Dear Dr. van der Meer,

We would like to thank you and the two reviewers for your thoughtful and comprehensive comments on our manuscript. Below is our response, which contains explanations of how we've integrated reviewer and editor comments into our revised manuscript. In addition to addressing line-by-line suggestions made by the reviewers, we have made major revisions to the way we introduce our model organism, *Balanophyllia elegans*. In particular, we provide more motivation for why we choose this organism and explain why it falls into the category of being a deep-sea coral. Additionally, we have added new text to the abstract, methods, and results to precisely define 'turnover time'. We hope these additions ease confusion and concern about our interpretation of the isotope feeding study results. Finally, we made major revisions to our discussion of the implications of our study for understanding the components of cold-water coral diet. First, we have edited the title of our manuscript from "Zooplankton as the primary diet for cold-water scleractinian corals (CWCs): implications for the CWC marine N cycle proxy and trophic ecology" to "Quantifying the $\delta^{15}N$ trophic offset in a cold-water scleractinian coral (CWC): implications for the CWC diet and the marine N cycle proxy". Second, we have substantially rewritten and re-titled Section 4.4 (now "Implications for components of CWC diet"). Finally, we have edited sentences within the conclusion (Section 4.6) so that the language we use is a bit weaker. Specifically, we have edited sentences to read: "**While our study was limited to a shallow field site**, our isotope feeding experiment, evaluated alongside previously published studies, **may point to the possibility that** deeper-dwelling CWCs **could** also rely on zooplankton prey as a fundamental component of their diet." And "…the $\delta^{15}N$ recorded by CWC may differ among individuals of the same species feeding on different zooplankton prey, **depending on food availability.**"

Before responding to the specific reviewer comments, we would also like to respond to additional concerns noted by you, the editor. You asked: "In your comments you mention a small city nearby, are there no effects from (the greater area of) Vancouver and Seattle and possibly Victoria? I know they are a bit further away, but still, not that far. I was wondering, do you have anoxic bottom water and/or sediments at or around your site?". First, while we do see some effects of the nearby Fraser River (as described in our main text), we do not see any anthropogenic signals in this region, and none are documented in the literature – the majority of which we cite in the manuscript to describe pertinent nutrient dynamics. This area is highly flushed by nutrient-rich waters from the open Pacific. While these anthropogenic signatures appear in hydrographically-restricted Puget Sound, WA (which is near Seattle) the fact that Friday Harbor is relatively free from pollution has made Friday Harbor Labs, where this work was done, a hub for marine research in the Pacific Northwest of the United States. As described in the main text, the extensive tidal mixing at this site also means that there is no anoxic bottom water. Corals here live on rocky walls, not near a zone with high sedimentary deposition.

Overall, we feel that the suggested revisions have greatly improved the clarity and scientific quality of the manuscript. We provide responses to specific comments and concerns below using *italicized font.*

Reviewer 1 Comments:

This manuscript presents a fairly comprehensive examination of the feeding of a non-symbiont bearing cold water coral sampled from relatively shallow depths. The authors present hydrographic data and environmental samples for baseline ecosystem values, a feeding study (long term, and multiple values from diets), and a smaller and more brief study on starvation effects from reduced feeding intervals. I enjoyed reading this work and have a few comments. The MS could be more concise in places and the authors should consider when they are using vocabulary that is unnecessarily complex as there will be non-native speakers reading this work (eg. LN 437, evinced, when indicated will work fine, you forced a native speaker to have to look it up, also adroitly on LN 672, portend and heeded in the abstract). Please edit for clarity of language throughout.

Response: We thank Reviewer #1 for their assessment of this manuscript and are pleased that they enjoyed reading it. We are grateful for the Reviewer's feedback on the accessibility of some of our vocabulary. We have revised the manuscript accordingly, and have removed less widely used native English terms including 'evinced (changed to indicated)', 'portend (changed to 'point to')', 'adroitly' (changed to competently), 'heeded (changed to 'taken into consideration')'.

The authors are quite thorough in their presentation of the *Artemia* diet that the corals were raised on, but they do mention that nauplii are hatched at monthly intervals. It would be useful to present the measured values of the *Artemia* across the timeline of the experiment as a supplemental figure, just to clearly present the lack of variability in the underlying food items being fed to the corals. I do not anticipate much variability here given the relatively clear asymptotic relationships presented in Figure 3, but I do think it is important to clearly present long term variability in the underlying food source. Alternatively to the supplement, you could just add values as small points along the indicated average values for the food items in Figure 3, but please ignore if it makes the figure harder to interpret.

Response: We agree that it is important to demonstrate the lack of variability in food eaten by corals. In the supplementary materials originally posted, we had included a figure (Figure S5) that documents the effect of long-term freezer storage on the d15N of Artemia nauplii. Additionally, Table S2 lists the average d15N of the Artemia diet hatched over multiple intervals and the corresponding 1 sigma SD. However, the figure and table captions in the supplement indeed could be expanded in order to make our results clearer. We have amended the captions associated with these supplementary figures and tables. We have also added a sentence to our methods (near where Table S2 and Figure S5 are cited in the main text) to specifically note that we do not see significant variability in the diet over the course of the experiment: "These results

show that there was limited variability in the diet of corals due to freezer storage and hatching of multiple individual batches of Artemia (Table S2, S3, Figure S5).”

