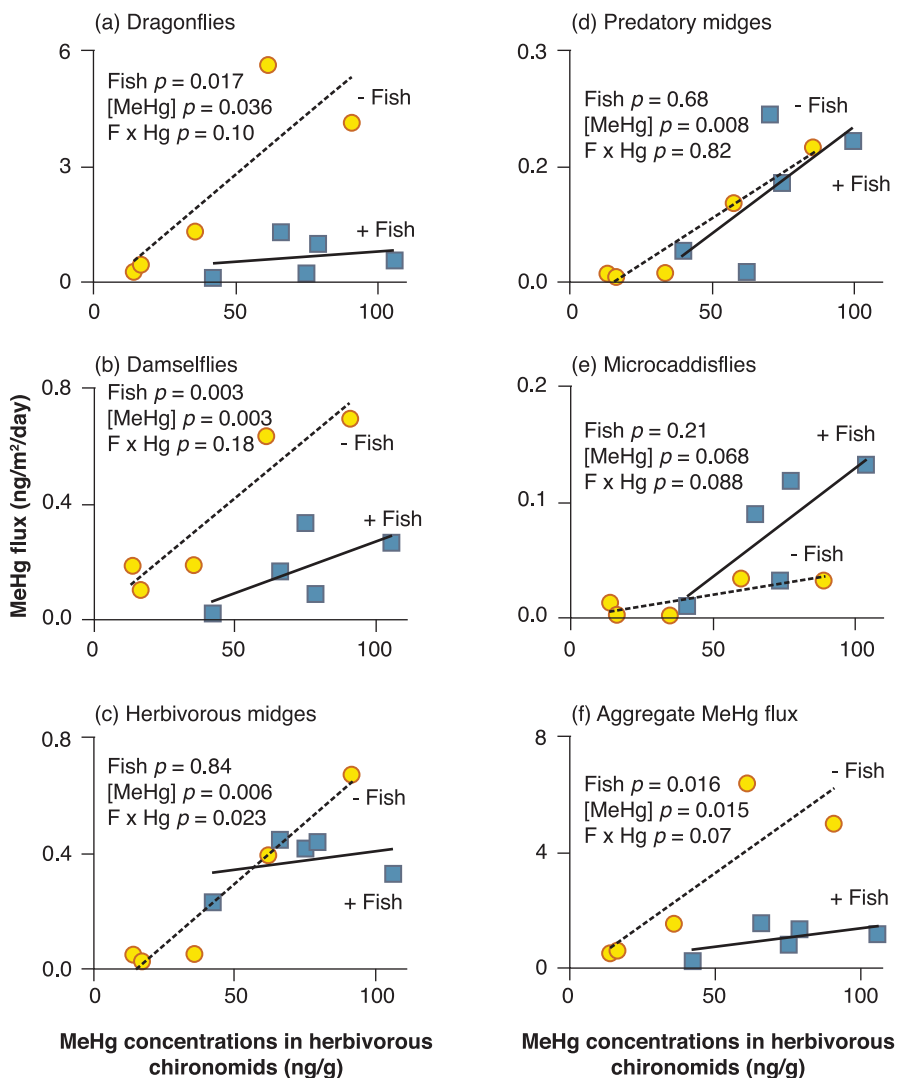


**Fig. 2** (a) The Eagle Mountain Fish Hatchery Experimental Pond Facility consists of ponds supplied with water from Eagle Mountain Lake, a large eutrophic reservoir near Fort Worth, Texas, USA (32°52'32.95"N, 97°28'29.00"W). Atmospheric deposition to the pond surfaces and the watershed of Eagle Mountain Lake contaminates ponds with Hg, allowing us to conduct studies without having to add Hg to the ponds. (b) Ponds are shallow with maximum and average depths of 1.2 and 0.6 m, respectively, and range in size from 0.23 to 0.54 ha. Ponds have earthen bottoms and contain complex communities of macrophytes, benthic invertebrates, reptiles, and amphibians that colonize the ponds (Williams et al. 2017). Ponds can be stocked with any combination of fish species, and fish will reproduce in ponds. Image reprinted with permission from Tweedy et al. (2013). Copyright 2013 American Chemical Society. (c) In Tweedy et al. (2013) and Chumchal et al. (2017), we captured emerging insects using 0.53 m × 0.53 m area (0.28 m<sup>2</sup>) floating emerging insect traps. (d) In Williams et al. (2017), dragonfly emergence was monitored with 1 m × 1.5 m (width × height) emergence platforms

