1 Introduction

Author Response

Dear Reviewers,
Thank you for your careful reading of our manuscript and for the constructive feedback. This is our second response to the reviewer comments, and in some cases our responses have been updated compared to the initial version. One significant change we made in this revision is the simplification of the model evaluation statistics for the global dataset: we have removed the Bayes factor likelihood analyses. With the additional data provided by McClelland et al. (2024), using only normalized bias, RMSE, NRMSE, and R^2 (Pearson and residual) makes the results clearer and easier to interpret. We would be happy to reinstate the previous analyses if preferred. Below, we provide a point-by-point response, indicating the changes made and the corresponding line numbers in the revised manuscript.

2 Answer to reviewer 1

2.1 Answers to the technical corrections and suggestions

Reviewer Comment

On line 18: Add reference for the threefold increase in environmental Hg and specify whether this data is a global average and the environmental medium that it comes from (ie. sediment and peat archives?)

Edit

Line 18
These 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 Geyman2025.

Reviewer Comment

Line 30: Volume concentration factor (6.4E6) – specify units if applicable.

Edit

Line 30
The bioconcentration process can result in high 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:

$$\mathrm{VCF} = \frac{C_{\mathrm{phytoplankton}}}{C_{\mathrm{water}}} \tag{1}$$

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

Reviewer Comment

Line 31: Sentence is overly casual – recommend removing or revising.

Edit

Line 37
MeHg concentrations that are elevated due to bioconcentration can be further increased by biomagnification along the aquatic food web.

Reviewer Comment

Line 34: Revise to: "Consumption of MeHg-contaminated seafood is the primary pathway of mercury exposure in humans, with elevated risk among coastal and seafood-reliant populations (Zhang et al. 2021)." This revised version better emphasizes exposure pathways while remaining sensitive to the context of seafood-dependent communities. If you choose to expand on health effects, a brief mention of methylmercury's neurotoxicity could provide a natural transition to your discussion of Minamata Bay. If you do retain the sentences in lines 34 – 37, also consider briefly clarifying Minamata Bay's specific contamination source, to not create a false sense of fear that these pollution levels are common.
Reference: Zhang, et al. (2021) Global health effects of future atmospheric mercury emissions. Nat. Commun. https://doi.org/10.1038/s41467-021-23391-7

Edit

Line 40
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 primary pathway of Hg exposure in humans, with elevated risk among coastal and seafood-reliant populations Sheehan2014, Zhang2021, Giuseppe2017, Trasande2006.
The risk associated with consuming seafood contaminated with MeHg gained significant attention after over 1000 fatalities occurred in Japan in 1956 due to the consumption of contaminated seafood from Minamata Bay Harada1995. 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 UNEP2013. The global state of Hg as a pollutant and the effect of the Minamata Convention is periodically reviewed in the Minamata Convention Effectiveness Evaluation Outridge2018Updated2018.

Reviewer Comment

Line 39: Rephrase to avoid starting with a number or acronym (e.g., "A total of 151 countries…").

Edit

Line 48
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. 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).

Reviewer Comment

Line 95: Add references for the coupled models (ie. GOTM, ECOSMO E2E and Mercy v2.0). Alternatively, the subheadings 2.3, 2.4, and 2.5 could be changed to 2.2.1, 2.2.2, and 2.2.3 respectively as they all fall under the “2.2 The models” subheading.

Author Response

I will update the subheadings to a lower level as you suggest untill model development, so the structure is:
2.1 The models
2.1.1 The hydrodynamical model
2.1.2 The physical setups
2.1.3 The MERCY v2.0 model
2.2.4 ECOSMO E2E
2.2 Model Development
Additionally I will add the references in addition to their respective paragraph the the introductary sentence on line 95 as fellows:

Edit

Line 96
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) GOTM1999 with the ECOSMO E2E ecosystem model Daewel2019 and the MERCY v2.0 Hg speciation and bioaccumulation model Bieser2022.

Reviewer Comment

Figure 1: Uses URL links within the figure caption which is generally not recommended. One possibility for rewording the caption is: “Several sub-images were used to create this figure. Image sources (used under Creative Commons licenses or in the public domain) are as follows: Filter feeder: Sabella spallanzanii (image by Wikipedia contributors, CC BY-SA 3.0, via Wikipedia).”

Edit

Caption Fig. 1
Filter feeder: *Sabella spallanzanii* (photo by Diego Delso, CC BY-SA 4.0, via Wikipedia), Suspension feeder: *Aplysina fistularis* (photo by Twilight Zone Expedition Team 2007, NOAA-OE, CC BY 2.0, via Flickr), Generalist feeder: *Crangon crangon* (photo by Etrusko25, Public Domain, via Wikipedia), Deposit feeder: *Buccinum undatum* (photo by Oscar Bos / Ecomare, CC BY 4.0, via Wikipedia), Benthic predator: *Hommarus gammarus* (photo by Bart Braun, Public Domain, via Wikipedia), Top predator: *Sepia officinalis* (photo by Nick Hobgood, CC BY-SA 3.0, via Wikipedia).

Reviewer Comment

Line 148: Provide justification or reference for the bprotected value used.

Edit

Line 169
The macrobenthos in the North Sea are estimated to have between 1.1 and 35.5 gC m^{-2} Heip1992, Daan2001. The value for $B_{Protected}$ is chosen as 1 gC m^{-2} for all macrobenthos except for the benthic predator where $B_{Protected}$ is 0.5 gC m^{-2}.

Reviewer Comment

Line 155: Maintain consistent MeHg/iHg order throughout the sentence for clarity.

Edit

Line 182
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.

Reviewer Comment

Line 176: Unsure of what units d-1 refers to.

Edit

Line 190
When organic carbon (detritus, labile DOM, and semi-labile DOM) is produced, 5% is allocated to semi-labile DOM. Additionally, detritus breaks down into semi-labile DOM at a rate of 0.001 d^{-1} (per day).

Reviewer Comment

Line 210: Include a reference for B10 value interpretation and the Jeffreys–Zellner–Siow prior assumption.

Author Response

As mentioned at the beginning of the document I would suggest to remove the BF10 values from the paper as I belive they introduce more uncertainty than that they clarify.

Reviewer Comment

Line 216: Rephrase for clarity. For example: "A BF10 factor below 1 supports the H1 hypothesis, while BF10 values < 0.1 and < 0.01 are considered strong and very strong evidence, respectively, in favor of the H0 hypothesis."