Fig 3 and others as appropriate: The y axis range could use a few more indicators of value here, could easily go from 5 to 20 with the same number of interval ticks in between and make it easier on the eye when comparing against multiple diet and consumer differences. Multiple figures with odd range choices, so have a look through and see where interpretation could be made easier for the reader.

Response. We have changed the y-axis range in Figures 3 and 4 in order to make the range clearer. We also considered the range in the rest of the figures in the text, and the tick marks and y-axis ranges were either intentionally chosen in order to minimize white space on the top and bottom of the figure and clearly display the full range of data. Alternatively, the range was chosen such that we could use the same range across multiple panels of a figure (as in Figure 7).

Regarding the starvation study, could you define the feeding regime as a percentage of your normal feeding rate so that you provide a more quantitative estimate of just how much less these animals were fed than their counterparts? It is fairly common in the literature to see conversations about % protein deficiency, and some effort in standardizing this feeding regime will make its inclusion in future meta analyses easier and also make it more likely to be compared against and included in future work. As is, it will be hard for future workers to feel confident assessing how much less they were fed, and it would behoove the authors to provide their assessment up front of just how much less was fed in the study.

Response. One of the challenges we encountered in our exploration of this deep-water species is that it is very difficult to estimate the ‘normal’ feeding regime given the lack of extensive studies of diet of this organism in situ. Our chosen feeding regime was based on the only previous study we’re aware of that explores the impact of feeding rate on growth of B. elegans (Crook et al. 2013), which shows that corals fed at our unstarved rate produced skeleton at much higher rates than the corals fed at our starved rates. We have, however, amended the text to note the percentage difference in feeding rate between our unstarved and starved corals and to reference the Crook paper more directly. We do not have direct measurements of the % protein in our artemia, but do report the starved feeding rate as a percentage of the control (not-starved) feeding rate.

I am surprised that I do not find a measurement of the DON d15N value included in this study. The authors have quite comprehensively measured values to account for most other potential sources, but have not provided a measurement to conclusively eliminate DON as a potential source (that I can find). Since one of the goals is to remove as many potential confounding variables from this accounting of feeding sources for non-symbiont CWC’s, this measure may help to further eliminate or confound the author’s conclusion, which would be interesting either

way the measurement value turned out. Coastal waters in an upwelling setting, so it is my understanding that this should be possible from environmental samples.

Response: It is true that previous studies reported that cold-water corals appear to be able to assimilate DON. However, we unfortunately do not have d15N DON data from our field study. Even so, we do not expect DON to be able to explain the elevated d15N of organic tissue that is observed. There are two components of DON: refractory and labile, which each have different d15N. At Friday Harbor, we don't know the partitioning of the d15N between these pools, but even if we did, the labile fraction (which would presumably be the pool available to corals) is expected to converge on the d15N value of SPOM (Bronk et al. 2002, Sigman and Fripiat 2019 their Fig. 4; Knapp et al. 2018, Zhang et al. 2020), given that the most recently produced DON is the most labile. As a result, consumption of DON would not explain the d15N of coral organic tissue. We have added text to the discussion to discuss this further.

DOI for Bronk et al.: https://doi.org/10.1016/B978-012323841-2/50007-5

DOI for Knapp et al.: https://doi.org/10.1029/2017GB005875

DOI for Zhang et al.: https://doi. org/10.1029/2020GB006551

DOI for Sigman and Fripiat: https://doi.org/10.1016/B978-0-12-409548-9.11605-7

Fig 5: I would like to see the local d15NO3 values added to this figure, to conclusively display the 6-9 per mil differences that have inspired such a comprehensive effort. Even if the baseline was only measured in Aug 2021, showing the difference between the baseline values and the skeleton and tissue values will help to highlight the extent of the potential offset problem that you are highlighting in your conclusion. You could also include an offset in panel B, highlighting both the variability and how much larger the offset is.

Response. We have added a horizontal bar to Figure 5a representing the average local d15NO3 value sampled during multiple food campaigns. Measured values for individual campaigns are shown in Figures 6 and 7.

Detailed comments:

LN 14: export is vague here, how about OM, or exported OM?

Response: We agree. We've changed 'export' to 'exported particulate organic matter'

LN 15: Unusual to unusually

Response: Changed.

LN 18: probably worthwhile to specify that the coral is non-symbiont bearing up front, save readers having to look and specify the time period instead of long-term

Response: Edited to 'asymbiotic scleractinan cold water coral Balanophyllia elegans'.

LN 21: Is this turnover time correct? You state further on that none of the corals came to equilibrium with their diets across 400 days, so what portion of turnover does 291 represent then? Also is not apt is quite vague, I think you mean does not provide sufficient resolution to track seasonality.