insect-mediated MeHg flux between ponds with and without fish was greatest in ponds with high MeHg contamination (Fig. 3f), suggesting that the effects of fish on insect-mediated MeHg flux would be expected to be greatest in highly Hg-contaminated ecosystems. In summary, we found that the potential for insect-mediated MeHg flux increased with MeHg contamination levels of the ponds but that the realized MeHg flux from individual insect taxa was determined by fish presence.

### 3.2 Nutrient Levels and Trophic State

In addition to fish predation, the population biomass of emerging aquatic insects is also determined by the level of primary production (Blumenshine et al. 1997). In aquatic systems, primary production can be limited by the nutrients nitrogen (N) and phosphorus (P) (Elser et al. 1990, 2007). In combination, high concentrations of N and P enhance primary production (Elser et al. 1990, 2007) and increase the biomass of primary and secondary consumers, including emerging insects (McCarty



**Fig. 3** Relationship between herbivorous chironomid MeHg concentration (a proxy for baseline MeHg contamination) and MeHg flux from (a) dragonflies, (b) damselflies, (c) herbivorous chironomids, (d) predatory chironomids, (e) microcaddisflies, and (f) an aggregate of all taxa in ponds with and without fish. Solid lines with blue squares represent ponds with fish (+ fish), and dashed lines with yellow circles represent ponds without fish (– fish). P-values from an ANCOVA testing for the main effects of chironomid MeHg concentration ([MeHg]) and fish presence (fish) and their interaction ( $F \times Hg$ ) on MeHg flux are included in each panel. The assumption of heterogeneous slopes was violated in the case of herbivorous chironomids; therefore, we report the treatment effect of fish at the average of the covariate. Note the scale of the y-axis differs for each taxon. Used with permission from Tweedy et al. (2013). Copyright 2013 American Chemical Society



**Fig. 4** Our experimental mesocosms are 550 l conical fiberglass tanks (0.6 m<sup>2</sup> surface area) located at the Texas Christian University mesocosm facility in Fort Worth, Texas, USA. Water is supplied from a nearby pond. The mesocosms were aerially colonized by aquatic insects and stocked with fish. Sediments collected from nearby ponds (LBJ National Grasslands, Decatur, TX, USA) contaminated with Hg from the atmosphere were added to the tanks to serve as a source of Hg. In Jones et al. (2013), mesocosms were covered with mesh netting to capture all emerging insects

1997; Davis et al. 2011; Greig et al. 2012). We hypothesized that nutrient addition would increase insect-mediated MeHg flux by increasing the biomass of emerging insects more in systems without fish than in systems with insectivorous fish.

To examine how nutrient addition and the presence of predatory fish may interact to affect insect-mediated MeHg flux, we conducted a mesocosm experiment at the Texas Christian University mesocosm facility in Fort Worth, Texas, USA (Fig. 4). We used a 2 × 2 factorial design in which two levels of nutrient addition (presence and absence of simultaneous N and P addition) were cross-classified with two levels of fish (presence and absence of juvenile green sunfish [*Lepomis cyanellus*]) (Jones et al. 2013). This experimental design allowed us to examine the main effects of nutrients and fish and their potential interaction effects on insect-mediated MeHg flux. Mesocosms were filled with water (day 1), and 51 and 52 days later, fish were stocked and nutrient additions began, respectively. Adult aquatic insects were allowed to aerially colonize the mesocosms from days 1 to 101 of the experiment. One hundred and two days after filling the mesocosms with water, we began capturing adult aquatic insects emerging from the mesocosms. We used tent-shaped

