

Peer Review File

Manuscript Title: Continental-scale nutrient and contaminant delivery by Pacific salmon

Reviewer Comments & Author Rebuttals

Reviewer Reports on the Initial Version:

Referees' comments:

Referee #1 (Remarks to the Author):

This paper analyzed regional changes from 1976-2015 in returns of Pacific salmon to their spawning grounds and the concentrations of nutrients and contaminants they bring with them. They demonstrate that increasing salmon populations have led to increasing inputs of “bright” and “dark” subsidies to freshwater ecosystems, despite declines in body size over that time. Nutrient subsidies exceed those of contaminants by orders of magnitude, but they could still pose a risk to consumers. This paper provides a novel and valuable contribution to the literature on resource subsidies, salmon transport, and contaminant literature by demonstrating the ways in which animals can be vectors of both important nutrients and harmful contaminants, and how the relative transport of both can vary due to changes in population size, body mass, trophic level, etc. The long-term analysis and regional scope presented here provides an especially unique view on how the “bright” and “dark” sides of subsidies can vary over time and space. The data compiled for this paper seem overall robust and sound, although I was surprised by the relatively sparse amount of body nutrient composition data available for these estimates, especially compared to contaminant data. The analyses seemed very robust, and I appreciated the effort put into modeling the uncertainty around these estimates. The only place where I thought insufficient information was included in the modeling approach was in regard to the example of bald eagle consumption, which I think is an important and illustrative component of the paper, so it would be helpful to understand more clearly how that was done. Your data and results presentation were all clear and helpful, and your conclusions seem robust and clearly presented. I did think you overstated the positive news a bit in the paper summary at the beginning, as it focused only the net positive benefits of salmon transport, whereas your bald eagle example and your human consumption benefit:risk analysis both showed some potential risks due to contaminant loads in salmon. The writing was very clear and easy to follow, and the paper was well referenced and supported by the literature. Overall, I think this is a very novel, interesting, and valuable contribution to the literature in several topic areas, and I think it will be of broad interest to readers.

A few more detailed comments and suggestions are as follows:

- It’s encouraging to see that the amount of nutrients exceeds the contaminants by several orders of magnitude, but the quantity of both needed for an effect in ecosystems also varies by orders of magnitudes, and that doesn’t seem to be currently addressed as clearly. That is, what are the likely environmental concentrations that will result from both the nutrients and the contaminants, and is that within acceptable levels or not? You include some discussion of this in your example with the bald eagle,

but it would be helpful to have some kind of ecosystem context about the concentration and/or areal deposition of these inputs. I know you decided not to include watershed area here, and I understand the complexities in doing so, but in reading how you calculated the salmon returns, it seems it would be possible to get some kind of watershed area estimate, at least for one or two of the regions, to provide an example. If not, is there another way you could illustrate for the reader not well versed in these topics how much greater magnitude you would expect to see nutrients vs. contaminants in a natural vs. impacted environment?

- Looking at your source data, I'm really surprised how much less nutrient data, and how less specific it seems to be by species and by region, than your contaminant data. I would imagine there would be much more nutrient data available, and I would guess the concentrations would be fairly variable by species, especially given the differences in size. Is there a reason you chose to use only these nutrient concentrations? Or are these really the only data available? If the latter, that seems like an important area for future research given all the work done on salmon subsidies.
- I did not see any information on how you estimated the trophic level of each species, which I think is important to understand.
- In Li 38, you say both nutrients and contaminants have increased 29% from 1976-2015, but in the next sentence you say they have increased at different rates from one another. I think I understand from reading the methods how you calculated the net sum and increase, but it would be worth clarifying this a bit in the main text.
- Li 41: This seems like an overly positive overview of your findings, given that some species provide a relatively greater source of contaminants than nutrients (Fig. 4), and your example of the bald eagle demonstrated the ability of these inputs to still provide a source of contaminants at levels of concern. I would temper your article summary with an acknowledgement of the magnitude of contaminants being transported by salmon and the potential for ecological consequences.
- You provided a detailed discussion about how salmon body size has changed over time, but I didn't see any/much discussion about how contaminant levels may have changed. It's unclear from looking at your source data how difficult that may be to provide, and you may be limited in your ability to provide a robust analysis for each contaminant by species and by region, but it would still be helpful to understand to what degree contaminant concentrations are increasing with time. It also wasn't clear if this change in concentration over time was included in your models, which seems like an important assumption to address.
- Li 63: Maybe "assimilation" would be a better word here than "uptake"
- Li 225-227: I'm not sure if it makes sense to say they transported more or less "than expected" when it appears you're comparing those numbers relative to 1 kg/ 1 mg standard, which appears rather arbitrary, but maybe I'm unclear about this comparison
- Li 249: why is *ecological* in italics here?
- Li 265: It is unclear how you arrived at these estimates for contaminant consumption by bald eagles. In the methods (Li 477-482) you give a broad overview of how "Exposure scenarios were estimated under various assumptions..." but very little detail is provided. Could you please provide more information about this?
- Li 266: A range of 1-100% assimilation for Hg seems very broad—is there no literature that can better inform an appropriate range for this estimate?

- Li 354: You say that changes in salmon population numbers were the most important factor driving changes in total nutrient and contaminant loads, which suggests you did a sensitivity analysis, but it would be helpful to say that directly. I saw the sensitivity analysis in your methods, but it wasn't clear just from reading the main text.

- Amanda Subalusky

Referee #2 (Remarks to the Author):

This is an interesting and novel/creative paper that describes shifts in modeled inland inputs of N, P, long chain fatty acids (EPA/DHA), and several contaminants with fluctuations in salmon stocks between 1976 and 2015. The authors construct detailed estimates of the proportions of contaminants and nutrients transported into individual systems from different salmon stocks over time and how they fluctuated with salmon stock abundance, differences in weight of the fish, and contaminant concentrations (although changes in tissue concentrations were not really the focus due to data limitations).

The results show that abundance was the major driver of the observed differences in fluxes across years and that pink salmon returns are particularly important. While the estimates and accounting of contaminants and nutrients flows in this paper seem reasonable, and the manuscript is well written, my main concern about this paper is that it presents all the calculations through the lens of a salmon only world and therefore does not provide context for how relevant the budgets are for overall ecosystem processes. My major suggestion for the authors is therefore to provide more context for the importance of salmon subsidies for both nutrient and contaminants in the paper. The authors need to convince the readers that the salmon associated fluxes considered are important for the four systems highlighted in the manuscript. The present version of the manuscript contains no information or discussion of this at all. It pivots to an exposure/risk discussion at the end but this is driven by concentrations not overall budgets, and the authors acknowledge in the methods that this is a weak point in the analysis.

The idea of a contaminant "subsidy" from a marine system to an inland system is a bit surprising since we normally think about the flow in the other direction. We do this because the sources coming from terrestrial systems are large and thus the reservoir in the water/sediment is large relative to offshore marine ecosystems. Global and continental scale budgets for contaminants and nutrients from other work indicate inbound fluxes from salmon presented here are negligible compared to what is already present in the terrestrial systems and being discharged offshore. From this perspective, the salmon are a relatively clean import to potentially contaminated terrestrial systems.

Flipping this idea adds to the novelty of the paper, so could be a good thing, but as mentioned above, the reader needs to be convinced that this subsidy is actually important. For example, even though fish biomagnify some contaminants, when you construct a budget for total mass in the system the fisheries

reservoir is usually negligible compared to what is present in water/sediment. The authors could address this point by comparing watershed budgets for contaminants and nutrients for the four specific regions highlighted in the manuscript to the estimated salmon-only associated fluxes in this manuscript.

The EPA/DHA flux is quite interesting and I don't know what happens to it when a salmon dies. In contrast to the contaminants and nutrients, I don't think there is a large flux of riverine discharges of EPA/DHA. Are the long chained fatty acids stable when the salmon die or do they degrade? I think the authors could focus on this story a bit more because it is very interesting.

Around line 248 - the tone of the manuscript shifts to ecological impacts of the shifts in budgets over time. This will depend on concentrations in individual fish and diet composition rather than the overall budgets so seem a bit disconnected from the first part. This statement seems very subjective "Pacific salmon concentrate transported contaminants" - since salmon are not highly contaminated compared to other foods and often are a relatively clean source of food for the animals consuming them. The pulsed exposure is simply the animals are eating a lot - so again I think this statement is misleading given the broader context of animals need to eat something and all food has contaminants. Perhaps a focus on relative changes over time rather than absolute risk/benefit ratios would be good but I recommend caution to the authors in these sections given the limited empirical data available for such calculations.

Lines 288 onward - I am not really convinced that this is important yet.

Methods: I am not an expert in salmon stock assessment methods but there are large teams of fisheries scientists devoted to this and estimating returns so I hope a reviewer with such expertise is included. On first pass - the methods for this section look reasonable to me.

As is typical, there are few data to estimate temporal patterns in contaminant or nutrient data in the salmon. This should be acknowledged more clearly in the main text. This will drive the exposure/risk/benefit results presented so those should be viewed as highly uncertain and I don't really think fit well into this work anyway.

Referee #3 (Remarks to the Author):

The manuscript entitled Shifts in Pacific salmon community alter continental-scale nutrient and contaminant delivery includes several key results. First, the paper documents how a shift in the proportion of salmonid species shifting over the course of a 40 year time frame alters the flow of important marine derived nutrients and deleterious contaminants across the Pacific Rim. Most individuals know the story with regards to the importance of marine derived nutrients, but few understand the shift in species composition over time and what that may mean from an ecosystem perspective. This paper does a good job of highlighting that change. Second, few link contaminants with salmon, from an ecosystem perspective and at the scale this paper delves into the topic. While there have been some papers on this topic (Baker, M.R., Schindler, D.E., Holtgrieve, G.W. and St. Louis, V.L.,

2009. Bioaccumulation and transport of contaminants: migrating sockeye salmon as vectors of mercury. *Environmental science & technology*, 43(23), pp.8840-8846.) they have not expanded the concept to the entire Pacific Rim. So the results that nutrients are orders of magnitude larger than contaminant delivery is original and significant, and the fact that species composition change and the resultant shift in what species dominates these return of nutrients at the Pacific Rim scale is unique. The data and methods, validity of approach and quality of presentation is sound. The quality of the data varies, but the authors recognize this in their methods section and allow the reader to assess the information as well as the original data in the supplementary material. The authors do a solid job of utilizing Bayesian statistics to help quantify both the variation, distribution, and uncertainty. This is critical to the results, in my opinion, and add credence to the interpretation due to the extreme difference in magnitude of contaminants to nutrients. The conclusions, robustness, validity and overall reliability is thus sound. There are several places where the manuscript can be improved. Rather than repeat my specific comments, they are embedded into the paper which is attached. The references are adequate and the clarity and context is clear and thoughtful. While I understand and utilize some of the statistics, I do not readily utilize Bayesian statistics so someone who does may have further insights into the analyses. I do believe the paper is in need of revisions but is a sound potential contribution to nature.

Line 51-The authors identify salmon but do not mention steelhead, which also have the same transboundary ecological effect. It may be useful to include them as well. Pacific Lamprey also have a similar migratory strategy.

Line 52- a myriad of?

Line 87- How did the authors account for uncertainty or variance in the annual return abundance estimates as well as the annual mean individual fish weight?

Line 89- ok this answers my previous question because you are using the posterior distributions.

Line 208- Do the authors have any hypotheses as to what may occur? potential mechanisms? this need not go into the paper but it would be goo to hear what the potential changes are and what drives such changes.

Line 236- It would be good for the authors to recognize the large body of literature on salmon and contaminant transport in the great lakes. there they have had the opportunity to study the potential mechanisms and differences of where contaminants accumulate and what it means to ecosystem function. again no need to get into too much detail but there are some important references in that literature.

Line 239-this has been stated multiple times in the paper.

Line 254-This is where perhaps some of the great lakes literature may be useful.

Line 315-Anytime the word Chinook is used it should be followed by salmon to discern between the fish, the wind, and the people

Line 317- What do the authors mean by infilling? snythetic data, some sort of interpolation or extrapolation? What method?

Line 320- Where does the assumed harvest rate come from and how does it temporally vary?

Line 325- This is an important disclaimer and it is good of the authors to have it in the methods. How different are these estimates from the ones used for management purposes?

Line 330- This is a large assumption because fisheries can often be quite selective on the size and thus the age of the fish. Was there any analyses conducted to verify this assumption or at least identify the variation between fish size caught and escaped? perhaps somewhere in the literature?

Line 336-ok this answers by previous question

Line 356-This is a confusing paragraph -

Post 2000 - 432 estimates

Pre 2000 - 25

Temporal trend of species*region combination - one species for > 4 years

Average species*region combination - 2 year

So if the authors cannot account for changes in contaminant concentrations over time then how do they go about focusing on temporal changes? This confuses me and a clearer explanation would be helpful.

Line 380-These assumptions and methods to deal with these assumptions all seem quite reasonable.

Line 407-What is the connotation of weakly informative prior to the overall model analyses?

Line 427-Was there misspecification of the model or were the results similar to the data?

Line 436-this makes sense

Line 456-this makes sense

Line 477-does this like salmon biomass change over time? if so is that important to include?

Line 499 -these references are over a decade old, are there others more recent or is this the standard typically used?

Line 520-do not know if the format for the first 9 citations is appropriate of the ones following the first 9.

Author Rebuttals to Initial Comments:

Key

Referee comment

Author response

New or edited text in the manuscript

Referee #1: Aquatic ecology

Referee #1 (Remarks to the Author):

This paper analyzed regional changes from 1976-2015 in returns of Pacific salmon to their spawning grounds and the concentrations of nutrients and contaminants they bring with them. They demonstrate that increasing salmon populations have led to increasing inputs of “bright” and “dark” subsidies to freshwater ecosystems, despite declines in body size over that time. Nutrient subsidies exceed those of contaminants by orders of magnitude, but they could still pose a risk to consumers. This paper provides a novel and valuable contribution to the literature on resource subsidies, salmon transport, and contaminant literature by demonstrating the ways in which animals can be vectors of both important nutrients and harmful contaminants, and how the relative transport of both can vary due to changes in population size, body mass, trophic level, etc. The long-term analysis and regional scope presented here provides an especially unique view on how the “bright” and “dark” sides of subsidies can vary over time and space. The data compiled for this paper seem overall robust and sound, although I was surprised by the relatively sparse amount of body nutrient composition data available for these estimates, especially compared to contaminant data. The analyses seemed very robust, and I appreciated the effort put into modeling the uncertainty around these estimates. The only place where I thought insufficient information was included in the modeling approach was in regard to the example of bald eagle consumption, which I think is an important and illustrative component of the paper, so it would be helpful to understand more clearly how that was done. Your data and results presentation were all clear and helpful, and your conclusions seem robust and clearly presented. I did think you overstated the positive news a bit in the paper summary at the beginning, as it focused only the net positive benefits of salmon transport, whereas your bald eagle example and your human consumption benefit:risk analysis both showed some potential risks due to contaminant loads in salmon. The writing was very clear and easy to follow, and the paper was well referenced and supported by the literature. Overall, I think this is a very novel, interesting, and valuable contribution to the literature in several topic areas, and I think it will be of broad interest to readers.

We greatly appreciate Dr. Subalusky’s expertise in ecological subsidies and her constructive feedback on our manuscript. Please find our responses and revisions organized with each of the detailed comments below.

A few more detailed comments and suggestions are as follows:

It’s encouraging to see that the amount of nutrients exceeds the contaminants by several orders of magnitude, but the quantity of both needed for an effect in ecosystems also varies by orders of magnitudes, and that doesn’t seem to be currently addressed as clearly. That is, what are the likely environmental concentrations that will result from both the nutrients and the contaminants, and is that within acceptable levels or not? You include some discussion of this in your example with the bald eagle, but it would be helpful to have some kind of ecosystem context about the concentration and/or areal deposition of these inputs. I know you decided not to include watershed area here, and I understand the complexities in doing so, but in reading how you calculated the salmon returns, it seems it would be possible to get some kind of watershed area estimate, at least for one or two of the regions, to provide an example. If not, is there another way you could illustrate for the reader not well versed in these topics how much greater magnitude you would expect to see nutrients vs. contaminants in a natural vs. impacted environment?

We agree with the referee that these are important questions for this research, and we explored many of these same ideas in depth as we considered the suite of questions to address in this manuscript. We identified three major knowledge gaps as current hurdles that, if resolved for at least a subset of the systems to which Pacific salmon return, would enable this line of questioning in the future. First, the context dependency of salmon-recipient systems (i.e., size, geomorphology and hydrology, nutrient status, food web structure, etc.) has a strong influence on the fate and processing of fluxed nutrients and contaminants (Walsh et al. 2020, Gerig et al. 2018) and constrains our ability to meaningfully estimate their environmental concentrations in recipient system compartments at the broad spatial scales considered in this paper. Second, while the effects of salmon-derived nutrients on ecological responses (such as primary production and plant and animal abundance and density) have been explored by many researchers and for many systems, the relationships between nutrients and these ecological responses are inconsistent among systems (Walsh et al. 2020). Further, there is very little research on the influence of the suite of contaminants that are efficiently biotransported on ecological processes. This is true even beyond the context of salmon biotransport; for example, we have poor understanding of how many of the PBT (persistent, bioaccumulative, and toxic) contaminants affect primary producers despite the well-known importance of primary producers to the bioaccumulation and biotransformation of PBT contaminants at the base of freshwater food webs. However, contaminant effects on ecological processes, including primary productivity and community respiration, is an emerging research area (Richmond et al. 2017, Beauvais-Flück et al. 2018, Gray and Bernhardt 2022) and studies working at the intersection of biotransport and ecological disruption by contaminants could fill important gaps in support of these broader salmon flux - ecosystem influence questions. Finally, and related to the previous challenge, we anticipate that the strongest direct effects of macronutrients and biomagnifying contaminants would involve organisms at opposite positions in the food web (i.e., in the lower and upper trophic levels, respectively) such that multi-trophic level analyses would best inform nutrient versus contaminant effects at an ecosystem level. Even still, the absence of common metrics for understanding nutrient (stimulating) and contaminant (disruptive) effects will make it difficult to reconcile these net effects from organismal to community to ecosystem levels (as Referee 1 suggests) without the development of new frameworks.

