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Comparing nearshore benthic and pelagic prey as mercury sources to lake fish: the importance of prey quality and mercury content

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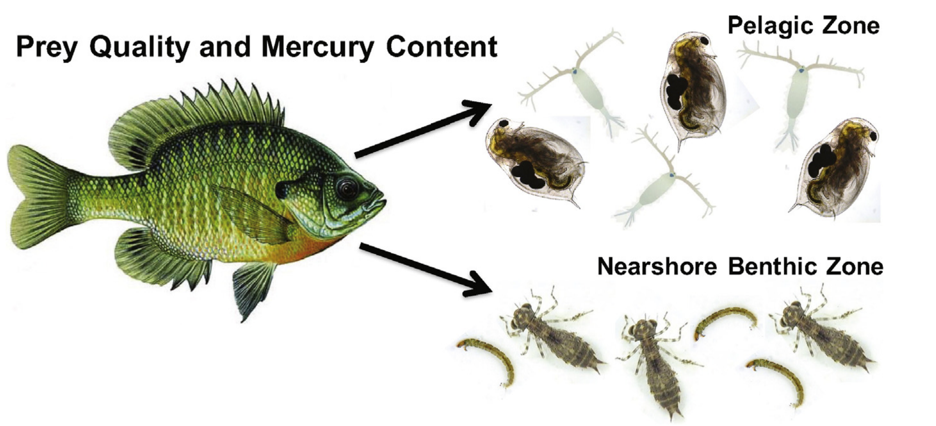
HIGHLIGHTS

- We examined habitat-specific feeding and Hg accumulation in lake fish.
- Zooplankton had higher Hg content than many benthic prey.
- Literature analysis shows lower Hg content in fish associated with benthivory.
- Model shows role of lower Hg, higher calories, growth dilution from benthivory.
- Growth dilution is important to understand habitat-specific Hg accumulation.

GRAPHICAL ABSTRACT



Bluegill image © courtesy of Joe Tomelleri.

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ABSTRACT

Mercury (Hg) bioaccumulation in fish poses well-known health risks to wildlife and humans through fish consumption. Yet fish Hg concentrations are highly variable, and key factors driving this variability remain unclear. One little studied source of variation is the influence of habitat-specific feeding on Hg accumulation in lake fish. However, this is likely important because most lake fish feed in multiple habitats during their lives, and the Hg and caloric content of prey from different habitats can differ. This study used a three-pronged approach to investigate the extent to which habitat-specific prey determine differences in Hg bioaccumulation in fish. This study first compared Hg concentrations in common nearshore benthic invertebrates and pelagic zooplankton across five lakes and over the summer season in one lake, and found that pelagic zooplankton generally had higher Hg concentrations than most benthic taxa across lakes, and over a season in one lake. Second, using a bioenergetics model, the effects of prey caloric content from habitat-specific diets on fish growth and Hg accumulation were calculated. This model predicted that the consumption of benthic prey results in lower fish Hg concentrations due to higher prey caloric content and growth dilution (high weight gain relative to Hg from food), in addition to lower prey Hg levels. Third, using data from the literature, links between fish Hg content and the degree of benthivory, were examined, and showed that benthivory was associated with reduced Hg concentrations in lake fish. Taken together, these findings support the hypothesis that higher Hg content and lower caloric content

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make pelagic zooplankton prey greater sources of Hg for fish than nearshore benthic prey in lakes. Hence, habitat-specific foraging is likely to be a strong driver of variation in Hg levels within and between fish species.

1. Introduction

In order to minimize mercury (Hg) exposure risks to humans and fish-consuming wildlife, there is a need to continue to refine and improve predictions of Hg concentrations in fish. Human consumption of fish is increasing worldwide (Fisheries and Agriculture Organization of the United Nations (FAO), 2014), and continues to be a primary source of Hg exposure to wildlife and humans (UNEP, 2003). Mercury exposure and its concomitant health risks are difficult to manage because fish Hg concentrations are highly variable, even within a species (Karimi et al., 2012; Sunderland, 2007). Fish obtain Hg from their diet (Hall et al., 1997), with Hg concentrations in fish prey, as well as bioenergetic factors such as fish growth and metabolism, known to influence fish Hg concentrations (Essington and Houser, 2003; Schindler et al., 1995; Trudel and Rasmussen, 2006; Ward et al., 2010).

To refine our understanding and improve predictions of fish Hg concentrations within and across systems, it is necessary to continue to identify and examine unexplored sources of Hg to fish. One potential source of variation that is not well understood is the effect of fish foraging in different habitats, where prey Hg and fish bioenergetic rates can differ widely. Many lake fish species consume invertebrate prey from both pelagic and nearshore benthic (shallow sediments and macrophytes along the shoreline) habitats for at least part of their lives (Schindler and Scheuerell, 2002; VanderZanden and Vadeboncoeur, 2002). For example, young-of-year largemouth bass (Hodgson et al., 1993; Post, 2003) and yellow perch of 1–3 years (Prout et al., 1990; Wu and Culver, 1992) eat both benthic and pelagic invertebrates (zooplankton) before switching to piscivory (Pelham et al., 2001; Post, 2003; Schindler et al., 1997a). Similarly, bluegill sunfish consume zooplankton as young-of-year, switch to benthic invertebrates as juveniles, then consume zooplankton as adults (Mittelbach and Osenberg, 1993; Osenberg et al., 1992; Werner and Hall, 1988). These cross-habitat diet shifts can occur on relatively short timescales, such as intermittently throughout the summer (Mittelbach, 1981) or on a diel basis (Baumann and Kitchell, 1974; Keast and Welsh, 1968). Further, piscivorous fish indirectly consume both benthic and pelagic prey by consuming forage fish. Evidence suggests that comparable amounts of benthic and pelagic-derived carbon are transferred to top predators. For instance, Vadeboncoeur et al. (2002) showed that an average of 65% of the diet of numerous forage and piscivorous fish species comes from benthic sources due to direct and indirect consumption. Clearly, cross-habitat prey consumption is neither rare nor insignificant. Therefore, the relative importance of benthic and pelagic sources of Hg to fish must be quantified to understand and predict patterns of Hg accumulation in lake fish.