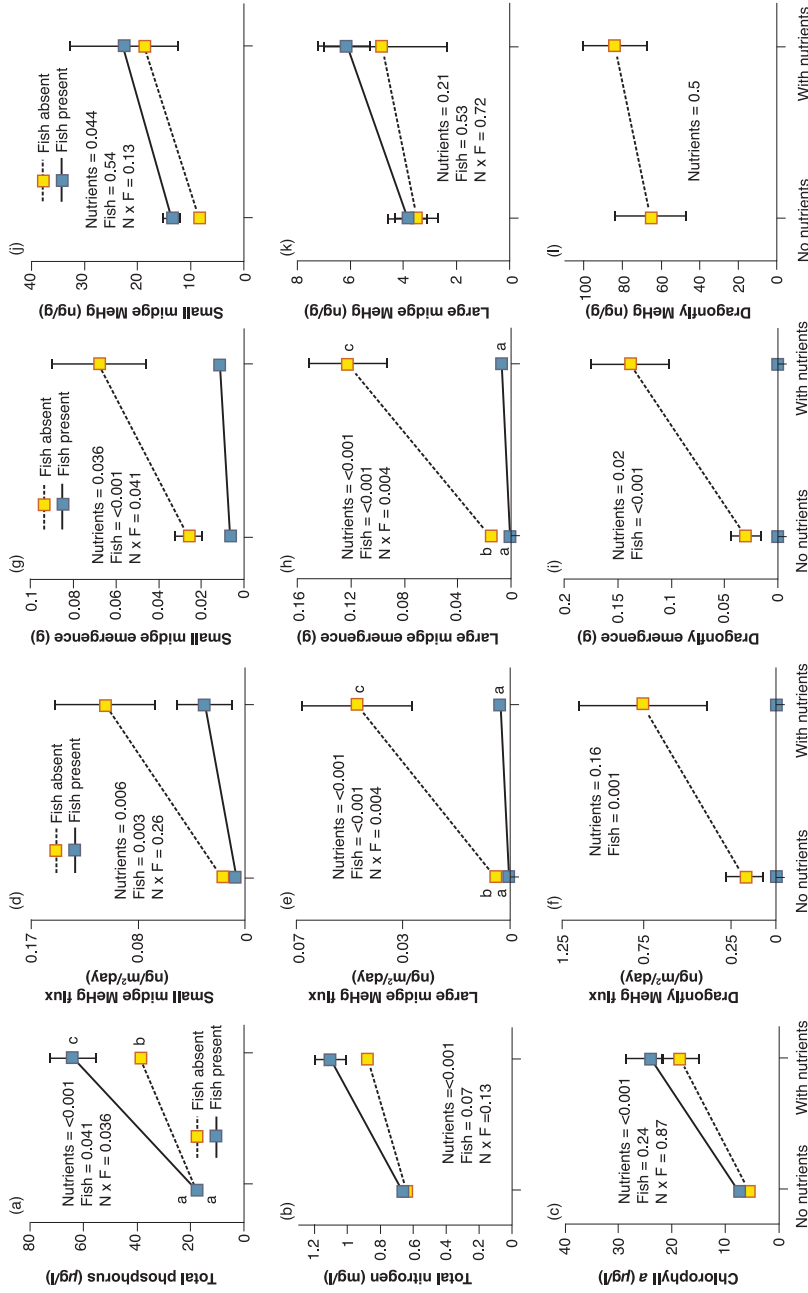
emergence traps that covered the entire surface of the mesocosm (Fig. 4) to capture all emerging insects including small midges (defined as Chironomidae <4.0 mm total length), large midges (Chironomidae  $\geq$ 4.0 mm total length), and dragonflies for 20 days.