These considerations led us to the conclusion that there is not yet sufficient data for estimating the net (or comparing the relative) ecosystem effects of salmon-supplied nutrients and contaminants in recipient systems. On the other hand, the underlying question about the potential impacts of these fluxes motivated our analyses about nutrient and contaminant exposures which we examined with the bald eagle/mercury assimilation and risk example and the human health risk-benefit quotient analysis. The former concerns exposure to one of the biotransported contaminants and reflects the direct consumption pathway by a specific consumer. The latter considers trade-offs more in line with the question of the net effects of salmon inputs for recipient systems by marrying the known health benefits of omega-3 fatty acid intake with the known health risks of contaminant exposure for people. We present these two assessments as examples of approaches for contextualizing the significance of salmon nutrient and contaminant inputs at broad spatial scales that can be built upon in subsequent studies.

We think a brief discussion of these challenges benefits the paper and provides important context for the intended role of the two analyses that we present. We have accordingly revised the text leading to the bald eagle and benefit-risk analyses as follows:

- L279: “We do not yet know how co-exposure to the nutrients and contaminants transported by salmon influence ecological responses within trophic levels (e.g., primary production), nor have studies explored how nutrient benefits may be balanced by contaminant effects

across trophic levels to inform their overall influence on ecosystem functioning. Further, the coupled fates (following excretion and decay) and influences of salmon-derived nutrients and contaminants are anticipated to vary among recipient systems to reflect both spatial and temporal spawning patterns and site-specific characteristics—including waterbody size, geomorphology and hydrology, nutrient status, and food web structure. Together, these factors will determine the importance of transported nutrients and contaminants relative to other sources.^{12,15,43}

Lacking the data needed to address these broader ecological questions, we examined salmon consumption exposure scenarios for preliminary insights on the potential significance of salmon inputs for recipient systems...”

- L310: The present study highlights salmon consumption as a mechanism for nutrient and contaminant co-exposure, yet the net effect of these co-exposures is presently unknown for consumers in recipient systems.”

We see the challenges described above as some of the most exciting next steps for this line of research and hope that this paper motivates future studies that address the questions of: 1) what are the shared versus distinct pathways and mechanisms of nutrient and contaminant release (i.e., excretion, deposition, or transfer) from Pacific salmon and uptake and/or use by various trophic levels?; and 2) when and where in recipient food webs do we see net benefits or net disadvantages of biotransported nutrient plus contaminant portfolios. We now highlight these ideas more clearly at L320: “Our work points to the need to understand the net effects of Pacific salmon inputs at local scales. Building on the long history of salmon-derived nutrient research, experimental field and laboratory-based studies that consider the distribution, fate, and processing of nutrient and contaminant inputs in concert by recipient food webs and in specialist consumer diets will inform questions about how Pacific salmon inputs interact to influence ecosystem functioning and wildlife populations at spawning grounds. Longer-term, the influence of these salmon-derived nutrients vs contaminants may reflect distinct mass balance patterns, such as differences in the proportions of marine-to-freshwater nutrients and contaminants that are subsequently exported by salmon smolts when they migrate to sea (e.g.,^{51,55}). We might find unique opportunities to investigate the ecosystem processing, storage, and effects of Pacific salmon nutrient and contaminant transport from the onset of anadromy should Pacific salmon freshwater habitat ranges expand with Arctic ice loss.⁵⁶”

References cited in response

- Beauvais-Flück R, Slaveykova VI, Cosio C. Molecular effects of inorganic and methyl mercury in aquatic primary producers: Comparing impact to a macrophyte and a green microalga in controlled conditions. *Geosciences*. 2018 Oct 29;8(11):393.
- Gray AD, Bernhardt E. Are nitrogen and carbon cycle processes impacted by common stream antibiotics? A comparative assessment of single vs. mixture exposures. *Plos one*. 2022 Jan 5;17(1):e0261714
- Richmond EK, Grace MR, Kelly JJ, Reisinger AJ, Rosi EJ, Walters DM. Pharmaceuticals and personal care products (PPCPs) are ecological disrupting compounds (EcoDC). *Elem Sci Anth*. 2017;5:66.
- Walsh JC, Pendray JE, Godwin SC, Artelle KA, Kindsvater HK, Field RD, Harding JN, Swain NR, Reynolds JD. Relationships between Pacific salmon and aquatic and terrestrial ecosystems: implications for ecosystem-based management. *Ecology*. 2020 Sep;101(9):e03060.

Looking at your source data, I'm really surprised how much less nutrient data, and how less specific it seems to be by species and by region, than your contaminant data. I would imagine there would be much more nutrient data available, and I would guess the concentrations would be fairly variable by species, especially given the differences in size. Is there a reason you chose to use only these nutrient concentrations? Or are these really the only data available? If the latter, that seems like an important area for future research given all the work done on salmon subsidies.

We were also surprised by the lack of published nutrient data and how few N and P measurements support the nutrient flux estimates in the Pacific salmon subsidies literature. Our assemblage of the available chemical composition data underlying our analyses (i.e., the accompanying Supporting Information File) was based on Web of Science and Google Scholar searches of the peer-reviewed literature and published reports using search terms including “elemental”, “nutrient”, “marine-derived nutrients”, “nitrogen” and “phosphorus” along with “salmon”. We are not the first authors to identify this data need as Ebel et al. 2015 (and likely others) have summarized that previous Pacific salmon flux studies tend to draw on two very similar estimates for %P (0.36% and 0.38%) from two early studies.

We also agree with the referee that this is an important area for future research and have added the following text to emphasize this need: (L330) “[Finally, our assemblage of the available Pacific salmon nutrient and contaminant data revealed the need for more species-specific and temporally-resolved information to ensure that full ranges are captured in modeling approaches. Routine monitoring of Pacific salmon nutrient and contaminant concentrations would additionally benefit research on marine food web responses to the interactions between chemical loading, biogeochemistry, temperature regimes, and food web structures.](#)”

References cited in response

- Ebel JD, Leroux SJ, Robertson MJ, Dempson JB. Ontogenetic differences in Atlantic salmon phosphorus concentration and its implications for cross ecosystem fluxes. *Ecosphere*. 2015 Aug;6(8):1-8.

I did not see any information on how you estimated the trophic level of each species, which I think is important to understand.

Our analyses use trophic level to characterize the relative food web positions of the five species as food web position relates to differences in the bioaccumulated concentrations of biomagnifying contaminants. For these purposes, we used the trophic levels previously reported by Qin and Kaeriyama (2016) who arrived at their estimates using robust empirical measurements from their own work combined with the results available in the published literature for Pacific salmon in North Pacific Ocean ecosystems. The mean and standard deviations provided by Qin and Kaeriyama yield a ranking, from highest trophic position to lowest, as follows:

1. Chinook salmon (4.3 ± 0.3)
2. Sockeye salmon (3.9 ± 0.1)
3. Coho salmon (3.9 ± 0.4)
4. Chum salmon (3.6 ± 0.3)
5. Pink salmon (3.5 ± 0.2)

We have revised the text to better identify this paper as the source of these estimates at L213, the captions of Figures 4 and 5, and the details of Extended Data Tables 7 and 8.

In Li 38, you say both nutrients and contaminants have increased 29% from 1976-2015, but in the next sentence you say they have increased at different rates from one another. I think I understand from reading the methods how you calculated the net sum and increase, but it would be worth clarifying this a bit in the main text.

Thank you for pointing out the confusion here. We have clarified the text at L38 as follows: “From 1976 to 2015, increases in salmon returns accounted for increases in nutrient and contaminant inputs of 29% and 19% respectively.” This revision specifies the values for both rates and should also improve understanding with the following sentence about the difference in rates of increase. We also note that it may seem odd that we report that nutrient inputs and total nutrient plus contaminant inputs both increased by 29%, but this simply reflects that nutrient inputs dominated total flux (nutrients make up >99.9 percent of the combined nutrient and contaminant flux). Hence, the total increase in nutrients + contaminants is essentially the same as the increase in nutrients alone.

Li 41: This seems like an overly positive overview of your findings, given that some species provide a relatively greater source of contaminants than nutrients (Fig. 4), and your example of the bald eagle demonstrated the ability of these inputs to still provide a source of contaminants at levels of concern. I would temper your article summary with an acknowledgement of the magnitude of contaminants being transported by salmon and the potential for ecological consequences.

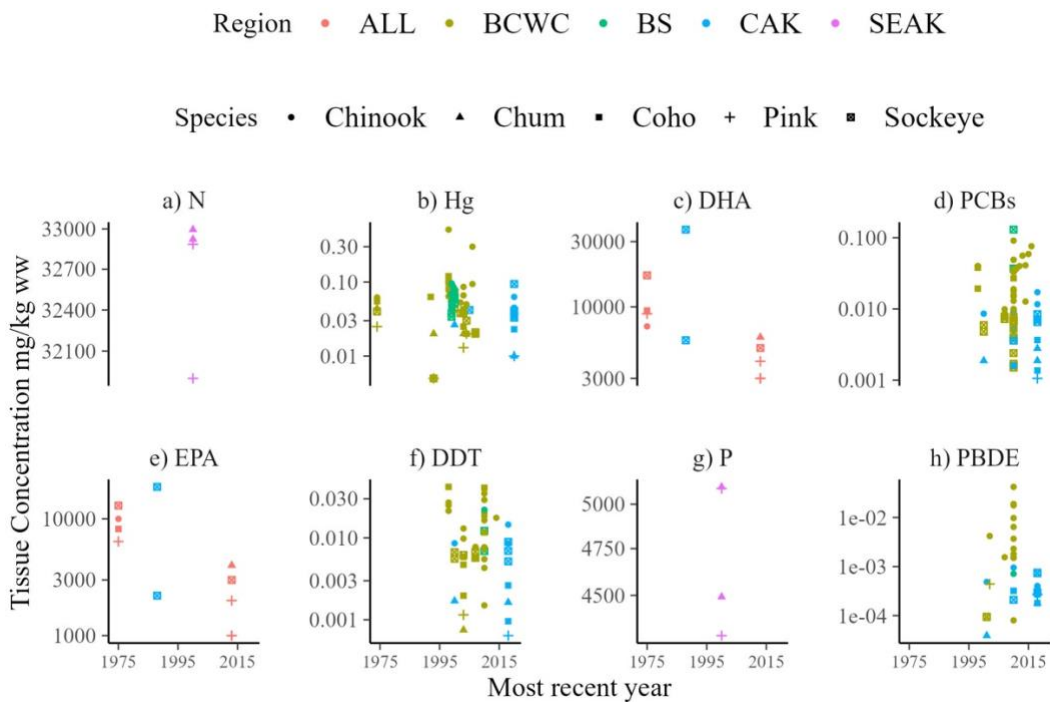
We agree with the referee and have added the following sentence to the summary at L42: “Even still, exposure levels of some contaminants (e.g., mercury) have the potential to represent concerns for some salmon predators.”

We also now better emphasize this conclusion in the main text at L306: “It follows that exposure to even small proportions of salmon-derived contaminants can be toxicologically relevant for upper trophic level consumers, reflecting that the contaminants stored in salmon tissues are bioavailable and efficiently assimilated by predators.”^{3,46}

You provided a detailed discussion about how salmon body size has changed over time, but I didn’t see any/much discussion about how contaminant levels may have changed. It’s unclear from looking at your source data how difficult that may be to provide, and you may be limited in your ability to provide a robust analysis for each contaminant by species and by region, but it would still be helpful to understand to what degree contaminant concentrations are increasing with time. It also wasn’t clear if this change in concentration over time was included in your models, which seems like an important assumption to address.

This is an important point. We were unable to analyze temporal trends in contaminants or nutrients for a number of reasons. Most importantly, more than half of the contaminant/nutrient concentration data were not specified by year. For example, Hg concentrations for Coho in Lockhart et al. 2005 (their Table 3) are given as an average of six samples, but the year in which those samples were taken is not listed. The range of data in Lockhart is 1970s to 2000s, making it impossible to estimate specific concentrations of Hg in a given year or even decade. Other data source papers were similar, though with smaller ranges of years (e.g., 1998-2014). This would not have been a problem if it pertained to only a small proportion of papers, but it was unfortunately common across the published sources of contaminant/nutrient concentrations. We describe limitations with the nutrient and contaminants data in the methods section (L399-443).

One way to address this is to assume, conservatively, that the concentrations reflect the most recent possible year of each report. The plot below shows that result. Several features stand out. First, data for all but two chemicals (EPA and DHA) are limited to 1990 or later. Second, if we ignore the regional and species variation, there does not appear to be any obvious trend in the concentrations (though, again, this interpretation is limited by uncertainty in the year of collection, species, and region).



To make this clear in the text, we have added the following to L136: “It is important to note that chemical concentrations were not available as time series, since many studies reported tissue concentrations averaged over multiple years and there were few data available over time within a single region or fish species.”

We also added the following clarification to the methods at L463 “Sample year is not included in these models due to lack of year-specific data for many contaminants.”

In addition to the two sentences above, it is worth noting that the models for tissue concentrations contained random effects for study authors and regions. The data for each author/region combination is usually from a single year. As a result, variation in authors/regions may also represent variation in years even if the sample year is not clearly reported. While we cannot measure variation in tissue concentrations over time, the variation attributable to the authors/regions is therefore attributable to time as well (in an indirect way). This variation is contained in the posterior predictive distributions. If we had solid data for tissue concentrations in each year/species/region combination, then presumably our estimates of contaminant flux in each year would have smaller prediction intervals, meaning that our current predictions are conservative with respect to temporal changes in tissue concentrations.

Li 63: Maybe “assimilation” would be a better word here than “uptake”

Thank you for this suggestion. We have changed “uptake” to “bioaccumulation” which is defined as the net result of chemical uptake, transformation, translocation, and elimination processes and therefore better describes the nutrients and contaminants stored in Pacific salmon for migratory transport.

Li 225-227: I’m not sure if it makes sense to say they transported more or less “than expected” when it appears you’re comparing those numbers relative to 1 kg/ 1 mg standard, which appears rather arbitrary, but maybe I’m unclear about this comparison

Thank you for this comment. Our wording here was unclear and we've revised the text to clarify what "more than expected" means: L236 "Consequently, pink salmon transported ~8% more nutrients than expected based on their return biomass alone (i.e., they transported 35% of total nutrients but only 27% of total contaminants on average each year), while Chinook and coho salmon respectively transported ~8% and 2% more contaminants than expected based on their returns (Fig. 4b)."

Li 249: *why is ecological in italics here?*

This formatting error has been corrected.

Li 265: *It is unclear how you arrived at these estimates for contaminant consumption by bald eagles. In the methods (Li 477-482) you give a broad overview of how "Exposure scenarios were estimated under various assumptions..." but very little detail is provided. Could you please provide more information about this?*

We thank the referee for this comment and opportunity to expand on our methods. Here, we took a coarse approach to provide bounding estimates on potential bald eagle mercury accumulation under various scenarios of the proportion consumed (from 1-100%) of salmon-transported Hg. These estimates make the simplifying assumptions that the entire bald eagle population consumes an equal share of the transported Hg and that salmon are the only source of Hg for this species population in order to ask how much Hg bald eagles would accumulate if they were the ultimate recipients of between 1-100% of the Hg that salmon transport annually and whether those accumulated levels have toxicological significance.