Studies have begun to measure concentrations of Hg in nearshore benthic and pelagic prey as sources to fish in freshwater (Back et al., 2003; Chetelat et al., 2011; Gorski et al., 2003) and marine (Chen et al., 2014; Chen et al., 2009) ecosystems. These studies provide crucial information to understand Hg patterns in lower trophic level organisms that are key sources of Hg into the food web (Cleckner et al., 1999; Folt et al., 2002). However, existing evidence regarding the relative importance of freshwater zooplankton and benthic invertebrates as sources of Hg to lake fish is sparse and contradictory. Two studies suggest that while some benthic invertebrates have lower Hg concentrations than zooplankton (Back et al., 2003; Gorski et al., 2003), predacious water scorpions and notonectids have the highest Hg concentrations among all invertebrates, consistent with higher Hg in predators due to biomagnification. Among zooplankton, cladocerans have significantly higher Hg concentrations than copepods (Back and Watras, 1995; Pickhardt et al., 2002; Pickhardt et al., 2005; Watras et al., 1998).

Patterns of Hg concentrations among fish provide indirect evidence that in general, pelagic prey may be more important sources of Hg to fish than benthic prey. Gorski et al. (2003) found higher Hg concentrations in fish (adult pike and large adult yellow perch) in a lake with a pelagic-based food web compared to a lake with a more benthic-based food web, even when fish trophic level, size and age were similar between lakes. Similarly, studies show that benthivorous lake fish have lower Hg concentrations than pelagic-feeding lake fish (Becker and Bigham, 1995; Kidd et al., 2003; Power et al., 2002; Willacker et al., 2013). Studies of estuarine and marine systems also found greater biomagnification of Hg (indicated by a higher slope of the Hg-δ^{15}N relationship) in pelagic compared to benthic food chains (Lavoie et al., 2010), and that a higher degree of pelagic feeding (determined from δ^{13}C) is associated with higher Hg concentrations in fish and shellfish (Chen et al., 2014; Chen et al., 2009; Karimi et al., 2013). Overall, these findings are consistent with higher Hg concentrations in zooplankton and other pelagic prey. Yet, there are numerous exceptions to this pattern. For example, one study found similar methylmercury (MeHg) concentrations among zooplankton and benthic invertebrates (Wyn et al., 2009). Also, benthic prey can be relatively more important Hg sources in contaminated (Eagles-Smith et al., 2008a; Eagles-Smith et al., 2008b) or shallow (Chumchal et al., 2008) lakes. Differences in relative Hg concentrations between benthic and pelagic invertebrates among studies likely depend on the taxa collected, and the sources of Hg to habitat-specific prey (e.g., concentrations of bioavailable Hg from sediments, consumption of detrital material versus periphyton or algae). Mercury concentrations for a given taxon can be highly variable (Tremblay et al., 1996), further complicating our ability to make general comparisons of Hg concentrations in lower trophic level taxa across ecosystems. Currently, there are insufficient data to assess the generality of these patterns across lake ecosystems, and compare the overall importance of benthic and pelagic invertebrates as sources of Hg to fish.

Past Hg studies also have not examined the potential influence of differences in benthic and pelagic prey quality on fish growth and subsequent somatic growth dilution of Hg (Karimi et al., 2007; Ward et al., 2010). Past research showed that rapid, efficient growth can reduce Hg concentrations in the body by decreasing the amount of Hg obtained from food relative to weight gain (Karimi et al., 2007; Karimi et al., 2010). This process of somatic growth dilution is hypothesized to be particularly important for MeHg, the organic, dominant form found in fish (Watras and Bloom, 1992), and other contaminants with low rates of efflux (excretion) that tend to persist in the body and biomagnify through the food chain (Karimi et al., 2010; Reinfelder et al., 1998). Among the factors that influence fish growth, those that most strongly increase growth efficiency (weight gain relative to consumption, and Hg intake) are more likely to result in somatic growth dilution (Karimi et al., 2007; Karimi et al., 2010; Trudel and Rasmussen, 2006). Such factors include prey quality (caloric content, digestibility), and fish activity level (including energy expended to capture and consume prey), with higher prey quality and lower fish activity level hypothesized to increase somatic growth dilution (Trudel and Rasmussen, 2006). Despite the growing recognition of the influence of growth dilution on Hg bioaccumulation, the relative importance of differences in fish growth from habitat-specific diets on fish Hg content is unknown.

The overarching goal of this study was to compare nearshore benthic versus pelagic prey as sources of Hg to fish based on differences in prey Hg content and caloric content using three different approaches. The