

Feeding strategy as a key driver of the bioaccumulation of MeHg in megabenthos

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Abstract. The bioaccumulation of methylmercury (MeHg) in the marine food chain poses a neurotoxic risk to human health, especially through the consumption of seafood. Although MeHg bioaccumulation at higher trophic levels is relatively well understood, MeHg bioaccumulation at the base of the food web remains underexplored. Given the neurotoxic effects of methylmercury on human health, it is essential to understand the drivers of bioaccumulation at every level of the food chain. In this study, we incorporate six megabenthos functional groups into the ECOSMO marine end-to-end ecosystem model, coupled to the MERCY marine Hg cycling model. We investigated how various feeding strategies influence the bioaccumulation of both inorganic Hg (iHg) and MeHg in marine ecosystems. We show that the feeding strategy significantly influences bioaccumulation and correlates stronger with iHg than the trophic level and that suspension feeders have elevated iHg levels while filter feeders have higher MeHg values. Additionally, we show that the bioaccumulation of both iHg and MeHg can be accurately modeled solely based on feeding strategies in low trophic-level megabenthos. However, when modeling higher trophic levels, incorporating the allometric scaling law dramatically improves the model performance. These results demonstrate the need for a holistic approach in which iHg, MeHg, and trophic levels of organisms are evaluated at both high and low trophic levels to identify what food web structures drive high MeHg concentrations in seafood.

1 Introduction

Mercury (Hg) is a naturally occurring element. In addition to its natural occurrence, it is also emitted through various anthropogenic activities, such as the burning of fossil fuels, small-scale artisanal gold mining, and the production of cement and ferrous metals (Pacyna et al., 2006). These ~~emissions have led to a threefold increase in environmental Hg compared to pre-anthropogenic levels~~anthropogenic emissions have significantly raised environmental Hg levels, with 78%, 85%, and 50% of atmospheric, upper ocean, and deep ocean Hg, respectively, originating from anthropogenic emissions (Geyman et al., 2025)

When elemental Hg (Hg^0) is emitted, it can undergo long-range atmospheric transport. In this way, it can be transported on a global scale and deposited in the oceans, thus increasing Hg levels in the marine environment (Durnford et al., 2010). Marine Hg^0 is volatile and can return to the atmosphere or be oxidized into dissolved Hg (Hg^{2+}) (Sommar et al., 2020). This Hg^{2+} can be reduced back to volatile elemental Hg^0 , or it can be methylated to the dangerous neurotoxin methylmercury (MeHg), which

occurs as monomethylmercury (MMHg⁺) or dimethylmercury (DMHg) (Jensen and Jernelov, 1969; Lin et al., 2021). In this paper, we will look at the bioaccumulation of three groups of Hg; total Hg (tHg) refers to all Hg, methylmercury (MeHg) refers to both MMHg⁺ and DMHg, and inorganic Hg (iHg) refers to all Hg that is not MeHg.

There are two key processes involved in bioaccumulation: bioconcentration and biomagnification. ~~Animals living in a polluted marine environment will~~ When animals absorb Hg directly from their environment, this is called bioconcentration. Both iHg and MeHg bioconcentrate. Since iHg is generally present in higher concentrations than MeHg, and its bioconcentration rate is higher, iHg is usually bioconcentrated faster than MeHg (Mason et al., 1996). The bioconcentration process can result in high ~~Hg concentrations in organisms, concentrations in aquatic organisms. This process is commonly quantified using the Volume Concentration Factor (VCF), a unitless ratio between the Hg concentration in phytoplankton and that in the surrounding water.~~

$$VCF = \frac{C_{\text{phytoplankton}}}{C_{\text{water}}} \quad (1)$$

where both $C_{\text{phytoplankton}}$ and C_{water} have the same units, for example, ng Hg μm^{-3} , and the VCF is unitless. For MeHg, very high volume concentration factors of up to ~~6.4E6 have been found (Schartup et al., 2018)~~ 6.4×10^6 have been reported in the literature (Lee and Fisher, 2016; Schartup et al., 2018).

~~These already high Hg concentrations can be increased even further by biomagnification~~ MeHg concentrations that are elevated due to bioconcentration can be further increased by biomagnification along the aquatic food web. Biomagnification refers to the increase in Hg with each successive trophic level in the food chain. The trophic transfer efficiency of MeHg (66-80%) is higher than that of iHg (7-46%), where MeHg accumulates at much higher levels in the food chain (Metian et al., 2020; Wang and Wong, 2003; Dutton and Fisher, 2012). ~~These concentrations can become harmful to humans when consumed, and the consumption of MeHg-polluted~~ MeHg is a neurotoxin whose overconsumption can decrease IQ points and raise the risk of heart attacks, and consumption of MeHg-contaminated seafood is the ~~main risk of exposure to Hg for the average person (Sheehan et al., 2014)~~ primary pathway of Hg exposure in humans, with elevated risk among coastal and seafood-reliant populations (Sheehan et al., 2014; Zhang et al., 2021; Genchi et al., 2017; Trasande et al., 2006).

The ~~danger posed by the consumption of MeHg-contaminated seafood received a great deal of attention when more than~~ risk associated with consuming seafood contaminated with MeHg gained significant attention after over 1000 ~~people died fatalities occurred~~ in Japan in 1956 due to the consumption of contaminated seafood ~~caught in Minamata Bay (?). from Minamata Bay (Harada, 1995).~~ Although this MeHg outbreak was a unique event linked to industrial waste disposal containing Hg, it highlighted the dangers of MeHg exposure. In order to reduce the risk of further outbreaks of MeHg intoxications, the Minamata Convention on Mercury was founded. A total of 151 countries have pledged to reduce their Hg emissions in support of the Minamata Convention and 128 countries have signed and ratified the convention (UNEP, 2013). The global state of Hg as a pollutant and the effect of the Minamata Convention is periodically reviewed in the Minamata Convention Effectiveness Evaluation (Outridge et al., 2018).

While there is considerable understanding of MeHg bioaccumulation in high trophic levels, less is known about the bioaccumulation drivers at the base of the food web. ~~The lower concentration of Hg at the base of the food web reduces the risk for~~

humans, which is why these animals do not receive the same monitoring recommendations from the ~~where~~ Hg concentrations
60 tend to be lower, resulting in reduced risk to humans. As such, these organisms are not prioritized in the current monitoring
strategies under the ongoing effectiveness evaluation of the Minamata Convention ~~as~~, which focuses primarily on fish, hu-
mans ~~and~~, and predatory wildlife (Evers et al., 2016). ~~Furthermore, the effectiveness evaluation noted that the concentrations~~
~~of~~ Additionally, the evaluation to date has shown that Hg and MeHg concentrations in water and sediment ~~are poorly correlated~~
~~with the concentrations in biota. Thus, Hg levels in water and sediment do not receive the same monitoring recommendations~~ do
65 not correlate well with levels in biota, leading to greater emphasis on biological monitoring over abiotic compartments.

Once Hg is bioconcentrated in primary producers, a strong link appears between the trophic level and Hg bioaccumulation (Madgett et al., 2021). This indicates that our understanding of Hg bioaccumulation in high trophic levels is greatly limited by our understanding of Hg bioaccumulation at the base of the food web.

~~Improving our understanding of bioaccumulation at the base of the~~ The benthic food web is ~~challenging, as the base of the~~
70 ~~food web is very complex~~ highly complex, making it challenging to improve our understanding of bioaccumulation within it
(Silberberger et al., 2018). There are several distinct groups of megabenthos with different feeding strategies, such as bivalves that filter feed, lugworms that feed on sediment carbon particles, active hunters and scavengers such as shrimps and crabs, and sponges that feed on suspended dissolved material. These different feeding strategies allow them to exploit a variety of food sources, but different food sources can have different Hg concentrations, and Hg originating from different food sources can
75 have different assimilation efficiencies. In this study, we hypothesize that the low-trophic-level biota feeding strategy has a significant impact on their Hg content.

We focus this study on the benthic food web. Although primary production in the North Sea can be highly variable due to factors such as wind (Daewel and Schrum, 2017), tidal mixing (Zhao et al., 2019) and nutrient availability (Richardson et al., 1998), primary production in coastal areas is generally dominated by pelagic phytoplankton, with the exception of extremely
80 shallow areas that are dominated by benthic macroalgae (Krause-Jensen et al., 2012; Cibic et al., 2022). ~~Especially in~~ In
well-mixed areas where pelagic phytoplankton dominate primary production, ~~while the pelagic phytoplankton are available for~~
~~consumption by megabenthos because of water column mixing, they can be consumed by megabenthos and~~ there is a strong
coupling between the benthic and the pelagic, called the benthic-pelagic coupling. In these well-mixed areas, megabenthos can reach high biomass since food is abundant in several ways, resulting in megabenthos with different feeding strategies in the
85 same ecosystem (Ghodrati Shojaei et al., 2016).

We hypothesize that the different feeding strategies of low-trophic-level megabenthos play an important role in creating the disconnect between Hg concentrations in the water and sediment and the concentrations at the base of the food web. We investigated whether the feeding strategy impacts bioaccumulation and hypothesized that feeding strategies influence the bioaccumulation of iHg and MeHg differently, contributing to the high variation in Hg levels at the base of the benthic food
90 web.

To test our hypotheses, we employed ~~two methods~~ three approaches. First, we ~~performed literature research~~ conducted a
literature review in which we collected field observations of ~~the content of~~ tHg, MeHg, and iHg ~~the trophic level, and~~
~~the concentrations, together with trophic level and~~ megabenthos feeding strategy. We then performed statistical analyses on

95 ~~this literature to see if patterns between bioaccumulation and feeding strategies exist in nature. Afterward, we conducted~~
~~an in-silico~~ these data to examine if we could find a relationship between feeding strategy and trophic level. Second, we
carried out a modeling experiment in which megabenthos with ~~various feeding strategies compete~~ different feeding strategies
competed under physical drivers in idealized scenarios ~~that are typical representative~~ of megabenthos-rich coastal oceans. The
megabenthos groups ~~are~~ were designed to differ only in their feeding strategies, allowing us to isolate this effect. This ~~was~~
~~done to verify whether we can reproduce~~ experiment was used to test whether the observed effects from our literature ~~study~~
100 review could be reproduced in a fully coupled model.

Finally, we ~~used the model to quantify the role of the feeding strategy in the bioaccumulation of Hg and investigated whether~~
~~it fully explains the observed differences or if other drivers need to be incorporated.~~

2 **Materials and methods**

1.1 **Literature research and statistics**

105 ~~To compare the findings with the literature, we collected field studies measuring Hg in megabenthos. The studies we used~~
~~are shown in the Table ??.~~ We categorized the megabenthos into the same feeding categories, "deposit feeder", "filter feeder",
~~"suspension feeder", "grazer" and "predator". To better look at the effect of the trophic level, we also added "primary producers"~~
~~as the base of the food web, "predators" as benthic predators, and "seabird" and "benthic fish" as top predators. We analyze~~
~~whether trophic level and feeding strategy influence megabenthos iHg, MeHg, and/or tHg content. The observations are~~
110 ~~analyzed by visualizing the data, performing a linear regression, and plotting a correlation matrix of the difference in bioaccumulation~~
~~between different feeding strategies. The total and partial R^2 of the linear regression of the effect of the feeding strategy,~~
analyzed data from a single study to evaluate whether the trophic level, and the feeding strategy are compared to analyze the
effect of both drivers on bioaccumulated iHg, MeHg and tHg ~~same dynamics observed in the model and the global dataset were~~
also present in a single geographical location. While none of these individual tests is conclusive on its own, consistent evidence
115 across all three approaches would support the conclusion that feeding strategy is an important driver of Hg bioaccumulation
and would warrant further empirical studies to investigate this role in more detail.

2 Materials and methods

2.1 **The models**

To ~~further~~ assess the importance of the feeding strategy, we modeled bioaccumulation in megabenthos, with the feeding strategy
120 being the only distinction between different groups of megabenthos. Then we compared our model to observations to evaluate
whether this approach allows us to accurately model bioaccumulation or if additional drivers should be taken into account.
We used a fully coupled 1D water column model that is run in 2 setups that resemble typical hydrological regimes found
in coastal oceans. We coupled the Generalized Ocean Turbulence Model (GOTM) (Burchard et al., 1999) with the ECOSMO

E2E ecosystem model ~~and the Merrey~~ (Daewel et al., 2019) and the MERCY v2.0 Hg speciation and bioaccumulation model
125 (Bieser et al., 2023).

2.2 ~~The hydrodynamical model~~

2.1.1 The hydrodynamical model

The hydrodynamics of the model are estimated using the GOTM, which is a 1D hydrodynamic model (Bolding et al., 2021). GOTM calculates the turbulence of a vertical 1D water column set-up by computing the solutions to the one-dimensional
130 version of the transport equation of momentum, salinity, and temperature. The model is nudged to observational data sets for temperature and salinity. The setups are based on gridded bathymetry data for water depth with 1/240° resolution (GEBCO Bathymetric Compilation Group, 2020), ECMWF ERA5 dataset for meteorological data (Wouters et al., 2021), Ocean Atlas for salinity and temperature profiles (Garcia H.E. et al., 2019), and the TPOX-9 atlas for tides (Egbert and Erofeeva, 2002), which is combined using the iGOTM tool (<https://igotm.bolding-bruggeman.com>). The GOTM model is coupled using the
135 Framework for Aquatic Biogeochemical Modeling (FABM) (Bruggeman and Bolding, 2014). The biogeochemical models are encoded in FABM. The FABM interfaces communicate the state variables between the GOTM model and the biogeochemical models.

