

Methylmercury in Marine Ecosystems: Spatial Patterns and Processes of Production, Bioaccumulation, and Biomagnification

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Abstract

The spatial variation of MeHg production, bioaccumulation and biomagnification in marine food webs is poorly characterized but critical to understanding the links between sources and higher trophic levels such as fish that are ultimately vectors of human and wildlife exposure. This paper discusses both large and local scale processes controlling Hg supply, methylation, bioaccumulation and transfer in marine ecosystems. While global estimates of Hg supply suggest important open ocean reservoirs of MeHg, only coastal processes and food webs are known sources of MeHg production, bioaccumulation, and bioadvection. The patterns observed to date suggest that not all sources and biotic receptors are spatially linked and that physical and ecological processes are important in transferring MeHg from source regions to bioaccumulation in marine food webs and from lower to higher trophic levels.

Key words: methylmercury, bioaccumulation, trophic transfer, biomagnification, bioadvection

Introduction

Mercury (Hg) is a pervasive and toxic environmental contaminant (U.S. EPA, 1997). Human exposure to Hg occurs primarily through the consumption of marine fish (Fitzgerald and Clarkson, 1991; U.S. EPA, 2002). The organic form of Hg, methylmercury (MeHg), is of greatest concern because it is a potent neurotoxin (Salonen et al., 1995; Grandjean et al., 1997; Sorensen et al., 1999) and because it accounts for > 95% of the Hg in fish (Bloom, 1992; Bank et al., 2007; Sunderland, 2007). Fish are commercially harvested from all over the globe including ecosystems distant from major anthropogenic sources of Hg pollution. This raises important scientific and policy questions regarding these sources of MeHg in the fish and shellfish (Chen et al., 2008).

Biogeochemical, physical, and ecological processes govern the distribution and movement of MeHg from source regions to bioaccumulation in marine food webs. There is great spatial variability in the concentrations of Hg across ocean basins (Lamborg et al., 2002; Hammerschmidt and Fitzgerald, 2004; Laurier et al., 2004; Sunderland and Mason 2008) and in the distribution of biogeochemical conditions favoring Hg methylation. However, the MeHg concentrations found in commercially harvested fish are an integration of feeding in deep and shallow waters across inshore and offshore habitats (Block et al., 2005; Hammerschmidt and Fitzgerald, 2006b). Moreover, commercially harvested fish come from all regions of the world making it particularly difficult to link human exposure to specific fisheries and sources of MeHg (Sunderland, 2007). Given its importance to human and environmental health, it is critical to understand the spatial distribution of MeHg production and fate in marine ecosystems.

The objective of this paper is to consider spatial patterns and mechanistic processes of MeHg production, bioaccumulation, and biomagnification across marine ecosystems from estuarine to coastal to open ocean. We discuss: 1) estimates of global sources and sinks of MeHg; 2) processes controlling Hg methylation, bioaccumulation, and transfer from estuaries to the continental shelf; and 2) latitudinal patterns of Hg bioaccumulation and biomagnification in marine food webs.

Scaling Global Sources and Fluxes of MeHg

On a global scale, the majority of methylated Hg found in the ocean is formed within the system from available inorganic Hg(II). Methylated Hg (both mono- and dimethyl- forms) represents a small percentage of total Hg in external sources including precipitation (<0.2% in coastal/open ocean; Bloom and Watras, 1989; Mason et al., 1992; Mason et al., 1997; Holz et al., 1999; Lamborg et al., 1999) and riverwater (ca. 2%; Coquery et al., 1997; Balogh et al., 1998; Benoit et al., 1998; Hurley et al., 1998; Choe and Gill, 2003; Balcom et al., 2004). When combined with estimates for the global precipitation and riverine flux of total Hg (THg; e.g., Mason et al., 1994; Cossa et al., 1996), these percentages suggest a total external flux of <0.04 Mmole MeHg y⁻¹.

