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Does trophic structure dictate mercury concentrations in top predators? A comparative analysis of pelagic food webs in the Pacific Ocean

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ABSTRACT

Large pelagic predators in the marine environment accumulate relative high levels of mercury (Hg), yet it is difficult to identify the ecological factors that control the fate and flow of contaminants in marine systems, in part due to the difficulty in experimenting with large, dynamic ecosystems. By comparing the eastern tropical Pacific (ETP) and central north Pacific (CNP) pelagic food webs, we determined how differences in trophic pathways, versus differences in baseline Hg conditions, might translate into varying levels of Hg contamination in upper trophic levels. We developed coupled contaminant-trophic mass balance models to estimate Hg concentrations or Hg-elimination rates for species groups in each region finding generally higher Hg concentrations in the ETP model. Specifically we found Hg concentrations of yellowfin, skipjack, bigeye, and albacore tunas were two- to four-fold greater in the ETP than the CNP. These estimated differences reflected previous empirical observations of Hg concentrations in tunas across these regions. Regional differences in tuna Hg concentrations can be solely explained by differences in diets of tuna and their prey, although changes in Hg input at the base of the food web can strongly influence Hg concentrations in top predators as well. The coupled models allowed us to test hypotheses on the sources of Hg variation in top predators at a food web scale, incorporating the indirect effects of different food web structures into our regional Hg estimates. Our ability to draw firm conclusions regarding causal effects underlying known differences in Hg levels across ocean regions is restricted by data limitations that led to different assumptions made to construct the food web models.

1. Introduction

Trophic transfer is the primary source of contaminants, such as mercury (Hg), to top pelagic predators in the marine environment (Morel et al., 1998). Structural differences in food webs can determine how mercury is transported throughout ecosystems (Carrer et al., 2000; Booth and Zeller, 2005) but the strength of influence on Hg concentrations in top predators is unknown. Variation in Hg concentrations can occur due to varying levels of Hg bioavailable at the base of the food web (Morel et al., 1998), variation in food chain length (Cabana et al., 1994) or variation in their diet composition, especially when alternative prey have markedly different Hg levels, i.e., feeding at different trophic levels (Chen et al., 2008) or depths (Choy et al., 2009). Variation between food webs in the production and consumption rates of species, or functionally equivalent species, can also influence the accumulation of contaminants and biomagnification up the food web (Trudel and Rasmussen, 2006).

A Hg mass balance model can be used to explore alternate hypotheses for regional variation of contaminant bioaccumulation in top pelagic predators. Hg accumulation is largely influenced by a combination of production, consumption and diet composition (Vander Zanden and Rasmussen, 1996; Trudel and Rasmussen, 2006), all of which are included in food web models. Thus, combining food web models with contaminant tracers provides a method of connecting the flow of contaminants with their ecological (trophic network) and physiological (consumption and metabolism) controls providing an integrative framework to study contaminant flows in a system context. For instance, these types of coupled models have been used to predict contaminant levels in aquatic species in the Lagoon of Venice (Carrer et al., 2000) in the absence of detailed data, and also to explore the effects of natural and anthropogenic changes in contaminant levels of pilot whales and cod in the Faroe Islands (Booth and Zeller, 2005).

Previously, Ferriss and Essington (2011) observed Hg concentrations in yellowfin and bigeye tuna approximately 30% higher in

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the eastern equatorial versus the central equatorial Pacific. In the absence of additional data on Hg concentrations throughout the food web and water column, the authors speculated that environmental factors affecting Hg cycling (and especially methylation) at the base of the food web could cause the observed regional variation in large predatory fishes. Differences in feeding habits can also dictate Hg levels in fish (Cabana et al., 1994; Harris and Bodaly, 1998;Laskowski, 1991; McIntyre and Beauchamp, 2007; Vander Zanden and Rasmussen, 1996), and diet studies confirm that the relative importance of dominant prey items of yellowfin and bigeye tuna varies throughout the Pacific Ocean (Allain, 2004; Brock, 1985; Buckley and Miller, 1994; King and Ikehara, 1956; Olson and Boggs, 1986; Tester and Nakamura, 1957; Watanabe, 1958, 1960). The influence of trophic structure on Hg levels in large predatory fish could be clarified by measuring Hg levels in plankton, lower, and higher trophic levels simultaneously. In lieu of this extensive sampling, models can be employed to test this hypothesis.

Contaminant-trophic mass balance models have not been used to explore regional variation in Hg levels of marine species despite the recognition that Hg can vary in relation to feeding habits (e.g., Vander Zanden and Rasmussen, 1996; Harris and Bodaly, 1998; McIntyre and Beauchamp, 2007). Large marine apex predators such as tunas (*Thunnus*) exhibit wide ranges of Hg concentrations (e.g., Greig and Krzynowek, 1979; Yamashita et al., 2005; Ferriss and Essington, 2011) and feed on prey assemblages that are taxonomically distinct across the eastern and central Pacific Ocean (Watanabe, 1960; Olson and Boggs, 1986). One hypothesis to explain these differences is that the pathways of Hg flow from lower to upper trophic level species are fundamentally different among ecosystems. For instance the eastern tropical Pacific (ETP) and the central north Pacific (CNP) ecosystems vary with respect to primary trophic pathways leading to apex predators and the composition of species that comprise middle and lower trophic levels (Cox et al., 2002a; Olson and Watters, 2003; Hinke et al., 2004). These structural differences may arise through differences in oceanography (Mann and Lazier, 1991; Lehodey, 2001), biogeography, and current and past fishing pressures (Cox et al., 2002b; Essington et al., 2002; Kitchell et al., 2002).