2.2 ~~The Merrey v2.0 model~~

2.1.1 The physical setups

140 The model runs in 2 setups, the first is a 41.5 m deep permanently mixed Southern North Sea set of 41.5 m deep and the second is a seasonally mixed 110 m Northern North Sea setup. These setups are described in more detail in Amptmeijer et al. (2025). The Southern North Sea setup is located at (54°15'00.0" N 3°34'12.0" E). It is a shallow station that is permanently mixed, meaning that megabenthos can feed directly from the phytoplankton and zooplankton bloom. The setup is chosen because it resembles perfect growth conditions for megabenthos, and most megabenthos in the observations are sampled from similar
145 circumstances. Because of this, most samples are from shallow well-mixed coastal areas, and we used this setup to evaluate the performance of the models.

The Northern North Sea setup is located at (57°42'00.0" N 2°42'00.0" E) and is only mixed in winter. This means that megabenthos cannot feed directly from the bloom, but are rather dependent on the sinking of detritus particles. In nature, these deeper areas typically have lower overall biomass. This setup is used to evaluate whether the models predict a difference in the
150 bioaccumulation of iHg and MeHg under a different hydrodynamic regime.

2.1.2 The MERCY v2.0 model

Hg cycling and speciation is modeled using the ~~Merrey~~-MERCY v2.0 model (Bieser et al., 2023). The ~~Merrey~~-MERCY v2.0 model is a comprehensive Hg cycling model that includes speciation between 7 forms of Hg and partitioning to both dissolved

organic matter (DOM) and detritus. It was originally developed as a 3D Hg cycling model of the North and Baltic Seas.
155 However, in this study, we use the 1D version of this model, which is driven using the GOTM model. This configuration is used, described, and evaluated in more detail in (Amptmeijer et al., 2025).

2.2 ECOSMO-E2E

2.1.1 ECOSMO E2E

The ecosystem model is based on the ECOSMO E2E (ECOSystem Model End-to-End) ecosystem model (Daewel et al., 2019).
160 This model extends the ECOSMO II model to have higher trophic levels while preserving consistency at lower trophic levels (Daewel et al., 2019). The version used in this study is the same as the version used and evaluated in (Amptmeijer et al., 2025). In this version, small modifications have been made, such as lowering the mortality rate of zooplankton and decreasing the efficiency of carbon uptake to make the model more suitable for bioaccumulation compared to the version published by (Daewel et al., 2019). ~~The model is evaluated and shown to reproduce the bioaccumulation of iHg and MeHg at the base of the food web within 1 standard deviation of observations for phytoplankton, microzooplankton, and mesozooplankton. Furthermore, the model accurately models the bioconcentration of both~~ Bioaccumulation is implemented to account for bioconcentration in all trophic levels and biomagnification in all consumers. Phytoplankton have a size-dependent uptake and release rate for the uptake and release of iHg. Based on observations by Pickhardt et al. (2006) that found higher MeHg in smaller phytoplankton but consistent iHg levels, phytoplankton have a size-dependent uptake rate and constant release rates. This means that diatoms
170 and flagellates bioaccumulate similar amounts of iHg, while the smaller flagellates accumulate more MeHg. The uptake and release rates of iHg and MeHg ~~and the biomagnification of MeHg within the range of observations in zooplankton are based on Tsui and Wang (2004) and on Wang and Wong (2003) for fish. An essential component of the ecosystem that interacts with bioaccumulation in megabenthos that was not overhauled for this study is the interactions between detritus and DOM and iHg and MeHg. The only Hg species assumed to partition to DOM and detritus are Hg^{2+} and $MMHg^+$, and this partitioning is~~ assumed to be an equilibrium that is instantaneous and is reestimated on every time step. The equilibrium is based on the K_{dw} values which are based on Allison et al. (2005) and Tesán Onrubia et al. (2020). This value is $\log_{10}(6.4)$ and $\log_{10}(6.6)$ for the partitioning of Hg^{2+} and $\log_{10}(5.9)$ and $\log_{10}(6.0)$ for the binding of $MMHg^+$ to detritus and DOM respectively. This is the same approach that is used and evaluated in Bieser et al. (2023).

2.2 Model development

180 To use the model to study bioaccumulation in megabenthos, the higher trophic level of the ECOSMO E2E model is altered. We exchanged the functional group macrobenthos, fish 1, and fish 2 with ~~5-6~~ megabenthos functional groups, as shown in Fig. 1. The megabenthos groups are separated by their feeding strategy: filter feeder, deposit feeder, generalist feeder, suspension feeder, predator, and top predator.

Filter feeders filter suspended particles from the water column. In our model, they can eat phytoplankton, zooplankton, and
185 detritus. Examples of filter feeders are mussels, tubeworms, and barnacles. The second group is **deposit feeders**. These animals

consume organic carbon from the sediment; in our model, they exclusively feed on organic carbon deposited in the sediment. This group would include gastropods and polychaete worms, such as the lugworm (*Arenicola marina*). The **generalist feeder** resembles animals such as ~~North-Sea~~ brown shrimp (*Crangon crangon*), which can utilize various feeding strategies. In our model, this group feeds on phytoplankton, zooplankton, detritus, and deposited material. We also include a **suspension feeder**.

190 Suspension feeders, such as sponges, can consume detritus and DOM. The consumption of DOM, which is too small to be consumed by filter feeders, differentiates suspension and filter feeders. A common strategy to consume DOM as a food source is the utilization of symbiotic bacteria such as chemosymbiotic bivalves from the families Lucinidae, Solemyidae, and Thyasiridae, and microbial biomes of high microbial assemblage sponges (Dufour, 2018; Olinger et al., 2021). Finally, we included 2 predators. The first predator is referred to as **the predator**, it feeds on the 4 benthic groups mentioned above, and
 195 it has an equal preference and grazing rate in all groups, but it will prioritize abundant groups. This preference is caused by making the food available for predation by the predators not linearly related to the abundance of the prey, but calculated as:

$$b_{\text{available}} = \begin{cases} b_{\text{biomass}}, & \text{if } b_{\text{biomass}} \geq b_{\text{protected}}, \\ b_{\text{biomass}} \frac{b_{\text{biomass}}}{b_{\text{protected}}}, & \text{if } b_{\text{biomass}} < b_{\text{protected}}. \end{cases}$$

in which,

- $b_{\text{available}}$: Portion of prey biomass in g C m^{-2} accessible to predators.
- 200 – $b_{\text{protected}}$: Level of prey biomass in g C m^{-2} below which hunting becomes less optimal or energetically inefficient.
- b_{biomass} : Total prey biomass in g C m^{-2} in the environment.

~~b~~The megabenthos in the North Sea are estimated to have between 1.1 and 35.5 gC m^{-2} (Heip et al., 1992; Daan and Mulder, 2001). The value for $B_{\text{protected}}$ is chosen as 1 g C m^{-2} for all megabenthos groups, and 0.5 g C m^{-2} except for the benthic predator where $B_{\text{protected}}$ is 0.5 gC m^{-2} . These values are chosen to protect megabenthos functional groups from
 205 extinction due to predation when their values are below the expected range. This relationship models 2 real-world interactions. First, when the concentration of prey is low, the small number of individuals can more likely survive under ideal circumstances and, therefore, may be less exposed to predation (Campanella Id et al., 2019). Secondly, several predators, such as the shore crab, adapt their behaviors to the density of the prey and learn to be more efficient in the hunting of more common prey (Chakravarti and Cotton, 2014). Our model is resolved in carbon content, while measurements are often
 210 in dry weight. The carbon fraction of dry weight generally ranges from 0.4 to 0.6, but can vary between different taxa (Gorokhova and Hansson, 2000; Jurkiewicz-Karnkowska, 2005). To ensure consistency across different functional groups with diverse feeding strategies, we maintain a 1:2 conversion ratio for carbon to dry weight for all megabenthos functional groups.

2.3 Assimilation efficiency of iHg and MeHg

2.2.1 Assimilation efficiency of iHg and MeHg

215 The assimilation efficiency (AE) of iHg and MeHg is a key parameter in correct biomagnification modeling. AE is based on laboratory experiments that analyze AE in phytoplankton (Metian et al., 2020; Wang and Wong, 2003). An assimilation efficiency of 0.95 for MeHg and 0.31 for iHg is chosen for everything except deposit feeding, which has a lower feeding efficiency of 0.07 for iHg and 0.43 for MeHg according to Dutton and Fisher (2012).

2.3 Semi-labile DOM

220 2.2.1 Semi-labile DOM

In the ECOSMO E2E model, only labile-DOM is resolved. This means that there is very little DOM. In our model, we want to incorporate a suspension feeder that would utilize DOM as a food source. Because of this, we added a DOM component referred to as semi-labile DOM. This semi-labile DOM has the same bacterial degradation rate as that of the detritus, and it has the same Hg partitioning behavior as labile DOM. ~~5% of the~~ When organic carbon (~~Detritus~~detritus+labile-DOM+semi-labile-
225 DOM) ~~formed, is formed, 5%~~ is formed as semi-labile DOM, and there is a breakdown of the detritus into semi-labile DOM of 0.001 d^{-1} (per day). Since the categorization of DOM is very complex, these rates are estimated to create a low maximum of 50 mg C m^{-3} . This is lower than the DOM concentrations typically found in the North Sea, but because it is unclear which fraction of DOM can be consumed by suspension feeders, this amount provides suspension feeders a unique food source that they can utilize while not outcompeting other megabenthos (Lønborg et al., 2024).

230 2.3 Allometric scaling model

2.2.1 Allometric scaling model

Finally, we run the model while taking into account other drivers of MeHg bioaccumulation to see whether it improves the model. There are three interactions that we take into account for this second model. First, the allometric scaling law, which states that larger animals have a lower base metabolic rate when normalized to body weight (da Silva et al., 2006). Secondly,
235 we account for the observations that MeHg bioaccumulation in fish increases as the water temperature increases, indicating that increased activity does not increase MeHg excretion while it increases MeHg uptake due to a higher grazing rate (Dijkstra et al., 2013). Finally, we assume that predators need to spend more energy on active metabolism to hunt their prey. Because of this, we assumed that the total relative respiration rate of predators and top predators is not altered, so both models have the same carbon cycle. However, MeHg is excreted at a lower rate of 0.002 d^{-1} , rather than their respiration rate, which is the same
240 base metabolic rate as the fish in the ECOSMO E2E model. This leads to a higher bioaccumulation of MeHg at higher trophic levels. The bioaccumulation of iHg is not altered between the two models. In the evaluation, the second model is referred to as the allometric scaling (AS) model.

2.3 ~~The physical setups~~Literature research and statistics

245 The model runs in 2 setups, the first is a 41.5 m deep permanently mixed Southern North Sea set of 41.5 m deep and the second is a seasonally mixed 110 m Northern North Sea setup. These setups are described in more detail in Amptmeijer et al. (2025). The Southern North Sea setup is located at (54°15'00.0" N 3°34'12.0" E). It is a shallow station that is permanently mixed, meaning that megabenthos can feed directly from the phytoplankton and zooplankton bloom. The setup is chosen because it resembles perfect growth conditions for megabenthos.

2.3.1 Literature research

250 To compare the findings with the literature, we collected field studies measuring Hg in megabenthos. The studies we used are shown in Table S1. We categorized the megabenthos into the same feeding categories, "deposit feeder", "filter feeder", "suspension feeder", "grazer", and "predator". To better assess the effect of the trophic level, we also added "primary producers" as the base of the food web, and "seabird" and ~~most megabenthos in the observations are sampled from similar circumstances.~~ Because of this, samples are sampled from shallow well-mixed coastal areas, and we used this setup to evaluate the performance ~~of the models~~ "benthic fish" as top predators. We analyzed whether trophic level and feeding strategy influence megabenthos iHg, MeHg, and/or tHg content. The total and partial R^2 of the linear regression of the trophic level and the feeding strategy were compared to analyze the effect of both drivers on bioaccumulated iHg, MeHg, and tHg.

The Northern North Sea setup is located at (57°42'00.0" N 2°42'00.0" E) and is only mixed in winter. This means that megabenthos cannot feed directly from the bloom, but are rather dependent on the sinking of detritus particles. In nature, these
260 deeper areas typically have lower overall biomass. This setup is used to evaluate whether the models predict a difference in the bioaccumulation of iHg and MeHg under a different hydrodynamic regime. We compared our model to observations in two ways. First, we compared it to all the data available in our global dataset. We acknowledge the limitation of this approach, as different geographical regions may have different Hg baselines, but it can provide insight into whether certain feeding strategies are consistently higher or lower in iHg, MeHg, or tHg. The most comprehensive dataset of MeHg bioaccumulation that we
265 could find was published by McClelland et al. (2024), we used this single dataset to verify if patterns observed in the model and the global dataset are also present in a single dataset. If certain patterns are present in our model, in globally aggregated data, and in a single large dataset, it becomes a compelling argument to form a hypothesis for further targeted empirical studies.