We have revised the text leading into this section of the main text to clarify that this analysis offers preliminary insights: L288 "Lacking the data needed to address these broader ecological questions, we examined salmon consumption exposure scenarios for preliminary insights on the potential significance of salmon inputs for recipient systems. Pacific salmon bioaccumulate contaminants from marine systems where contaminants are broadly distributed and dilute and subsequently concentrate these contaminants in freshwater areas of high spawning densities (i.e., contaminant focusing),³ such that their spawning periods can represent pulsed exposure events to PBT contaminants for organisms that exploit salmon resources.^{5,7,42,46,47} As a coarse example, we considered the potential exposure and risk scenarios of Hg for the bald eagle (*Haliaeetus leucocephalus*), a common salmonid predator and scavenger along the west coast of North America using our estimates of Hg delivery combined with the estimated eagle population size and associated biomass across Alaska, British Columbia, Washington, Oregon, and California.^{48,49} Assuming all ~65,000 bald eagles consumed equivalent proportions of returning salmon, they would accumulate 1.06 or 106 mg Hg if they consumed 1% or 100% of the transported Hg, respectively (Fig. 5a). We further estimated that by accumulating 1% of this Hg, the bald eagle population would achieve a whole-body concentration of 0.20 mg Hg kg⁻¹ wet weight and a blood Hg concentration of approximately 0.24 mg Hg kg⁻¹ wet weight, just exceeding the lowest concentration anticipated to have an adverse health effect (i.e., above the lowest observed adverse effect level, LOAEL) for piscivorous avifauna,⁵⁰ but falling below the moderate or high risk categories for reproductive impairment. In contrast, bald eagles would be exposed to concentrations corresponding to moderate, high, and severe risks of reproductive impairment if they assimilated 7%, 10%, and 14% of the transported Hg, respectively.⁵⁰ It follows that exposure to even small proportions of salmon-derived contaminants can be toxicologically relevant for upper trophic level consumers, reflecting that the contaminants stored in salmon tissues are bioavailable and efficiently assimilated by predators.^{3,51}"

We have also updated the methods section to clarify our approach so that it now reads:

L544 “To estimate the range of possible exposure to Hg from salmon subsidies in a model wildlife taxon, the bald eagle, we first compiled estimates of bald eagle population size (65,740 adult birds) across Alaska, British Columbia, Washington, Oregon, and California, from State and federal wildlife agency reports.^{48,49} We then estimated total mass of bald eagles across the study area using an average female feather-free mass of 5.4 kg. Exposure scenarios were estimated under various assumptions of the proportion of annual Hg subsidy consumed by the bald eagle population, both from direct consumption of migrating salmon, as well as indirectly from Hg transferring to bald eagles through aquatic and terrestrial consumers. For the 100% consumption estimate, we divided the full amount of the annual average salmon Hg input (~7 kg) by the total bald eagle population biomass to estimate the potential whole-body Hg concentration. We calculated similar estimates across a gradient of proportional exposure, down to consumption of 1% of the total annual Hg input by salmon. We then estimated bald eagle blood concentrations across this range of exposure levels using standard equations for avian taxa⁵⁰ to convert body concentrations (i.e., muscle) to blood concentrations and compared those blood concentrations to various benchmarks of impairment.⁵⁰”

Li 266: A range of 1-100% assimilation for Hg seems very broad—is there no literature that can better inform an appropriate range for this estimate?

Thank you for this question. While there are studies documenting how contaminant concentrations in specific food webs increase with the return of spawning salmon, there is very little data on the proportion of Pacific salmon-transported contaminants that accumulate in specific predators. We also have a poor understanding of how salmon-supplied contaminant exposures compare to other exposure sources (except for the few small-scale studies discussed in the manuscript involving grizzly bears and stream-resident fish in Great Lakes tributaries). Because of these data shortcomings, our intent is to offer preliminary estimates that provide coarse bounds on how much Hg accumulation is mathematically possible by a single predator population across the range of feasible exposure scenarios and at the continental scale. Because these estimates only account for Hg exposure via salmon consumption, the high- and low-exposure scenarios are conservative in that they do not account for background Hg burdens from other food sources (i.e., how salmon-derived Hg adds to the extant Hg accumulated by a specific consumer). Further, we do not account for long-term biological retention of Hg due to chronic or repeated exposure conditions. Subsequent research on the proportion of biotransported contaminants that accumulate in specific consumers at local to large spatial scales will be important for informing more ecologically-relevant ranges of contaminant accumulation in recipient biota from direct and indirect salmon pathways.

Li 354: You say that changes in salmon population numbers were the most important factor driving changes in total nutrient and contaminant loads, which suggests you did a sensitivity analysis, but it would be helpful to say that directly. I saw the sensitivity analysis in your methods, but it wasn't clear just from reading the main text.

We thank the referee for pointing this out. We have revised the corresponding text at L133 to read: “Variance partitioning from a sensitivity analysis indicated that mean individual fish weight explained <2% of these increases. Instead, return abundance and/or chemical concentration were the most important variables, explaining >98% of the variation in transport (Supplementary Information Fig. 1).”

We also revised the Supplementary Information Figure 1 caption to specify that it shows the results of the sensitivity analysis: “*Sensitivity analysis showing contributions of variation in weight (mean weight of individual fish in kg ww), post-harvest returns (millions of fish), and chemical*

composition (mg kg^{-1} ww) to the average annual flux of nutrients and contaminants from marine to freshwater ecosystems by salmon."

- Amanda Subalusky

This is an interesting and novel/creative paper that describes shifts in modeled inland inputs of N, P, long chain fatty acids (EPA/DHA), and several contaminants with fluctuations in salmon stocks between 1976 and 2015. The authors construct detailed estimates of the proportions of contaminants and nutrients transported into individual systems from different salmon stocks over time and how they fluctuated with salmon stock abundance, differences in weight of the fish, and contaminant concentrations (although changes in tissue concentrations were not really the focus due to data limitations). The results show that abundance was the major driver of the observed differences in fluxes across years and that pink salmon returns are particularly important.

We thank the referee for their interest and feedback on our manuscript. Please find our detailed responses to the questions and ideas provided below.

While the estimates and accounting of contaminants and nutrients flows in this paper seem reasonable, and the manuscript is well written, my main concern about this paper is that it presents all the calculations through the lens of a salmon only world and therefore does not provide context for how relevant the budgets are for overall ecosystem processes. My major suggestion for the authors is therefore to provide more context for the importance of salmon subsidies for both nutrient and contaminants in the paper. The authors need to convince the readers that the salmon associated fluxes considered are important for the four systems highlighted in the manuscript. The present version of the manuscript contains no information or discussion of this at all. It pivots to an exposure/risk discussion at the end but this is driven by concentrations not overall budgets, and the authors acknowledge in the methods that this is a weak point in the analysis.

We appreciate the referee's comments and recognize from them that we did not provide sufficient background about the importance of marine-to-freshwater subsidies nor the specific influence of Pacific salmon in recipient systems. Ecological subsidies research is premised on the relevance of energy, nutrients, and organic matter produced in one system and transferred to another (i.e., allochthonous materials) and sets out to characterize the degree to which these flows modify the structure and/or productivity of the subsidized food webs (Polis et al. 1997, Subalusky and Post 2019, Walters et al. 2020). Among migratory fish species, the anadromous (i.e., freshwater fish that mature in marine systems before returning to freshwaters as spawning adults) and semelparous (i.e., reproducing once per lifetime) Pacific salmon species we include in our analyses are unique in that they represent both material subsidies and process subsidies (Flecker et al. 2010); the former are defined as resource subsidies that result in direct changes in recipient ecosystem resource pools and the latter are defined as effects on recipient ecosystem process rates that result from migratory animal activities in those systems (e.g., feeding). The importance of salmon subsidies for recipient ecosystems represents a tradeoff for commercial fisheries and underlies Pacific salmon population management strategies (Schindler et al. 2013). Salmon-derived subsidies research since the 1990s has documented their influence on diverse ecological processes in freshwaters and adjacent terrestrial systems which has been summarized by several syntheses (e.g., Gende et al. 2002, Naiman et al. 2002, Schindler et al. 2003, Janetski et al. 2009, among others). From this body of research, the idea that spawning Pacific salmon are influential in recipient systems is well-supported in the systems where they have been studied. Below, we provide a brief overview of this research which includes results from studies where salmon subsidies are modulated as carcass additions and from studies that compare systems that do and do not receive returning salmon.

Pacific salmon accrue more than 95% of their biomass during their ocean residency and subsequently import substantial amounts of energy and hundreds of metric tons of nutrients to recipient systems, many of which are nutrient poor or oligotrophic. These nutrient subsidies are

released through consumption of live salmon, gametes, and carcasses and local food web fertilization from fish excretion and carcass decomposition. The importance of these subsidies for recipient systems is supported by multiple lines of evidence across studies: stimulating primary production, nutrient uptake in plant and animal tissues, increased growth rates and sizes of consumers, resident fish communities, and young of the year salmon, phenological patterns in salmon predators and scavengers, and the phylogenetic dispersion of riparian plants, among others; collectively these measures point to the potential for Pacific salmon to increase recipient system productivity (Naiman et al. 2002, Schindler et al. 2003, Janetski et al., 2009, Schindler et al. 2013, Walsh et al. 2020, and references therein). Further, the spatial influence of salmon subsidies are extended when predators, scavengers, emergent aquatic insects, floods, and subsurface flow can carry carcasses or salmon subsidies to riparian and terrestrial food webs where the nutrients are subsequently used by organisms across trophic levels (Schindler et al. 2003). Accompanying these fluxes of energy and nutrients are the fluxes of contaminants also stored in Pacific salmon tissues, which we discuss in more detail below. Beyond their provisioning of nutrients and energy, Pacific salmon engineer recipient ecosystems by altering sediment composition export, disturbing benthic communities, and altering the local hydrology as they build their spawning redds in stream beds (Schindler et al. 2003, Janetski et al. 2009, Walsh et al. 2020). Recent research also shows that some streams are vulnerable to hypoxia where salmon spawning densities are high and combine with drought conditions (Sergeant et al. 2023).

There is considerable context dependency in the influence of animal resource subsidies, including salmon subsidies, for recipient systems as we know that input effects depend on input quantity, quality, timing and duration as well as the recipient system's abiotic and food web characteristics (Subalusky and Post 2019, Gende et al. 2002, Janetski et al. 2009, Walsh et al. 2020). The extent to which Pacific salmon represent material subsidies depends on how their return biomass relates to the size of the recipient ecosystem, the recipient system's baseline availability of energy and nutrients, and how effectively Pacific salmon subsidies are mobilized and retained in the recipient system (Flecker et al. 2010). Recently, Walsh et al. (2020) reviewed 31 studies investigating 172 relationships between salmon density and ecological responses in recipient terrestrial and freshwater ecosystems in western North America. From this work, they identified 104 non-isotopic ecological indicators from 30 of the studies that revealed consistent patterns with salmon density, including positive relationships with food provisioning for bears and freshwater fish, abundance of scavengers and passerines, and freshwater fish growth rates and sizes; they also report a consistently negative relationship between salmon density and the proportional change in stream invertebrates and algal biomass pre- and post-spawning reflecting the influence of salmon bioturbation on benthic communities (Walsh et al. 2020). It is also important to note that the influence of Pacific salmon on recipient systems has not been studied for all systems to which they return and that there is an apparent bias to study salmon influence in British Columbia and Bristol Bay, in streams, and where runs are dominated by pink and sockeye salmon and spawning densities are high (Janetski et al. 2009, Walsh et al. 2020).

As the referee identifies, the manuscript would benefit from more context about the importance of salmon subsidies for recipient systems. Accordingly, we revised the introductory section by adding the following text:

L55 “Pacific salmon accrue more than 95% of their biomass at sea and later deliver the energy and nutrients stored in their tissues as they release gametes, excrete, decompose, and are consumed by predators and scavengers in recipient food webs. These inputs of allochthonous material have diverse influences in aquatic and terrestrial systems, including stimulating primary and secondary production, enhancing nutrient uptake in plant and animal tissues, increasing growth rates and sizes of resident consumers, and altering the phylogenetic dispersion of riparian plants.^{5,13–18} Predators, emergent aquatic insects, floods, and subsurface flows can extend the spatial influence of these

subsidies to riparian and terrestrial food webs where they are subsequently used by organisms across trophic levels.¹⁶ The effects of salmon subsidies in recipient systems are broad yet context-dependent, and vary according to the quantity, quality, timing, and duration of inputs as well as the abiotic and food web characteristics of the recipient system.^{5,9,12,15,17}

References cited in response and added to manuscript (excluding those already cited in the manuscript)

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The idea of a contaminant “subsidy” from a marine system to an inland system is a bit surprising since we normally think about the flow in the other direction. We do this because the sources coming from terrestrial systems are large and thus the reservoir in the water/sediment is large relative to offshore marine ecosystems. Global and continental scale budgets for contaminants and nutrients from other work indicate inbound fluxes from salmon presented here are negligible compared to what is already present in the terrestrial systems and being discharged offshore. From this perspective, the salmon are a relatively clean import to potentially contaminated terrestrial systems. Flipping this idea adds to the novelty of the paper, so could be a good thing, but as mentioned above, the reader needs to be convinced that this subsidy is actually important. For example, even though fish biomagnify some contaminants, when you construct a budget for total mass in the system the fisheries reservoir is usually negligible compared to what is present in water/sediment. The authors could address this point by comparing watershed budgets for contaminants and nutrients for the four specific regions highlighted in the manuscript to the estimated salmon-only associated fluxes in this manuscript.

The referee is correct that we much more commonly think of unidirectional material flows from land to sea and in the contexts of flowing waters and soil erosion (Gerig et al. 2020). Conventional contaminant transport models mostly exclude transboundary biological transport (Schiesari et al. 2018), but considerable evidence now supports that the upstream (upgradient) fluxes by migratory animals such as anadromous salmon can involve the mass transport of materials in a manner that strengthens metacommunities and metaecosystems. Many studies have shown that salmon nutrient and contaminants inputs are not negligible relative to other sources in recipient systems, but rather lead to measurable increases in the nutrient and contaminant status of the recipient systems. For example, Holtgrieve and Schindler (2011) assessed recipient system dynamics in an Alaskan stream with moderate densities of spawning salmon for seven years and showed that dissolved nitrogen and phosphorus concentrations increased on average by 190% and 390%, respectively. Similar work by Kyle (1996) reported 33% higher total phosphorus concentrations in lakes in the Alaskan Peninsula with sockeye salmon returns relative to those where natural barriers exclude spawning salmon (Naiman et al. 2002). Inferences from isotopic signatures, though not without their caveats, have supported estimates that marine-derived nitrogen biotransported by salmon can represent up to 70% of the overall lake sediment nitrogen burden (Naiman et al. 2002). As discussed below, we are not aware of any studies that have compared the magnitudes of salmon-derived fatty acids (EPA and DHA) to other sources in recipient systems. However, dispersing animals such as Pacific salmon are expected to be the

dominant pathways of EPA and DHA subsidy fluxes from marine to freshwater and terrestrial systems and these fluxes are expected to be more substantial than those from terrestrial to aquatic systems (Twining et al. 2016, Gladyshev et al. 2009).

Contaminant transport by migrating salmon can also represent an important source to recipient systems and lead to contamination hot spots. Ewald et al. (1998) were the first to document returning salmon as contaminant biovectors by reporting that PCB and DDT concentrations in arctic grayling (a resident aquatic predator) sampled from lakes upstream of the Gulf of Alaska that receive runs of spawning sockeye salmon were significantly higher than arctic grayling in lakes that do not receive salmon. Further, they showed that atmospheric deposition of PCBs and DDTs did not differ between the two lake catchment areas nor were atmospheric contaminant deposition levels related to arctic grayling contaminant concentrations (Ewald et al. 1998). Five years later Krümmel and co-authors reported recipient lake surface sediment PCB congener profiles matching those in spawning sockeye salmon returning to those lakes and that sediment PCB concentrations were not only higher in lakes receiving salmon than lakes that do not receive salmon, but that sediment PCB concentrations and accumulation rates were correlated with salmon densities (Krümmel et al. 2003). Here too the authors found that salmon PCB fluxes were greater than atmospheric pathways to these lakes. Finally, we point to studies documenting the importance of salmon-derived contaminants for specialist consumers like resident rainbow trout (Gregory-Eaves et al. 2007) and coastal grizzly bears in British Columbia who alter their exposures (both concentrations and compositions) to persistent organic pollutants (POPs) and mercury by consuming large amounts of returning salmon biomass when it is available (Christensen et al. 2005, Noël et al. 2014), even achieving hair concentrations above proposed neurotoxicity effect levels (Noël et al. 2014). This work has also estimated that salmon contribute an estimated mean 70-90% of bear POP burdens (Christensen et al. 2005) and that POP elimination via defecation by grizzlies is less when POPs are acquired from salmon vs plant sources due to differences in the fugacity of the chemicals in the different POP mixtures and the digestibility of the food types (Christensen et al. 2013).

Collectively, the large body of research on the significance of salmon nutrient and contaminant fluxes for recipient systems indicates that Pacific salmon can be comparable, if not the most important, sources of these materials and that Pacific salmon can carry different chemicals and congener mixtures than may arrive in systems by other pathways due to their physicochemical properties. Another key distinction between Pacific salmon and other sources of nutrients and contaminants in recipient systems is that salmon-derived nutrients and contaminants are packaged as food and in chemical forms that are directly bioavailable to local food webs (Blais et al. 2007, Baker et al. 2009) such that they will be more efficiently (i.e., higher amounts and more quickly) assimilated by recipient food webs than abiotic pools, even if the abiotic pools contain larger amounts of these materials.