Author Response

We removed this part from the paper to increase clarity.

Reviewer Comment

Figure 2 caption: Final sentence seems to have been cut down short. Recommend: "This contrasts the iHg concentration (<100 ng g-1 d.w.) for all animals, except starfish, eel, and sponges." The caption should also clarify that the data shown came from a literature review. If each point comes from a separate study, consider citing sources directly in the figure legend.

Author Response

We removed this image, it does not convey informaiton relevant for the paper that are not present in the new barplots (Fig. 4) at line 372

Reviewer Comment

Line 256: Typo. Should read: "...followed by deposit feeders with up to 5 g C m-2."

Edit

Line 299

Filter feeders have the highest biomass, which is up to 10 g C m^{-2} followed by deposit feeders with 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}.

Reviewer Comment

Figure 7: Recommend removing plot titles and reformatting to look more like Figure 3. The Hg species should be identified in the y-axis label, and the order of the Hg species should match Figure 3 (MeHg, iHg, tHg). Will also need to be repeated for figure 8.

Author Response

I will redo the plots with the updated layout script as shown in Fig. 1. I will also combine Fig. 7 and Fig. 8 so that the differences between the base model and allometric scaling model are easier to evaluate.

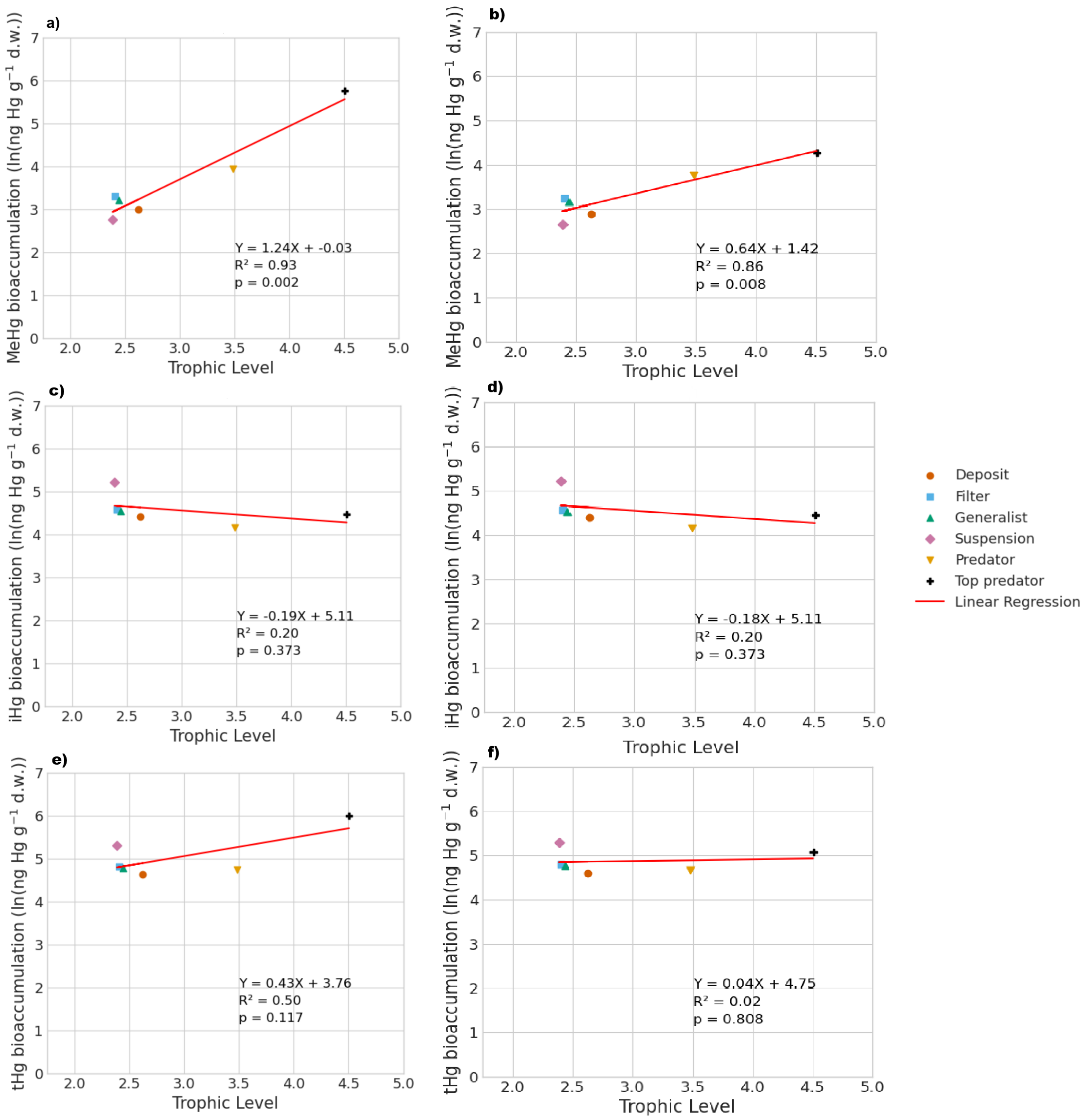

Figure 1: The inluence of trophic level on the bioaccumulation of MeHg, iHg, and tHg in both the AS (panels a, c, e) and the base model (panels b, d, f). In the AS model, the relationship with trophic level is stronger, where ln(MeHg)=1.24TL-0.03, compared to the base model, which is ln(MeHg)=0.64TL+1.42. TL represents trophic level, and MeHg is expressed in ng Hg g^{-1} d.w. For iHg, the bioaccumulation patterns are nearly identical, with ln(MeHg)=-0.19TL+5.11 for the AS model and ln(MeHg)=-0.18TL+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(MeHg)=0.43TL+3.76) compared to the base model (ln(MeHg)=0.04TL+4.175), driven by the stronger association between MeHg and trophic level in the AS model.

Reviewer Comment

Table 2 and 3 captions: Define AS as allometric scaling in the caption only

Edit

Updated caption Table 2
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 frm the allometric scaling model (AS).

Edit

Updated caption 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.