2.4 **Model evaluation**

2.3.1 Model evaluation using a global dataset

270 The goal of the model is to evaluate how well we can ~~model represent~~ the bioaccumulation of iHg and MeHg while only taking into account the feeding strategy and trophic interactions. To this extent, the model's result is its performance. If the model performs well, we can conclude that only ~~taking into account~~ accounting for feeding strategies and trophic interactions explains a large amount of the variability in Hg bioaccumulation. Initially ~~we performs~~, we performed this comparison between

observations and the modeled Southern North Sea setup. This ~~is~~ was done because most samples are collected from shallow areas ~~that are rich in macrobenthos. Our well-mixed~~ with high megabenthic biomass, which the well-mixed Southern North Sea setup ~~would resemble the majority of the observations better than the seasonally mixed Northern North Sea. Afterward~~ better resembles. Afterwards, the models ~~are~~ were compared to the Northern North Sea models and the AS model to evaluate the effect of hydrodynamics and increased bioaccumulation in higher trophic level animals on our conclusions. The ~~feeding strategy "grazer"~~ grazer feeding strategy was omitted, as the ECOSMO E2E model does not include benthic algae to graze on. The modeled generalist was compared to the sum of the deposit and filter ~~feeder~~ feeders from the observations, and the modeled top predator to the benthic fish and seabird feeding strategies ~~from the observations.~~

~~We first calculated the normalized bias (modeled—observed)/modeled for the average modeled and observed values. Then, we performed a Monte Carlo simulation in which we estimated the mean and standard deviation of the observed and yearly mean of the modeled data of the last 10 years of the simulation. Over 100,000 iterations, we estimated the probability that the modeled value is within 2 standard deviations of the observations, so it checks if the modeled mean is not outside 95% of the observations. After this, we quantified the probability that the modeled mean is of the same distribution as the observations by performing a Bayes factor analysis. The Bayes factor value is estimated by first estimating the likelihood of the modeled mean under the H0 hypothesis, which assumes that the modeled and observed data share the same distribution, and the H1 hypothesis, which assumes that they do not share a distribution. The likelihood of the H1 hypotheses over the H0 hypotheses is the BF10 value. The BF10 factor is estimated using a Jeffreys–Zellner–Siow prior assumption so we assume no prior knowledge. Finally, the total model performance is evaluated by calculating the Root Mean Square Error (RMSE), the Normalised Root Mean Square Error (NRMSE), and the R^2 of the model for iHg and MeHg. In general, a normalized bias between <0.5 can be seen as low. The probability that the model values are not within 2 standard deviations is considered bad and indicates that the modeled mean is a considerable outliers compared to the data. A BF10 factor below 1 indicates that the modeled distribution is more likely the same as the observed distribution, and a BF10 <0.1 can be considered strong evidence and a BF10 <0.01 as very strong evidence in favor of the H0 hypotheses. A lower RMSE shows better model predictive capacity and an NRMSE below~~ Model performance was evaluated using normalized bias, RMSE, NRMSE, and the R^2 (Pearson and residual) (see Table S2 for details). Normalized bias and NRMSE values below 0.5 is indicative of a good fit, while the R^2 is a value between 0 and indicate low bias and a good fit. R^2_{Pearson} quantifies how well differences between feeding strategies are captured, while R^2_{Residual} reflects agreement with absolute observed values.

2.3.2 Evaluation of the model using a single dataset

We used MeHg bioaccumulation and trophic level data from 476 individuals across 53 taxa of benthic invertebrates as published by McClelland et al. (2024) to verify if the interactions that occur in both our model and the global dataset are consistent when data from 1, and closer to geographical location is studied. These data were selected as they are the largest study we could find with both trophic level and MeHg concentrations. When several animals of the same group were sampled, the dataset presents mean values per group per location, which we use as one datapoint in our analyses. Although feeding strategies in the dataset were broadly aligned with our classifications, we reassigned them to match the functional groups in our model. For example,

shrimps were categorized as generalist feeders, which group is not present in McClelland et al. (2024), and isopods, which can be small benthic predators, were labeled as deposit feeders because their prey type is not represented in our model.

310 The data is sampled from two locations in the Canadian Arctic, Cape Bathurst (CB), which has a depth of 22 m and is located at 70°41'42.79" N, 128°50'21.34" W, and the eastern coast of Herschel Island in the Mackenzie Trough (MT), which has a depth of 116 m and is located at 69°36'44.96" N, 138°33'45.25" W. It must be noted this dataset is selected as it is extensive, but the region does have notable differences to the North Sea, where our model is run. It has extensive ice cover in winter, it is colder, and is geographically distant from the model location. It does, however, provide us with an opportunity to test if our
315 model conclusions can be verified using field observations from a single study.

To isolate the effect of the feeding strategy on MeHg bioaccumulation, we first transformed MeHg concentrations to their natural logarithm and fit a linear model with trophic level as predictor using the base R `lm()` function. The significance of the deviation from the predicted MeHg concentration at the trophic level was assessed using a one-sample *t* test. To improve interpretability, we calculated the percentage differences using $\text{Percentage difference} = 100 \times \left(\frac{\text{MeHg}_{\text{obs}}}{\text{MeHg}_{\text{pred}}} - 1 \right)$ based on the
320 residuals of the linear fit. This is visualized on a bar graph showing the percentage difference in MeHg concentration caused by the feeding strategy. The error bars represent the 1 shows a better fit Standard Error (SE). The same analysis was then performed to estimate differences in MeHg bioaccumulation related to phylum.

3 Results and discussion

2.1 Literature study

325 ~~The results of our literature study, depicted in Fig. ??, demonstrate that the feeding strategy affects the bioaccumulation of different benthic groups. If we only look at the groups that would represent the base of the benthic food web (filter feeder, suspension feeder, grazer, deposit feeder, and generalist) and perform an ANOVA, we see that there is greater significance of the effect.~~ As a final test, linear models were fitted on the natural logarithm of bioaccumulated MeHg concentrations using trophic level, phylum, and feeding strategy as predictor variables (using the `lm()` function in R). Estimated marginal means (EMM) for each feeding strategy were calculated with the `emmeans()` function of the `emmeans` package and compared
330 against the overall mean to assess deviations. This analysis was also performed separately for the MT and CB locations to verify the consistency of the effects of the feeding strategy (~~p = 0.001~~ on the-. The EMMs were transformed to a percentage difference with the earlier used equation and the estimated percentage difference due to feeding strategy and its significance is shown.

3.1 **Model evaluation**3.1.1 **Evaluation of the Hg cycling and pelagic bioaccumulation**

The marine cycling and speciation of Hg, in addition to the bioaccumulation in phytoplankton and zooplankton, is an essential driver of the bioaccumulation of iHg than on the bioaccumulation of MeHg ($p=0.09$). If we compare the median iHg and MeHg between organisms with different feeding strategies, we see that iHg is lowest in the benthic predator, followed by the deposit feeder, the top predator, the generalist, and the filter feeder, and the highest values are in the suspension feeders. Suspension feeders have by far the highest iHg concentrations and are more than double that of food web. Observed and modelled dissolved tHg concentration, the second highest group, the filter feeders. At the same time, MeHg shows a very different pattern in which suspension feeders have low values, roughly half of that of filter, deposit, and generalist feeders, whereas the predators and top predators are higher.

Figure ?? illustrates the correlation between the bioaccumulation of iHg, MeHg, and tHg. We observe a strong correlation ($R^2=0.49$, $p<0.001$) between MeHg and trophic levels, while no correlation is found between iHg and trophic levels ($R^2<0.02$, $P=0.474$). The linear fit of percentage of tHg that is MeHg, and the intercept of the equations for the iHg and MeHg intercept at trophic level 3.6, which means that below trophic level 3.6 the majority of tHg will on average be iHg. Hg content of phytoplankton and zooplankton is shown in Table 1. The concentration of dissolved tHg and the percentage of MeHg of dissolved tHg are compared to observations by Coquery and Cossa (1995), while the bioaccumulation of tHg in phytoplankton and zooplankton is compared to observations by Nfon et al. (2009). It must be noted that the observations by Nfon et al. (2009) are not from the North Sea itself, but from the better-studied nearby Baltic Sea. The average dissolved tHg concentration is 1.7 and 2.1, pM in the Northern and Southern North Sea, respectively. This is well within 1 standard deviation of the 1.7 ± 0.7 pM observed by Coquery and Cossa (1995). The MeHg concentration was observed to be between 0.5 and 4.3% of tHg, with an average of 3% in the North Sea. The percentage MeHg in our model is 2.3% and 2.0% on average, which falls well within that range.

In Table 2 we show the results of a linear regression taking into account both the trophic level and For bioaccumulation, we could not find separate reliable measurements of MeHg and iHg in phytoplankton and zooplankton in the North Sea, and we therefore evaluated the tHg content. This was measured in diatoms to be 10 ± 5 ng Hg mg^{-1} . This means that the feeding strategy, the relative fit of each model explains Hg bioaccumulation based on both factors. The trophic level and feeding strategy are adapted to the natural logarithms of iHg, tHg, and MeHg. This shows that we can explain the bioaccumulation of $\ln(\text{MeHg})$ very well ($R^2=0.72$) with a linear model that takes both drivers into account, while the bioaccumulation of iHg is poorly explained ($R^2=0.11$) and the bioaccumulation of tHg has an average fit ($R^2=0.46$). For mean bioaccumulation in our model in diatoms is lower, with 5.8 ng Hg mg^{-1} and 9.0 ng Hg mg^{-1} in the Northern and Southern North Sea, respectively, but still within 1 standard deviation of the measurements. Observations labeled as zooplankton and mysis were compared to our modeled microzooplankton and mesozooplankton, respectively. All modeled values fall within 1 standard deviation of the observed tHg concentration, with one exception:

mesozooplankton in the Northern North Sea, which is 13.5% more than 1 standard deviation above the observations. This is mostly driven by a high iHg content, as the MeHg content is similar in microzooplankton and mesozooplankton.

This similarity in the MeHg content of microzooplankton and mesozooplankton in our model is caused because, even though mesozooplankton have a higher trophic level, they prefer to feed on larger diatoms which have a lower MeHg bioconcentration rate than smaller flagellates, which are preferred by microzooplankton. The high iHg content, especially in the Northern North Sea, is caused by the consumption of detritus by zooplankton in the model. While there is a shortage of data on bioaccumulation at the base of the food web.

In Fig. ?? we show the pairwise comparison of the correlation between the bioaccumulation of iHg, especially in the North Sea, which complicates model evaluation, the dissolved tHg concentration, the percentage of MeHg, and the tHg content of phytoplankton and zooplankton agree well with observations. With the exception of the 13.5% elevated tHg content in Northern North Sea mesozooplankton, all modeled values fall within 1 standard deviation of the observations. Because of this, we conclude that the model replicates marine Hg cycling and bioaccumulation at the base of the food web in line with observations, with the caveat that we do not have measurements of zooplankton in the Northern North Sea to verify or reject the elevated levels in that setup. This shows a clustering in which filter and deposit feeders have similar MeHg concentrations, but MeHg concentrations are lower in grazers and suspension feeders. The strong difference between suspension and filter feeders is especially notable as they both feed on pelagic organic carbon. Overall, this demonstrates that nuanced differences in MeHg bioaccumulation where the concentration in the suspension feeders < grazers < deposit feeders < filter feeders. For iHg the pattern is different; deposit feeders, filter feeders, and grazers have similar iHg, while the iHg content of suspension feeders is much higher.

3.2 Model results

Table 1. Dissolved tHg (pM), MeHg (% of tHg), and tHg concentrations in biota (ng Hg mg⁻¹ d.w.) across North Sea regions.

	Observed	NNS	SNS
tHg _{dissolved} (pM)	1.7 ± 0.7	1.7 ± 0.26	2.0 ± 0.28
MeHg (% of tHg)	3 (0.5–4.3)	2.3 ± 0.23	2.0 ± 0.31
Diatoms tHg (ng Hg mg ⁻¹)	10 ± 5	7.0 ± 1.1	8.3 ± 1.6
Flagellates tHg (ng Hg mg ⁻¹)		13.9 ± 3.0	14.3 ± 3.0
Microzooplankton tHg (ng Hg mg ⁻¹)	37.5 ± 31.3	67.4 ± 29.3	40.3 ± 11.4
Microzooplankton MeHg (ng Hg mg ⁻¹)		7.1 ± 2.1	10.5 ± 2.7
Mesozooplankton tHg (ng Hg mg ⁻¹)	62.5 ± 12.5	86.7 ± 15.1	72.3 ± 19.6
Mesozooplankton MeHg (ng Hg mg ⁻¹)		6.9 ± 2.6	10.5 ± 1.7

3.1.1 BiomassMegabenthic biomass

Although ~~While~~ our megabenthos groups only vary in ~~feeding rate and, therefore, have no~~ their feeding strategies and lack
390 a direct real-world counterpart~~to compare to~~, it is important to ~~validate that they survive~~ ensure that all functional groups
have consistent biomass in the model and thus the results originate from the modeled interactions, and are not altered due
to unrealistically high or low modeled biomass. The yearly progression of ~~megabenthos in the Southern North Sea setup the~~
megabenthos biomass is shown in Fig. 2. Filter feeders have the highest biomass, which is up to 10 g C m^{-2} followed by deposit
feeders with ~~5 up to up to 5~~ g C m^{-2} , generalist feeders with up to 3 g C m^{-2} , and suspension feeders with up to 1 g C m^{-2} .
395 Higher trophic levels have lower biomass, with up to 0.2 g C m^{-2} for the predator and 0.5 g C m^{-2} for the top predator. This
shows that after a simulation period of 20 years, all megabenthos have a stable population, while biomass is highest at the base
of the food web. -

3.1.2 Bioaccumulation

3.2 Bioaccumulation in the model

400 The modeled bioaccumulation ~~of iHg, MeHg, and tHg is shown in Fig. 3 and the evaluation in the AS model in the Southern~~
North Sea is shown in ~~Table 3. Note Fig. 3, note~~ that the values are expressed in ng Hg mg C^{-1} , as this is the best proxy in
our model to show the dietary uptake of Hg per energy and nutrients consumed. There is a very high concentration of iHg in
the sediment, detritus, and DOM. These values are ~~0.22, 0.83, and 1.9~~ 0.60, 1.1, and 2.6 ng Hg mg C^{-1} for iHg and ~~0.038,~~
~~0.0046, and 0.0082~~ 0.089, 0.0067, and 0.012 ng Hg mg C^{-1} for MeHg. The high amount of iHg in organic carbon is in line with
405 observations that found values of up to $0.114\text{--}1.192 \text{ ng Hg mg d.w.}$ in sediment in the Scheldt estuary and that DOM strongly
binds up to $1.0 \text{ ng Hg mg}^{-1}$ (Zaferani and Biester, 2021; Haitzer et al., 2002; Muhaya et al., 1997), which would approximate
our modeled ~~1.9~~ 2.6 ng Hg mg C^{-1} if we assume a carbon to weight ratio of 1:2. These high iHg values in DOM lead to
high values in suspension feeders in both setups. The bioaccumulation of MeHg is very different from that of iHg and has
the highest bioaccumulation in the top predators and predators, followed by deposit feeders and suspension feeders. In Fig. ??
410 4a, c, and e the relationship between the trophic level and the bioaccumulation of iHg~~and MeHg in megabenthos~~, MeHg, and
tHg in megabenthos in the model is shown. There is an increase in the MeHg content with trophic levels that are not present
for iHg. For iHg, there is weak anti-correlation ($R^2 = 0.20$), which is mainly caused by the extremely high iHg content of the
low-trophic-level suspension feeders. There is no positive relationship between the bioaccumulation of tHg and the trophic
level ($R^2 = 0.02$), while this is present in the ~~allometric scaling model~~ AS model ($R^2 = 0.50$); this indicates that our base model
415 underestimates the bioaccumulation at higher trophic levels.