We have revised the section on the ecological importance of salmon-derived nutrients and contaminants to better reflect this important background information as follows:

L260 “It is difficult to predict the ecological importance of nutrient and contaminant inputs based solely on their magnitudes. Salmon-derived nutrients are ecological subsidies of essential elements and compounds, i.e., donor-controlled resources with positive ecological benefits (e.g., enhanced productivity) for recipient systems,^{4,20} whereas PBT contaminants are either entirely the result of anthropogenic production (PCBs, DDTs, and PBDEs) or are greatly enhanced by it (Hg), with exposures expected to impair rather than enhance biological function. The potential significance of both salmon-derived nutrients and contaminants in recipient systems is well-established. For example, returning salmon enrich dissolved N and P concentrations and N transported by salmon can represent a substantial fraction of lake sediment stores.^{13,39} Early work on salmon contaminant

transport similarly showed that spawning returns can be significant sources of persistent organic pollutants to sediments and resident biota, including grizzly bears who increase their contaminant exposures by consuming large amounts of returning salmon when they are available.^{6,7,40–42} Contaminant transport by Pacific salmon has also been studied in the Laurentian Great Lakes where salmon introduced in the 1950s migrate from the lakes to tributaries for spawning. There, stream-resident fish that capitalize on energy-dense salmon eggs substantially enhance their exposure to the PCBs and DDTs that efficiently partition to high-fat tissues while reducing their exposure to Hg for which salmon egg concentrations are low relative to other dietary sources.^{43–45}

While the referee's question about how salmon nutrient and contaminant fluxes compare to the magnitudes of other sources at watershed scales is interesting, we contend that watersheds are the wrong unit of study. This is because returning Pacific salmon do not uniformly distribute within the watersheds to which they return. Rather, they aggregate at their freshwater spawning grounds, and the sizes and densities of these aggregations vary both within and among species. It would therefore be more insightful to compare nutrient and contaminants fluxes by salmon with those of other sources specifically in those areas where salmon return. As discussed above, this question has been previously addressed by researchers for specific nutrients, contaminants, and ecosystem contexts (Naiman et al. 2002, Ewald et al. 1998). Importantly, these results indicate that the amounts supplied by salmon can be comparable to existing pools and other inland sources. These studies support the premise—that salmon are significant sources of nutrients and contaminants in recipient systems—that we build on with our study. In other words, accepting the premise that Pacific salmon are important to the inland systems to which they return, we set out to quantify salmon nutrient fluxes across the marine-to-freshwater boundary for the full latitudinal extent of their migration runs in order to estimate, for the first time, the magnitudes of those fluxes. We build on that first principles objective by 1) adding measures of the accompanying contaminant fluxes that represent chemical tradeoffs to nutrients and 2) assessing how both nutrient and contaminant fluxes at the continental scale varied over a 40-year time period corresponding with changes in the Pacific salmon community. Then, because the structure of the five-species Pacific salmon community varies from the northern to the southern extent of the range of their migration runs, we compare fluxes among four sub-regions and ask how variation in community structure influences the amounts of nutrients and contaminants across the four spatially demarcated marine-to-freshwater boundaries. In other words, our intent for the scope of this first paper is not to compare the influence of salmon-derived nutrients and contaminants among the four regions but rather to compare their quantities and ratios as a reflection of the properties of the returning salmon communities (differences in species composition and numbers and sizes of fish). We think these analyses are important precursors to future research about salmon subsidies at large spatial scales, including many of the ideas presented by the referee.

We have removed the statement about watershed area as it could be misleading (by specifically emphasizing watersheds as units for Pacific salmon inputs). We have also revised this section to better position the regional analyses and future directions in the manuscript as follows:

L163 “The distribution of freshwater spawning grounds is a principal driver of how salmon-derived nutrients and contaminants are dispersed among recipient ecosystems. Further, the structure of the Pacific salmon community varies from the northern to the southern extent of their migration runs (Extended Data Fig. 1, Extended Data Table 1). To build on the continental-scale estimates described above, we considered how community composition affects the magnitudes of nutrient and contaminant inputs at regional scales by defining four marine-to-freshwater boundaries following broad patterns of Pacific salmon migration: the northern Bering Sea (BS), Central Alaska (CAK), Southeast Alaska (SEAK), and a region encompassing British Columbia and the west coast of the United States (BCWC) (Fig. 1). These regional groupings allowed for the best matching of

data sources needed to generate return estimates while facilitating our assessment of how the relative return biomass of each species related to nutrient and contaminant transport patterns.

[...] We anticipate that insights about the influence of Pacific salmon for specific ecosystems will come from studies assessing recipient food web responses to the temporal dynamics of nutrient and contaminant loading (e.g., where and when various spawning populations overlap) by salmon and relative to other sources of these materials.”

References cited in response and added to manuscript (excluding those already cited in the manuscript)

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The EPA/DHA flux is quite interesting and I don't know what happens to it when a salmon dies. In contrast to the contaminants and nutrients, I don't think there is a large flux of riverine discharges of EPA/DHA. Are the long chained fatty acids stable when the salmon die or do they degrade? I think the authors could focus on this story a bit more because it is very interesting.

We are uncertain as to the fate of EPA/DHA after salmon die. There are both direct (egg and carcass consumption) and indirect (dissolved nutrient uptake) effects of salmon (Kiernan et al. 2010), and it is most likely that EPA/DHA enter the food web by direct pathways (Figueroa-Munoz et al. 2022). However, these compounds are measurable in Chinook salmon feces (Elvines et al. 2023), suggesting that they may remain intact and biologically available when part of particulate matter, so could be taken up by filter feeders. Whether they remain available for microbial uptake once they are in the dissolved phase is unknown, though we would expect a short half-life owing to hydrolysis and photolysis (Kieber et al. 1997).

We highlight the knowledge gap about nutrient vs contaminant co-processing on ecosystem functioning at L279: “We do not yet know how co-exposure to the nutrients and contaminants transported by salmon influence ecological responses within trophic levels (e.g., primary production), nor have studies explored how nutrient benefits may be balanced by contaminant effects across trophic levels to inform their overall influence on ecosystem functioning. Further, the coupled fates (following excretion and decay) and influences of salmon-derived nutrients and contaminants are anticipated to vary among recipient systems to reflect both spatial and temporal spawning patterns and site-specific characteristics—including waterbody size, geomorphology and hydrology, nutrient status, and food web structure. Together, these factors will determine the importance of transported nutrients and contaminants relative to other sources.”^{12,15,43}

References cited in response

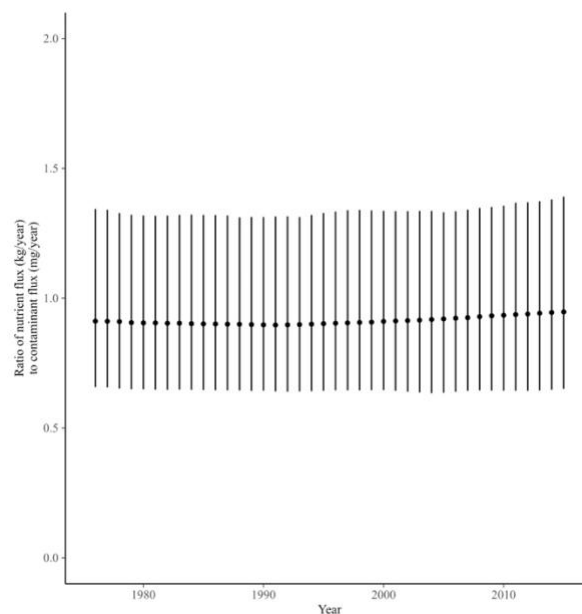
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Around line 248 - the tone of the manuscript shifts to ecological impacts of the shifts in budgets over time. This will depend on concentrations in individual fish and diet composition rather than the overall budgets so seem a bit disconnected from the first part. This statement seems very subjective “Pacific salmon concentrate transported contaminants” - since salmon are not highly contaminated compared to other foods and often are a relatively clean source of food for the animals consuming them. The pulsed exposure is simply the animals are eating a lot - so again I think this statement is misleading given the broader context of animals need to eat something and all food has contaminants. Perhaps a focus on relative changes over time rather than absolute risk/benefit ratios would be good but I recommend caution to the authors in these sections given the limited empirical data available for such calculations.

We hope that our responses above and the associated revisions now provide a suitable amount of background information for contextualizing our study within the broader Pacific salmon subsidies literature. The major theme of this body of research is that the subsidies are ecologically important, and we build on the prior work in this section of our manuscript by providing an initial exploration of the potential influence of Pacific salmon fluxes at the continental scale. Our study is the first to consider a spatial scale as broad as western North America and our analyses about the ecological relevance of these fluxes allows the study to extend beyond an accounting of inputs. We take two approaches. First, the bald eagle mercury consumption example serves as an end-member analysis of how the total annual mercury flux by Pacific salmon could influence recipient food webs (L293-308). As described above, Pacific salmon represent enriched

contaminant sources for consumers like grizzly bears who switch their diet away from lesser-contaminated foods to capitalize on salmon prey (Christensen et al. 2005, Christensen et al. 2013, Noël et al. 2014). Our estimates that bald eagle consumption of even small proportions of the incoming mercury could lead to toxicologically-relevant concentrations should inspire future research for salmon-specialist consumers. We see this as a fruitful topic as there is limited research to date about the ecological impact of salmon-derived contaminants in recipient food webs. Second, we assessed the human health tradeoffs of omega-3 fatty acid versus contaminant exposure from consuming each of the five Pacific salmon species (L312-319) as a first pass at addressing the question (also identified by the referee here) about how Pacific salmon compare to other foods as dietary sources of nutrient and contaminants.

We liked the referee's idea about considering relative changes in transported nutrients to contaminants over time. In the section above this one about species-specific transport patterns (L195), we compared the relative contributions of each species to total nutrient versus total contaminant fluxes and how those relative contribution trends have changed over 40 years as the community structure shifted (Fig. 4b). Below, we show these data for the community level with time plotted on the x-axis; the figure shows the median (points) and 95% interval (vertical lines). As the referee points out, the absence of temporally-resolved nutrient and contaminant tissue concentrations inhibits our ability to analyze temporal change in those values, so our species-specific nutrient-to-contaminant ratios are fixed. The analysis shown below therefore reflects changes in the community structure over time instead. We see a slight increase in the median trend over time as well as a high level of uncertainty. We can add this analysis to the main text or supporting information if the referee and editor find it helpful, though it is somewhat redundant with the population patterns shown in Fig 4b.



Our statement that Pacific salmon concentrate transported contaminants refers to the phenomenon by which contaminants that are relatively diluted and widely distributed in marine waters become relatively concentrated in the food web through the processes of partitioning and biomagnification. The movement of large numbers of migratory fish like Pacific salmon and associated transport of the bioaccumulated contaminants from across spatially dispersed marine habitats to inland spawning areas concentrates contaminant inputs as large numbers of fish congregate in relatively small habitat areas (streams and lakes). This is a process known as

“contaminant focusing” and is performed by various migratory animals, including Pacific salmon (Blais et al. 2007, Kallenborn and Blais 2015, Gerig et al. 2020).

We have revised the language at L290 to describe this process more clearly: “Pacific salmon bioaccumulate contaminants from marine systems where contaminants are broadly distributed and dilute and subsequently concentrate these contaminants in freshwater areas of high spawning densities (i.e., contaminant focusing),³ such that their spawning periods can represent pulsed exposure events to PBT contaminants for organisms that exploit salmon resources.”^{5,7,42,46,47”}

Lines 288 onward - I am not really convinced that this is important yet.

We hope that our responses and revisions following from the referee’s constructive comments now support these ideas as future research directions. We also revised the text here to include the referee’s ideas about exploring the net effects of salmon inputs for recipient systems (L320): “Our work points to the need to understand the net effects of Pacific salmon inputs at local scales. Building on the long history of salmon-derived nutrient research, experimental field and laboratory-based studies that consider the distribution, fate, and processing of nutrient and contaminant inputs in concert by recipient food webs and in specialist consumer diets will inform questions about how Pacific salmon inputs interact to influence ecosystem functioning and wildlife populations at spawning grounds.”

Methods: I am not an expert in salmon stock assessment methods but there are large teams of fisheries scientists devoted to this and estimating returns so I hope a referee with such expertise is included. On first pass - the methods for this section look reasonable to me.

Thank you. We agree that stock assessments generated by fisheries experts are valuable and relevant to this work. As such, our estimates build upon the previously published estimates of total salmon abundance (pink, chum, sockeye), harvests (all species), and escapements from fisheries (comprehensiveness varies with species) from stock assessment reports. We speculate, based on their insights and questions, that Referee #3’s specialty appears to be in fisheries management and Pacific salmon.

As is typical, there are few data to estimate temporal patterns in contaminant or nutrient data in the salmon. This should be acknowledged more clearly in the main text. This will drive the exposure/risk/benefit results presented so those should be viewed as highly uncertain and I don’t really think fit well into this work anyway.

Thank you for this suggestion. Similar comments and questions were posed by the other two referees. Accordingly, we have made the following revisions to clarify and better describe how we approached the issue of temporal tissue concentration change:

L136: “It is important to note that chemical concentrations were not available as time series, since many studies reported tissue concentrations averaged over multiple years and there were few data available over time within a single region or fish species.”

L463 “Sample year is not included in these models due to lack of year-specific data for many contaminants.”

We have also revised the Methods to emphasize that temporal changes in contaminant and nutrient flux are driven by changes in Pacific salmon returns, not changes in individual-level fish tissue concentrations: L414 “This is a source of uncertainty in our analysis because we cannot account for changes in contaminant concentrations over time. Because increases or decreases in the flux of any given analyte over time are driven by yearly changes in Pacific salmon returns, not changes in analyte tissue concentration, all temporal changes in chemical or nutrient flux are described at the

population or community level. As a result, our analyses focus on the influence of temporal changes to the Pacific salmon community as principal drivers of the shifts in subsidy transport between 1976 and 2015.”

We repeat here part of our related response to Referee 1 as it may be useful for understanding how time is incorporated in our modeling approach: It is worth noting that the models for tissue concentrations contained random effects for study authors and regions. The data for each author/region combination is usually from a single year. As a result, variation in authors/regions may also represent variation in years even if the sample year is not clearly reported. While we cannot measure variation in tissue concentrations over time, the variation attributable to the authors/regions is therefore attributable to time as well (in an indirect way). This variation is contained in the posterior predictive distributions. If we had solid data for tissue concentrations in each year/species/region combination, then presumably our estimates of contaminant flux in each year would have smaller prediction intervals, meaning that our current predictions are conservative with respect to temporal changes in tissue concentrations.

Overview comments: The manuscript entitled *Shifts in Pacific salmon community alter continental-scale nutrient and contaminant delivery* includes several key results. First, the paper documents how a shift in the proportion of salmonid species shifting over the course of a 40 year time frame alters the flow of important marine derived nutrients and deleterious contaminants across the Pacific Rim. Most individuals know the story with regards to the importance of marine derived nutrients, but few understand the shift in species composition over time and what that may mean from an ecosystem perspective. This paper does a good job of highlighting that change. Second, few link contaminants with salmon, from an ecosystem perspective and at the scale this paper delves into the topic. While there have been some papers on this topic (Baker, M.R., Schindler, D.E., Holtgrieve, G.W. and St. Louis, V.L., 2009. Bioaccumulation and transport of contaminants: migrating sockeye salmon as vectors of mercury. *Environmental science & technology*, 43(23), pp.8840-8846.) they have not expanded the concept to the entire Pacific Rim. So the results that nutrients are orders of magnitude larger than contaminant delivery is original and significant, and the fact that species composition change and the resultant shift in what species dominates these return of nutrients at the pacific rim scale is unique. The data and methods, validity of approach and quality of presentation is sound. The quality of the data varies, but the authors recognize this in their methods section and allow the reader to assess the information as well as the original data in the supplementary material. The authors do a solid job of utilizing Bayesian statistics to help quantify both the variation, distribution, and uncertainty. This is critical to the results, in my opinion, and add credence to the interpretation due to the extreme difference in magnitude of contaminants to nutrients. The conclusions, robustness, validity and overall reliability is thus sound. There are several places where the manuscript can be improved. Rather than repeat my specific comments, they are embedded into the paper which is attached. The references are adequate and the clarity and context is clear and thoughtful. While I understand and utilize some of the statistics, I do not readily utilize Bayesian statistics so someone who does may have further insights into the analyses. I do believe the paper is in need of revisions but is a sound potential contribution to nature.

We thank the referee for their insightful and constructive comments on the manuscript. Please find our responses and revisions organized with each of the detailed comments below.

Detailed comments embedded in the manuscript file:

L51: The authors identify salmon but do not mention steelhead, which also have the same transboundary ecological effect. It may be useful to include them as well. Pacific Lamprey also have a similar migratory strategy.

We thank the referee for this comment and have revised the first lines of the main text to better situate Pacific salmon as an example of both the broader category of migratory animals that carry resource subsidies and, more specifically, as part of the large group of anadromous fishes that connect marine and freshwater food webs. The text now reads: L48 “[Migratory animals that carry nutrients and organic matter from donor to recipient ecosystems \(i.e., spatial subsidies\) strengthen transboundary ecological networks.^{1,2,10,11} Anadromous fishes are particularly important to the coupling of marine and freshwater food webs in temperate aquatic systems.¹² Among them, the five species of semelparous Pacific salmon that return to freshwaters to spawn at the end of their life cycles – Chinook salmon \(*Oncorhynchus tshawytscha*\), chum salmon \(*O. keta*\), coho salmon \(*O. kisutch*\), pink salmon \(*O. gorbuscha*\), and sockeye salmon \(*O. nerka*\) – exemplify the delivery of subsidies obtained from marine food webs to inland systems 100s-1000s of km away from the oceans where they grew.^{12,13}”](#)

L52: suggest “a myriad of”.

We revised myriad to “many”.

L87: *How did the authors account for uncertainty or variance in the annual return abundance estimates as well as the annual mean individual fish weight?; followed by L89: ok this answers my previous question because you are using the posterior distributions.*

Thank you, we are glad that the text provides the information needed to understand our approach to accounting for uncertainty in fish abundance and fish weight.