3 Answers to reviewer 2

Author Response

Dear reviewer,
Thank you for your comments and taking the time to review the paper. Before I get to answering your specific comments, I want to respond to what I agree is a very general criticism of the paper that should be properly addressed, which is related to using data from different geographic areas. The issue is that there is very little data on MeHg bioaccumulation at the base of the food web, and almost nothing in the North Sea. This complicates model validation and is the reason why the decision was made to simply try to use all data available. However, 2 recent papers came out with a lot of data, of which one paper, by McClelland et al., 2024 samples 476 benthic animals from two locations in the Canadian Arctic. While this is a different location, it does allow us to evaluate if certain patterns between feeding strategies are consistent in samples from the same geographic location. Because of this, we expanded the paper by verifying if the observed patterns from the model and global dataset analyses are also present in a single dataset.

This is introduced in the methods section in line 258 in the section:
2.3.3 Evaluation of the model using a single dataset
The results are presented in line 434 in section:
3.5 The role of the feeding strategy on MeHg bioaccumulation in a single case stud

3.1 Direct answers on reviewer comments

Reviewer Comment

Since the primary objective of the study is to model Hg bioaccumulation, I recommend that the model evaluation be presented as part of the Results and Discussion rather than the Methods. This change would strengthen the narrative and reduce redundancy—many of the points currently discussed in Section 3 could be streamlined. I suggest restructuring Section 3.1 to serve as the model evaluation, followed by subsequent sections explaining key discrepancies between model output and observations (currently in Section 4).

Author Response

The manuscript is overhauled in detail. Currently the paper has the following structure:

- 3 Results
  - 3.1 Model evaluation
    - 3.1.1 Evaluation of the Hg cycling and pelagic bioaccumulation
    - 3.1.2 Megabenthic biomass
  - 3.2 Bioaccumulation in the model
  - 3.3 The allometric scaling law in high trophic level animals
  - 3.4 Bioaccumulation in the global dataset
  - 3.5 Comparing model and observations
    - 3.4.1 The effect of feeding strategy on bioaccumulation
    - 3.4.2 The statistical performance of the model
    - 3.4.3 The effect of water column mixing
    - 3.4.4 Deposit feeders
  - 3.5 The role of the feeding strategy on MeHg bioaccumulation in a single case study
- 4 Discussion
  - 4.1 The role of feeding strategy on the bioaccumulation of MeHg
  - 4.2 The AS model
  - 4.3 Bioconcentration of iHg
  - 4.4 Model structural limitations
  - 4.5 Data-related limitations
  - 4.6 Potential improvements
- 5 Summary and conclusion

This allows way the paper has the model evaluate as part of the results to streamline the results section.

Author Response

We will also update Fig. 6 to show the bioaccumulation in the AS model, as shown in Fig. 5. This because this is the better performing version of the model and we can therefore

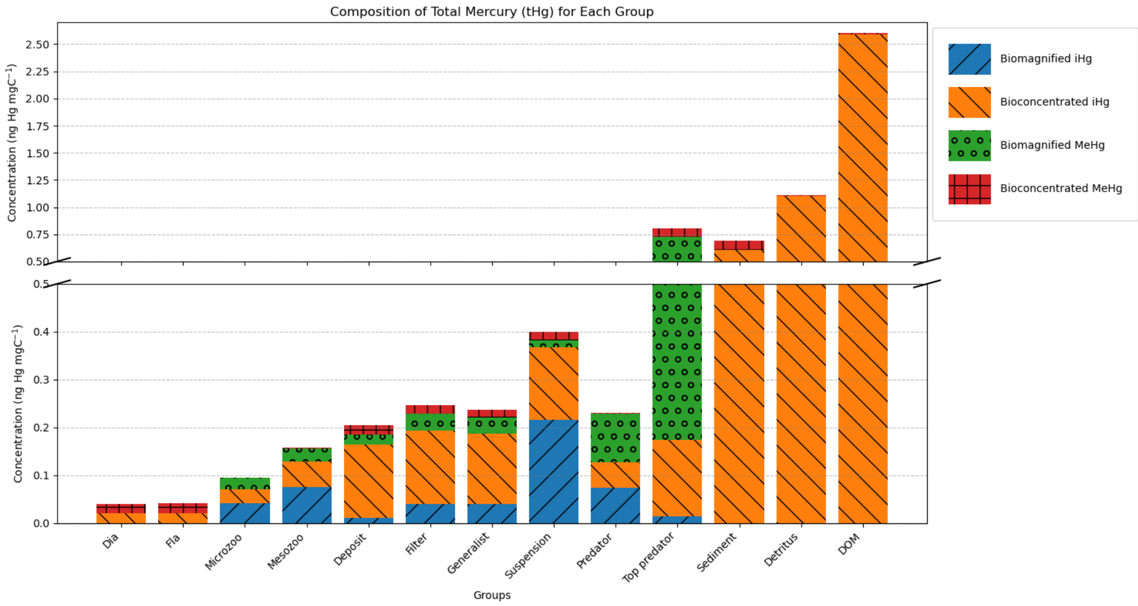

Figure 2: Modeled bioconcentration and biomagnification of iHg and MeHg. Partitioning to detritus and DOM is colored as bioconcentration. The y-axis is cut to show the high and low values. Notably is the high iHg to mgC ratio of detritus and DOM, leading to elevated iHg in suspension feeders. Additionally, higher trophic level animals have higher biomagnified MeHg.

better anlyse this version.

Author Response

I would also add this section ad the end of the model evaluation segment

Edit

Line 500

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. Our model is run in the North Sea, while most of the field observations are from different regions. This means that 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 bentho-pelagic coupling, which indicates that the performance of the ECOSMO E2E-MERCY-GOTM coupled system should be critically evaluated before it can be used for predictive bioaccumulation modelling in deeper water.

Author Response

I will add this to the beginning of the model evaluation section to show the Hg cycling and bioaccumulation in the pelagic is in line with observations.

Edit

3.2 Evaluation of the Hg cycling and pelagic bioaccumulation

Line 266

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 and MeHg in the benthic food web. Observed and modelled dissolved tHg concentration, the percentage of tHg that is MeHg, and the Hg content of phytoplankton and zooplankton is shown in Table 2. 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.

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 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 MeHg is caused because, even though mesozooplankton have a higher trophic level, they prefer to feed on larger diatoms which have less MeHg 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, 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.

Table 1: Dissolved total Hg (pM), MeHg (% of tHg), and Hg 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 (ng Hg mg^{-1})	10 ± 5	7.0 ± 1.1	8.3 ± 1.6
Flagellates (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

Author Response

I would suggest to add the below expansion of the discussion about what drives the role in feeding strategy.