3.2.1 The effect of feeding strategy on bioaccumulation

~~The range and average~~

3.3 Bioaccumulation in the gobal dataset

In Table 2 we show the results of a linear regression using the global dataset taking into account both the trophic level and the feeding strategy; the relative fit of each model explains Hg bioaccumulation based on both factors. The trophic level and feeding strategy are adapted to the natural logarithms of iHg, tHg, and MeHg. This shows that we can explain the bioaccumulation of ln(MeHg) very well ($R^2=0.72$) with a linear model that takes both drivers into account, while the bioaccumulation of iHg is poorly explained ($R^2=0.11$) and the bioaccumulation of tHg has an average fit ($R^2=0.46$). Furthermore, we show the unique contributions of the fit of each driver, the partial R^2 . Note that feeding strategy and trophic level can sometimes co-correlate, especially in the case of high MeHg bioaccumulation in predators, benthic fish, and seabirds, as predators are naturally higher in trophic level than the prey they consume. The feeding strategy has an explanatory power larger than that of the trophic level for tHg and iHg, while it is similar for MeHg. Despite the limitations mentioned above, this still shows that the partial R^2 for the feeding strategy is double that of the trophic level, demonstrating the importance of the feeding strategy for the bioaccumulation of tHg at the base of the food web.

Table 2. R-squared and Partial R-squared Results for ln(THg), ln(iHg), and ln(MeHg)

Model	ln(tHg)	ln(iHg)	ln(MeHg)
Full Model R-squared	0.46	0.11	0.72
Partial R-squared (Feeding Strategy)	0.22	0.089	0.32
Partial R-squared (Trophic Level)	0.10	0.012	0.31

3.4 The allometric scaling law in high trophic level animals

In Table 3 we show the model performacne against the global dataset of the base and the AS model. This shows that if we take the allometric scaling law into account, the model results for high-trophic level animals increase considerably. In Fig. 4b, d, and e we show the relation between the natural logarithm of bioaccumulation and the trophic level of the AS model in the Southern North Sea setup. The normalized bias in the predator and top predators decreased from -0.37 and -0.82 to -0.26 and -0.24, respectively. Our base model does agree well with both observed iHg ($R^2=0.84$) and MeHg ($R^2=0.86$) in the Southern North Sea setup, but this is mostly driven by accurate predictions in the lower trophic levels while there is a normalized bias of -0.84 in the Top Predators. This is improved dramatically in the AS model with the reduction of the normalized bias of top predators to -0.32 which improves the overall R^2 of the model to >0.99 .

3.5 Comparing model and observations

3.5.1 The effect of feeding strategy on bioaccumulation

Table 3. Statistical analysis of model performance for iHg and MeHg levels by feeding strategy for Southern North Sea (SNS) and Northern North Sea (NNS). The predator and top predator of both the default setup and Allometric Scaling (AS) model is shown. For all individual feeding strategies the normalised bias is shown, and for the full model the RMSE, NRMSE, R^2_{Pearson} , and R^2_{Residual} is shown.

	SNS		NNS	
	iHg	MeHg	iHg	MeHg
<u>Suspension</u>	0.18	1.09	-0.18	0.24
<u>Filter</u>	1.48	-0.28	1.45	-0.69
<u>Deposit</u>	1.01	-0.36	0.34	-0.75
<u>Generalist</u>	1.31	-0.35	1.23	-0.73
<u>Predator</u>	0.41	-0.37	0.07	-0.77
<u>Top predator</u>	-0.22	-0.80	-0.46	-0.92
<u>Predator (AS)</u>	0.41	-0.31	0.07	-0.75
<u>Top predator (AS)</u>	-0.22	-0.12	-0.46	-0.67
Overall Model Performance				
<u>RMSE</u>	40	132	40	146
<u>NRMSE</u>	0.36	0.35	0.35	0.39
<u>R^2_{Pearson}</u>	0.61	0.86	0.24	0.94
<u>R^2_{Residual}</u>	<0	<0	<0	<0
<u>RMSE (AS)</u>	40	22.8	40	108
<u>NRMSE (AS)</u>	0.36	0.061	0.35	0.29
<u>R^2_{Pearson} (AS)</u>	0.61	>0.99	0.24	0.99
<u>R^2_{Residual} (AS)</u>	<0	0.96	<0	<0

The mean annual average and range of the ~~annual average values of the~~ bioaccumulation of iHg and MeHg in our model and the range and mean of measured iHg and MeHg are shown in Table 4. We additionally visualised in Fig. 5 the modeled values of the AS model in the Southern North Sea compared to the observations. In Fig. 5a the bioaccumulation of MeHg and in Fig. 5b the bioaccumulation of iHg is visualised. All values fall within the range of observations, except for the modeled top predator in the base model. In the ~~allometric scaling-AS~~ model, the top predator has values for both iHg and MeHg in both the Southern North Sea and the Northern North Sea that are within the range of observations. ~~Although~~ The most notable observation for iHg bioaccumulation is that, although the variation in measured iHg is considerable, suspension feeders consistently have high iHg values. ~~MeHg is bioaccumulated more efficiently and has a higher assimilation efficiency. Because of this, MeHg content is not as dependent on the feeding strategy but is mostly dependent on the trophic level. The~~ In both the Southern North Sea setup and the observation the mean MeHg is lowest in suspension feeders (9-17 and 8 ng Hg g⁻¹ d.w. respectively) while it is very similar for deposit feeders (22 and 35 ng Hg g⁻¹ d.w. respectively), filter ~~feeder~~ feeders (28 and 39 ng Hg g⁻¹ d.w.) respectively), and generalist feeders (19-26 and 40 ng Hg g⁻¹ d.w.)-It respectively). MeHg is notably higher for predators and

highest for top predators ~~with a median value of 36 and 59 in the observations with 77 and 381 ng Hg g⁻¹ d.w. respectively~~ which is close to the 54 and 337 in the AS model for predator and top predator than the 49 and 73 ng Hg g⁻¹ in the base model respectively.

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3.5.2 Trophic level vs bioaccumulation

The relationship between the trophic level and the bioaccumulation of iHg, MeHg, and tHg for the literature study is shown in Fig. ??, and for the model is shown in Fig. ?. In both the literature study and

Table 4. Comparison of modeled and observed Hg and MeHg bioaccumulation in different feeding strategies for the Southern North Sea (SNS), Northern North Sea (NNS), and field observations. Values are presented as ranges with means in parentheses. Units are ng Hg g d.w. for iHg and MeHg, and% for MeHg percentage. The bottom two rows are the predator and top predator from the AS model (AS).

	Model (SNS)			Model (NNS)			Observations		
	iHg	MeHg	% MeHg	iHg	MeHg	% MeHg	iHg	MeHg	% MeHg
Suspension	141-213 (180)	14-20 (17)	9	72-186 (125)	6-14 (10)	7	58-515 (152)	1-26 (8)	5
Filter	85-109 (97)	23-32 (28)	22	80-120 (96)	10-15 (12)	11	3-82 (39)	2-173 (39)	50
Deposit	73-93 (83)	19-26 (22)	21	41-71 (55)	7-12 (9)	14	9-113 (41)	2-231 (35)	46
Generalist	82-105 (94)	21-29 (26)	22	71-114 (90)	8-13 (11)	11	3-113 (40)	2-231 (40)	50
Predator	62-67 (65)	47-50 (49)	43	45-51 (49)	16-19 (18)	27	9-329 (46)	4-367 (77)	63
Top predator	83-91 (88)	69-76 (73)	45	51-71 (61)	26-39 (32)	34	69-266 (113)	77-895 (381)	77
Predator (AS)	45-48 (47)	52-55 (54)	54	45-51 (49)	18-20 (19)	28	9-329 (46)	4-367 (77)	63
Top predator (AS)	62-66 (64)	320-348 (337)	84	51-71 (61)	109-147 (127)	68	69-266 (113)	77-895 (381)	77

3.5.2 The statistical performance of the model

Our model estimates that suspension feeders have the highest iHg values, which is in line with observations. In our model, there is no strong correlation between trophic level and iHg bioaccumulation. In the literature study, Rthe high iHg values are caused by the very efficient Hg scavenging of small DOM particles. These small particles have the highest Hg/C ratio (as was shown in Fig. 3) and can only be consumed by suspension feeders. This leads to very high iHg and low MeHg in suspension feeders. The result that our model partially replicates the high iHg values in the suspension feeders indicates that we underestimated this effect or that additional factors were contributing to the high iHg levels found. In Orani et al. (2020), it is demonstrated that the extremely low MeHg/Hg ratio in suspension-feeding sponges may be caused by the demethylation of MeHg by symbiotic bacteria. Our study expands on this by showing that the high iHg and low MeHg values can partially be explained by the consumption of DOM by suspension feeders, but the proposed demethylation could explain why we cannot fully replicate the observations. Based on this, it is likely that the unique bioaccumulation values in suspension feeders are caused by a combination of their ability to feed on DOM, together with biochemical processes that occur in their symbiotic bacteria. Notably, while not statistically significant, our model overestimates the mean iHg values with a normalized bias of 0.61 and 0.77 for filter feeders and 0.60 and 0.60 for generalist feeders in the Southern North Sea and Northern North Sea,

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respectively. In Fig 3 we see that the majority of this iHg originates from bioconcentration. This discrepancy is described in more detail later in the paper.

The $R^2_{\text{Pearson}} < 0.01$ and in our R^2_{Pearson} is high (>0.86) for MeHg in all setups and exceeds 0.99 in the AS model, indicating that the model captures the relative differences between feeding strategies well. For iHg, performance is lower, particularly in the Northern North Sea ($R^2_{\text{Pearson}} = 0.20$). In both cases, there is a strong correlation between the bioaccumulation of MeHg and trophic level. The ability to reproduce absolute bioaccumulation is more limited. Only the AS model in the Southern North Sea shows good agreement ($R^2_{\text{Residual}} = 0.49$ for the literature study and 0.96), while all other setups yield $R^2 = 0.81$ in our model. Our model does have a lower effect on the trophic level on MeHg bioaccumulation. Figure ?? shows the relationship between the trophic level and bioaccumulation in the allometric scaling model. There is a notable increase in the correlation between the bioaccumulation of MeHg and trophic level, suggesting that using the mean of the observations would outperform the model.

This can be explained, as baseline MeHg levels vary between sampling regions. Notably, the AS model in the Southern North Sea performs well both in reproducing overall MeHg levels and in explaining variability across feeding strategies. Even when excluding predators and tHg with the trophic level compared to the base model, top predators, R^2_{Pearson} remains high (0.80), suggesting that feeding strategy effects are captured across trophic levels and are not just driven by high MeHg levels in predatorial feeding strategies. In contrast, the Northern North Sea has a high R^2_{Pearson} ($=0.94$) but low R^2_{Residual} (<0) so it captures the effect of feeding strategies while not being able to replicate absolute MeHg concentrations.

The natural logarithm of the modeled bioaccumulation of iHg, MeHg and tHg in the permanently mixed Southern North Sea using the allometric scaling model is shown against the trophic level. Notably is the stronger slope (1.24) in bioaccumulation of MeHg, which is notably higher than the slope in the default setup (0.66). The slope in the allometric scaling model overlaps much better with the observed relationship of 1.14.

3.6 The allometric scaling law in high trophic level animals

In Table 3 we show that if we take the allometric scaling law into account the model results for high-trophic level animals increase considerably. In Fig. ?? we show the relation between the natural logarithm of bioaccumulation and the trophic level of the allometric scaling model in the Southern North Sea setup. This increases the linear fit to $1.24x - 0.26$, which has a slope very similar to the observed $1.14x + 0.389$. Additionally, the normalized bias in the predator and top predators decreased from -0.37 and -0.82 to -0.26 and -0.24, respectively. This is an improvement in the model and shows that while the feeding strategy is an essential driver of Hg bioaccumulation, other differences between high- and low-trophic level animals should also be taken into account when modeling MeHg bioaccumulation.