External inputs of MeHg are not enough to account for our estimates of the pool of MeHg in phytoplankton in the world's oceans, thus internal sources of MeHg must dominate. For example, phytoplankton (as represented by oceanic suspended particulate matter) has been measured to contain about 6 ng MeHg g⁻¹ C (Topping and Davies, 1981; Mason and Fitzgerald, 1991). As global primary production is 43.5 Pg C y⁻¹ (Behrenfeld and Falkowski, 1997), it appears that at least 1.3 Mmoles y⁻¹ of MeHg must be supplied to the phytoplankton pool to

explain the concentrations observed. This suggests that methylation of Hg within the ocean must exceed external sources by >30 fold and dominate as a source of MeHg in the ocean.

In the rest of this section, we consider internal sources of MeHg and ask whether any one particular biogeochemical process or source region may lead to more MeHg production or bioaccumulation on a global scale than another. The potential sources considered here include: 1) methylation in marine sediments 2) methylation in or near submarine hydrothermal systems and 3) methylation in the pelagic water column. A summary of these estimated flux strengths and the approach used to make them is shown in Table 1. The flux of MeHg from sediments is estimated to be 8% of the total Hg load (Fitzgerald et al., 2007), estimated in different ways for the various ocean locations. For example, coastal total Hg loadings were taken to be similar in areal flux as that occurring in Long Island Sound or Chesapeake Bay ($\sim 0.3 \mu\text{mole Hg m}^{-2} \text{ y}^{-1}$; Mason et al., 1999; Balcom, et al., 2004), and applied to an area equivalent to 1% of total ocean area. The continental shelf/slope region was recently studied by Hammerschmidt and Fitzgerald (2006a) where they determined an average total Hg concentration in shelf sediments to be $0.1 \text{ nmole Hg gdw}^{-1}$, which may then be scaled up by assuming sedimentation rates of $480 \text{ g m}^{-2} \text{ y}^{-1}$ (Bothner et al., 1981) and shelf/slope (<1000 m depth) area of 12% of total ocean area ($0.24 \text{ Mmole y}^{-1}$). For deep-sea contributions, the 8% rule was applied to a total Hg load of 2 Mmole y^{-1} , estimated in a global model (Lamborg et al., 2002). The methylation of Hg associated with seawater circulation in submarine hydrothermal systems was estimated by multiplying measured fluid concentrations by estimates of water circulation (Elderfield and Schultz, 1996; Lamborg et al., 2006), suggesting an upper estimate of 0.4 Mmole y^{-1} . This is an upper end estimate because the highest rate of water circulation (1 Sv) was used, and the true flow is likely to be much less. Finally, the

rate of methylation within the oceanic water column was estimated by requiring that it balance the other sources of MeHg to the upper ocean (from shallow sediments, primarily) and the loss of MeHg in sinking particle fluxes, estimated by applying the ratio of MeHg to THg in particles to the modeled THg flux of 9 Mmole y^{-1} (Topping and Davies, 1981; Mason and Fitzgerald, 1991; Lamborg, et al., 2002).

To the first order, the various estimates suggest that the internal sources of MeHg production are of roughly comparable size, and that combined they provide about the right amount of this species to balance the annual biological uptake rates. It is likely, however, that they are not equivalent in the fraction of the flux that is anthropogenically mobilized, with the shallower water pools containing a larger percentage of “pollution” Hg (e.g., Lamborg et al., 2002; Kraepiel et al., 2003; Sunderland and Mason, 2007). Moreover, each of these sources, although incompletely understood at present, will have different bioaccumulation and food web pathways to various fish species. For example, although deep-sea sources of MeHg to the ocean could be significant (ca. 0.2 Mmole y^{-1}), extremely low biomass and densities of marine organisms in the deep oceans and limited vertical migration of deep-sea biota and slow rates of vertical water mixing reduces the likelihood of significant MeHg transfer to shallower food webs (e.g., Fitzgerald et al., 2007). Kraepiel and colleagues (2003) suggested, however, that deep-sea sources of MeHg determined bioaccumulation rates in the surface based on a time trend analysis of Hg content in tuna, but temporal data needed to rigorously test their hypothesis is lacking. It appears more likely that water column and shallow sediment sources supply most of the MeHg accumulating in fisheries.