Nutrient addition led to an increase in nutrient concentrations (Fig. 5a, b) and chlorophyll a concentration (a proxy for primary producer biomass, Fig. 5c) in the water column. Nutrient additions increased insect-mediated MeHg flux from small and large midges and dragonflies (Fig. 5d–f) primarily by enhancing biomass of emerging adults (Fig. 5g–i). This experiment suggests that an increase in nutrients can lead to an increase in emerging insect biomass and enhanced flux of MeHg from aquatic to terrestrial ecosystems.

The effects of nutrient additions on MeHg concentrations in emerging adult aquatic insects were inconsistent among taxa. Methyl mercury concentrations in small midges were enhanced by nutrient additions (Fig. 5j), whereas the MeHg concentrations in large midges and dragonflies were not affected by nutrient additions (Fig. 5k, l). An increase in nutrients has been hypothesized to lead to reduced contaminant concentrations in aquatic organisms because an increase in primary production or consumer growth rates without a concomitant increase in contaminant levels could reduce the amount of MeHg available per algal cell or per gram of consumer tissue (i.e., the bloom dilution and somatic growth dilution hypotheses, respectively) (Pickhardt et al. 2002; Karimi et al. 2007, 2010). The predictions of the bloom and growth dilution hypotheses were not supported here nor in some other studies (reviewed in Jones et al. 2013) suggesting that more work is needed to determine the conditions under which bloom and growth dilutions occur.

The presence of fish led to a decrease in insect-mediated MeHg flux from small and large midges and dragonflies (d–f), primarily by reducing biomass of emerging adults (Fig. 5g–i). In this study, all insects were suppressed, not just the largest taxa like in Tweedy et al. (2013). Fish suppression of small midges in this study and not Tweedy et al. (2013) may have occurred because the fish species differed between studies. Alternatively, the fiberglass mesocosms used in this study were less environmentally complex than the experimental ponds used in Tweedy et al. (2013) which contained abundant macrophytes that provided a refuge from predation. The effects of nutrient additions and fish presence were interdependent such that the effects of nutrients on insect-mediated MeHg flux were more pronounced when fish were absent, and the effects of fish on insect-mediated MeHg flux were more pronounced when nutrient concentrations were high (Fig. 5d–f).





**Fig. 5** Two-way interaction plots illustrating the main effects of nutrient additions (nutrients) and fish presence (fish) and their interaction effect (N x F) on (a–c) water quality, (d–f) emerging insect MeHg flux, (g–i) emerging insect biomass, and (j–l) emerging insect MeHg concentration in experimental mesocosms. Water samples were collected twice a month throughout the experiment after nutrient additions began. Values for water quality represent the treatment combination average (± S.E.) of four sampling dates (a–c). Values for MeHg flux and MeHg concentration represent the treatment combination average (± S.E.) collected during 20 days (g–i). MeHg concentrations were not determined in dragonflies from tanks with fish because fish completely eliminated dragonfly emergence (l). Copyright 2013 Wiley. Used with permission from Jones et al. (2013)

### 3.3 *Drying Disturbance, Pond Permanence, and Seasonality of Insect Emergence*

Drying disturbance is a key ecological factor affecting the community structure of small ponds (Batzer and Wissinger 1996; Wellborn et al. 1996). Small ponds (0.005–1 ha) exist across a permanence gradient from permanent (that do not dry and often contain fish) to semi-permanent (that dry periodically and therefore usually do not contain fish) (Chumchal and Drenner 2015; Chumchal et al. 2016). Because pond permanence determines if fish are present or absent, and fish presence suppresses emergence of large-bodied adult aquatic insects, permanence may control insect-mediated MeHg flux.