L209: *Do the authors have any hypotheses as to what may occur? potential mechanisms? this need not go into the paper but it would be good to hear what the potential changes are and what drives such changes.*

A handful of studies have addressed the question of how physiological changes during Pacific salmon migrations influence tissue contaminant concentrations. Each of the four studies referenced here focused on sockeye and/or Chinook salmon, but can inform hypotheses for the Pacific salmon community more broadly. Ewald et al. (1998) is the first study we are aware of to identify spawning Pacific salmon as contaminant biovectors to freshwaters. Along the 410 km spawning migration from the Gulf of Alaska to spawning lakes associated with Alaska’s Copper River, muscle tissue concentrations of PCBs and DDTs increased in mature fish and further in spent fish and these increases corresponded in decreases of muscle lipid content. In other words, lipid depletion during migration was not coupled with contaminant elimination from the body but rather, in the case of these two lipophilic contaminant types, magnification within tissues and redistribution to gonadal tissues. DeBruyn et al. (2004) reported similar patterns in lipophilic organic contaminant (PCBs, PCDDs, and PCDFs) magnification in sockeye salmon returning to Great Central Lake (British Columbia) and showed that concentrations increase with migration distance. Finally, Kelly and co-authors (2007, 2011) build on these results in the context of Fraser River sockeye and Chinook populations. Together these studies show that lipophilic contaminant and mercury concentrations increase with migration and that these concentration magnifications balance decreases in weight such that wet weight body burdens remain relatively constant. These studies also report that magnification factors are highest for high K_{ow} (lipid partitioning coefficient) compounds which suggests that the relative composition of the chemical profile may change with migration.

As far as we’re aware, there has not been corresponding research about how migration affects adult tissue N&P composition, and this adds to the knowledge gaps discussed above in response to Referee 1 about variation in Pacific salmon macronutrient concentrations and body burdens both within and among species. Of interest, related work by Ebel et al. (2015) and references therein indicates that %P varies with life stage in Atlantic salmon; however, this is distinct from the question of whether catabolism in the period between freshwater entry and spawning and senescence (or direct consumption in or near spawning grounds) alters whole-body nutrient burdens in a manner that informs flux estimates. If we assume that macronutrient concentrations are proportionally consistent with body size (i.e., %N and %P do not change), we can hypothesize that whole body nutrient concentrations would not change but that whole body fish burdens would decrease as fish weights decrease during migration. The degree to which nutrient burdens decrease would also be expected to vary as a function of the length of the spawning run. For fatty acids, changes during migration are likely to be important. Lipid depletion during the spawning migration (McVeigh et al. 2007) leads to proportional loss of omega-3 fatty acids (Phelger et al. 1995), which would change the ratio of omega-3 fatty acids relative to contaminants and thus alter the risk-benefit ratio for consumers.

Collectively, the results of this limited body of research suggest that nutrient:contaminant *concentration* ratios and nutrient:contaminant *loading* ratios may both change during spawning

migrations in a manner that depends on the composition of the nutrient and contaminant profiles considered, the species (as high lipid content fish will accumulate higher levels of persistent organic pollutants), and the distance traveled during migration. These hypotheses are compelling and a promising direction for future research about the bright and dark sides of salmon subsidies.

References cited in response

- deBruyn AM, Ikonomou MG, Gobas FA. 2004. Magnification and toxicity of PCBs, PCDDs, and PCDFs in upriver-migrating Pacific salmon. *Environ Sci Technol* 38:6217–6224.
- Ebel JD, Leroux SJ, Robertson MJ, Dempson JB. 2015. Ontogenetic differences in Atlantic salmon phosphorous concentration and its implications for cross ecosystem fluxes. *Ecosphere* 6(8)L136.
- Ewald G, Larsson P, Linge H, Okla L, Szari N. 1998. Biotransport of organic pollutants to an inland Alaska lake by migrating sockeye salmon (*Oncorhynchus nerka*). *Arctic* 1:40-47.
- Kelly BC, Gray SL, Ikonomou MG, Macdonald JS, Bandiera SM, Hrycay EG. 2007. Lipid reserve dynamics and magnification of persistent organic pollutants in spawning sockeye salmon (*Oncorhynchus*
- *nerka*) from the Fraser River, British Columbia. *Environ Sci Technol* 41:3083–3089.
- Kelly BC, Ikonomou MG, MacPherson N, Sampson T, Patterson DA, Dubetz C. 2011. Tissue residue concentrations of organohalogenes and trace elements in adult Pacific salmon returning to the Fraser River, British Columbia, Canada. *Environmental Toxicology and Chemistry* 30(2):367-376.
- McVeigh BR, Healey MC, Wolfe F. Energy expenditures during spawning by chum salmon *Oncorhynchus keta* (Walbaum) in British Columbia. *Journal of Fish Biology*. 2007 Dec;71(6):1696-713.
- Phleger CF, Laub RJ, Wambeke SR. Selective skeletal fatty acid depletion in spawning Pacific pink salmon, *Oncorhynchus gorbuscha*. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*. 1995 Jul 1;111(3):435-9.

L236: It would be good for the authors to recognize the large body of literature on salmon and contaminant transport in the Great Lakes. There they have had the opportunity to study the potential mechanisms and differences of where contaminants accumulate and what it means to ecosystem function. Again no need to get into too much detail but there are some important references in that literature.

We thank the referee for this helpful suggestion. Please see our response below where we fully address this alongside the related comment at L254.

L239: this has been stated multiple times in the paper.

We thank the referee for pointing this out. The first sentences of this paragraph have been revised to better frame the focus of this section. They now read: “[Our analyses show that salmon-mediated nutrient transport was balanced by the co-occurring transport of contaminants, and that both nutrient and contaminant inputs to North America increased from 1976 to 2015](#)” (L252).

L254: This is where perhaps some of the Great Lakes literature may be useful.

Thank you for pointing out that we neglected to include the Great Lakes Pacific salmon literature; we agree that insights from that work enhance our discussion here. We have revised this section in response to feedback from the other referees as well. It now reads:

L260 “It is difficult to predict the ecological importance of nutrient and contaminant inputs based solely on their magnitudes. Salmon-derived nutrients are ecological subsidies of essential elements and compounds, i.e., donor-controlled resources with positive ecological benefits (e.g., enhanced productivity) for recipient systems,^{4,20} whereas PBT contaminants are either entirely the result of anthropogenic production (PCBs, DDTs, and PBDEs) or are greatly enhanced by it (Hg), with exposures expected to impair rather than enhance biological function. The potential significance of both salmon-derived nutrients and contaminants in recipient systems is well-established. For example, returning salmon enrich dissolved N and P concentrations and N transported by salmon can represent a substantial fraction of lake sediment stores.^{13,39} Early work on salmon contaminant transport similarly showed that spawning returns can be significant sources of persistent organic pollutants to sediments and resident biota, including grizzly bears who increase their contaminant exposures by consuming large amounts of returning salmon when they are available.^{6,7,40–42} Contaminant transport by Pacific salmon has also been studied in the Laurentian Great Lakes where salmon introduced in the 1950s migrate from the lakes to tributaries for spawning. There, stream-resident fish that capitalize on energy-dense salmon eggs substantially enhance their exposure to the PCBs and DDTs that efficiently partition to high-fat tissues while reducing their exposure to Hg for which salmon egg concentrations are low relative to other dietary sources.^{43–45} This work demonstrates how complex interactions among salmon contaminant profiles and partitioning dynamics, salmon resource use, and spawning habitat factors interact to determine the ecosystem contexts under which salmon provisioning can overshadow physicochemical influences on contaminant bioaccumulation in recipient food webs.^{43,44} We do not yet know how co-exposure to the nutrients and contaminants transported by salmon influence ecological responses within trophic levels (e.g., primary production), nor have studies explored how nutrient benefits may be balanced by contaminant effects across trophic levels to inform their overall influence on ecosystem functioning. Further, the coupled fates (following excretion and decay) and influences of salmon-derived nutrients and contaminants are anticipated to vary among recipient systems to reflect both spatial and temporal spawning patterns and site-specific characteristics—including waterbody size, geomorphology and hydrology, nutrient status, and food web structure. Together, these factors will determine the importance of transported nutrients and contaminants relative to other sources.”^{12,15,43}”

References added:

- Gerig BS, Chaloner DT, Janetski DJ, Moerke AH, Rediske RR, O'Keefe JP, de Alwis Pitts DA, Lamberti GA. Environmental context and contaminant biotransport by Pacific salmon interact to mediate the bioaccumulation of contaminants by stream-resident fish. *Journal of Applied Ecology*. 2018 Jul;55(4):1846-59
- Gerig BS, Janetski DJ, Chaloner DT, Lamberti GA. Contaminant Biotransport by Pacific Salmon in the Great Lakes. *Frontiers in Ecology and Evolution*. 2020 Jun 24;8:199
- Gerig BS, Chaloner DT, Rediske RR, Paterson G, Lamberti GA. Pacific salmon as vectors of environmental contaminants: An experimental test confirms synoptic surveys in natural streams. *Environmental Pollution*. 2023 Nov 1;336:122355

L315: *Anytime the word Chinook is used it should be followed by salmon to discern between the fish, the wind, and the people*

Thank you, and we agree. We have revised the text here to say “Chinook and coho salmon return estimates” and also clarified where appropriate in the main text, extended data, and supplementary information files.

L317: What do the authors mean by infilling? synthetic data, some sort of interpolation or extrapolation? What method?

Thank you for this question. We have revised the sentence (now L375) to be more specific:
“Some infilling at the population level, using averages of adjacent values, was necessary for missing values.”

L320: Where does the assumed harvest rate come from and how does it temporally vary?

The assumed harvest rates for central Alaska Chinook salmon are from Rogers 1987, who published the first comprehensive dataset of the annual return of each species of Pacific salmon, 1952 to 1985. Co-author Ruggerone worked with Rogers during this time. Rogers made these calculations as part of the international effort to allocate Japanese high seas catches back to North America and Asia and to estimate harvest rates in those fisheries (see references within Rogers 1987). Chinook salmon runs to central Alaska are small compared with the Bering Sea region where catch and escapement counts were used to estimate run size and harvest rates. The annual harvest rate of 50% (all years) for the relatively small runs in central Alaska was assumed, based on experience with the mixed stock salmon fisheries that primarily targeted sockeye salmon in which harvest rate was known. The assumed harvest rate approach represented only 4% of the total Chinook salmon escapement estimates. Coho escapement is typically not estimated in western and central Alaska, but coded-wire tags provide some information on harvest rates in Southeast Alaska. We used the Rogers 1987 assumption for coho harvest rates by region. Harvest rates were fixed over time at 0.6 for western and central Alaska, and 0.7 for Southeast Alaska. The Alaska coho escapement estimates represented approximately 60% of the total. To help readers understand the relative importance of this assumption, we added the following sentence to this paragraph in the Methods: L382 “Abundance estimates based on assumed harvest rates represented approximately 4% and 60% of the total for Chinook and coho salmon estimates, respectively.”

L325: This is an important disclaimer and it is good of the authors to have it in the methods. How different are these estimates from the ones used for management purposes?

The initial values (i.e., input values) used in our dataset are the same as those published in reports by management agencies, but our goals are different from harvest managers. Here, our goal is to expand escapement counts to the entire management region. In contrast, harvest managers typically focus on the more accurate counts from indicator stocks. To clarify, we modified this section as follows: L383 "All return values are approximations showing the year to year magnitude by species and region; while they are suitable for the broad spatial and temporal questions explored herein, harvest managers typically rely upon a subset of indicator stocks that provide the most accurate information for management."

L330: This is a large assumption because fisheries can often be quite selective on the size and thus the age of the fish. Was there any analyses conducted to verify this assumption or at least identify the variation between fish size caught and escaped? perhaps somewhere in the literature?; followed by the comment at L336: ok this answers the previous question.

Thank you, we are glad that the text addresses this question. A number of studies have been published and the degree and direction of selectivity vary by gear and species/age of the fish. We used the simple assumption that fish weight in the escapement was similar to that in the fishery. Some examples are pasted below:

1. "Size selection by the commercial fishery was highly variable over time, but overall, smaller-than-average Chinook salmon were caught, inconsistent with the declining trends in age and size of returning fish. In contrast, the recreational fishery and presumably the subsistence fishery regularly removed larger-than-average fish." (Kendall and Quinn 2011)

2. "Specifically, we found evidence of stronger size selectivity on sockeye populations with smaller-bodied fish and less directional selection on populations dominated by larger-bodied fish. These results reveal the complex variation in the intensity and selectivity of fishing that can result from exploitation of populations that differ in age and size at maturity and shape." (Kendall and Quinn 2009).

References:

Kendall & Quinn. 2011. Length and Age Trends of Chinook Salmon in the Nushagak River, Alaska, Related to Commercial and Recreational Fishery Selection and Exploitation. Trans. Am Fish. Soc. 140:611-622.

Kendall & Quinn. 2009. Effects of population-specific variation in age and length on fishery selection and exploitation rates of sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 66: 896–908

L356: This is a confusing paragraph -

Post 2000 - 432 estimates

Pre 2000 - 25

*Temporal trend of species*region combination - one species for > 4 years*

*Average species*region combination - 2 year*

So if the authors cannot account for changes in contaminant concentrations over time then how do they go about focusing on temporal changes? This confuses me and clearer explanation would be helpful.

We thank the referee for identifying the confusion in our description of our approach and, in response, revised this section of the Methods to emphasize that temporal changes in contaminant and nutrient flux are driven by changes in Pacific salmon returns, not changes in individual-level fish tissue concentrations (which we could not analyze): L414 “This is a source of uncertainty in our analysis because we cannot account for changes in contaminant concentrations over time. Because increases or decreases in the flux of any given analyte over time are driven by yearly changes in Pacific salmon returns, not changes in analyte tissue concentration, all temporal changes in chemical or nutrient flux are described at the population or community level. As a result, our analyses focus on the influence of temporal changes to the Pacific salmon community as principal drivers of the shifts in subsidy transport between 1976 and 2015.”

We have also added the following changes at L136 in response to a similar comment from Referee 1: “It is important to note that chemical concentrations were not available as time series, since many studies reported tissue concentrations averaged over multiple years and there were few data available over time within a single region or fish species.”

As well as the following to L463: “Sample year is not included in these models due to lack of year-specific data for many contaminants.”

L380: These assumptions and methods to deal with these assumptions all seem quite reasonable.

Thank you.

L407: What is the connotation of weakly informative prior to the overall model analyses?

We have added the following clarification to this statement: L470 “Priors parameter values were then chosen to reflect the range of probable values plus some error, yielding weakly informative priors.⁸² Such priors place low probability on unreasonably large or small values of analyte concentrations, but have little influence on the among-species or among-region concentrations.”

L427: Was there misspecification of the model or were the results similar to the data?

The models showed good fit. We have added a statement to the main text to clarify this on L497: “...Failure to do so indicates a misspecification of the model. All posterior predictive checks indicated reasonable fit to the data (Supplementary Information Figs. 6 and 7).”

We have also added a section to the Supplementary Information that shows the visual posterior predictive checks, along with Bayesian P-values, for each model in this study.

L477: does this like salmon biomass change over time? if so is that important to include?

Our estimate of the bald eagle population size and corresponding biomass reflects a compilation of the most recent estimates available for each state or province because annual estimates were not available from all sources. To clarify, here we are also using the average annual Hg input of ~7 kg/year. In other words, we do not attempt to pair a given year’s Hg input with that same year’s bald eagle biomass. As we also note in response to referee 1 above, the purpose of this analysis is not to estimate bald eagle exposure to Hg from salmon consumption with certainty, but rather to provide bounding estimates of what exposures would result from consuming various proportions of the amount of Hg that salmon transport each year (i.e., the whole body and blood concentrations if 1 vs 100% of the total annual input were consumed equally by the entire bald eagle population). While we would expect in this analysis that an increase in the bald eagle population size would correspond with a decrease in individual bird internal concentrations (and vice versa for a decrease in bald eagle population size), the stable population estimate we use serves our purpose of presenting plausible exposure ranges for these consumption scenarios.

L499: these references are over a decade old, are there others more recent or is this the standard typically used?

A variety of methods are used to assess relative risks and benefits of food consumption, with varying combinations of harmful and beneficial compounds, as summarized recently by Thomsen et al. (2022). However, the most common method is to compare dietary intake against dietary reference values (the value below which no harm would be expected to occur), as we have done. This method remains in regular use (Wang et al. 2013 has >20 citations in the past 3 years). As an example, the same approach we used was applied recently by Keva et al. (2022) for harmful (methylmercury) and beneficial (PUFA) compounds in fish in Finnish lakes. We have chosen to cite the older Wang et al. (2013) paper because they included multiple contaminants rather than solely methylmercury.

References cited in response

- Keva O, Kiljunen M, Hämäläinen H, Jones RI, Kahilainen KK, Kankaala P, Laine MB, Schilder J, Strandberg U, Vesterinen J, Taipale SJ. Allochthony, fatty acid and mercury trends in muscle of Eurasian perch (*Perca fluviatilis*) along boreal environmental gradients. *Science of the Total Environment*. 2022 Sep 10;838:155982
- Thomsen ST, Assunção R, Afonso C, Boué G, Cardoso C, Cubadda F, Garre A, Kruisselbrink JW, Mantovani A, Pitter JG, Poulsen M. Human health risk–benefit assessment of fish and other seafood: a scoping review. *Critical Reviews in Food Science and Nutrition*. 2022 Sep 22;62(27):7479-502

L521: do not know if the format for the first 9 citations is appropriate of the ones following the first 9.

Thank you, this formatting error has been fixed.

Reviewer Reports on the First Revision:

Referees' comments:

Referee #1 (Remarks to the Author):

I appreciate your very detailed responses to my and the other reviewers' comments and questions, as well as the additional text and references you have added to the ms to address them. I feel satisfied after reading your responses and accompanying references that the best available data was used in the modeling approaches. I remain surprised about the lack of detailed data available on several parameters (e.g., nutrient concentration by species across ontogeny and migration), but I recognize that is beyond the scope of this paper, and I appreciate the text you have added calling for more work in these areas. Your explanation of the trophic level estimates as well as the bald eagle consumption example was also helpful, and I appreciate the additional text and citations added to the ms addressing these topics as well. I think your revised statement about the potential risks raised through coupled nutrient-contaminant transport is a good addition that better highlights the potential concerns. Overall, I thought you addressed my comments thoroughly and I have no other concerns with the ms. I think it's a very interesting ms that is likely to be highly cited and to spur more research in this important area.