Processes Controlling MeHg Production, Bioaccumulation, and Trophic Transfer

Hg Transformation in Coastal Sediments. Estuarine and coastal sediments are repositories for Hg where substantial external inputs from direct atmospheric deposition and riverine input are deposited and recycled (Stordal et al., 1996; Turner et al., 2001; Laurier et al., 2003; Balcom et al., 2004). Here, the methylation of Hg is dependent on the physical regime of the estuary and the sediment (e.g., degree of bioturbation, hydrodynamics at the sediment water interface: SWI), sediment chemistry (e.g., organic matter (OM) content, iron content, sulfate and sulfide concentration), and the movement of Hg from sediments to biotic receptors through physiochemical, physiological, and ecological processes. The biogeochemical factors in sediments greatly influence the transformation of inorganic Hg to MeHg that, in turn, determines its potential for bioaccumulation and biomagnification in food webs.

Estuarine and coastal sediments are areas of high MeHg production due to *in situ* biogeochemical conditions including high organic matter and sulfate. Microbial processes including sulfate reduction utilize these substrates to produce high concentrations of MeHg if conditions are optimal. Of the factors that are likely to control sediment MeHg and methylation rates are the inorganic Hg loading to the sediment as well as the geochemical factors that influence the availability of the inorganic Hg, and the supply of OM to sulfate-reducing bacteria. Moreover, the great spatial and temporal variation in estuarine biogeochemistry also results in areas of high MeHg production, release and bioaccumulation. These coastal sediments are also subject to significant fluctuations in water level and salinity that result in redox transitions in the zone close to the SWI.

MeHg can be transferred from surface sediments to the water column via passive diffusion, advection, and resuspension (Bloom et al., 1999). Efflux into the water column may be controlled by the location of the redoxcline (Merritt and Amirbahman, 2008). For example, oxic or suboxic surface sediments may impede direct MeHg release into the water column (Gagnon et al., 1996, Bloom et al., 1999). This may be a consequence of sorption to certain surface sediments, especially Fe-oxyhydroxides, or increased rates of MeHg demethylation close to the SWI (Merritt and Amirbahman, 2008). The location of the redoxcline, in turn, is controlled by factors such as OM content, sediment physical mixing by the benthic infauna, rate of microbial respiration, and hydrodynamics at the SWI. Lambertsson and Nilsson (2006) observed the highest MeHg concentration in sediments with the highest OM content, and a progressive upward movement of MeHg production maxima with increasing sediment OM.

The abundance of benthic infauna may influence MeHg cycling rates and concentration. At high bioturbation rates, the introduction of oxidants, such as O₂ and Fe(III), deepens the sediment redoxcline (Aller, 1978, 1994; Hines et al., 1999) and this may influence porewater MeHg concentration. Burrowing macrofauna also leads to bioirrigation that may enhance sulfate transport and oxidizing conditions (Furukawa et al., 2000) thereby affecting MeHg production rates. Recently, Benoit et al. (2006) suggested that in the presence of a high burrow density, oxidizing conditions may extend deeper in the sediment and result in a lower sediment methylation rate. They also proposed that intermediate burrow densities (~500 burrows m⁻²) may provide optimum conditions for the enhancement of methylation by preventing the buildup of significant dissolved S(-II). In addition to influencing the direct transfer of MeHg to the

overlying water, benthic fauna also may be important in biotransfer of MeHg to hyperbenthic organisms and on to pelagic food webs, as discussed later.

Complex interactions among physical, chemical and biological factors in the coastal zones contribute to the variation in MeHg production from inorganic Hg at the local scale (patchiness). These zones are sites of significant sedimentation of river-borne particulate matter, and as a result, act as storage areas for sediment contaminants including Hg. Areas within the coastal zone that have sediments with small grain size, high OM content, and shallow redoxcline may lead to levels of MeHg production, release and bioaccumulation. In contrast, areas within coastal zones that are subaerially exposed at times, and in the areas where a relatively high water velocity occurs, the coarse sediment grain size and a low OM content results in a relatively deep oxic/suboxic environment. In these regions, net MeHg production may be diminished and MeHg release and bioaccumulation may be suppressed by enhanced adsorption and demethylation. This local scale spatial heterogeneity in MeHg production and concentration likely affects flux of MeHg to the water column and bioaccumulation by benthic and pelagic organisms.