Edit

Line 488

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 Weil2019.

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 Eklof2017.

Author Response

Additionally I would add the following component to the concluding remarks

Edit

Line 536

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 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 ability to accurately predicht MeHg bioaccumulations 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.

Reviewer Comment

The purpose of Figure 3 is unclear. It is not evident why the authors chose to use Hg data from different ecosystems and plot them against trophic level (referred to as feeding strategy in the figure). Since ecosystems differ in baseline inorganic Hg and MeHg concentrations, the MeHg–trophic level relationship should be examined within each ecosystem independently.

Author Response

We removed the image, instead we performed the ecosystem specific analyses based on the McClelland et al. (2024). The original purpose of Fig. 3 was to have a slope for MeHg bioaccumulation to compare our model too, but this is now done by Fig. 6 on line 462 was is based on a single geographical location and therefore does not have the same concerns.

Reviewer Comment

For model evaluation, I strongly suggest plotting modeled versus observed concentrations of speciated Hg (inorganic and MeHg) for each modeled feeding strategy. This would provide a clearer and more direct assessment of model performance.

Author Response

We will do this by making a barplot for both MeHg and iHg with a broken axis for MeHg so we can show both higher and lower trophic levels. I would also suggest to only do this for the MeHg so it can show both lower and higher trophic levels. We will show Fig. 3 for MeHg and Fig. 4 for iHg..

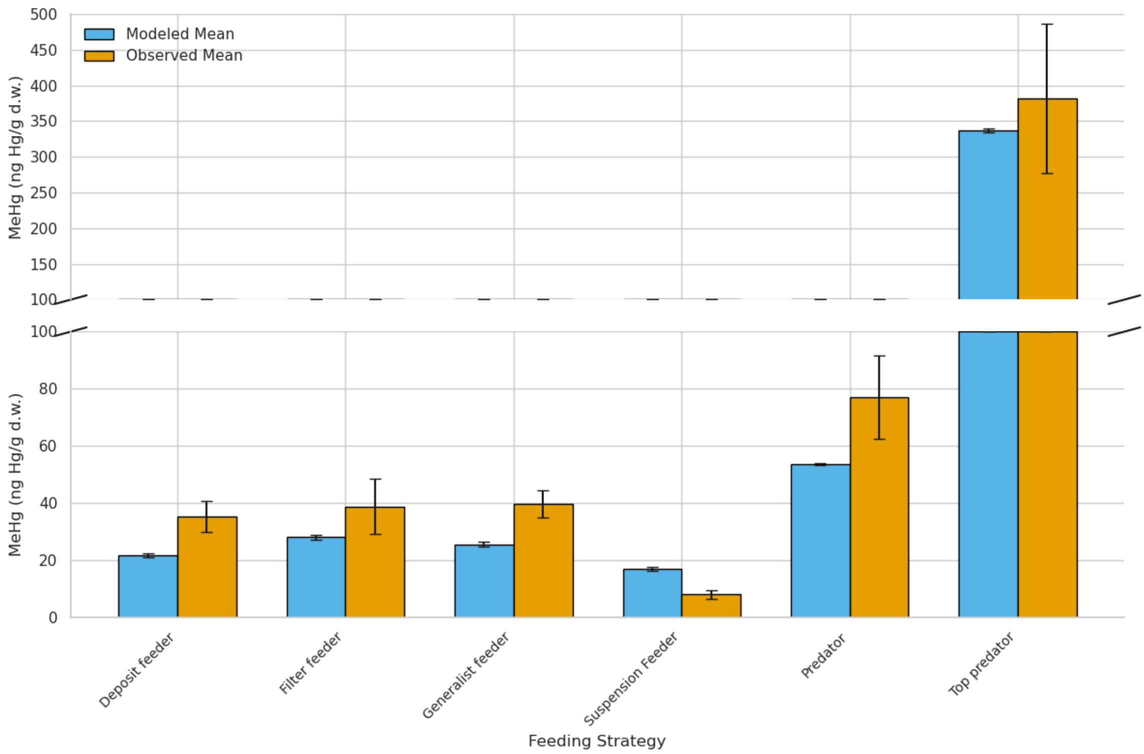

Figure 3: Mean bioaccumulation of MeHg in both model and observations is shown, with error bars representing 1 SE. The model's predictions do not consistently match observations within 1 SE, yet they display a comparable trend: Top Predators have the highest MeHg levels, followed by predators, with generalists and filter feeders showing similar MeHg, which are higher than those found in deposit feeders. Both model and observations show that suspension feeders have the lowest MeHg levels among the feeding strategies.

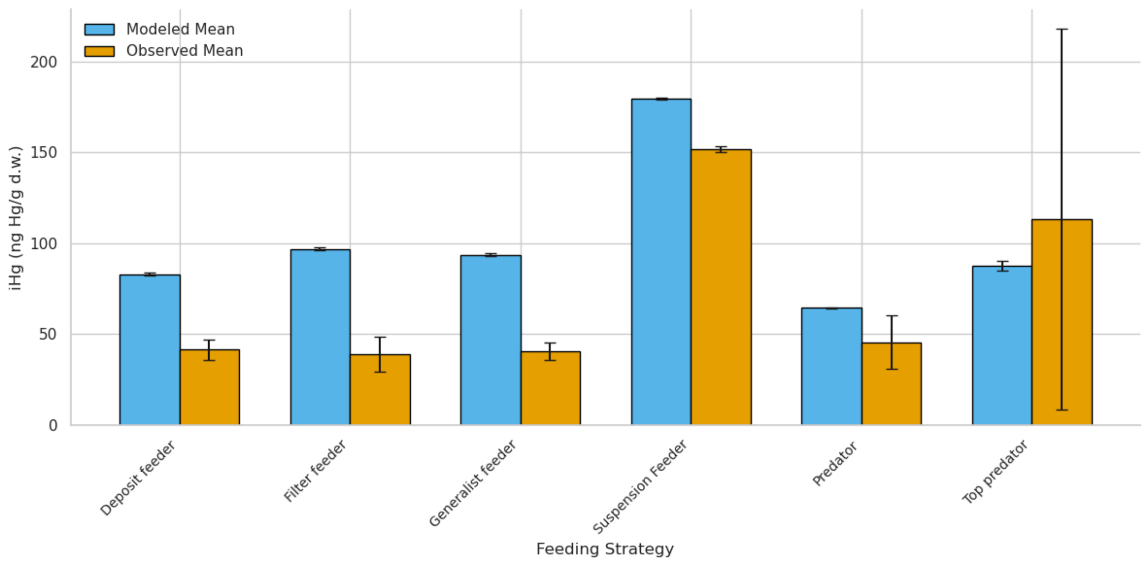

Figure 4: Mean bioaccumulation of iHg in both the model and observations. Error bars represent 1 SE. The model accurately shows increased iHg levels in suspension feeders. However, for all other feeding categories, except top predators, the iHg content is overestimated. In top predators, observed iHg levels are higher and not reflected in the model, though these elevated iHg levels have a very high SE.