One additional comment... there was a tremendous amount of interesting text and information in your response to reviewers. This level of detail is clearly not suited for including in a short format paper in Nature, but you may want to consider developing an additional paper that gets a bit more into the weeds on these topics. I imagine this is going to be an important research topic in coming years, particularly as NSF moves more towards funding contaminant research, and researchers will be looking for papers that lay out these important questions to guide future research.

-Amanda Subalusky

Referee #1 (Remarks on code availability):

I did review the supplemental data files and github page where the code is stored, and I reviewed about half of the code files. There was very clear explanatory information, and the code seemed clear and well-organized such that someone could run it themselves. They note that the original salmon escapement and biomass data is not posted there, although the other data are, and they provide contact info for whom to contact for the correct raw data. I did not install and run the code.

Referee #2 (Remarks to the Author):

General comments:

I have reviewed the revised manuscript and appreciate the authors thorough responses to all of my questions. I think perhaps the authors misunderstood my initial/overarching question from the last round of review. I appreciate that “subsidies” are a well-established framework in ecology when looking at the functioning of ecosystems, and that salmon-derived fluxes have been shown to be “important” for specific food webs in past literature. However, it would be nice to quantitatively compare the relative importance of salmon-derived subsidies to the other mass fluxes of contaminants and nutrients to freshwater ecosystems. This could be done at multiple spatial scales, and the answer in terms of the relevance/relative magnitudes of salmon-derived fluxes, will depend on the spatial scale chosen.

In the abstract, the authors emphasize their spatial domain is all of continental North America. Perhaps in all ecosystems where salmon are spawning, salmon-derived nutrient/contaminant subsidies may be important. But, when you look at nutrient and contaminant fluxes from all of continental North America, the total efflux from terrestrial systems will be much greater than the “subsidy” from salmon described here. So, my biggest question about this study still relates to trying to understand the relative importance of salmon-derived fluxes compared to total contaminant/nutrient inputs to freshwater ecosystems. For example, the authors report “kg/year” for contaminant subsidies at the continental scale. How does this compare to other estimates of inputs: A) to all of North America B) to ecosystems where spawning occurs. I am convinced of the importance for B) but not for A). I think readers are likely to be confused by this as well, so I recommend the authors try to think about how to place this nice work into the broader context of contaminant and nutrient budgets that are available (such that they are) for North America and any specific ecosystems that could help to elucidate this point. Even if some bounding estimates are drawn from the literature - it will help frame the relative importance of the fluxes derived in this paper. The emphasis on salmon for specific food webs seems fine to me and does not need to be changed, but when talking about the salmon-derived mass fluxes to ecosystems, I really think this broader context is needed.

I don’t think this changes the central messages of the paper or the novelty of this work, but it is important for framing and appealing to other disciplines. I also think work relating overall contaminant mass budgets to the specific ecology of individual ecosystems is very limited so there is an opportunity for the authors to step into this space here. I particularly like this paper because it nicely represents the coupled nature of natural ecological processes and anthropogenic contaminants.

Specific comments:

Abstract lines 31-32 - again some caveat like “recipient ecosystems” or “focusing regions” is needed here otherwise it sounds like a generalized phenomenon that applied to all of continental North America.

Lines 63-64: These lines are so vague they don’t really seem to say anything so could be deleted.

Lines 80-81 - the implication here is that the authors conducted a temporally resolved analysis of nutrient and contaminant concentrations when calculating fluxes rather than just biomass shifts so this

should be clarified. Same comment for lines 84-85.

Line 134: I don't really understand how chemical concentration emerges as the most important variable in the sensitivity analysis if only one time period/value is included. Does this relate to the specification of uncertainty as a PDF for contaminant concentrations based on the literature data in the Bayesian modeling? Most of this can be clarified in the methods but a brief note here would be helpful to avoid confusion as well.

Line 158-159 - a note that this is the salmon-derived flux on would be useful here.

Line 162 - this would be a good place to add a comment on how much this matters for the overall contaminant/nutrient budgets available - in addition to the salmon-derived fluxes discussed.

Line 173 - Suggest: Regional "salmon-derived" nutrient + contaminant transport....

Referee #3 (Remarks to the Author):

The manuscript entitled Shifts in Pacific salmon community alter continental-scale nutrient and contaminant delivery includes several key results. First, the paper documents how a shift in the proportion of salmonid species shifting over the course of a 40 year time frame alters the flow of important marine derived nutrients and deleterious contaminants across the Pacific Rim. Most individuals know the story with regards to the importance of marine derived nutrients, but few understand the shift in species composition over time and what that may mean from an ecosystem perspective. This revised paper continues to do an excellent job of highlighting that change. Second, few link contaminants with salmon, from an ecosystem perspective and at the scale this paper delves into the topic. While there have been some papers on this topic (Baker, M.R., Schindler, D.E., Holtgrieve, G.W. and St. Louis, V.L., 2009. Bioaccumulation and transport of contaminants: migrating sockeye salmon as vectors of mercury. *Environmental science & technology*, 43(23), pp.8840-8846.) they have not expanded the concept to the entire Pacific Rim. So the results that nutrients are orders of magnitude larger than contaminant delivery is still original and significant, and the fact that species composition change and the resultant shift in what species dominates these return of nutrients at the pacific rim scale is unique. The data and methods, validity of approach and quality of presentation is sound. The quality of the data varies, but the authors recognize this in their methods section and allow the reader to assess the information as well as the original data in the supplementary material. The authors do a solid job of utilizing Bayesian statistics to help quantify both the variation, distribution, and uncertainty. This is critical to the results, in my opinion, and add credence to the interpretation due to the extreme difference in magnitude of contaminants to nutrients. The conclusions, robustness, validity and overall reliability is thus sound. There were several places where the manuscript was improved and clear responses were given by the

authors, thank you.

The suggested improvements were made, additional references were added, and the clarity and context for the paper became more clear.

I do believe this paper is of quality to be accepted at this point

-George Pess

Referee #4 (Remarks to the Author):

This is an interesting and well-written paper summarizing the potential changes in nutrient and toxin transport by Pacific salmon into watersheds. I thought the general framework of the Bayesian models was good, and the model checks and diagnostics were all reasonable and appropriate. All the technical details seemed correct, including the specification of priors based on data from other species. I also appreciated that the authors made the code available on Github, and that the code was well organized, so that it was easy to recreate what they did.

On the other hand, like the other reviewers, I was surprised by the lack of data on toxin and nutrient concentrations in Pacific salmon. There really isn't enough data to fit the the nutrient concentration models. For example, for nitrogen, there were only 10 data points, of which 5 were numbers from the USDA database on chemical composition in various types of food (eg. salmon, chinook, fillet). The database doesn't say how many fillets were analyzed to get these numbers, whether they were caught at sea or came from hatcheries, what region they were from etc. Thus, the regions for which the model attempts to estimate a random effect are: All (the 5 points from USDA), BC/WC (1 point) SEAK (4 points), and the data-source random effect is the exact same grouping of the 10 points. This tiny number of data points is really not enough to estimate the model coefficients for N and P. In fact, Suppl. Info figure 2 shows the posteriors are nearly identical to the priors for the N and P models, particularly for the random effect standard deviations. The only other parameter in these two models (other than the gamma scalar) is the intercept, which is also very similar to the prior. I suspect you would get very similar results if you just estimated mean N concentration and P concentration with a simple intercept-only model, or even just used the USDA numbers directly as the best estimate of the concentration of N and P, rather than attempting a hierarchical model.

The analysis of patterns in the ratio of nutrients to contaminants (Figure 4) seems weak, since the models assume that the nutrient concentration is constant across all species, regions and years (with variability that can be higher in some regions) and the levels are based on a very small number of data points (and some weakly informative priors). The contaminant concentrations are potentially different

between species and regions, but any patterns over time are driven by the differences in number or weight of fish. The authors do explain all this in the methods, but the results and discussion on this point (195-249) seem to go beyond what the actual analysis can support. This study had no data on the ratio of nutrients to contaminants in individual fish or even species of fish, so the discussion about trophic levels of each species and how that influences bioaccumulation, etc. seems rather speculative.

In summary, I think this is an important topic and the general structure of the analysis is sound, so I would support publication with some modifications. I don't think the very small number of data points for the nutrient analysis is sufficient to support the complexity of the analysis and conclusions. I suggest two possible solutions to the small number of nutrient data points. One is to find more data. Would it be possible to collect a few fish and measure N and P? Alternatively, there may be data available at USDA, FWS, ADFG, NMFS, etc. if you talk to the right people. I would support publication as is if you had ~30 fish for each nutrient. If it really isn't possible to get more data, then I would suggest estimating mean N and P concentration from a meta-analysis so that you can bring in the data from multiple species more rigorously. Then, you could re-write the paper to make it clear that the N and P concentrations are assumed to be constant, and that all the trends and patterns in the results are driven by escapement and fish size information (which comes from large data sets). The contaminant concentration data sets are larger so better justified.

Specific comments.

456. (eq 1). Since the text indicates a log link for the gamma likelihood, the model for the mean should be written as $\log(\mu) = \beta_1 x_1 + \dots$

Also, clarify that the X_1 - X_{n-1} variables are dummy variables for species.

468. These priors are somewhat informative, particularly for the intercept for N and P.

Suppl. Info. Fig 3 should use the same color for the prior and posterior as the other figures. Also, Suppl. Info. Fig 2 and 3 have x and y axis labels reversed.

Referee #4 (Remarks on code availability):

The code is excellent and everything runs.

Author Rebuttals to First Revision:

Key

Referee comment

Author response

New or edited text in the manuscript

Referee #1: Aquatic ecology

Referee #1 (Remarks to the Author):

I appreciate your very detailed responses to my and the other reviewers' comments and questions, as well as the additional text and references you have added to the ms to address them. I feel satisfied after reading your responses and accompanying references that the best available data was used in the modeling approaches. I remain surprised about the lack of detailed data available on several parameters (e.g., nutrient concentration by species across ontogeny and migration), but I recognize that is beyond the scope of this paper, and I appreciate the text you have added calling for more work in these areas. Your explanation of the trophic level estimates as well as the bald eagle consumption example was also helpful, and I appreciate the additional text and citations added to the ms addressing these topics as well. I think your revised statement about the potential risks raised through coupled nutrient-contaminant transport is a good addition that better highlights the potential concerns. Overall, I thought you addressed my comments thoroughly and I have no other concerns with the ms. I think it's a very interesting ms that is likely to be highly cited and to spur more research in this important area.

One additional comment... there was a tremendous amount of interesting text and information in your response to reviewers. This level of detail is clearly not suited for including in a short format paper in Nature, but you may want to consider developing an additional paper that gets a bit more into the weeds on these topics. I imagine this is going to be an important research topic in coming years, particularly as NSF moves more towards funding contaminant research, and researchers will be looking for papers that lay out these important questions to guide future research.

(Remarks on code availability):

I did review the supplemental data files and github page where the code is stored, and I reviewed about half of the code files. There was very clear explanatory information, and the code seemed clear and well-organized such that someone could run it themselves. They note that the original salmon escapement and biomass data is not posted there, although the other data are, and they provide contact info for whom to contact for the correct raw data. I did not install and run the code.

-Amanda Subalusky

Thank you, Dr. Subalusky, for your feedback and support of our manuscript. We want to note that we were able to find some additional Pacific salmon N and P estimates (see Referee #4 response below), though we also continue to be surprised how limited these data are in the literature. We agree that a more detailed paper about nutrient and contaminant dynamics in the context of biotransport would be valuable to this area of research going forward, and are considering one as a follow-up to this manuscript.

General comments:

I have reviewed the revised manuscript and appreciate the authors thorough responses to all of my questions. I think perhaps the authors misunderstood my initial/overarching question from the last round of review. I appreciate that “subsidies” are a well-established framework in ecology when looking at the functioning of ecosystems, and that salmon-derived fluxes have been shown to be “important” for specific food webs in past literature. However, it would be nice to quantitatively compare the relative importance of salmon-derived subsidies to the other mass fluxes of contaminants and nutrients to freshwater ecosystems. This could be done at multiple spatial scales, and the answer in terms of the relevance/relative magnitudes of salmon-derived fluxes, will depend on the spatial scale chosen.

In the abstract, the authors emphasize their spatial domain is all of continental North America. Perhaps in all ecosystems where salmon are spawning, salmon-derived nutrient/contaminant subsidies may be important. But, when you look at nutrient and contaminant fluxes from all of continental North America, the total efflux from terrestrial systems will be much greater than the “subsidy” from salmon described here. So, my biggest question about this study still relates to trying to understand the relative importance of salmon-derived fluxes compared to total contaminant/nutrient inputs to freshwater ecosystems. For example, the authors report “kg/year” for contaminant subsidies at the continental scale. How does this compare to other estimates of inputs: A) to all of North America B) to ecosystems where spawning occurs. I am convinced of the importance for B) but not for A). I think readers are likely to be confused by this as well, so I recommend the authors try to think about how to place this nice work into the broader context of contaminant and nutrient budgets that are available (such that they are) for North America and any specific ecosystems that could help to elucidate this point. Even if some bounding estimates are drawn from the literature - it will help frame the relative importance of the fluxes derived in this paper. The emphasis on salmon for specific food webs seems fine to me and does not need to be changed, but when talking about the salmon-derived mass fluxes to ecosystems, I really think this broader context is needed.

I don’t think this changes the central messages of the paper or the novelty of this work, but it is important for framing and appealing to other disciplines. I also think work relating overall contaminant mass budgets to the specific ecology of individual ecosystems is very limited so there is an opportunity for the authors to step into this space here. I particularly like this paper because it nicely represents the coupled nature of natural ecological processes and anthropogenic contaminants.

We appreciate the referee’s continued interest in our paper and their ideas on how to better contextualize the nutrient and contaminant fluxes that we estimate. We first want to clarify that we use “continental-scale” in this manuscript to describe the full extent of the spatial area (i.e., the inland waters of continental North America from the northern Bering Sea to coastal California) to which Pacific salmon return during their spawning migrations. In other words, the continental-scale context of our analyses is restricted to Pacific salmon-receiving systems in western North America; we identify the spatial scope of these migration runs at L83-85: “We examined 40-y trends (1976-2015) in nutrient and contaminant transport defined by the upgradient migration of Pacific salmon from the eastern Pacific Ocean to freshwaters spanning western Alaska to northern California (Fig. 1a, Fig. 1b).” We do not scale our estimates of Pacific salmon nutrient and contaminants inputs to the areas of North America for which there are not migration runs, nor do we assert that Pacific salmon inputs of nutrients and contaminants are important to the ecosystems beyond their physical reach. We have revised wording about the geographic scope to address the potential for misunderstanding in several places; specifically in response to the referee’s concern with the abstract, we replaced “continental” with “western” at L36.

We also appreciate the referee's perspective that frames of reference are useful for contextualizing the amounts of nutrients and contaminants transported by Pacific salmon. We took a two-pronged approach to adding this broader context. First, we compared our estimates of upgradient salmon fluxes (from marine to freshwater) to fluxes by riverine transport in the opposite direction (from freshwater to marine), following the referee's suggestion of using bounding estimates from the literature. We were able to find robust estimates for riverine nitrogen and mercury export to the North Pacific Ocean that broadly overlapped with the marine habitat area of Pacific salmon such that the salmon and river fluxes are generally analogous; we also added text to the Supplementary Information describing our approach (see below). This addition allowed us to acknowledge that Pacific salmon contributions to nutrient and contaminant budgets are small, while also highlighting important caveats to comparisons of biotic and abiotic fluxes. Second, we better positioned our work in the broader context of animal resource subsidies and their importance to advancing the classic resource subsidy paradigm by comparing our estimates of Pacific salmon N and P fluxes to those by other organisms from the literature. As shown in the new Fig. 1c, these include N and P transfers among habitats or ecosystems by mass aquatic insect emergence events, terrestrial and aerial migrations, egg laying, and excretion pathways. The new text comes at the end of the section detailing the annual average magnitudes of Pacific salmon nutrient and contaminant fluxes; to make room for this addition, we removed the paragraph describing the modeling approach as this content was repetitive of the methods.

L105-116: "Upgradient transport by Pacific salmon counters the physical, downstream transport of nutrients and contaminants from terrestrial to freshwater and marine ecosystems. The magnitudes of chemical transfer (i.e., fluxes) by biological and physical mechanisms are on different scales—for example, estimates of annual dissolved inorganic N and Hg fluxes by rivers to the eastern North Pacific Ocean are greater than one and three orders of magnitude larger, respectively, than our estimates of Pacific salmon transport (Supplementary Information)^{23,24}—yet are not directly comparable given that animals concentrate bioavailable forms of nutrients and contaminants in recipient ecosystems,³ whereas physical fluxes are dominated by inorganic compounds that become diluted as they enter coastal and open ocean habitats.²⁵ Increasing recognition of the ecological importance and budget contributions of biological fluxes has helped advance the study of resource subsidies since the 1990s.^{9,20} Estimates of Pacific salmon N and P transport from this study are among the largest documented contributions of biological vectors to large scale nutrient distribution (Fig. 1c);^{9,22} we lack analogous comparisons for paired nutrient and contaminant fluxes."