MeHg Bioaccumulation at the Base of the Food Web. Hg methylation in the pelagic zone is also a potentially important source for MeHg bioaccumulation. In the water column it is readily concentrated by phytoplankton the biological conduit for transferring the contaminant to pelagic and benthic food webs (Lindqvist et al., 1991; Watras and Bloom, 1992; Mason et al. 1996). Concentration factors of MeHg from water to aquatic organisms are overwhelmingly largest in phytoplankton, where values can be $>10^5$, compared to subsequent increases to higher trophic levels of only 2-3 times (Baeyens et al., 2003; Hammerschmidt and Fitzgerald 2006b; Pickhardt

and Fisher, 2007; IAEA, 2004). Bioconcentration factors in phytoplankton can vary up to six orders of magnitude between different metals but generally less than one order of magnitude for a given metal across taxa (Fisher, 1986; Fisher and Reinfelder, 1995). Temporal or spatial variations in MeHg bioconcentration in phytoplankton could be transferred to higher trophic levels, although relatively few field measurements have been made, so it is important to examine those factors likely to influence its bioaccumulation in phytoplankton.

It is important to understand the mechanisms underlying MeHg uptake in phytoplankton in order to understand geographic and seasonal variability in contamination of marine food chains. There is evidence for both passive and active uptake of Hg and MeHg by phytoplankton (Moye et al., 2002; Pickhardt and Fisher, 2007). In San Francisco Bay-Delta waters, Hg and MeHg were enriched about 10^4 times out of ambient water by dead cells but 10^5 times in living cells (Pickhardt and Fisher, 2007). Passive uptake of Hg and MeHg sorbed primarily to cell surfaces is not unlike many other particle-reactive metals (Fisher et al., 1984; Fisher 1985). However the mechanisms for active uptake of MeHg remain unclear. Hg and MeHg could be bound to some organic compounds that are actively acquired by cells (Roditi et al., 2000; Brandt et al., 2008) or act as a surrogate for a compound that is actively taken up. Once taken up, MeHg penetrates more significantly into the cytoplasm of algal cells than inorganic Hg (Pickhardt and Fisher, 2007; Mason et al., 1996) and results in higher herbivore assimilation efficiencies and greater transfer in the food web (Reinfelder and Fisher, 1991).

Variations in dissolved organic matter (DOM) concentration and composition may account for spatial and temporal variations in MeHg bioavailability to phytoplankton. DOM derives from

both autochthonous and allochthonous sources (Fenchel et al., 1998), and such variations are more pronounced in estuarine and coastal waters than in the open ocean (Thurman, 1985; Cauwet 2002), reflecting the more variable biological productivity in coastal systems and input from terrestrial sources. Metals complexed by DOM in natural waters are generally less bioavailable to phytoplankton than free metal ions (Campbell, 1995). Once bound to DOM ionic mercury can undergo photochemical reduction to elemental mercury, which in turn could influence volatilization and bioavailability (Ravichandran, 2004). Ionic Hg in natural waters is primarily bound to organic complexes, often involving multidentate chelation sites (Lamborg et al., 2003; Han and Gill, 2005). Inorganic and MeHg have strong affinities for thiol groups in DOM (Hintelmann et al., 1997; Benoit et al., 2001; Amirbahman et al., 2002; Haitzer et al., 2003; Han et al., 2006). MeHg also displays a strong affinity for natural colloidal matter (1 kDa - 0.45 μm , particularly colloidal material <10 kDa) (Choe and Gill, 2001; Bilinski et al., 2000), mainly with thiol-type functional groups (Guentzel et al., 1996), but the influence of colloidal matter on the bioavailability of MeHg in plankton remains largely unknown.