Reviewer Comment

Section 3.2.3, which addresses the effect of feeding strategy on bioaccumulation, is central to the manuscript's aims, yet it is not discussed in sufficient depth. In contrast, the manuscript devotes substantial space to explaining Hg vs. trophic level patterns (Section 3.2.4), which are already well-established in the literature. I recommend condensing the discussion in 3.2.4 and focusing more on how feeding strategies influence MeHg and inorganic Hg transfer, particularly in benthic food webs.

Author Response

To adress this we removed the segment about trophic level as it is indeed very established. To compensate for this we expanded by validating the the identified role of the feeding strategy is also present in the single dataset published by McClelland et al. (2024). Additionally we expanded the discussion in segments

Reviewer Comment

Figure 4 is difficult to interpret. It is unclear whether the data are empirical or simulated. A more straightforward approach might be to present Hg concentrations across feeding strategies as a bar chart with error bars. If the intent is to show correlations between feeding strategies, a correlation coefficient would be more appropriate.

Author Response

Figure 4 is removed from the manuscript. Rather we added 2 bar charts comparing iHg and MeHg bioaccumulation in the model and observations in line 372.

Reviewer Comment

Section 3.3, on allometric scaling, should appear earlier in the manuscript. When reading Sections 3.2.3 and 3.2.4, I repeatedly found myself wondering about the effects of allometric scaling on the results. Figures 7 and 8 could be consolidated to allow readers to compare model performance with and without allometric scaling more clearly.

Author Response

We moved the segment about the allometric scaling model forward to section 3.3 so it is discussed before the main comparisons between the model and observations are made. Additionally we concolodated Fig. 7 and 8 untill the new Fig.3 Line 347.

Reviewer Comment

Lines 340–350: This content would be better integrated into the allometric scaling section.

Author Response

The majority of this was added to the section about the AS model in the discussion section (Line 475).

Reviewer Comment

As the authors note, the model is implemented for the North Sea, yet many of the empirical datasets used for comparison originate from other regions. This mismatch raises concerns about the validity of the model evaluation. Comparing model output to observations from ecologically distinct systems—each with different baseline Hg and MeHg levels, food web structures, and biogeochemical conditions—complicates interpretation and undermines the credibility of the evaluation. I strongly recommend either (1) limiting the model evaluation to observed data from the North Sea, or (2) running separate models parameterized for the specific ecosystems from which the empirical data are drawn.

Author Response

I agree with this concern of data being drawn from different locations. Unfortunately, there is not enough data from the North Sea to evaluate the model purely on data from the North Sea. I think the biggest concern is that there might be a cocorrelation between certain areas with high MeHg and the feeding strategies that are commen there. I hope that involving the evaluation component purely based on the McClelland et al. (2024) data adresses this concern to some degree. The model is not purely designed to be a predictive model for different megabenthos species in the North Sea, rather it is aimed to analyse if feeding strategy is a significant driver of MeHg bioaccumulation. The aim is to show that running a model in an idealized 1D setup resembling coastal conditions results in differences in the bioaccumulation caused by feeding strategies. Notably, our model shows higher MeHg in filter feeders compared to deposit feeders and extremely elevated levels of iHg in suspension feeders consuming DOM. We find it convincing the same pattern occurs in our model, the global dataset and the McClelland et al. (2024) dataset, but I fully agree that better measurements are necessary to validate models before they can be used in a predictive capacity. Our hope is that this manuscripts helps the message that studies to measrurements of biaoccumulation in the benthic food web can be relevant to increase our understandig of bioaccumulation in higher trophic levels.

4 Answer to reviewer 3

4.1 General answer

Author Response

Thank you for your great comments. Before I go into the individual comments in detail, I want to acknowledge a limitation in the paper that you flagged in several of your comments. This is related to the evaluation of the model output and the problem that the combining of data from various locations brings. This was done because, although data on Hg bioaccumulation can be found more often, studies measuring both MeHg and Trophic Level are less common. That being said, two big studies came out in 2024 that after I did the original data analyzes and I can include these papers. Although 2 papers sounds small, they have a lot of samples and drastically improve the sample size. Especially the paper by McClelland et al. (2024) can really supplement the paper. They sampled 476 benthic animals from two locations in the canadian Arctic. We added a third component to the paper where we verify that the patterns observed in our model and the global dataset are also present in the single dataset published by McClelland et al. (2024).
This is introduced in the methods section in line 258 in the section:
2.3.3 Evaluation of the model using a single dataset
The results are presented in line 434 in section:
3.5 The role of the feeding strategy on MeHg bioaccumulation in a single case stud

4.2 Specific Comments

Reviewer Comment

Data on mercury concentrations in marine megabenthos were compiled and examined for differences in bioaccumulation by feeding strategy. It appears a relatively small number of studies were used (n = 12, Table 5) compared to available published data on mercury in marine megabenthos. What criteria were used for the literature review and selection of papers?

Author Response

The papers were selected with a focus on having both trophic level and MeHg concentrations estimated in marine megabenthos. These studies are indeed less common than studies sampling only metal concentration, including total Hg. While verifying new literature, I did find two new papers that were published last year that I would now include in the analyses Bradford et al., 2024; McClelland et al., 2024. The study by McClelland et al. (2024) has a very substantial dataset that allows us to verify our hypothesis purely based on this data. Which has become a major component of the paper. I hope this addresses your concern.