Although insect emergence and associated insect-mediated MeHg flux from permanent ponds is not interrupted by drying disturbances, insect-mediated MeHg flux in semi-permanent ponds ceases during drying disturbances. Insect-mediated MeHg flux in semi-permanent ponds restarts after ponds refill with water and are recolonized by aquatic insects (Batzer and Wissinger 1996). We hypothesized that as insect populations reestablished in recently refilled semi-permanent fishless ponds, insect-mediated MeHg flux would recover and eventually reach higher levels in semi-permanent fishless ponds than permanent fish ponds. We also hypothesized that the effects of pond permanence on insect-mediated MeHg flux were dependent on season because insect development is regulated by temperature, photoperiod, and food availability, all of which vary seasonally (Corbet 1980). Specifically, we expected that insect-mediated MeHg flux would be lower in winter than in summer.

To test the two hypotheses above, we conducted a two-phase experiment in ten experimental ponds near Fort Worth, Texas, USA (Fig. 2a, b) (Chumchal et al. 2017; Williams et al. 2017). In spring 2013, we filled ten dry ponds with water and stocked them with bluegill. On April 1, 2014, five of the ten ponds were drained and fish removed to simulate drying disturbance. The five dried ponds were refilled with water on May 13, 2014, to simulate semi-permanent ponds without fish. After drying disturbance and refilling of semi-permanent ponds, aquatic insect communities were reestablished by recruitment of insect populations from eggs deposited by aerially colonizing adults that migrated from nearby waterbodies (Chumchal et al. 2017). Phase I of the experiment focused on recovery of insect-mediated MeHg flux immediately after the drying disturbance and refilling of semi-permanent ponds (Chumchal et al. 2017). In phase II of the experiment, we examined the seasonality of insect-mediated MeHg flux from permanent fish ponds and semi-permanent fishless ponds from winter through summer 2015 (Williams et al. 2017). Phase II began 8 months after the semi-permanent ponds were refilled.

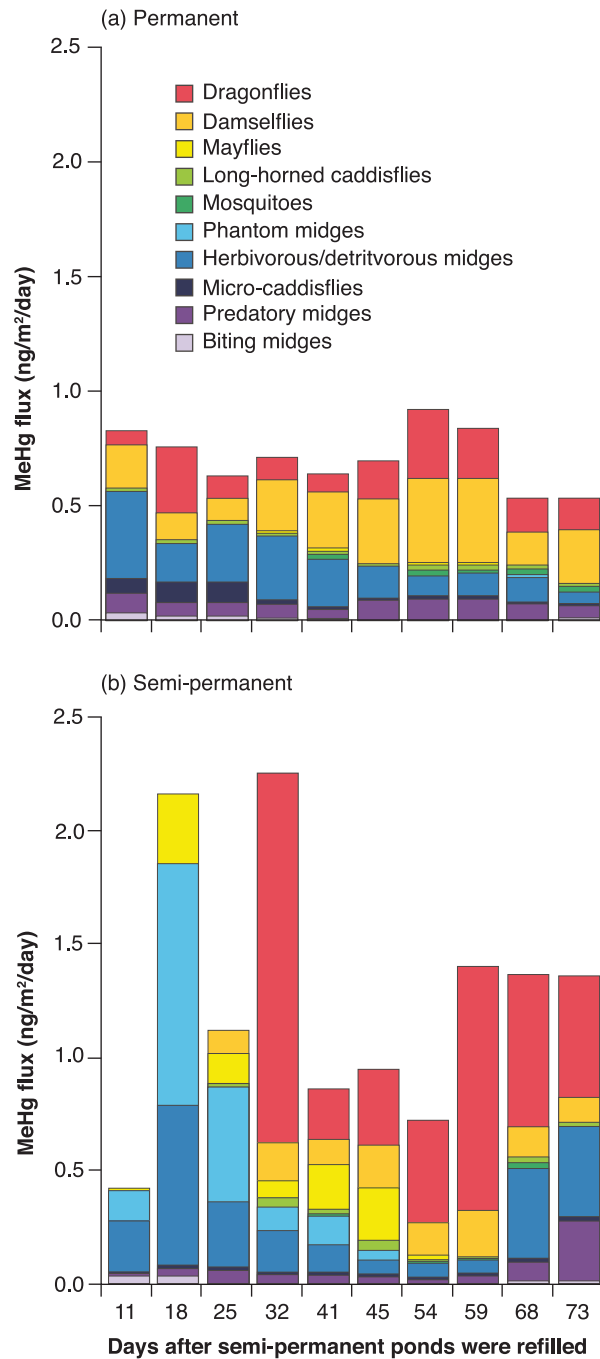
*Phase I: Recovery of insect-mediated MeHg flux in semi-permanent ponds after a drying disturbance.* In phase I, we used floating emergence traps (Fig. 2c) to collect emerging insects. We collected emerging insects over a 73-day period that began immediately after ponds were refilled. During the 73-day period after semi-permanent ponds were refilled, aggregate MeHg flux from semi-permanent ponds was greater than aggregate MeHg flux from permanent ponds (although the