Because the composition and concentration of DOM (including thiol enriched material) varies seasonally and spatially, its influence on the bioavailability of MeHg should also vary spatially and temporally. Further, for low to moderate DOM concentrations, the relationship of DOM concentration and bioavailability of MeHg to phytoplankton appears variable (Gorski et al., 2008). Until more is known about DOM's influence on the uptake kinetics of MeHg in phytoplankton and the rate of production (e.g., from algal blooms) and decomposition of thiol-rich DOM compounds, it will be difficult to predict how regions will vary with regard to MeHg bioconcentration patterns.

From bioconcentration in primary producers, MeHg is potentially transferred to primary and secondary consumers through several physical and biological processes that have important consequences on the fate of the contaminant in pelagic and benthic trophic pathways. The uptake of MeHg by marine consumers in estuarine and coastal ecosystems can occur directly from sediments or via the water column. For benthic organisms, MeHg can be taken up directly from the bulk sediments or from porewater. In addition, organic matter in sediments reduces the bioavailability of MeHg to benthic fauna due to potential effects on feeding rates, changes in K_d , or changes in the solubilization of MeHg in the gut of deposit feeders (Mason et al., 1999; Lawrence and Mason, 2001; Mason, 2002). MeHg bioconcentrated by phytoplankton is incorporated into the pelagic food web by local zooplankton communities grazing on phytoplankton, and subsequently transferred to resident or transient planktivorous biota (Mathews and Fisher, 2008). Alternatively, through pelagic-benthic coupling, suspension-feeding benthic invertebrates transport MeHg from the water column to the sediment-water interface, making it available to benthic food webs. These sediment MeHg repositories are available to benthic infauna and epifauna (e.g., crustaceans, polychaetes) because of those organisms' direct contact with the substrate and their deposit feeding on detrital matter (Lawrence and Mason, 2001). The relative importance of these two pathways is not known but ongoing studies suggest greater bioaccumulation by pelagic feeding species.

Ecological Transfer of MeHg from Estuaries to the Continental Shelf. Recent investigations suggest that MeHg production in coastal sediments is important to local and potentially offshore biota (Benoit et al., 2003; Hammerschmidt and Fitzgerald, 2006b), however little information

exists on the spatial connectivity between these sources and bioaccumulation by marine food webs that span contiguous ecoscapes: i.e., estuarine, coastal, and open ocean habitats.

Kneib (1997, 2000) defined “nekton trophic relay” as the movement of intertidal carbon production across boundaries within marsh and estuarine ecoscapes. This horizontal bioadvection of energy is mediated by a sequence of predator-prey interactions that actively transport carbon biomass across interconnected habitats. Because of the bioaccumulating properties of MeHg, any trophic transfer of carbon resources likely results in the concomitant bioadvection of MeHg (Fitzgerald et al. 2007). To this end, Kneib’s (1997) conceptual “trophic relay” model provides a framework for describing the spatial connectivity between MeHg sources and a continuum of marine trophic assemblages.

Resident nekton complete their entire life history in the estuary or coastal regions and bioaccumulate MeHg through the passive uptake of contaminants from ambient water, and to a larger extent, through dietary uptake of zooplankton or small benthic invertebrates. Resident nekton also undergo daily migrations between estuaries that include movements between intertidal and subtidal habitats. These regular movement patterns result in the spatiotemporal overlap of resident nekton with larger predatory residents and transient nekton, the latter representing species that seasonally utilize estuaries for foraging, refuge, and reproduction. This sequence of predator-prey interactions effectively translocates MeHg from near-shore sediment repositories to estuarine pelagic food webs, and subsequently exposes higher trophic level coastal and oceanic organisms to MeHg contamination.