Reviewer Comment

More information on the measurement of mercury burdens in the megabenthos studies seems important to include for interpretation and standardization. Sometimes megabenthos tissues cannot be sampled consistently due to differences in exoskeleton and body form. What tissue types were measured for mercury? (e.g., whole body [including exoskeleton], internal viscera, muscle). How was inorganic mercury concentration determined? (i.e., the studies in Table 5 do not include inorganic mercury). Are the modelled concentrations for whole body of megabenthos (e.g., Figure 6)?

Author Response

The bioaccumulation in the model and the output in Fig. 6 is shown to be in ng Hg per mg carbon. In the model we tried to isolate the effect of the feeding strategy on bioaccumulation, so the conversion to dry weight assumes a 1:2 ratio. Most measurements indeed express bioaccumulation in dry weight and the carbon content of biota is seldom measured alongside Hg. The conversion from carbon to dry weight does indeed introduce uncertainty, but it is within reasonable levels. For example. the soft part of molluscs are for example found to have between 36% and 48% carbon per dry weight while the carbon content of artrophods (mysis mixta) was found to be 51.4% (Gorokhova & Hansson, 2000; Jurkiewicz-Karnkowska, 2005). The complications is that the study aims to look at the feeding strategy, which does very between phyla. Filter feeders can, for example, be either arthropods in the form of barnacles, molluscs in the form of bivalves, annelids in the form of of fan worms, or echinoderms in the form of brittle stars, because of this a standard 1:2 conversion ratio between carbon and dry weight was kept consistent over all feeding strategies.
We added these citations to the manuscript at the end of the model development section (line 152)

Edit

Line 176 Our model is resolved in carbon content, while measurements are often in dry weight. The carbon fraction of dry weight generally ranges from 0.4 to 0.6, but can vary between different taxa (Gorokhova & 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.

Reviewer Comment

The empirical mercury data for megabenthos were pooled across geographic locations where environmental mercury exposure may have differed. How were potential confounding effects of geographic variation and feeding strategy resolved? Were the findings of feeding strategy influence on mercury burdens consistent with individual studies from specific geographic areas?

Author Response

I agree that this is an issue. We tried to validate our model findings using data, but data is not sufficiently available for all geographic locations to robust individual analyses. In order to address your concerns, we added the analyses solely based on the data presented (McClelland et al., 2024). Based on this, we can see that the results of our studies are consistent between the model, by pooling all geopgraphical locations and by analysing two individual locations.

Reviewer Comment

Organism bioaccumulation is described as involving two key processes: bioconcentration and biomagnification (lines 26-34). A more nuanced discussion is suggested here on exposure pathways and also clarification on the mechanistic processes that were modelled. Uptake of aqueous inorganic mercury and methylmercury into the food web occurs via bioconcentration in primary producers. However, consumers are typically exposed to mercury primarily through their diet and not via bioconcentration from water.

Edit

Line 134

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) which 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 and flagellates bioaccumulate similar amounts of iHg, while the smaller flagellates accumulate more MeHg. The uptake and release rates of iHg and MeHg in zooplankton are based on Tsui and Wang (2004) and on W. 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 are the interactions between detritus and DOM and iHg and MeHg. The only Hg^{2+} and $MMHg^{+}$ are assumed to partition to detritus and DOM, 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_{ow} values which are based on Allison et al. (2005) and Tesán Onrubia et al. (2020). This value is log10(6.4) and log10(6.6) for the partitioning of Hg^{2+} and log10(5.9) and log10(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) and Amptmeijer et al. (2025).

Reviewer Comment

Figure 6 shows modelled concentrations in biota, where bioconcentrated and biomagnified mercury are differentiated. These model results are not consistent with known trophic transfer processes of mercury. In higher trophic level biota, very little of the total mercury burden is inorganic mercury (e.g., in contrast with modelled result for a top predator) and most mercury is obtained from diet rather than water (bioconcentration). In Figure 6, much of the bioaccumulated mercury is attributed to bioconcentration. E.g., see Wang and Wang, Environmental Pollution 2019, Volume 252, Part B, September 2019, Pages 1561-1573, and other studies cited therein.

Author Response

This image stems from an admittedly awkward design choice in the paper. As stated in the paper, we aimed to enhance the model's performance over its previous version by modifying how iHg and MeHg are released during respiration. While some species have relatively high iHg concentrations, it is typically much higher and is better depicted in the Allometric Scaling (AS) model. The image presented is of the base model, which shows MeHg levels that, while in the observed range, are below average observations. Additionally, while some experimental studies such as presented by W. Wang and Wong (2003) find that bioconcentration can be a major exposure route in fish, I agree that it is typically expected to be smaller, as is the case in the AS model.
To improve this in the manuscript moved the segment about the AS model forward, and by default used graphs of the Southern North Sea AS model, as it ia sthe best agreement with observatiosn. In the AS model, top predators have 80-90% of tHg from MeHg from biomagnification, which is more in line with the observations by W. X. Wang and Tan (2019). Bioconcentration remains a significant route in the model, but based on W. Wang and Wong (2003) this is in line with obervations. The new image is shown on line 334 and shown below for clarity.

Reviewer Comment

The focus of this study is on megabenthos, i.e. consumer organisms. However, a key process that warrants more modelling attention is the process of methylmercury entry in the food web via primary producers. Figure 6 shows modelling results for diatoms and dinoflagellates. How do those mercury concentrations compare with empirical data for phytoplankton? How can the inorganic mercury and methylmercury in primary producers be a result of biomagnification, as indicated in the figure?

Author Response

The labeling in Fig. 6, my apology that is indeed mislabeled. I will correct this as shwon in Fig. 5. I think the question surrounding the comparison with phytoplankton aligns with your question about the model validation in the technical comments section "Line 195. Provide more detail on how the model performance was evaluated.". Since the model is quite extensively evaluated for the bioaccumulation in megabenthos, I will add the following paragraph about the evaluation of the model performance in the pelagic before the evaluation of the bioaccumulation in benthos.