difference was not statistically significant), indicating that insect-mediated MeHg flux had rapidly recovered in semi-permanent ponds following drying disturbance (Fig. 6a, b). The taxonomic composition of insect-mediated MeHg flux was relatively consistent in permanent ponds throughout the experiment (Fig. 6a) but changed in semi-permanent ponds as the insect communities underwent succession after refilling (Fig. 6b). In the permanent ponds, both small and large taxa (e.g., midges and dragonflies, respectively) contributed to the MeHg flux during the 10-week experiment (Fig. 6a). In semi-permanent ponds, we detected MeHg flux from the eight smallest insect taxa 11 days after refilling (Fig. 6b). The three largest taxa (mayflies, damselflies, and dragonflies) did not emerge and contribute to the MeHg flux from semi-permanent ponds until days 18, 25, and 32, respectively (Fig. 6b). This phase of the study demonstrated the potential for rapid recovery of insect-mediated MeHg flux following drying disturbance. The rapid rate of recovery of insect-mediated MeHg flux following drying disturbance in our study was likely due to the proximity of our experimental ponds to nearby permanent waterbodies that served as sources of adult aerially colonizing insects (Niemi et al. 1990) and warm water temperatures (mean = 27.8 °C in this experiment) that facilitated insect growth and development (Corbet 1980; Gillooly and Dodson 2000).

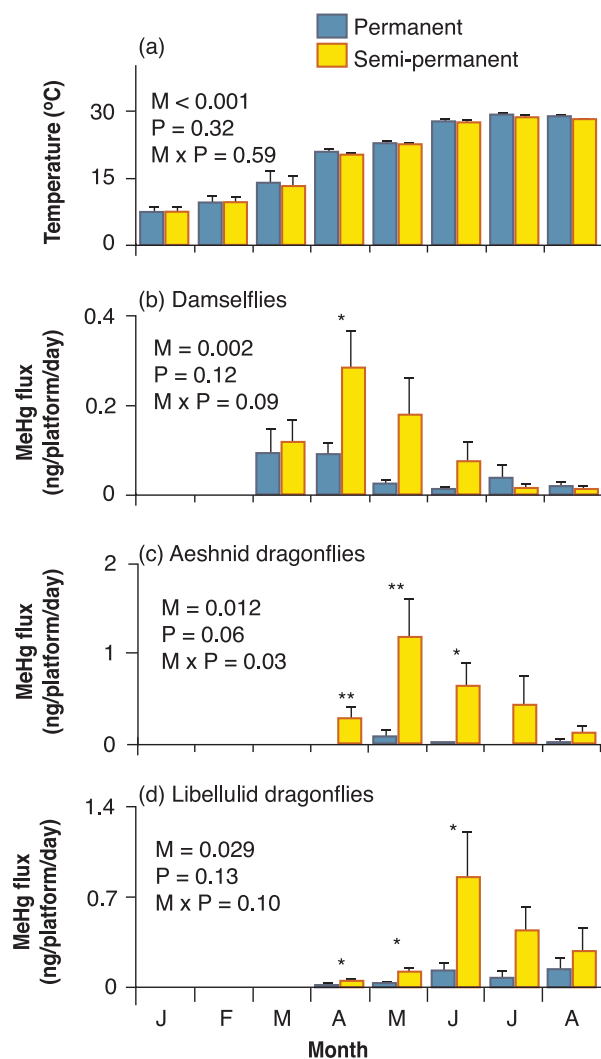
*Phase II: Seasonality of insect-mediated MeHg flux from permanent fish ponds and semi-permanent fishless ponds.* In phase II of the experiment, we examined the seasonality of insect-mediated MeHg flux from permanent fish ponds and semi-permanent fishless ponds from winter through summer 2015, beginning 8 months after the semi-permanent ponds were refilled. Because odonates (dragonflies and damselflies) dominated the flux during phase I, we focused on odonate-mediated MeHg flux during phase II. Odonate emergence was monitored with emergence platforms (Fig. 2d), and water temperature data were collected using temperature loggers.