New text for the Supplementary Information: "Herein, we estimated the annual average transport of N and Hg by Pacific salmon from the North Pacific Ocean to inland ecosystems in western North America between 1976-2015 to be 9,175 MT yr⁻¹ and 7 kg yr⁻¹, respectively. We related these fluxes to literature-based estimates of riverine flows moving N and Hg in the opposite direction – from terrestrial and freshwaters in western North America to coastal and open ocean habitats. For N, we used the 1990 model riverine flux estimates from Kroeze and Seitzinger (1998).¹ Table 3 of that paper provides estimates of annual dissolved inorganic nitrogen export by rivers to the eastern North Pacific for three latitudinal regions. We combined estimates for the 20-45th and 45-66th parallels, for an overall estimate of 270,418 MT N yr⁻¹; this estimate is 29.5 times and greater than one order of magnitude larger than our estimate of the magnitude of Pacific salmon N flux. For Hg, we used the riverine Hg flux estimates from Liu et al. (2021).² Supplementary Table 11 provides estimates for Hg inputs to coastal waterbodies. We combined the Hg flux estimates for the North-eastern Pacific and California Current for a total flux of 4.9 MT yr⁻¹; this estimate is 700 times and three orders of magnitude greater than our estimate of the magnitude of Pacific salmon Hg flux."

References for riverine N and Hg fluxes:

Kroeze C, Seitzinger SP. Nitrogen inputs to rivers, estuaries and continental shelves and related nitrous oxide emissions in 1990 and 2050: a global model. *Nutrient Cycling in Agroecosystems*. 1998 Oct;52:195-212.

Liu M, Zhang Q, Maavara T, Liu S, Wang X, Raymond PA. Rivers as the largest source of mercury to coastal oceans worldwide. *Nature Geoscience*. 2021 Sep;14(9):672-7.

While space constraints prohibit a more detailed comparison of Pacific salmon versus abiotic fluxes of nutrients and contaminants at large spatial scales—which in our view would justify a subsequent study—we agree with the referee that relating our estimates to the more commonly considered unidirectional flows enhances this manuscript and broadens its relevance to other disciplines.

Specific comments:

Abstract lines 31-32 - again some caveat like “recipient ecosystems” or “focusing regions” is needed here otherwise it sounds like a generalized phenomenon that applied to all of continental North America.

Thank you, we’ve revised the summary paragraph to better specify that our discussion of nutrient and contaminant inputs by Pacific salmon refers to recipient systems in western North America (L36). The first sentence of the summary paragraph also identifies the spatial scope for Pacific salmon subsidies as recipient ecosystems (L29).

Lines 63-64: These lines are so vague they don’t really seem to say anything so could be deleted.

Thank you for this feedback. The purpose of this sentence is to acknowledge that the ecological influence of salmon-derived nutrient subsidies will vary among recipient systems due to characteristics of the salmon run(s) and of the systems to which they return. This was added in response to the previous feedback about how the influence of salmon is not uniform among their spawning areas. We have revised this sentence to be more clear and use this opportunity to better position this paper within the broader area of animal resource subsidy literature. L61: “The ecological influence of salmon subsidies in recipient systems, as with all animal resource subsidies, are context-dependent, and vary according to input quantity, quality, timing, and duration as well as the abiotic and food web characteristics of recipient systems.”^{5,9,12,15,17}

Lines 80-81 - the implication here is that the authors conducted a temporally resolved analysis of nutrient and contaminant concentrations when calculating fluxes rather than just biomass shifts so this should be clarified. Same comment for lines 84-85.

We have been careful to emphasize that this research centers on the influence of the Pacific salmon community over nutrient and contaminant biotransport. We state this in the summary paragraph (L34-38), introductory text (L64-67), and figure captions (Extended Data Fig. 2). We also describe our approach in the relevant section “Community change alters biotransport” of the main text (L118-141), including the statement: L137 “It is important to note that chemical concentrations were not available as time series, as many studies reported tissue concentrations averaged over multiple years and there were few data available over time within a single region or fish species. Thus, the contribution of chemical concentrations in the sensitivity analysis is driven by among-species variation (Supplementary Information Fig. 1).” Moreover, we provide full details about the analysis approach and nutrient and contaminant data limitations in the Methods. We are confident that these explanations make it clear to readers that the temporal changes in nutrient and contaminant fluxes are due to changes in Pacific salmon biomass and community structure.

Line 134: I don’t really understand how chemical concentration emerges as the most important variable in the sensitivity analysis if only one time period/value is included. Does this relate to the specification of uncertainty as a PDF for contaminant concentrations based on the literature data in the Bayesian modeling? Most of this can be clarified in the methods but a brief note here would be helpful to avoid confusion as well.

We agree that this was confusing. As suggested, we've added a sentence here to clarify how chemical concentration can contribute even though it isn't measured as a time-series: L139 "Thus, the contribution of chemical concentrations in the sensitivity analysis is driven by among-species variation (Supplementary Information Fig. 1)." In other words, while escapement was always important to explain flux, much of the residual variation could be explained by differences in concentrations (mg/kg chemical) among species or regions. For example, an area dominated by Chinook salmon can have higher fluxes of Hg than an area dominated by pink salmon, since Chinook salmon have higher Hg concentrations. This difference would occur even if the area had the same magnitude of escapement.

Line 158-159 - a note that this is the salmon-derived flux on would be useful here.

Thank you, the sentence has been revised to read: L159 "Contemporary increases in pink salmon return biomass (of ~62,000 MT) were particularly influential, accounting for ~80% of the increase in salmon-derived nutrient + contaminant transfer to North America between 1976 and 2015 (Extended Data Table 5)."

Line 162 - this would be a good place to add a comment on how much this matters for the overall contaminant/nutrient budgets available - in addition to the salmon-derived fluxes discussed.

This section focuses on temporal changes in nutrient and chemical transport by Pacific salmon. As described above, we instead added the broader budget context earlier in the manuscript to follow the discussion of annual average fluxes at L105-116.

Line 173 - Suggest: Regional "salmon-derived" nutrient + contaminant transport....

Thank you, the sentence has been revised to read: L176 "Regional nutrient + contaminant transport by Pacific salmon varied between 2,800 MT yr⁻¹ in CAK and 4,700 MT yr⁻¹ in BCWC (Extended Data Table 3)."

Referee #3: Fisheries/Pacific salmon

Referee #3 (Remarks to the Author):

The manuscript entitled Shifts in Pacific salmon community alter continental-scale nutrient and contaminant delivery includes several key results. First, the paper documents how a shift in the proportion of salmonid species shifting over the course of a 40 year time frame alters the flow of important marine derived nutrients and deleterious contaminants across the Pacific Rim. Most individuals know the story with regards to the importance of marine derived nutrients, but few understand the shift in species composition over time and what that may mean from an ecosystem perspective. This revised paper continues to do an excellent job of highlighting that change. Second, few link contaminants with salmon, from an ecosystem perspective and at the scale this paper delves into the topic. While there have been some papers on this topic (Baker, M.R., Schindler, D.E., Holtgrieve, G.W. and St. Louis, V.L., 2009. Bioaccumulation and transport of contaminants: migrating sockeye salmon as vectors of mercury. Environmental science & technology, 43(23), pp.8840-8846.) they have not expanded the concept to the entire Pacific Rim. So the results that nutrients are orders of magnitude larger than contaminant delivery is still original and significant, and the fact that species composition change and the resultant shift in what species dominates these return of nutrients at the pacific rim scale is unique. The data and methods, validity of approach and quality of presentation is sound. The quality of the data varies, but the authors recognize this in their methods section and allow the reader to assess the information as well as the original data in the supplementary material. The authors do a solid job of utilizing Bayesian statistics to help quantify both the variation, distribution, and uncertainty. This is critical to the results, in my opinion, and add credence to the interpretation due to the extreme difference in magnitude of contaminants to nutrients. The conclusions, robustness, validity and overall reliability is thus sound. There were several places where the manuscript was improved and clear responses were given by the authors, thank you.

The suggested improvements were made, additional references were added, and the clarity and context for the paper became more clear.

I do believe this paper is of quality to be accepted at this point.

-George Pess

Thank you, Dr. Pess, for your input and support of the manuscript. Your expertise helped us improve the paper.

This is an interesting and well-written paper summarizing the potential changes in nutrient and toxin transport by Pacific salmon into watersheds. I thought the general framework of the Bayesian models was good, and the model checks and diagnostics were all reasonable and appropriate. All the technical details seemed correct, including the specification of priors based on data from other species. I also appreciated that the authors made the code available on Github, and that the code was well organized, so that it was easy to recreate what they did.

Thank you for the positive feedback and recognition of the code organization.

On the other hand, like the other reviewers, I was surprised by the lack of data on toxin and nutrient concentrations in Pacific salmon. There really isn't enough data to fit the the nutrient concentration models. For example, for nitrogen, there were only 10 data points, of which 5 were numbers from the USDA database on chemical composition in various types of food (eg. salmon, chinook, fillet). The database doesn't say how many fillets were analyzed to get these numbers, whether they were caught at sea or came from hatcheries, what region they were from etc. Thus, the regions for which the model attempts to estimate a random effect are: All (the 5 points from USDA), BC/WC (1 point) SEAK (4 points), and the data-source random effect is the exact same grouping of the 10 points. This tiny number of data points is really not enough to estimate the model coefficients for N and P. In fact, Suppl. Info figure 2 shows the posteriors are nearly identical to the priors for the N and P models, particularly for the random effect standard deviations. The only other parameter in these two models (other than the gamma scalar) is the intercept, which is also very similar to the prior. I suspect you would get very similar results if you just estimated mean N concentration and P concentration with a simple intercept-only model, or even just used the USDA numbers directly as the best estimate of the concentration of N and P, rather than attempting a hierarchical model.

We, too, were surprised at the paltry amount of data for N and P, particularly given the importance of these elements in past studies of the ecosystem importance of salmon fluxes. Our initial literature searches revealed that multiple studies simply cite the same 3-4 reports of salmon nutrient concentrations, leading to a small number of independent estimates. However, motivated by your comments, we were able to find additional N and P estimates from the literature (from 7 studies). This raised the total n to 48 and 39 for N and P, respectively. (Note: 16 of the additional N data were from the Donaldson 1967 study already in our database. Previously we had a single value from that report, but we were able to find the underlying 16 data points that generated that mean) With these new data, we were able to estimate a species fixed effect in the N and P models.

One important point about the N and P concentrations is that we did not expect a prior for the species to show much variation in these measures due to stoichiometric constraints. For example, in the few estimates that reported both N and P concentrations ($n = 5$) in the same fish, the N:P ratios only varied from 6.2 to 8.4. While N and P can vary relative to total biomass, their variation is expected to be much less than variation in contaminants, which are not subject to the same stoichiometric constraints (and nutrients don't biomagnify as some contaminants do). Thus, as the new N and P models show, there is only minimal variation in species concentrations of N and P. We view that as unsurprising; the new Fig 1c shows how the stoichiometric relationship between N and P for individual organisms is also apparent at population to community levels of biological organization and even among input types (whole bodies to laid eggs to excreta). The main benefit of fitting the models for N and P is to provide posterior estimates of uncertainty in the mean values of nutrients so that we can account for that in the downstream predictions of nutrient transport.

Finally, as the referee suggests, we were not clear enough in reporting the number of individual fish involved in the data summaries. We have now added the following text to the methods to emphasize that the literature data reports summary statistics, but those summaries represent at least 6,731 individuals.

L463: “We obtained a total of 363 estimates of nutrient and contaminant concentrations in Pacific salmon. These estimates are summaries of measures from at least 6,798 individual fish (33 estimates did not report a sample size). This ranged from 15 estimates of DHA and EPA (42 individuals each) to 83 estimates of Hg (2,768 individuals).”

The analysis of patterns in the ratio of nutrients to contaminants (Figure 4) seems weak, since the models assume that the nutrient concentration is constant across all species, regions and years (with variability that can be higher in some regions) and the levels are based on a very small number of data points (and some weakly informative priors). The contaminant concentrations are potentially different between species and regions, but any patterns over time are driven by the differences in number or weight of fish. The authors do explain all this in the methods, but the results and discussion on this point (195-249) seem to go beyond what the actual analysis can support. This study had no data on the ratio of nutrients to contaminants in individual fish or even species of fish, so the discussion about trophic levels of each species and how that influences bioaccumulation, etc. seems rather speculative.

We agree that there is speculation here, though we view it as justified on several grounds. First, the ratio estimates in Figure 4 are simply a derived quantity from the posterior distributions of the nutrient/contaminant models (adjusted for mean body size of salmon). Thus, the raw data enter into these estimates by constraining the posteriors of contaminants and nutrients. As the referee mentions, we do not have any data on ratios in individual fish. Indeed, spurring additional study on these patterns is one of the main goals of this section, as we note at L250: “These nuanced results point to complex interactions at the community ecology-ecosystem ecology interface that are ripe for further exploration in the context of Pacific salmon migration and marine-to-freshwater subsidies.”

Second, the patterns shown in Figure 4 emphasize the relative concentrations of contaminants to nutrients as a function of trophic level, suggesting biomagnification as a possible mechanism generating variation in continental scale flux. They confirm well-known patterns of contaminant biomagnification in higher trophic levels, particularly for the lipophilic contaminants in this study (e.g., PCBs). Namely, nutrients are likely evolutionarily constrained to certain concentrations/ratios whereas man-made contaminants are not. In other words, we would be surprised if we *did not* find magnification in Chinook salmon relative to pink salmon. In our view, the fact that the trophic patterns emerge ultimately from data on raw nutrient/contaminant concentrations (i.e., data that were not collected with the purpose of analyzing biomagnification) gives support to the reliability of the main flux estimates in the manuscript, while emphasizing the role of trophic biomagnification as a mechanism.

We hope that the new analysis allays some of the concerns regarding the consistency of N and P. We also note that there is no a priori expectation that nutrients would increase with trophic level (or vary much across fish species). Thus, the patterns in Figure 4, while speculative relative to the direct flux estimates, are also biologically reasonable. For example, using only the raw data, we made a quick calculation of mean nutrients per fish and contaminants per fish for each species and then calculated the ratios (nutrient:contaminant). The results qualitatively match with those of Figure 4, showing that the relative concentration of nutrients in pink salmon (0.6) is 4-5 times higher than Chinook salmon and 1.5-2 times higher than chum, coho, and sockeye salmon (see table below), matching with results of the full analysis in Figure 4.

Species	Contaminants (mg/fish)	Nutrients (kg/fish)	Nutrient:contaminant Ratio
Chinook	0.79	0.37	0.47
Coho	0.25	0.18	0.72
Chum	0.2	0.17	0.8
Sockeye	0.14	0.13	0.95
Pink	0.03	0.07	2.68

The estimates in the table above are complicated by the fact that no single study measured all nutrients and contaminants, so these are just mean comparisons among groups of fish from different studies/regions, etc. In the main analyses in Figure 4, however, we account for this uncertainty using the multilevel models, rather than the point values above. Thus, we view the estimates in Figure 4 as more robust than estimates from the raw data, while agreeing with the general sentiment that raw data on the ratios would be ideal.

In summary, I think this is an important topic and the general structure of the analysis is sound, so I would support publication with some modifications. I don't think the very small number of data points for the nutrient analysis is sufficient to support the complexity of the analysis and conclusions. I suggest two possible solutions to the small number of nutrient data points. One is to find more data. Would it be possible to collect a few fish and measure N and P? Alternatively, there may be data available at USDA, FWS, ADFG, NMFS, etc. if you talk to the right people. I would support publication as is if you had ~30 fish for each nutrient. If it really isn't possible to get more data, then I would suggest estimating mean N and P concentration from a meta-analysis so that you can bring in the data from multiple species more rigorously. Then, you could re-write the paper to make it clear that the N and P concentrations are assumed to be constant, and that all the trends and patterns in the results are driven by escapement and fish size information (which comes from large data sets). The contaminant concentration data sets are larger so better justified.

Thank you for this suggestion. As mentioned above, we were able to find additional data on N and P and now have 48 and 39 data points, respectively. This removed our previous assumption of constancy across species for N. We hope that the additional data, along with the *a priori* expectation that N and P should have far lower variation among species than any contaminant, are sufficient to allay concerns about sample size. The idea of a meta-analysis is good. From our view, our modeling approach is similar. For example, our use of informative priors (based on literature values from other fish species) and authors as varying intercepts essentially functions as a meta-analysis with the data providing further information in the models. We also note that our use of Bayesian methods with informative priors is a common approach for dealing with small sample sizes since it can formally incorporate other information into the model (McNeish, 2016).

McNeish, D. (2016). On using Bayesian methods to address small sample problems. *Structural Equation Modeling: A Multidisciplinary Journal*, 23(5), 750-773.

Specific comments.