3.6 The effect of water column mixing

3.5.1 The effect of water column mixing

Finally, if we compare our 2 setups, we find that our model predicts MeHg bioaccumulation three times higher in the shallow permanently mixed Southern North Sea setup than in the deeper seasonally mixed Northern North Sea setup. In our model, this is mostly caused because the megabenthos in the shallow Southern North Sea can feed directly from the ~~phyto-and~~ phyto- and zooplankton bloom. This gives them greater access to protein-rich food that strongly binds to MeHg. In the Northern North Sea, the ecosystem revolves around the sinking of detritus. Since detritus binds less MeHg than living material, there is a reduction in overall Hg bioaccumulation in the Northern North Sea compared to the Southern North Sea, but especially for MeHg. This means two things. First of all, in the well-mixed Southern North Sea, filter feeders have a competitive advantage as they can filter out fresh food and feed on relatively high trophic level zooplankton. Filter feeders have the highest MeHg values at the base of the benthic food web, and therefore a higher concentration of filter feeders will lead to a higher fraction of filter feeders in the predator diet and thus more MeHg. Additionally, since the filter feeders feed on living pelagic material with higher MeHg values, the filter feeders themselves also have higher MeHg. Thus, predators and, consequently, the top predators have higher MeHg values in the Southern North Sea compared to the Northern North Sea as a result of the increased water column mixing. In Fig. 6 we show the correlation between the natural logarithm of bioaccumulated Hg and the trophic level in the Northern North Sea. Interestingly, the trophic level of megabenthos is higher in the Northern North Sea, while the bioaccumulation level is lower. This is because the detritus is cycled more often in the pelagic before it is consumed by megabenthos, ~~because~~ because the detritus is in constant equilibrium with the water column for its partitioning of Hg and MeHg, this does not translate to higher bioaccumulation. This lower bioaccumulation results in lower concentrations of MeHg in high trophic levels of fish.

4 Comparing model and observations

~~First, we compare the values for iHg. The probability that the model is within 2 standard deviations of the observation is >0.95 in all cases. In most cases, the BF10 factor is <0.1 , which provides strong evidence in favor of the null hypotheses, indicating that the distribution of the model output closely matches the distribution of the observations and suggests that the model accurately reproduces the properties of the observations. The only instance where the BF10 factor >0.1 for iHg is for suspension feeders. This comparison yields several interesting results. Our model estimates that suspension feeders have the highest iHg values, but comparing our model with field observations shows that the observed values are even higher. In our model, the high iHg values are caused by the very efficient Hg scavenging of small DOM particles. These small particles have the highest Hg/C ratio (as was shown in~~

530 3.1 The role of the feeding strategy on MeHg bioaccumulation in a single case study

In addition to using the global bioaccumulation dataset to evaluate our hypothesis that the feeding strategy is a key driver of bioaccumulation, we also evaluate if our hypothesis holds true when analyzing a comprehensive published dataset from a single

study. The fit of the linear model against the natural logarithm of the bioaccumulated MeHg based on the data published by McClelland et al. (2024) is shown in Fig. 3)-7. The R^2 is similar with 0.43 and can only be consumed by suspension feeders. This leads to very high iHg and low MeHg in suspension feeders. The result that our model partially replicates the high iHg values in the suspension feeders indicates that we underestimated this effect or that additional factors were contributing to the high iHg levels found. In Orani et al. (2020), it is demonstrated that 0.45 in the CB and MT respectively, while the bioaccumulation is a bit lower in the extremely low MeHg /Hg ratio in suspension-feeding sponges may be caused by the demethylation of MeHg by symbiotic bacteria. Our study expands on this by showing that the high iHg and low MeHg values can partially be explained by the consumption of DOM by suspension feeders. CB ($\log(\text{MeHg}_{\text{BA}})=0.137+1.14*\text{TL}$) compared to that in the MT ($\log(\text{MeHg}_{\text{BA}})=0.256+1.39*\text{TL}$), where MeHg_{BA} is the bioaccumulated MeHg in ng Hg mg^{-1} d.w. and TL is the trophic level. The influence of the feeding strategy on MeHg bioaccumulation based on the results of McClelland et al. (2024) is shown in Table 5. While the only significant effect is deposit feeders in the MT having less MeHg than would be expected on their trophic positions, some other effects are consistent, albeit not significant in both locations. The strongest effect is that filter feeders have consistently higher MeHg (residuals are 0.7 in the CB and 0.8 in the MT), while deposit feeders have lower MeHg (residuals are -0.2 in the CB and -0.5 in the MT). The results of the same analyses for phyla are shown in Table 6. Here we see two consistent significant effects. Molluscs have elevated MeHg levels (residuals are 0.61 in the CB and 0.51 in the MT) while arthropods have reduced MeHg values (residuals are -0.35 in the CB and -0.30 in the MT). The percentage difference in MeHg bioaccumulation per feeding strategy is visualised in Fig. 8 and per phyla in Fig. 9. The average percentage difference between observed and the expectation based on trophic level is 102% and 128% in the CB and MT respectively for filter feeders, while deposit feeders have 19 and 37% less MeHg than would be predicted based on trophic level alone in the CB and MT respectively. In the analysis per phylum, we see that molluscs have highly elevated MeHg levels with an increase of 66% and 85% respectively in the CB and MT. The largest reduction in observed MeHg compared to the predicted values based on trophic level is in arthropods; here there is a decrease compared to the predicted values of 29% and 26% in the CB and MT respectively.

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Table 5. Mean residuals ($\pm$ SE) of $\log(\text{MeHg})$ by feeding strategy and region, after trophic level correction. Significant deviations ($p < 0.05$) are marked with *.

Region	Feeding Strategy	<i>n</i>	Mean Residual $\pm$ SE	p-value
CB	Deposit feeder	16	-0.208 ± 0.181	0.268
CB	Filter feeder	3	0.704 ± 0.286	0.133
CB	Predator	6	0.203 ± 0.331	0.568
MT	Deposit feeder	15	-0.467 ± 0.159	0.011*
MT	Filter feeder	5	0.824 ± 0.395	0.105
MT	Generalist	3	-0.143 ± 0.319	0.698
MT	Predator	12	0.277 ± 0.226	0.247

Table 6. Mean residuals ($\pm$ SE) of log(MeHg) by phylum and region, after trophic level correction. Significant deviations ($p < 0.05$) are marked with *.

Region	Phylum	<i>n</i>	Mean Residual $\pm$ SE	p-value
CB	Annelida	6	0.229 $\pm$ 0.424	0.612
CB	Arthropoda	11	-0.349 $\pm$ 0.137	0.0294*
CB	Echinodermata	3	-0.198 $\pm$ 0.584	0.767
CB	Mollusca	5	0.611 $\pm$ 0.211	0.0446*
MT	Annelida	5	-0.405 $\pm$ 0.377	0.343
MT	Arthropoda	12	-0.304 $\pm$ 0.111	0.0196*
MT	Echinodermata	5	-0.188 $\pm$ 0.509	0.730
MT	Mollusca	13	0.509 $\pm$ 0.231	0.0482*

The results of the final analyses are shown in Table 7. Despite the lower sample size, which reduces statistical power, the results indicate that filter feeders consistently have higher MeHg levels than predicted based on their trophic position and phyla, while deposit feeders tend to have lower MeHg concentrations. These results are stronger in the MT with a change of 118% and -40% in filter and deposit feeders respectively than in the CB with a change of 7.2% and -14.8% in filter and deposit feeders respectively. It must be stated that this final analysis is included to address potential concern between the co-correlation of phyla and feeding strategy, but the ~~proposed demethylation could explain why we cannot fully replicate the observations. Based on this, it is likely that the unique bioaccumulation values in suspension feeders are caused by a combination of their ability to feed on DOM, together with biochemical processes that occur in their symbiotic bacteria. Notably, while not statistically significant, our model overestimates the mean iHg values with a normalized bias of 0.61 and 0.77 for filter feeders and 0.60 and 0.60 for generalist feeders in the Southern North Sea and Northern North Sea, respectively. In Fig 3 we see that the majority of this iHg originates from bioconcentration. This discrepancy is described in more detail later in the paper~~problem of the reduced sample size has to be addressed. In the CB, where the increase in MeHg in filter feeders is rather low after correcting for both trophic level and feeding strategy, there are only three filter feeders, which are molluscs, and they make up 3/5 mollusc samples in this location, meaning that results should be seen with skepticism as filter feeders and molluscs have too much overlap. On the other hand, in the MT, there are five filter feeders from multiple phyla (Mollusca and Echinodermata) and the effect is considerably stronger with filter feeders having 118% more MeHg than would be expected based on their trophic level and phyla.

4 Discussion

4.1 The role of feeding strategy on the bioaccumulation of MeHg

Table 7. The effect of feeding strategy on MeHg bioaccumulation per Region compared to the prediction accounting for both trophic level and feeding strategy. Significant ($p < 0.05$) is marked with *. There is still a consistent increase in filter feeders and a consistent decrease in deposit feeders. This is effect is larger in the MT with a relative percentage increase of 118% in filter feeders and a decrease of 40% in deposit feeders.

Feeding Strategy	% Diff (MT)	p-value (MT)	% Diff (CB)	p-value (CB)
Deposit feeder	-40.0	0.034*	-14.8	0.888
Filter feeder	118.0	0.034*	7.2	0.888
Generalist	-25.9	0.563	—	—
Predator	3.0	0.895	9.4	0.888

Overall we find that the feeding strategy plays an important role in the bioaccumulation of MeHg in our model, the global dataset, and the single dataset published by McClelland et al. (2024). Because of this, we find it convincing that the role of the feeding strategy in MeHg bioaccumulation deserves further attention in both modeling and empirical studies.

4.2 The AS model

Our base model fails to reproduce the high values in the top predators, but this is improved in the allometric scaling-AS model. The normalized bias is reduced from -0.84 to -0.32, but the BF10 factor is reduced only from 0.53 to 0.37. This shows that while the modeled mean is closer to the observed mean, there is no strong indication that the modeled values are from the same distribution as the observations. In the allometric scaling-0.80 to -0.22. In the AS model, we get a linear relationship of $1.24x - 0.26$ ($R^2=0.93$), which is very similar has a similar slope to the $1.14x + 0.389$ found in the field observations. The drastic 0.387 and $1.39 + 0.256$ found in CB and MT station of the McClelland et al. (2024) dataset respectively. The improvement in the allometric scaling-AS model compared to the base model indicates that the lower MeHg release rates in high-trophic-level animals should be taken into account. We tried to run the model with the lower MeHg release rate in all megabenthos, but this resulted in unrealistically high values in both the base and top of the food web, so we cannot just use the lower MeHg release rate at every trophic level. Because of this, we conclude that the in addition to the feeding strategy, the difference in the release rate of MeHg-related MeHg related to body size, metabolic rate, or activity also likely has a significant contribution to the high MeHg values in high-trophic-level animals.

The last difference between our model and observations is that our model deposit feeders have considerably higher MeHg bioaccumulation compared to generalist feeders, filter feeders, and suspension feeders. This is not the case in the field observations where deposit feeders are similar to filter feeders and generalist feeders in MeHg. Interestingly, we already gave deposit feeders a lower assimilation efficiency compared to other functional groups. Since we do not model actual organisms, this difference can be caused by other differences in the organisms, such as their metabolic rate, or the assimilation efficiency of deposit feeders should be even lower. A final option is that the Meray v2.0 model is mainly focused and verified on pelagic Hg cycling, so we potentially overestimate the sediment MeHg content or the AE of sediment-bound MeHg.

The natural logarithm of the modeled bioaccumulation of iHg and MeHg in the permanently mixed Northern North Sea setup. While the slope is somewhat similar (0.60 vs 0.66) the overall bioaccumulation of MeHg is notably lower than in the permanently mixed Southern North Sea.

600 5 Bioconcentration of iHg

~~The~~

4.1 Bioconcentration of iHg

The largest bias in our model, which remains uncorrected in the ~~allometric scaling AS~~ model, is the overestimation of iHg in the filter ~~, deposit,~~ and generalist feeders. Although the modeled iHg values are not out of the observed range, the consistently high
605 normalized bias indicates that the model overestimates the ~~bioaccumulation~~ bioaccumulation of iHg. In Fig. 3 we can see that the vast majority of iHg in filter ~~, deposit,~~ and generalist feeders originates from bioconcentration. The most important driver of bioconcentration is the ratio between uptake and release rate, or the uptake-release ratio. Our model has an uptake-release ratio of $210 \text{ l g}^{-1} \text{ d.w.}$ This is derived from Tsui and Wang (2004), as it represents the lowest ratio found in the literature. The exact rate was obtained by withdrawing the modeled carbon excretion rate and deducting this from the measured iHg release
610 rate to have an ~~iHg specific release rate,~~ iHg-specific release rate; this rate was found to be 0.04 d^{-1} , as presented in Amptmeijer et al. (2025). Other studies such as Pan and Wang (2011) found higher uptake-release ratios between 424 and $781 \text{ l g}^{-1} \text{ d.w.}$

~~To address this uncertainty, we tested an alternative scenario in which we doubled the bioconcentrated iHg release rate, 0.04 d^{-1} to 0.08 d^{-1} , thus lowering the uptake-release ratio to $105 \text{ l g}^{-1} \text{ dw.}$ This adjustment resulted in a normalized bias in the Southern North Sea of -0.09 , 0.15 and 0.15 for the deposit, filter, and generalist feeders, respectively. This shows how the
615 uptake and release rates of iHg can impact the iHg content of megabenthos, and that the uptake-release ratio used in the model is likely overestimated.~~

The discrepancy between the modeled and observed iHg can be caused by several factors. First, iHg concentrations in North Sea megabenthos could be higher than those reported in other coastal zones. However, there are no empirical data to support or
620 invalidate this conclusion at the moment. Secondly, translating experimentally obtained uptake and release rates to observations of iHg might depend on the drivers that are not captured in the model. In either case, it is hard to verify the root of this high normalized bias, as the bioaccumulation of iHg is comparatively understudied compared to the bioaccumulation of MeHg, both in models and empirical studies.