During the experiment, temperature and odonate-mediated MeHg flux varied with month (Fig. 7). Temperature increased from winter to summer in permanent and semi-permanent ponds (Fig. 7a). Odonate-mediated MeHg flux was first detected for damselflies (Fig. 7b) in March and for aeshnid and libellulid dragonflies in April (Fig. 7c–d). Peak MeHg flux from damselflies, aeshnid dragonflies, and libellulid dragonflies occurred in April, May, and June, respectively. Methyl mercury flux from aeshnid dragonflies was suppressed in permanent ponds with fish.

These seasonal patterns in MeHg flux were caused by changes in emerging odonate biomass over time and not MeHg concentrations (Williams et al. 2017). This phase of the study demonstrated that at the warm temperate latitude where the study occurred (32°N), odonate-mediated MeHg flux is regulated by the interaction of season and pond permanence. Season is an important factor regulating MeHg flux because odonate-mediated MeHg flux does not occur during cold seasons. For all three taxa, most odonate-mediated MeHg flux occurred primarily in the spring and early summer. During periods of insect emergence, MeHg flux was affected by pond permanence and fish such that semi-permanent ponds without fish had higher MeHg flux than permanent ponds with fish.



**Fig. 6** Average MeHg flux (ng/m<sup>2</sup>/d) for ten emerging insect taxa collected on ten sampling dates from (a) permanent and (b) semi-permanent ponds following drying disturbance. In the legend, taxa are listed in order of body length, from largest to smallest. Copyright (2017) Wiley. Used with permission from Chumchal et al. (2017)



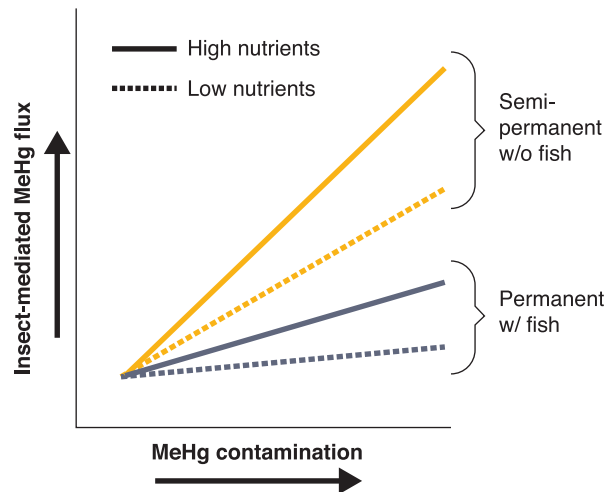
**Fig. 7** (a) Average ( $\pm$  S.E.) monthly water temperature and (b) damselfly-, (c) aeshnid dragonfly-, and (d) libellulid dragonfly-mediated MeHg flux in permanent and semi-permanent ponds.  $P$ -values from repeated measure ANOVAs examining the main effects of month (M), pond permanence (P), and the month  $\times$  pond permanence interaction (M  $\times$  P) are shown on each panel. When a significant month  $\times$  pond permanence interaction was detected, we tested for simple effects of pond permanence in a given month. The symbols \*\* and \* represent a significant simple effect between semi-permanent and permanent ponds equivalent to  $p \leq 0.05$  and  $p \leq 0.10$ , respectively. Copyright 2017 Wiley. Used with permission from Williams et al. (2017)