Consistent with the “trophic relay” concept, the bioadvection of MeHg from estuaries to coastal and open ocean ecoscapes is contingent upon larger-scale movement patterns by transient nekton. Seasonal migrations and ontogenetic shifts in habitat use by these transient species physically translocates MeHg contaminants to coastal environments. Moreover, these species are subjected to periodic predation pressure from oceanic apex fishes. For example, large epipelagic predators (e.g. porpoises, tuna, billfishes, and sharks) have cosmopolitan distributions owing to their highly migratory behavior. Moreover, these species are opportunistic feeders of schooling fish and cephalopods, and will seasonally utilize coastal habitats during brief foraging events (Collette and Klein-MacPhee, 2002 and references therein). During these seasonal visits, transient apex predators feed on coastal prey and in the process serve as conduits for the bioadvection of MeHg to offshore fisheries. An understanding of these complex migrations, shifts in habitat use, and predator-prey interactions is necessary to determine the relative importance of this ecologically-mediated translocation of MeHg in marine systems.

Spatial Patterns of MeHg Biomagnification in Ocean Food Webs

In studies of aquatic food webs thus far, MeHg bioaccumulated by lower trophic levels biomagnifies with increasing trophic level. However, factors such as geographic differences in Hg emissions, deposition, and the structure of marine food webs in addition to spatial variation in the processes described earlier all influence the fate of MeHg in marine ecosystems. This suggests the hypothesis that there are spatial differences in food web bioamagnification of MeHg. To date, inter-comparison between existing food web studies is problematic because of differences in units used (e.g. dry versus wet weight basis), measurements of whole organisms

vs. specific tissues, and uneven coverage of ecosystems. Therefore, a limited number of studies are available for comparison of trophic transfer across marine systems.

One way to compare biomagnification across food webs is to plot the linear relationships between $\text{Log} (\mu\text{g THg g}^{-1} \text{ wet weight})$ and $\delta^{15}\text{N}$ values: $\text{Log} [\text{THg}] = a\delta^{15}\text{N} + b$ (Kidd et al., 1995) and use the regression slope as a measure of biomagnification rate and the intercept as the baseline value for primary producers. A comprehensive study of a marine arctic food web in Lancaster Sound, Canada, at $\sim 74^{\circ}\text{N}$ examined a food web of 27 species from particulates to mammals that had a slope of 0.2 (Atwell et al., 1998). Nearby, a study of a northern Baffin Bay food web (ice algae to seal) revealed a similar slope of 0.197 and 0.22 for THg and MeHg, respectively (Campbell et al., 2005). The similarity of the slopes for MeHg and THg regressions and the observed increase in the % of MeHg with trophic level suggests that MeHg is the main form of mercury being bioaccumulated. A Gulf of Maine food web including ten size categories of plankton up to whales exhibited regression slopes of 0.14 and 0.23 for THg and MeHg, respectively (Harding et al., unpub.). In contrast, a study focused on upper trophic levels in the Gulf of Farallones, California, (krill to sea lion) had a slightly higher slope of 0.32 (Jarman et al., 1996). Thus, the rates of biomagnification across the above food webs were similar despite the differing food-chain coverage.

While the geographic coverage of Hg food web studies in the world's oceans is not comprehensive, the few available studies permit a limited assessment of spatial variation of bioaccumulated and biomagnified MeHg. For example, in comparing five food chain studies across latitudes between 76°N and 74°S , the concentrations of total Hg in microplankton were

within the same order-of-magnitude (Table 2). This was also true for higher trophic categories of mesoplankton, macroplankton, pelagic, plankton feeding fish, and fish-eating mammals. Sea lion Hg burdens in the Gulf of Farallones are an exception, however, liver concentrations were measured instead of muscle tissue (Campbell et al., 2005). Furthermore, MeHg concentrations in a simplified food chain in Long Island Sound were of the same magnitude as those measured in an arctic food chain (Campbell et al., 2005; Hammerschmidt and Fitzgerald, 2006b).

Based on the comparison of these studies, there is currently no evidence for a latitudinal pattern of Hg bioaccumulation. This is similar to findings in freshwater ecosystems (Campbell et al., 2003). Nor is there a difference between the northern and southern hemispheres despite the anthropogenic enhancement of atmospheric Hg in the northern hemisphere (Mason et al., 1994). However, fully characterizing these patterns will require more detailed site studies and greater geographic coverage of MeHg in marine food webs.