5 Model limitations

~~Our model is designed to have the same~~

625 4.1 Model structural limitations

The GOTM-MERCY-ECOSMO coupled system captures the influence of feeding strategy on MeHg bioaccumulation, but performance differs between regions. The Southern North Sea setup performs well in pelagic Hg cycling and benthic bioaccumulation, whereas the Northern North Sea setup underestimates MeHg in all benthic groups and shows unexpectedly high mesozooplankton iHg, which cannot be validated due to a lack of data. The model predicts lower MeHg bioaccumulation in deeper water, which is not true for the observations by McClelland et al. (2024). This suggests that MeHg fluxes from the pelagic to the benthic system are underestimated. In shallow waters, megabenthos can feed directly on the phytoplankton and zooplankton blooms, which leads to a strong benthic-pelagic exchange of organic carbon and Hg. In deeper waters, megabenthos mainly rely on detritus that sinks from the euphotic, which, in our model, carries less MeHg. But the higher performance in shallow conditions combined with the reduced performance in deeper conditions indicates that the model could be improved in areas driving deep water MeHg bioaccumulation, such as sediment Hg chemistry, deep-water Hg speciation, the benthic-pelagic coupling, or the transport of Hg to deeper water due to the sinking of organic material.

4.2 Data-related limitations

Combining the results of the model and the literature studies is difficult due to the high uncertainty in most drivers, including the organic material content of dry weight, and the result should be viewed with skepticism. For example, the data analyses by McClelland et al. (2024) were prepared to mimic consumption by predators: for small arthropods, their skin was not removed, but for gastropods and bivalves, the shell was not taken into account for the weight as predators would typically not eat this. The concentration of MeHg per unit energy is arguably the key measure in bioaccumulation. Predators need to ingest a specific energy amount, so if a prey is composed of half organic material and half non-organic components, such as shell, its MeHg content per dry weight is halved. However, predators would consume double the dry weight to obtain the energy, and thus the same MeHg. In general, the energy appears to be consistent with Ash Free Dry Weight (AFDW), as such ideally we would normalize all measurements of MeHg bioaccumulation per AFDW (Weil et al., 2019). Unfortunately, doing this conversion reliably on published data is not possible as AFDW varies with the age and body size of animals, which information is not always registered and made available (Eklöf et al., 2017).

4.3 Potential improvements

The model has the same rates for all megabenthos groups. This allows us to isolate the effect of the feeding strategy, but it should be taken into account that this also means that the model is limited in its ability to predict bioaccumulation of iHg or MeHg in specific animals. ~~Furthermore, when our model is compared to the data in the literature, it should be noted that field studies measuring Hg at the base of the food web are rare.~~ Our model is run in the North Sea, while most of the field observations are from different regions. ~~This is somewhat mitigated by aggregating large amounts of data and comparing it to our idealized water column scenarios to identify general trends, but it must be noted that comparison can always be improved by having more data to compare it to. The first and most notable limitation is that some field studies that analyzed megabenthos benthos did not differentiate between iHg and MeHg and that most studies did not estimate the trophic level of means that~~

660 this study should be seen as a hypothesis-generating work that identifies the role of feeding strategies on the bioaccumulation of iHg and MeHg as a potential direction for further empirical studies, rather than a complete classification. Based on this work, however, it appears that the inclusion of megabenthos with different feeding strategies could improve the performance of MeHg bioaccumulation models. At the same time, our analyses demonstrate the underperformance of the model in simulating the deep water benthic-pelagic coupling, which indicates that the animals. This is especially problematic when comparing Hg levels with our model.

665 The difference in bioaccumulation between the permanently mixed Southern North Sea setup and the seasonally mixed Northern North Sea setup is caused by several assumptions in the model. Notably, instant partitioning between dissolved Hg and Hg associated with detritus. The complication with this is that the partitioning coefficients are based on the $\log(k)^{ow}$ values of Hg, while it has been demonstrated that the binding of Hg to organic material also depends on its sulfate content (Seelen et al., 2023). Since the performance of the ECOSMO E2E model is a Redfield-ratio-based model, we did not take the
670 freshness of the organic material into account, but this might play a role and should be investigated in further studies.

A final interaction that we did not take into account is *in vivo* Hg speciation. This is not taken into account because at the moment there is too much uncertainty about the role this plays in Hg bioaccumulation. However, the earlier mentioned demethylation in sponges by Orani et al. (2020) and additional studies that demonstrate Hg speciation in cuttlefish by Gente et al. (2023) and Hg methylating bacteria in copepods by Gorokhova et al. (2020) indicate that the bioaccumulation of iHg and MeHg may
675 not be fully independent processes. These could be important interactions, and especially *in vivo*, methylation could be a driver of high MeHg values, but more empirical studies must be performed on the rates of this before this can be incorporated in models in a meaningful way. E2E-MERCY-GOTM coupled system should be critically evaluated before it can be used for predictive bioaccumulation modelling in deeper water.

5 Summary and conclusion

680 In this study, we analyze the role of the trophic level and the feeding strategy on the bioaccumulation of iHg and MeHg. We did this by performing a literature study and running a fully coupled 1D model in two idealized setups representing two different hydrodynamics-hydrodynamic regimes in which macrobenthic-megabenthic communities can live. Our study estimates that the trophic level predicts up to 32% of the variability of MeHg in the benthic food web. If we include both the feeding strategy and the trophic level, this increases to 72%. We show that several feeding strategies have significant differences.

685 We show that there are notable differences between feeding strategies. iHg is higher in suspension feeders and MeHg is low in suspension feeders and grazers, while filter feeders have the highest MeHg followed by deposit feeders. Our model expands on this by demonstrating that we can accurately model the bioaccumulation of iHg and MeHg at the base of the food web by only taking the feeding strategy into account.

690 Because We find it convincing that both our model results, the literature study in which we aggregate all measurements, and the literature study where we take samples from a single study all suggest similar patterns where feeding strategy is an important driver of bioaccumulation at the base of the food web, even if these results should be seen with skepticism due to the

large uncertainty in the model. Because feeding strategy in our base model ~~agrees well with both~~ correlates well with observed iHg ($R^2=0.860.61$) and MeHg ($R^2=0.940.86$) in the Southern North Sea setup, ~~we conclude that you can accurately model~~ the it appears that the feeding strategy is a key driver controlling the bioaccumulation of both iHg and MeHg at the base of the food web ~~based on the feeding strategy~~. However, this strong performance is mostly because 4 out of our 6 megabenthos groups are low trophic level non-predators, and our base model starts to underperform considerably in its ability to model MeHg bioaccumulation in higher trophic levels. This problem is solved by taking into account the allometric scaling law and assuming that MeHg removal from the organism is not linked to the total but rather to the base metabolic rate. Because of this, we accept our hypothesis that the feeding strategy is an essential driver of the bioaccumulation of iHg and MeHg in low-trophic-level animals, but other differences in the organisms between high- and low-trophic-level animals should also be taken into account when predicting MeHg values in high-trophic-level fish. Our model and observation focus on lower-trophic-level benthic invertebrates, with some high-trophic-level animals added to create context. The importance of this for the bioaccumulation of MeHg in animals of high trophic levels is that all biomagnification is an exponential function starting at the base of the food web. Therefore, a change in MeHg at the base of the food web will correspond to a similar relative increase at the top of the food chain. Because the feeding strategy has such a large impact on the base of the food web, high trophic-level animals ~~would~~ could have considerably different MeHg values depending on the species composition of the base of the food web.

Interestingly, despite the lower biomagnification potential of iHg, its high abundance in certain low-trophic-level animals can lead to higher tHg in ~~low trophic level~~ low-trophic-level animals than in higher-trophic-level animals. This discrepancy can distort risk perception, as safety assessments often rely on tHg measurements that do not distinguish between iHg and MeHg. ~~Such animals~~ Animals, such as suspension-feeding bivalves, may have high Hg values while remaining safe for human consumption. Our findings demonstrate the importance of Hg speciation data in marine organisms to help improve food safety guidelines and inform regulatory policies.

5.1 Societal relevance & future work

Our study highlights the critical role of benthic diversity in driving MeHg bioaccumulation. Both trophic interactions and the feeding strategy significantly influence MeHg bioaccumulation, which has important implications for seafood safety and fisheries management. Understanding these processes can help explain the spatial and temporal variability in the MeHg content of fish, which is crucial for policymakers to develop effective regulations that safeguard human health and marine ecosystems.

~~Our findings~~ Filter feeders and molluscs typically accumulate more MeHg than other organisms at similar trophic levels. This pattern is consistent not only in our models but also in available data. This raises a hypothesis that expanding bivalve populations, as seen in mussel or oyster farming, might affect MeHg bioaccumulation in higher trophic levels. This is supported by the observations that fish in lakes invaded by zebra mussels have higher Hg levels than fish in lakes without zebra mussels Blinick et al. (2024). However, such ecological alterations also impact other bioaccumulation factors like biomass distribution and trophic interactions. While our findings support the role of filter feeders and molluscs in MeHg dynamics and higher

725 bioaccumulation in top predators, the complexity of ecological situations requires further case-specific studies to understand if and when bivalve communities lead to increased MeHg transfer.

Modeling studies can help our understanding of the factors influencing MeHg bioaccumulation, but the ability to accurately predict MeHg bioaccumulation needs to be carefully validated. Our findings reveal that filter-feeding molluscs and DOM-utilizing suspension feeders have different Hg bioaccumulation patterns compared to other megabenthos. Modeling bivalve aquaculture or DOM-consuming suspension feeders can help explore their potential role in altering MeHg bioaccumulation. Understanding how functional traits like feeding strategy influence MeHg transfer remains key to improving both predictive models and environmental risk assessments.

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Our findings suggest that fish from food webs dominated by filter feeders would have the highest MeHg content, since filter feeders have the highest MeHg content in both our model and observations. It also creates an indication that the introduction of bivalve communities in the form of mussel or oyster farming could increase MeHg levels in higher food chains. However, such changes in the ecosystem would inevitably change other factors in the ecosystem, including biomass and trophic interactions that are also essential drivers for MeHg bioaccumulation. ~~This means that~~ While our model should be seen as a hypothesis-generating work that requires empirical validation, it does suggest that case-by-case studies are needed to fully understand how changes in the base of the food web will affect the concentration of MeHg in high trophic level fish.

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~~We~~ Based on our results, we strongly recommend targeted field studies that systematically measure iHg, MeHg, and trophic levels in diverse marine communities to assess how the structure of the food web influences the bioaccumulation of MeHg in seafood.

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Readability suggestions for this paper were generated using rAI tools such as ChatGPT (OpenAI), while AI-based spell checks such as Grammarly and Writefull were used to correct spelling. In addition, AI tools helped optimize the R and Python scripts and provide coding suggestions. All suggestions were implemented only after critical manual evaluation. Finally, Google Scholar and Perplexity were used to find sources for literature research, which were consequently manually read, verified, and cited.

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Author contributions

750 The contributions per author are listed in Table 8.

Conflict of interest

None of the authors declare any conflict of interest.

Table 8. Contributions per Author. Authors are: David Johannes Amptmeijer (DA), Andrea Padilla (AP), Sofia Modesti (SM), Prof. Dr. Corinna Schrum (CS), and Dr. Johannes Bieser (JB).

<u>Contributor role</u>	<u>Role definition</u>	<u>Authors</u>
Conceptualisation	<u>Conceptualized the study</u>	<u>DA, JB, CS</u>
	<u>Developed the research objectives</u>	<u>DA, JB, CS</u>
Methodology	<u>Implementation of the model into FABM</u>	<u>DA</u>
	<u>Compiled the database of megabenthos iHg and MeHg observations</u>	<u>DA, AP</u>
Evaluation	<u>Evaluated the model performance against observations</u>	<u>JB, DA, AP, SM</u>
	<u>Performed statistical tests on the observations</u>	<u>DA, AP, SM</u>
Writing	<u>Writing of the original draft</u>	<u>DA</u>
	<u>Review of the original draft and quality control</u>	<u>AP, SM, JB, DA</u>
<u>Supervision</u>	<u>Supervised the development of the work</u>	<u>CS, JB, DA</u>
<u>Funding acquisition</u>	<u>Acquired funding via the GMOS-Train ITN</u>	<u>JB</u>

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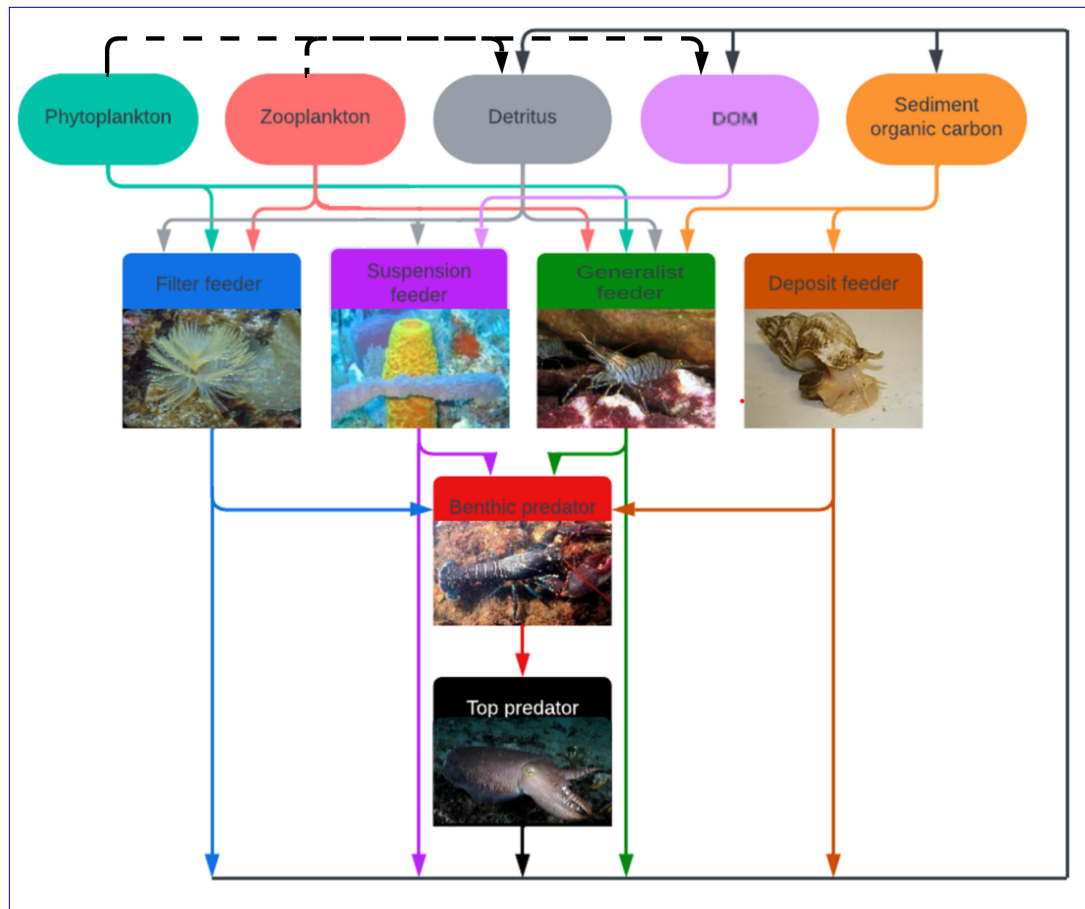