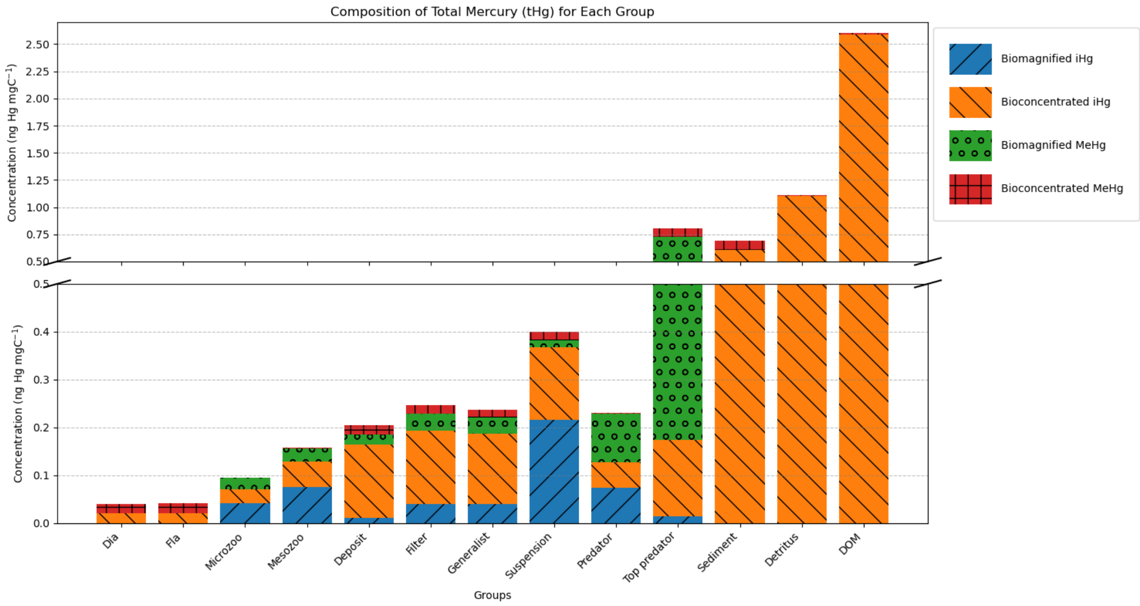

Figure 5: Modeled bioconcentration and biomagnification of iHg and MeHg. Partitioning to detritus and DOM is colored as bioconcentration. The y-axis is cut to show the high and low values. Notably is the high iHg to mgC ratio of detritus and DOM, leading to elevated iHg in suspension feeders. Additionally, higher trophic level animals have higher biomagnified MeHg.

Edit

Line 267

4.2.1 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 and MeHg in the benthic food web. Observed and modelled dissolved tHg concentration, the percentage of tHg that is MeHg, and the Hg content of phytoplankton and zooplankton is shown in Table 2. 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.
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 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, 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.

Table 2: 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

5 Technical Corrections

Reviewer Comment

Line 8. Is the inorganic mercury in filter feeders elevated, or more specifically, is it found as a higher proportion of total mercury compared to other megabenthos?

Author Response

No, filter feeders do not have elevated iHg levels. The iHg levels in filter feeders are large part of tHg, but filter feeders have similar iHg as most other macrobenthos but elevated MeHg levels, thus a reduced proportion of iHg of tHg. The main megabenthos group that has notably increase in iHg are the suspension feeders. They are defined by their ability to eat DOM (resembling sponges), where filter feeders cannot filter out dissolved particles. Suspension feeders on the other hand, have both elevated iHg levels and an elavated iHg to tHg ratio. This is true both in the model and in the observation in Meditereanean Sea sponges by Orani et al. (2020).

Reviewer Comment

Line 18. Cite a reference for this statement.

Edit

Line 18
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).

‘

Reviewer Comment

Line 26-27. Does bioconcentration only occur in a polluted environment? Is the model then only relevant for polluted environments?

Edit

Line 27
There are two key processes involved in bioaccumulation: bioconcentration and biomagnification. When animals absorb Hg directly from their environment; this is called bioconcentration.

Reviewer Comment

Line 45. The first effectiveness evaluation of the Minamata Convention has not been completed. Rephrase this text.

Edit

Line 51
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 where Hg concentrations 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 ef-

fectiveness evaluation of the Minamata Convention, which focuses primarily on fish, humans, and predatory wildlife Evers2016EvaluatingSteps. Additionally, the evaluation to date has shown that Hg and MeHg concentrations in water and sediment do not correlate well with levels in biota, leading to greater emphasis on biological monitoring over abiotic compartments.

Reviewer Comment

Line 51-52. Some megabenthos are not lower trophic level biota (e.g., are secondary consumers) and thus are not necessarily representative of processes at the base of the food web.

Edit

Line 60
The benthic food web is highly complex, making it challenging to improve our understanding of bioaccumulation within it (Silberberger et al., 2018).

Reviewer Comment

Line 74. Perhaps change "in silico" to "a modelling experiment"

Edit

Line 83
Afterward, we conducted a modeling experiment in which megabenthos with various feeding strategies compete under physical drivers in idealized scenarios that are typical of megabenthos-rich coastal oceans.

Reviewer Comment

Line 86-89 and elsewhere. Use past tense to describe work that was completed.

Author Response

I will change that anywhere in the manuscript. For example in line 80 it is refrased as:

Edit

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 look at the effect of the trophic level, we also added "primary producers" as the base of the food web, and "seabird" and "benthic fish" as top predators. We analyzed whether trophic level and feeding strategy influence megabenthos iHg, MeHg, and/or tHg content. The observations were analyzed by visualizing the data, performing linear regression, and plotting a correlation matrix of the differences in bioaccumulation between different feeding strategies. 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.

Reviewer Comment

Figure 1. What is the black line that connects biota to detritus, DOM and sediment organic carbon?

Author Response

I will update the caption of the figure as stated in Fig. 6. I also added a dotted black line to show mortality from phytoplankton and zooplankton.

Reviewer Comment

Line 186. Rephrase “samples are sampled”

Edit

Line 116
Because of this, most samples are from shallow, well-mixed coastal areas, and we used this setup to evaluate the performance of the models.

Reviewer Comment

Section 3.1. How do the results of this analysis compare with published findings reported in the literature?

Author Response

In the literature there is relatively little attention to direct role of feeding strategy or phyla on bioaccumulation. Several individual papers remark things such as that mussels have higher values than crustaceans but I could not find our main connclusion supported in the literature. That being said, I hope the expansian of the paper by doing the further analyses with the data presented by McClelland et al. (2024) is convincing that while this interaction itself is not supported as a conclusion in literature studies, published data does support our conclusions.

Reviewer Comment

Line 255. Unclear meaning – “validate that they survive in the model”

Edit

Line 296
While our megabenthos groups only vary in their feeding strategies and lack a direct real-world counterpart, it is important to 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 biomass in the model.