We focus on Hg in this study as it is a global public health concern due to its neurotoxic properties. Humans are primarily exposed to Hg through consumption of fish that have elevated Hg levels. Many nations set consumption advisories that identify species-specific limits on weekly or monthly consumption of fish based on average Hg levels (Nesheim and Yaktine, 2006). Yet, variation in Hg within fish species can be substantial and exceed variation between species (Cope et al., 1990; Wagemann et al., 1998; Hammerschmidt and Fitzgerald, 2006b; Levinton and Pochron, 2008). For example, large marine apex predators such as tunas are common targets of consumption advisories, but exhibit wide ranges of Hg concentrations within species (Greig and Krzynowek, 1979; Kai et al., 1988; Yamashita et al., 2005; Kaneko and Ralston, 2007; Ferriss and Essington, 2011). An improved understanding of the fate and flow of Hg in Pacific food webs could lead to more informed consumption advisories for these highly mobile, apex predators that support some of the world's largest fisheries.

The objective of this study is to explore the extent to which known regional variation in mercury concentrations of yellowfin (*Thunnus albacares*), skipjack (*Katsuwonus pelamis*), albacore (*T. alalunga*), and bigeye (*Thunnus obesus*) tunas can be explained by differences in diet and food web structure. We will identify and compare the distribution of Hg across the food webs of the CNP and ETP, using Ecopath and mercury mass balance models. The models will serve as tools to compare the Hg pathways and pools in these systems. These models will also provide insights into the sensitivity of Hg concentrations in tunas to changes in their diet and those of their prey.

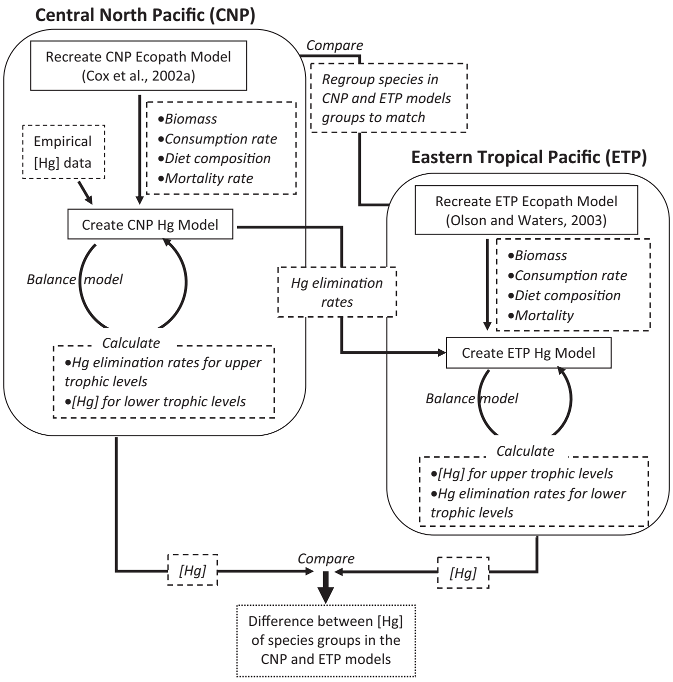

Fig. 1. Conceptual diagram of the creation of the coupled Ecopath and mercury mass balance models, the steps used to balance the models, and explore regional differences in Hg concentrations.

2. Methods

The mass balance models used in this study consist of a set of linear equations representing the flow of biomass or Hg through each functional group. We first reaggregated the functional groups in existing Ecopath models of the CNP and ETP to a comparable set of groups and recalculated the biomass and ecotrophic efficiency for each assemblage. We created a Hg mass balance model for each region to calculate the Hg elimination rate or the total amount of Hg in each biomass pool based on the consumption rate, biomass, diet composition and mortality parameters from the Ecopath models. We populated the CNP Hg model with regionally-specific empirical Hg data for the higher trophic level species and estimated Hg elimination rates for those species. We then incorporated the estimated elimination rates into the ETP Hg model (assuming consistent elimination rates within species groups across regions) and estimated Hg concentrations for upper trophic level species in that region. We sought to determine if previously observed regional differences in Hg concentrations in apex predators could be predicted by differences in food web structure (Fig. 1).

2.1. Model creation

The Ecopath model (Polovina, 1984; Christensen and Pauly, 1992) balances biomass gains and losses for each functional group using the following expression:

$$B_i \cdot \left(\frac{P}{B}\right)_i \cdot EE_i = BA_i + Y_i + \sum_{j=1}^{n} B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ij} \qquad (1)$$

where the biomass (B), production to biomass ratio (P/B) and ecotrophic efficiency (EE) (the fraction of production used in the system) of prey group i are balanced with the biomass accumulation (BA) and mortalities due to fisheries (Y), and predation by group j. Predation mortality is calculated using the biomass of predator group j, the consumption to biomass ratio (Q/B) and the fraction of group i in the diet of group j (DC). Ecopath uses matrix inversion