Figure 1. The overview of the modeled megabenthos functional groups and how they interact with each other and functional groups in the ECOSMO E2E model. There are 5 macrobenthic-megabenthic functional groups. The filter feeder feeds on pelagic detritus, zooplankton, and phytoplankton. The suspension feeders feeds-feed on pelagic detritus, phytoplankton, zooplankton, and DOM. The generalist feeds on phytoplankton, zooplankton, pelagic detritus, and sediment organic carbon. The deposit feeder feeds on sediment organic carbon. The benthic predator feeds on the other 4 megabenthos functional groups and the top predator solely feeds on the benthic predator. The arrows indicate trophic interactions where the arrow goes from the prey to the predator and the arrows have the same colour as the prey. The black lines represent loss of organic material due to mortality. When megabenthos die, their organic carbon is transferred to pelagic DOM and detritus, as well as the sediment, shown by the solid black arrow. In contrast, when pelagic organisms die, their organic carbon is transferred to DOM and detritus, indicated by the dotted black arrow. Several sub-images have been used in this image. Sources of the images are: filter Filter feeder: *Sabella spallanzanii* (photo by Diego Delso, suspension-CC BY-SA 4.0, via Wikipedia), Suspension feeder: *Aplysina fistularis* (photo by Twilight Zone Expedition Team 2007, generalist-NOAA-OE, CC BY 2.0, via Flickr), Generalist feeder: *Crangon crangon* (photo by Etrusko25, deposit-Public Domain, via Wikipedia), Deposit feeder: *Buccinum undatum* (photo by Oscar Bos / Ecomare, benthic-CC BY 4.0, via Wikipedia), Benthic predator: *Hommarus gammarus* (photo by Bart Braun, and-top-Public Domain, via Wikipedia), Top predator: *Sepia officinalis* (photo by Nick Hobgood, CC BY-SA 3.0, via Wikipedia).

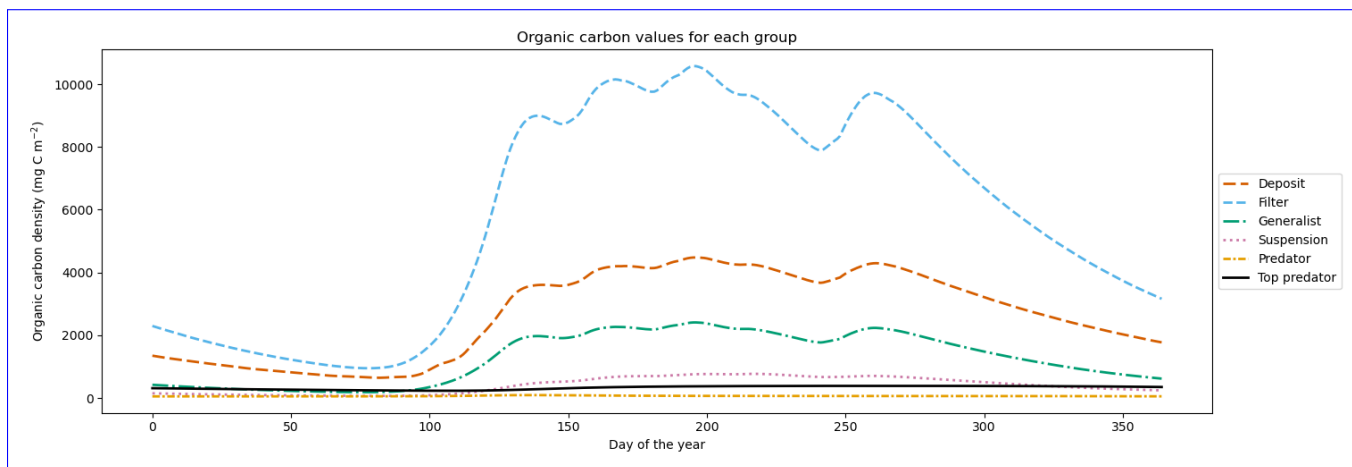


Figure 2. Megabenthos biomass in the modeled Southern North Sea, dominated by filter feeders, followed by deposit feeders, generalist feeders, suspension feeders, predators, and top predators. Biomass fluctuates between 10 and 15 gC m⁻² and all functional groups have stable populations

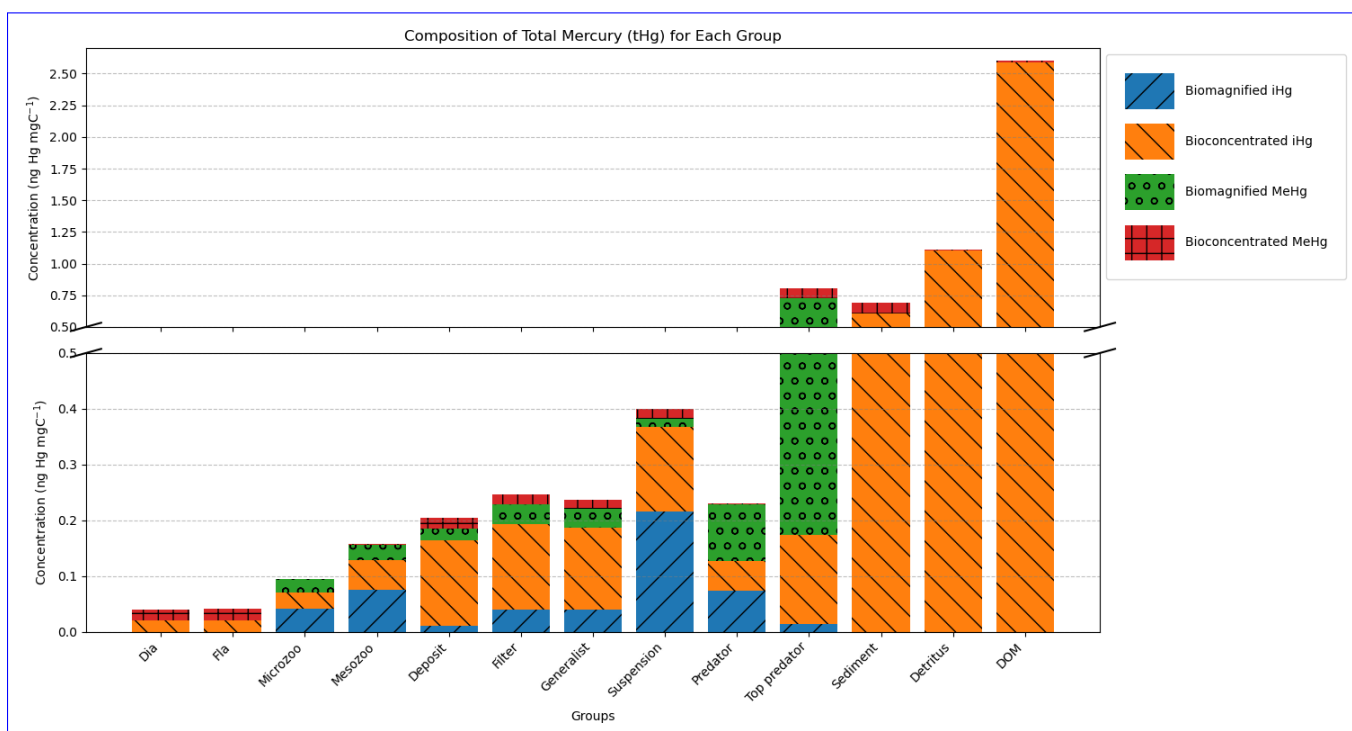


Figure 3. Modeled bioconcentration and biomagnification of iHg and MeHg. Partitioning to detritus and DOM is colored as bioconcentration. The y-axis is cut to show the high and low values. Notably is the high iHg to mgC ratio of detritus and DOM, leading to elevated iHg in suspension feeders. Additionally, higher trophic level animals have higher biomagnified MeHg

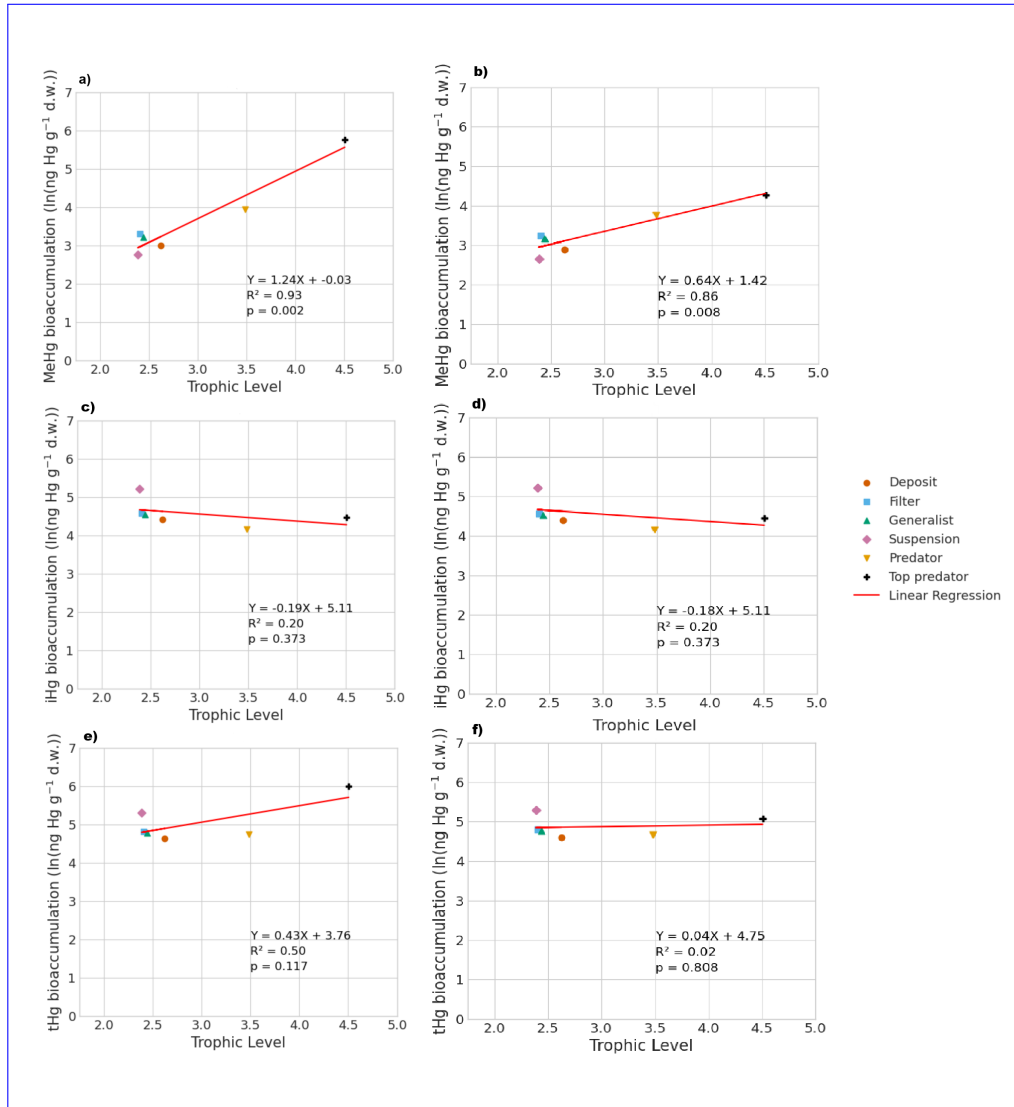


Figure 4. The influence of trophic level on the bioaccumulation of MeHg, iHg, and tHg in both the AS (panels a, c, e) and the base model (panels b, d, f). In the AS model, the relationship with trophic level is stronger, where $\ln(\text{MeHg}) = 1.24\text{TL} - 0.03$, compared to the base model, which is $\ln(\text{MeHg}) = 0.64\text{TL} + 1.42$. TL represents trophic level, and MeHg is expressed in $\text{ng Hg g}^{-1} \text{d.w.}$ For iHg, the bioaccumulation patterns are nearly identical, with $\ln(\text{MeHg}) = -0.19\text{TL} + 5.11$ for the AS model and $\ln(\text{MeHg}) = -0.18\text{TL} + 5.11$ for the base model, both showing a weak inverse correlation with trophic level, largely due to higher iHg levels in low trophic level feeders. In terms of tHg, there is a higher increase in bioaccumulation in the AS model ($\ln(\text{MeHg}) = 0.43\text{TL} + 3.76$) compared to the base model ($\ln(\text{MeHg}) = 0.04\text{TL} + 4.175$), driven by the stronger association between MeHg and trophic level in the AS model.