Reviewer Comment

Figure 6. How do mercury concentrations per unit carbon (reported in Figure 6) compare to literature reported values that do not take carbon content into account?

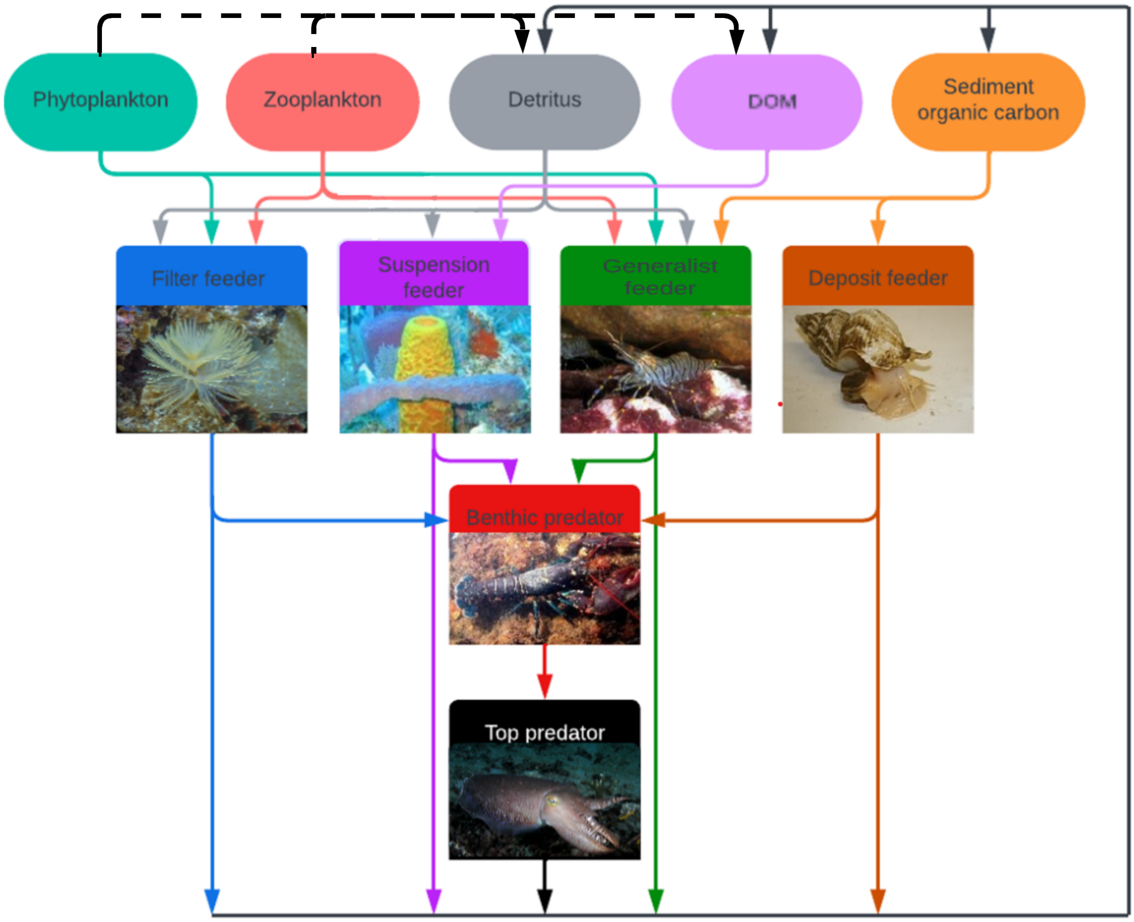

Figure 6: The overview of the modeled megabenthos functional groups and how they interact with each other and functional groups in the ECOSMO E2E model. There are 5 macrobenthic functional groups. The filter feeder feeds on pelagic detritus, zooplankton, and phytoplankton. The suspension feeders feed 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.

Author Response

As described in above, the conversion factor of carbon to dry weight is assumed to be a 1:2 ratio for all functional groups. This conversion is indeed a source of uncertainty. I expanded on this in the suggested expansion of the paper at the beginning of the revieuw, Additionally we added a segment on line 516 where we discuss data related uncertainty.

Reviewer Comment

Line 310-313. Are there published empirical studies that support this model prediction regarding filter feeders?

Author Response

There is published emperical data, as described at the beginning of these answer, that supports our conclusion. But no studies direclty comparing filter feeders in the way we did in this study with other feeding strategies. So our conclusion comes from the combination of having measurements that show elevated MeHg levels in filter feeders combined with a modeling explanation as why this might be because they are filter feeders.

Reviewer Comment

Line 361. Does the bioaccumulated inorganic mercury originate from water or dietary exposure?

Author Response

The majority of this in all catagories except suspension feeders is via bioconcentration, thus uptake from the water. We added the following to clarify this:

Edit

Line 489
In Fig. 6 we can see that the vast majority of iHg in filter, deposit, and generalist feeders originates from bioconcentration, thus direct uptake from the water is the dominant pathway of iHg bioaccumulation in our model in these feeding strategies.

Reviewer Comment

Line 394. Explain further what is meant by "in vivo mercury speciation".

Author Response

We removed the segment about in vivo mercury speciation. It is not the focus on this paper, and either we would need to long to explain it properly or it does not really contribute to this dicussion as it is not relevant for most of the animals we looked at.

Reviewer Comment

Line 411. Where are these regression results presented earlier in the manuscript?

Author Response

They are from Table 3 where the model is evaluated, but I can better describe the table outcome in text. I would add the following part to the end of section 3.3. where I discuss the results of the allometric scaling model.

Edit

Line 335
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 allometric scaling model with the reduction of the normalized bias of top predators to -0.32 which improves the overal R^2 of the model to >0.99.

Reviewer Comment

Line 436-437. This comment about bivalve communities is speculative.

Reviewer Comment

Line 441-442. Consider concluding the paper with a recommendation for future work on model development.

Author Response

I will answer these comments together by suggesting a rewrite of the closing remarks. I agree that it is speculative, but I do think, especially considering the addition of the further analyses that also point to molluscs as being higher in MeHg, that it is a logical next step to take into account based on the results of this study. We rephrased it as follows to make it clear that our work should be seen as hypothesis-generating modeling work that suggests investigating the potential relevance of benthic community for MeHg bioaccumulation might be relevant.

Edit

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. 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.
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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