## 4 Conceptual Model

Based on the results of our experiments, we developed a conceptual model of the influence of MeHg contamination and ecological factors on insect-mediated MeHg flux. In the model (overviewed below), we propose that the potential for insect-mediated MeHg flux increases with the level of MeHg contamination of the ecosystem but that the realized MeHg flux is determined by ecological factors such as pond permanence, fish presence, nutrient levels, and trophic state (Fig. 8).

**Methyl Mercury Contamination of Ecosystems** The potential for insect-mediated MeHg flux is set by Hg contamination of the ecosystem (Tweedy et al. 2013; Fig. 8). Our model predicts that insects from more contaminated sites will have higher concentrations of MeHg and therefore have the potential to transport more MeHg per unit of insect biomass to terrestrial ecosystems. The model would not apply to ecosystems with MeHg contamination levels high enough to be toxic to insects.

**Pond Permanence and Fish Presence** Pond permanence regulates insect-mediated MeHg flux by determining the presence and absence of insectivorous fish (Chumchal and Drenner 2015). Our model predicts that systems without fish will have higher insect-mediated MeHg flux relative to those with fish and that the suppression of MeHg flux by fish will be greater in high-nutrient than low-nutrient systems (Fig. 8).



**Fig. 8** Conceptual model of the influence of MeHg contamination of ecosystems and ecological factors regulating emerging insect biomass on insect-mediated MeHg flux. The potential for insect-mediated MeHg flux increases with MeHg contamination of the ecosystem but the realized MeHg flux is determined by ecological factors. Semi-permanent ponds without fish have higher insect-mediated MeHg flux than permanent ponds with fish. High-nutrient ponds have higher insect-mediated MeHg flux than low-nutrient ponds. This model applies during seasons when insects are emerging

This model is based on the results of our experiments conducted with large-bodied centrarchids that are ubiquitous and abundant in the Southern United States. These fish have large mouth gapes that allow them to consume large insects such as dragonflies. Small-bodied fish with smaller gapes (e.g., three-spined stickleback [*Gasterosteus aculeatus*]) might not have the same effect on large-bodied insects and instead could suppress insect-mediated MeHg flux from smaller taxa (Greig et al. 2012). Although, in our region (the southern Great Plains of the United States), drying is the primary disturbance that creates fishless lentic systems, other disturbances (e.g., winterkill) that eliminate fish may impact insect-mediated MeHg flux in other regions (Wellborn et al. 1996).

**Nutrient Levels and Trophic State** Nutrients regulate insect-mediated MeHg flux by enhancing emerging insect biomass (Fig. 8). Our model predicts that systems with high concentrations of nutrients will have elevated insect-mediated MeHg flux. The enhancement of insect-mediated MeHg flux by nutrients will be greater in semi-permanent ponds without fish than in permanent ponds with fish. This model was developed based on the results from our experiments conducted in oligomesotrophic and eutrophic systems (Jones et al. 2013) and may not apply to hyper-eutrophic systems that experience anoxia and fish kills.

## 5 Conclusions

Almost 20 years ago, Chapman (2002) suggested that “ecological understanding must be integrated into toxicology for a better, more coherent whole.” Our community-level experiments demonstrate how concepts such as the “dark side” of aquatic insect subsidies can be more fully understood by integrating the fields of toxicology and ecology. Although the integration of the fields of ecology and toxicology is just beginning (e.g., Chumchal and Drenner 2015; Schiesari et al. 2018), it has great potential to further our understanding of environmental contamination.

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