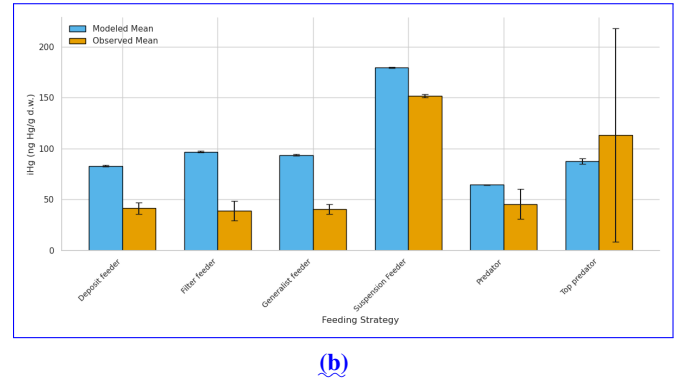
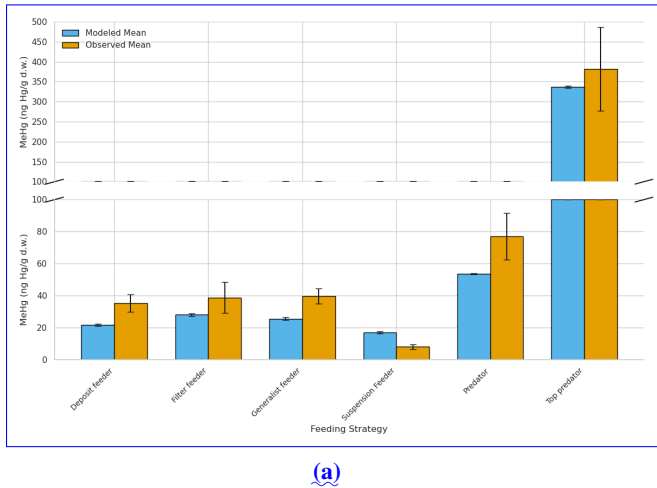


Figure 5. Comparison of bioaccumulation across feeding strategies between the Southern North Sea AS model and observations. The bars represent the mean with the error bar showing 1SE. Figure 5a) shows MeHg bioaccumulation. Notably is that Top predators show the highest levels, followed by predators, with generalists and filter feeders at intermediate levels and deposit feeders at lower levels. Suspension feeders have the lowest MeHg. 5b) shows iHg Bioaccumulation. Suspension feeders show increased iHg, while all other categories except top predators are overestimated by the model. Top predators have high observed iHg not fully captured by the model.

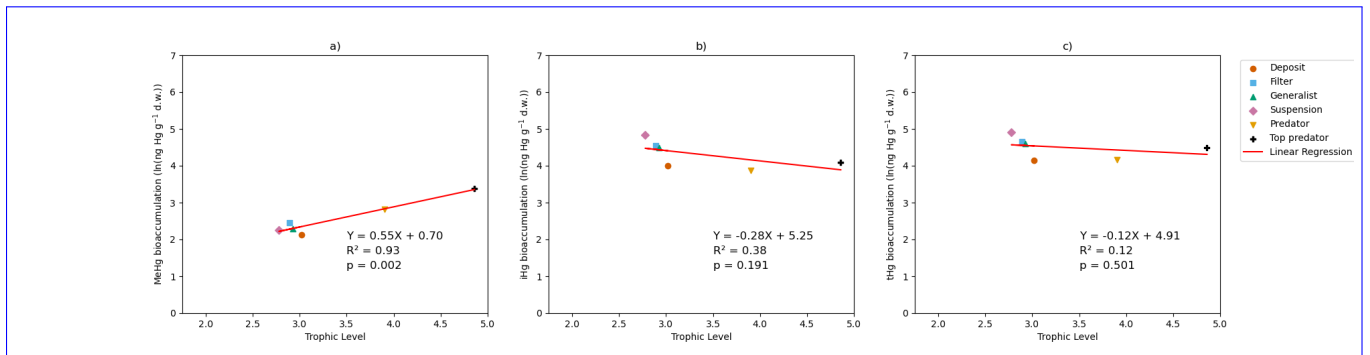


Figure 6. The natural logarithm of bioaccumulation for a) MeHg, b) iHg, and c) tHg in the permanently mixed Northern North Sea model shows that while the slope for MeHg bioaccumulation is comparable in the Northern and Southern North Sea with a slope of 0.55 and 0.64 respectively, its overall level of MeHg bioaccumulation is lower than in the Southern North Sea. Similar as in the Southern North Sea, there's no significant correlation between trophic level and iHg bioaccumulation.

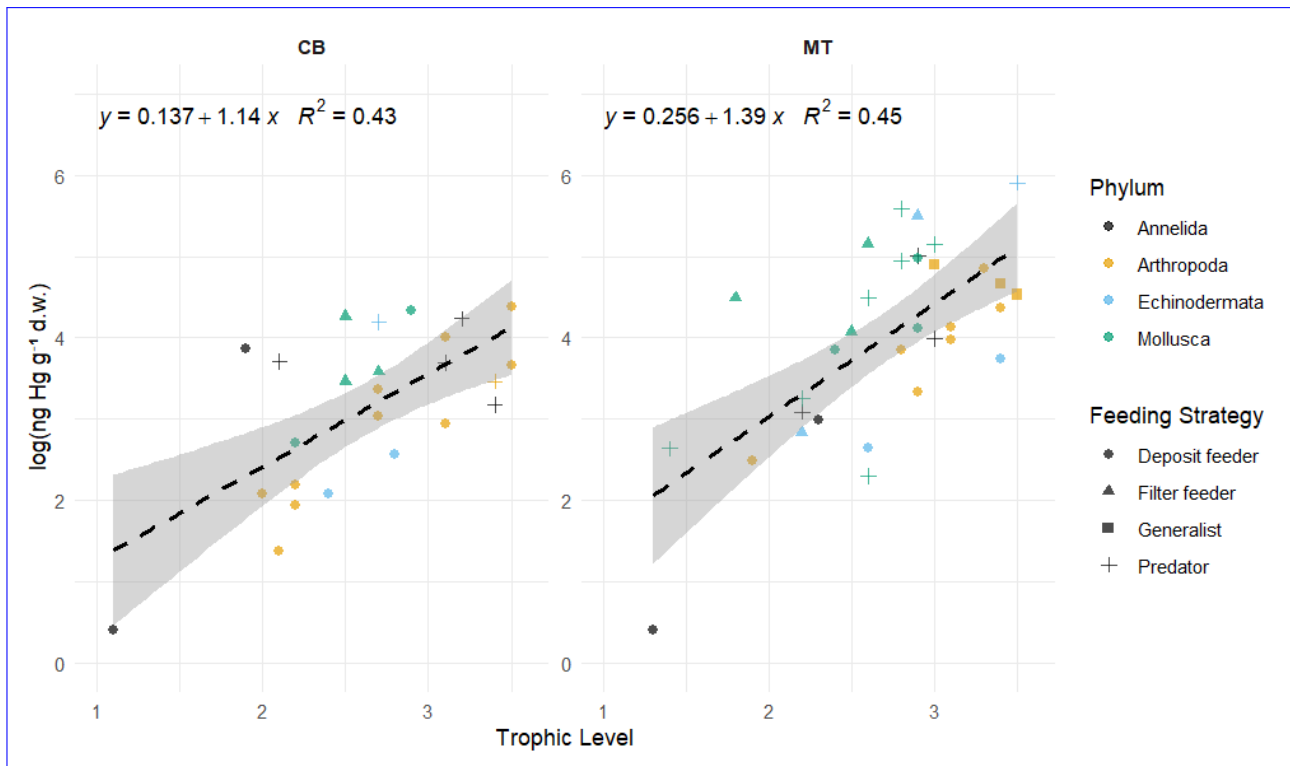


Figure 7. The linear fitted model between the natural logarithm of the bioaccumulated MeHg in $\text{ng Hg mg}^{-1} \text{ d.w.}$ and the Trophic Level in the data presented by McClelland et al. (2024). For extra clarity the different Phyla shown with different colors while the different feeding strategies are marked with different symbols. In both the CB and MT setups there positive relationship between trophic level and the bioaccumulation of MeHg, but R^2 is only 0.43 and 0.45 in the CB and MT respectively, so it does not explain the full variation in bioaccumulation.

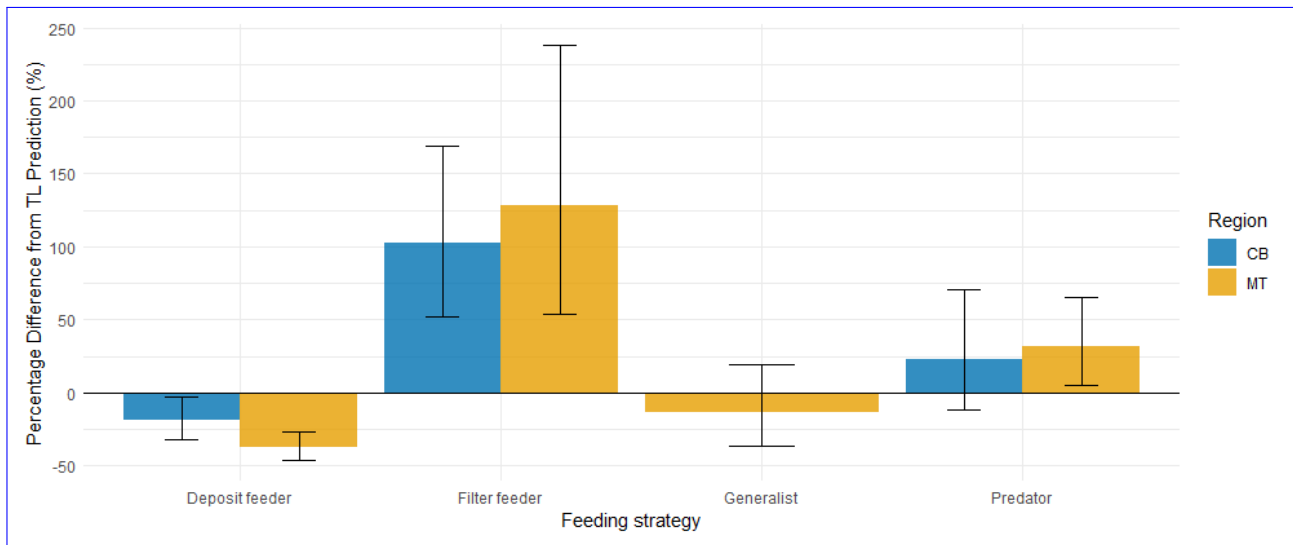


Figure 8. Percentage difference from trophic level predicted MeHg concentrations by feeding strategy, with error bars showing ± 1 SE. In both CB and MT regions, filter feeders have elevated MeHg levels relative to trophic level based expectations, while deposit feeders are reduced. Predators display higher MeHg than predicted, though the effect is smaller than in filter feeders; in CB, this increase does not exceed one SE. Generalist feeders have a slight reduction compared to expectations, but this is well within one SE, and were not present in CB for cross-region comparison.

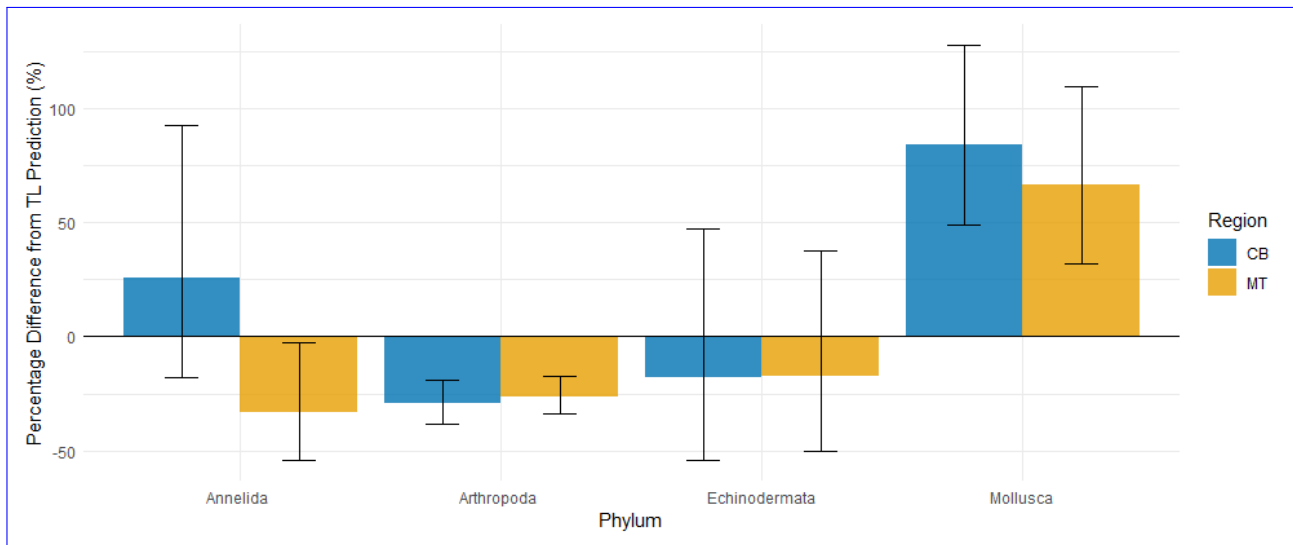


Figure 9. Percentage difference from the predicted MeHg bioaccumulated based on trophic level per phyla, the error bars represent ± 1 SE. The notable phyla are Mollusca and Arthropoda, while Mollusca have a notable increase in MeHg bioaccumulation compared to the prediction of 85% and 66% respectively in the CB and MT, there is a reduction of 26% and 29% in Arthropoda in the CB and MT respectively. Annelida are inconsistent with an increase in the CB and decrease in the MT compared to the predictions. Echinodermata have a mean reduction compared to the prediction in both the CB and the MT, but the SE is much larger than the mean effect.