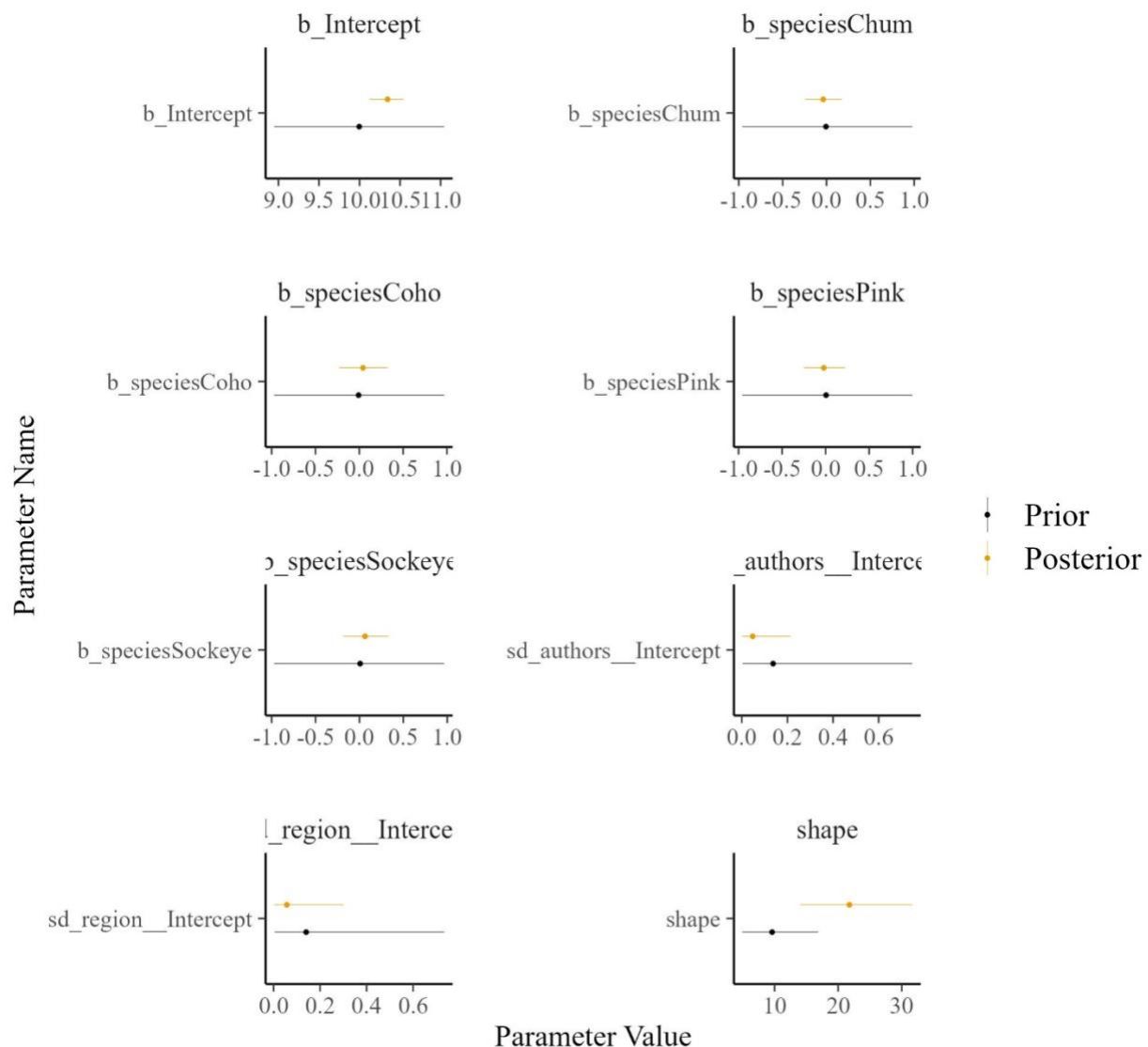
456. (eq 1). Since the text indicates a log link for the gamma likelihood, the model for the mean should be written as $\log(\mu) = \beta_0 + \beta_1 x_1 + \dots$

Also, clarify that the X_1 - X_{n-1} variables are dummy variables for species.

Both are fixed. Thank you.

468. These priors are somewhat informative, particularly for the intercept for N and P.

We assume the referee is referring to the prior parameter values listed in the Supplementary Information. Yes, they are informative and derived from literature values given in Supplementary Information Table 1, in this case from Gende et al., (2002). Those are plotted also against the posteriors in Supplementary Information Fig. 2. In that figure, the intercept and betas do indeed appear highly informative. However, it's worth noting that they are somewhat visually skewed by sharing the same axis values as contaminants (which have orders of magnitude smaller intercepts). The plot below shows the prior and posterior for N where each parameter has its own scale. In this view, the similarities in the prior and posterior are mostly in the central tendency, but there are clear differences in the uncertainty, indicating somewhat less informative priors than in Supplementary Information Fig. 2. Nevertheless, we believe that informative priors are justified here given the knowledge of likely N and P values from stoichiometry.



Suppl. Info. Fig 3 should use the same color for the prior and posterior as the other figures. Also, Suppl. Info. Fig 2 and 3 have x and y axis labels reversed.

Thank you, these issues have been corrected.

(Remarks on code availability):

The code is excellent and everything runs.

Thank you!

Reviewer Reports on the Second Revision:

Referees' comments:

Referee #2 (Remarks to the Author):

I want to thank the authors for their thorough responses to all the reviewer questions and patience with this process. I think they have now responded to all my concerns and the paper is ready for publication. I have just two very minor phrasing suggestions for the abstract:

Lines 28-29: The movement of large amounts of nutrients by migrating animals has ecological benefits "for consumers" in recipient ecosystems,^{1,2} which may be offset by co-transported contaminants.^{3,4}

From 1976 to 2015, increases in salmon returns accounted for increases in nutrient and contaminant inputs of 30% and 20% "from this source," respectively.

I think these clarifications will fully resolve any concerns I had.

Congratulations to the authors on their nice work!

Referee #4 (Remarks to the Author):

The revision is much improved and I appreciate the authors detailed response to all the points I raised. The larger sample size (number of studies) for N and P largely addresses one of my comments from the last revision. Given the model structure and priors it does seem to be possible to estimate the parameters. I still have a few (hopefully minor) issues with the modeling.

1. Now that I see the sample size (number of fish) for each study, it is clear that, as expected, studies with larger sample sizes have more variable values of each chemical because these are means. It might be worth trying some models that model the variance as a function of $1/n$ to be consistent with the fact that the data are means in most studies. Without this, there may be some bias in the estimates when the sample sizes are larger in some species/regions than others. This is easier to do with a gaussian model than gamma. You might want to try this on a few of the chemicals to make sure it doesn't change the species effects (it didn't for Hg but I didn't try the others). This can be added to the supplement.

2. One thing I failed to note last time is that there seem to be some divergences in nearly all of the brms models, which is an indication of convergence problems in the NUTS algorithm. You might want to clarify how you checked for convergence, e.g. Rhat, bulk ESS, lack of divergences. Did you disregard the divergences because they seemed not to be clumped in any particular parameter values? If so, this

should be spelled out in the supplement (with some figures or tables), and mentioned in line 549-551.

Figure 5. Why is the x axis negative in a and positive in b? They are described in the caption as being the same numbers.

466. "Data were not available for all combinations of subsidy x species x year x region" isn't consistent with the data. I would say "Data were only available for a small fraction of combinations..."

I think this is getting close to being publishable, as soon as you justify your convergence criteria, and justify why you didn't model the variable sample size.

Elizabeth Babcock

Referee #4 (Remarks on code availability):

The code all looks good. I ran all the brms models. This is the model I ran to see if sample size should be included in the estimate of variance. The fixed effects coefficients were very similar to the coefficients in the original models.

```
hg_model3 <- brm(bf(log(mean_concentration_standardized) ~ 0 + species + (1|authors) +  
(1|region),  
sigma~1+offset(log(sqrt(n)))),  
data = hg_data,  
prior = c(prior(normal(-5.5, 2), class = "b"),  
prior(exponential(2), class = "sd")),  
cores = 4,  
file = "models/hg_model3.rds",  
file_refit = "on_change")
```

Author Rebuttals to Second Revision:

Key

Referee comment

Author response

New or edited text in the manuscript

Referee #2: Toxicology/mercury

Referee #2 (Remarks to the Author):

General comments:

I want to thank the authors for their thorough responses to all the reviewer questions and patience with this process. I think they have now responded to all my concerns and the paper is ready for publication.

Thank you for your positive assessment of the manuscript and your contributions to the review process. We have accepted your suggestions, with minor modifications, as described below.

I have just two very minor phrasing suggestions for the abstract:

Lines 28-29: The movement of large amounts of nutrients by migrating animals has ecological benefits "for consumers" in recipient ecosystems,^{1,2} which may be offset by co-transported contaminants.^{3,4}

We adopted this suggestion, with a change to broaden the beneficiaries to "recipient food webs". This is because many of the ecological benefits related to salmon-derived nutrient inputs have to do with increases in primary production, etc., that are measured at the ecosystem scale. Therefore, "food webs" is more encompassing than "consumers".

L28-29: "The movement of large amounts of nutrients by migrating animals has ecological benefits for recipient food webs,^{1,2} which may be offset by co-transported contaminants.^{3,4}"

From 1976 to 2015, increases in salmon returns accounted for increases in nutrient and contaminant inputs of 30% and 20% "from this source," respectively. We adopted this suggestion, with the minor revision noted below. This does not change the meaning of the phrasing suggested by the referee.

L36-38"From 1976 to 2015, increases in salmon returns accounted for increases in salmon-derived nutrient and contaminant inputs of 30% and 20%, respectively."

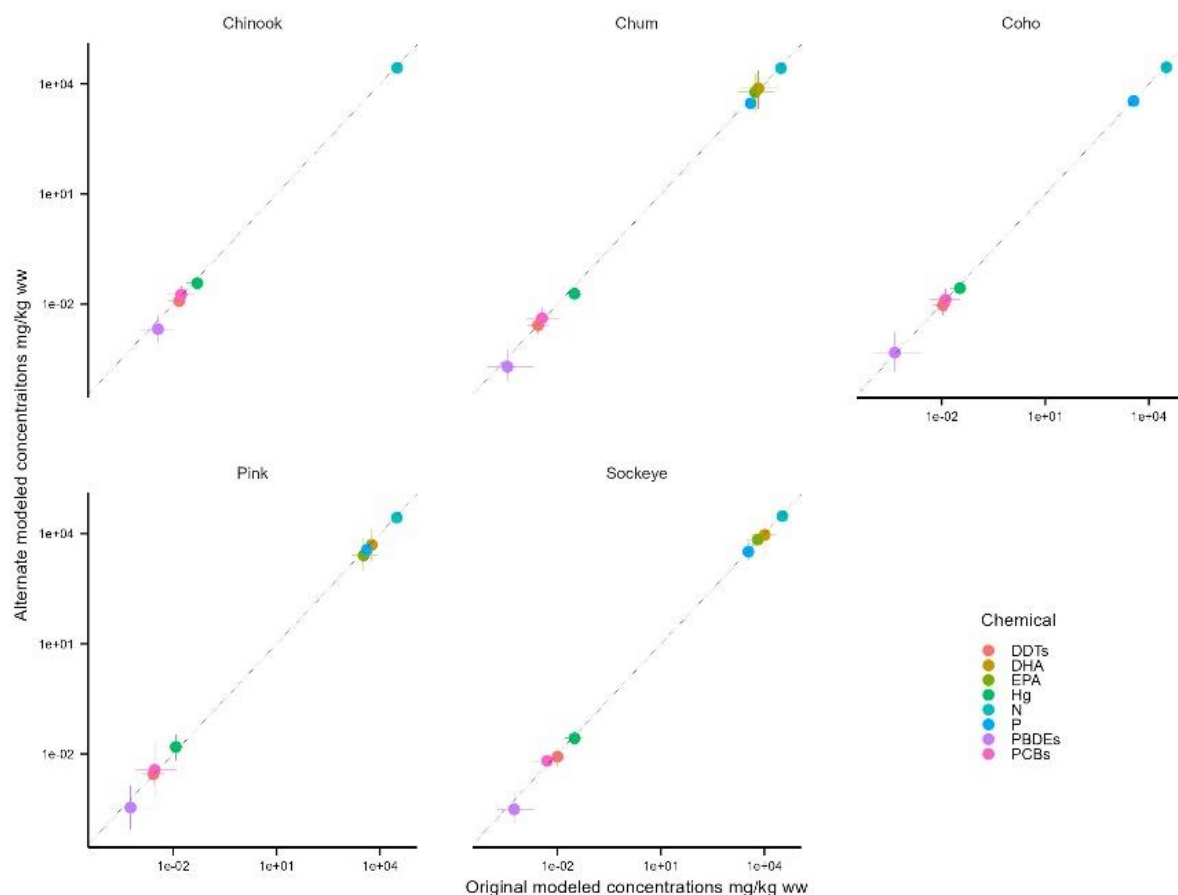
I think these clarifications will fully resolve any concerns I had.

Congratulations to the authors on their nice work!

The revision is much improved and I appreciate the authors detailed response to all the points I raised. The larger sample size (number of studies) for N and P largely addresses one of my comments from the last revision. Given the model structure and priors it does seem to be possible to estimate the parameters. I still have a few (hopefully minor) issues with the modeling.

1. Now that I see the sample size (number of fish) for each study, it is clear that, as expected, studies with larger sample sizes have more variable values of each chemical because these are means. It might be worth trying some models that model the variance as a function of $1/n$ to be consistent with the fact that the data are means in most studies. Without this, there may be some bias in the estimates when the sample sizes are larger in some species/regions than others. This is easier to do with a gaussian model than gamma. You might want to try this on a few of the chemicals to make sure it doesn't change the species effects (it didn't for Hg but I didn't try the others). This can be added to the supplement.

Thank you and we agree. Your code below really helped in getting these models to fit. We have now re-run each of the contaminant/nutrient models with the Gaussian model with sigma varying as a function of sample size and placed the results in the SI. One challenge with this was that 33 of the data points did not have sample sizes. Excluding those from the Gaussian model below meant that 2-3 nutrients could not be modeled for coho or Chinook salmon (as well as some other data being left out). We did not attempt to do a multiple imputation, though that could perhaps help here. More importantly, as you mentioned, the alternate model produced similar estimates as the original Gamma model for all contaminants/nutrients (Fig. S10 below). Given the potential data loss with sample sizes, we chose to keep the Gamma model for the main inferences in the manuscript. But we are also happy that two different approaches seem to arrive at similar conclusions. That is always reassuring. We have added text describing this analysis to the SI (page 15 – section “Alternate model structure”).



2. One thing I failed to note last time is that there seem to be some divergences in nearly all of the brms models, which is an indication of convergence problems in the NUTS algorithm. You might want to clarify how you checked for convergence, e.g. Rhat, bulk ESS, lack of divergences. Did you disregard the divergences because they seemed not to be clumped in any particular parameter values? If so, this should be spelled out in the supplement (with some figures or tables), and mentioned in line 549-551.

Thank you. We did indeed fail to mention how we checked for convergence. We have added the text below to showing that we checked convergence using Rhat (<1.1). Following your mention of the divergent transitions, we also added a follow-up in the Supplementary Information (Supplementary Figs. 8 and 9) where we re-ran the Hg model with increased adapt delta (0.9 instead of the default of 0.8). No inferences were changed, but we think this addition helps to demonstrate the robustness of our models. As an aside, we also learned that the Stan team now recommends Rhat < 1.01 , rather than the oft-used 1.1 (<https://mc-stan.org/misc/warnings.html>), so that cutoff (i.e., 1.01) is now included in our comparison of Rhats in Fig. S10.

L675: “We assessed model convergence by ensuring that all Rhats were <1.1 .⁸⁰ Some model diagnostics indicated divergent transitions. We explored the implications of these transitions by visualizing parameter-specific Rhats and/or re-fitting the models with increased target average acceptance probabilities and comparing inferences (“adapt delta”) (Supplementary Information Figs. 8 and 9). Finally, some of the nutrient and contaminant data contained both a mean literature value and a corresponding sample size (n). To determine if including sample size in the modeling approach would alter inferences of those concentrations, we fit an alternative model in which Gaussian variance was scaled by $1/n$ and compared to

the Gamma model described above. Differences were minimal and are reported in Supplementary Information Fig. 10.”

Figure 5. Why is the x axis negative in a and positive in b? They are described in the caption as being the same numbers.

Thank you for catching this error. We made the correction and updated the figure in the manuscript.

466. *"Data were not available for all combinations of subsidy x species x year x region" isn't consistent with the data. I would say "Data were only available for a small fraction of combinations..."*

We agreed and have re-worded as suggested.

I think this is getting close to being publishable, as soon as you justify your convergence criteria, and justify why you didn't model the variable sample size.

Thank you.

Elizabeth Babcock

(Remarks on code availability):

The code all looks good. I ran all the brms models. This is the model I ran to see if sample size should be included in the estimate of variance. The fixed effects coefficients were very similar to the coefficients in the original models.

```
hg_model3 <- brm(bf(log(mean_concentration_standardized) ~ 0 + species + (1|authors) +  
(1|region),  
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data = hg_data,  
prior = c(prior(normal(-5.5, 2), class = "b"),  
prior(exponential(2), class = "sd")),  
cores = 4,  
file = "models/hg_model3.rds",  
file_refit = "on_change")
```

Thank you. This code was super helpful! It's also really nice to have a referee dive into the code and provide feedback. We hope it will be useful to others in the future as well.

Reviewer Reports on the Third Revision:

Referees' comments:

Referee #4 (Remarks to the Author):

This all looks good. The authors have done a great job addressing all my questions about the models. I support publication as is.

Referee #4 (Remarks on code availability):

The authors made all the alternative model runs I suggested. Everything looks fine.

Author Rebuttals to Third Revision:

Referee #4 (Remarks to the Author):

This all looks good. The authors have done a great job addressing all my questions about the models. I support publication as is.

Thank you, we greatly appreciate your feedback for an improved manuscript.

Referee #4 (Remarks on code availability):

The authors made all the alternative model runs I suggested. Everything looks fine.

Thank you