Conclusions

At the local scale, MeHg production and bioaccumulation in coastal and pelagic systems are both strongly influenced by biogeochemical conditions including the concentration and nature of organic matter in sediments and in water. In contrast, trophic transfer and bioadvection of MeHg from estuaries to coastal oceans are largely controlled by ecological factors such as predator-prey interactions and migratory behaviors of different trophic groups. At the global scale, major sources of MeHg production in coastal zones and the deep ocean are not the marine habitats where fish with the highest MeHg concentrations are harvested, nor do food webs in different ocean regions differ greatly in their bioaccumulation and biomagnification despite great spatial

variation in Hg emissions and MeHg production. These patterns all suggest that sources and biological receptors such as pelagic fish species and their human consumers are not related spatially and that physical and ecological processes are important in transferring MeHg from source regions to bioaccumulation in marine food webs. To fully understand the fate of MeHg in the marine environment, these sources and transfer processes need to be identified, quantified, linked, and evaluated with ecosystem models.

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Table 1. Estimates for the MeHg production strength of various regions in the ocean.

Location	Est. MeHg Hg Flux (Mmole y ⁻¹)	Estimation Method	References
Sediments	0.5 ^a	8% of total Hg load	Fitzgerald et al., 2007
<i>Coastal</i>	0.06	~ 1 Mmole y ⁻¹ total Hg loading (1% of ocean area, loadings like Long Island Sound and Chesapeake Bay)	Mason et al., 1999; Balcom, et al., 2004
<i>ShelfSlope</i>	0.2	~ 2 Mmole y ⁻¹ total Hg loading (12% of ocean area, loadings according to references at right)	Hammerschmidt and Fitzgerald 2006a; Fitzgerald et al., 2007
<i>Deep-sea</i>	0.2 ^b	~ 2 Mmole y ⁻¹ total Hg loading	Lamborg, et al., 2002.
Hydrothermal Fluids	<<0.4 ^b	Measured fluid Hg concentrations multiplied by global fluid flow estimates.	Elderfield and Schultz, 1996 Lamborg et al., 2006
Water Column	0.4	Measured particulate Hg concentrations multiplied by global estimates of particle flux	Topping and Davies, 1981 Mason and Fitzgerald, 1991 Lamborg, et al., 2002
Bioaccumulation (for comparison)	0.2 – 1.3	Estimates of fish Hg accumulation as well as phytoplankton accumulation	Topping and Davies, 1981 Mason and Fitzgerald, 1991 Behrenfeld and Falkowski, 1997

^aThis value is the sum of the coastal, shelf and deep-sea fluxes.

^bBoth of these fluxes are delivered largely to the deep sea, where current data suggest concentrations of methylated Hg species that are too low to be consistent with this input, implying net demethylation in the deep sea if these inputs are accurate.

Table 2. Latitudinal variation of mercury concentrations ($\mu\text{g THg/g}$ wet weight) in various trophic levels of well-studied ecosystems.

Geographical Location	Lancaster Sound ^a	N. Baffin Bay ^b	Gulf of Maine ^c	Gulf of Farallones ^d	Ross Sea, Antarctica ^e
Latitude	~74 ⁰ N	~76 ⁰ N	~44 ⁰ N	~38 ⁰ N	~74 ⁰ S
Sampling Date	1988-90	1998	2001-2003	1993/94	1989-91
Microplankton	<0.004	0.003	0.002±0.001	–	0.007±0.001
Mesoplankton	0.012±0.002 ^f	0.025±0.017	0.003±0.001	–	0.013–0.007 ^h
Macrozooplankton	0.012-0.02 ^h	0.020±0.009	0.006±0.001	0.006 (0.006-0.008) ^g	0.015±0.005
Pelagic fish (muscle)	0.038±0.006	0.04	0.047±0.028	0.02 (0.018-0.022)	0.068±0.066
Seal or porpoise (muscle)	0.214±0.006	0.68±0.29	0.501±0.297	3.8 (0.96-1.46)	0.37

a – Atwell et al. (1998), b – Campbell et al. (2005), c – Harding et al. (unpubl.), d – Jarman et al. (1996), e – Bargagli et al. (1998), f – mean±SD, g – geometric mean (±1SD), h – range.