Response: We appreciate the reviewer noting this point of confusion. We use 'turnover time' as it is commonly used to quantify growth and turnover in biological tissue and in coral tissue specifically (e.g. Cerling et al. 2007; Tanaka et al. 2018). The turnover rate (λ) is often expressed as a half-life (defined as ln(2)/ λ) or as an e-folding time (1/ λ). The e-folding time can also be thought of as the time interval in which an exponentially growing quantity increases by a factor of e If [N]initial and [N]final are the coral tissue at the beginning of experiment respectively and at the time = 1/ λ, and $\frac{[N]final}{[N]initial} = e^{-\lambda t}$*, then at the time t=1/λ, we have* $\frac{[N]final}{[N]initial} = \frac{1}{e} = 0.37$*, meaning that 37% of the original tissue remains. The number 291 (days) corresponds to the e-folding time (1/λ) specified in Eq. 1, and for our scenario, it represents the time at which 63% of coral organic tissue N has been replaced with new N from coral diet. We have edited the text in the abstract and throughout the rest of the text to make it clear that we are referring to the e-folding time when we discuss turnover in units of days.*

We also appreciate the comments about the choice of 'apt'. We have edited the text to read: "is not able to provide sufficient resolution to track seasonality of diet $\delta^{15}N$*."*

LN 26: replace latter with phytoplankton

Response: Done.

LN 28: lose portend and heeded, goal should be easy to read and interpret clearly for all readers, including the non-native speakers. Indicate would suffice and is clear for everyone. Further on, is it really a sensitivity, or just an unaccounted for feeding strategy that is fairly similar in other sites?

Response: We have edited out portend and heeded. We agree that our results inform us about the feedings strategies of B. elegans and other cold-water corals. We have changed the final sentence of the abstract to read: 'These results point to a feeding strategy that may result in a dependence of cold-water coral $\delta^{15}N$ *on regional food web structure. This dependence must be taken into consideration in paleoceanographic studies of ocean N cycling.'*

Intro

LN 41: belongs in methods, not the intro

Response: While we agree that most equations should go in the methods, we feel it is important to define delta notation before using it extensively in the introduction. From a brief survey of the literature, the definition of delta notation is commonly offered in the introduction section of papers, for example in Wang et al. (2017).

LN 44: not :, should be . to end sentence

Response: Changed.

LN 58: intercalated…

Response: We interpret this comment as suggesting that this term in unnecessarily complex. We use 'intercalated' here in the geological sense, but agree that it would be more appropriate to change for a more general audience. We have changed 'intercalated' to 'in'.

LN 65: you use a semi colon, but I do not find the two parts of the sentence to be particularly clearly related, please edit for clarity

Response: Edited.

LN 70: ambiguous they, CWCs

Response: Changed.

LN 87: avoid excessive referencing, no need for 9 in the first and 7 in the second batch here to make this point. With this sort of coverage in the literature, it seems that these points are well contended, so pick the most relevant and go with those.

Response: Thank you for this suggestion. We have now pared down the number of references cited in these sections but included an 'e.g.' at the beginning of each reference list to show that the citations included are not exhaustive.

LN 93: I would specify zooplankton food web structure here, or lower trophic level structure.

Response: We thank the reviewer for this comment. We have edited this to read as: 'lower trophic-level food web structure'.

LN 98: passed on instead of communicated

Response: Done

LN 105: fully to further

Response: Done

LN 106: Specify the non-symbiont bearing nature of the spp here.

Response: Done

LN 108-118: Edit for brevity, combine your experimentation with each question that was asked and clearly and concisely indicate why you performed two feeding studies, a size fractionation of zoops, and underlying measurements of d15N and hydrographic conditions from the environment.

Response: Done

Methods:

LN 205: Here is where I would specify just how deficient the diet was in the starvation feeding study.

Response: Done

LN 238: Go with intermediate instead of undefined

Response: We think that undefined is more appropriate here. Intermediate suggests something in the middle whereas undefined means unspecified. In case it is more accessible, we have changed 'undefined' to 'unspecified' here.

LN 262: I would be wary of reporting an SD of 0 for analytical replicates. You are probably better off here reporting the sample precision across your runs. Either way, please clarify your analytical precision for d13C and d15N of bulk materials.

Response: Reporting an SD of 0 was a typo. We have replaced it with the correct value (0.3 permil).

LN 266: The denitrifier method is pretty standard these days, check the spelling on LN 266, and I think you can lose most of the detail here 266-274. Keep the reference standards used and the precision details, but a lot of this can go unless your aim is to establish the method for future reference here… At the very least, edit for brevity here.

Response: We corrected the spelling on LN 266 and removed excessive details describing the method.

Results:

LN 306: This model equation should be presented in methods and not in the results. I am somewhat skeptical of model output based on the fact that you have pretty clear visual evidence that animals did not completely come into equilibrium with their diets. Some discussion as to the assumptions within the model that lead to the unexpectedly short turnover time estimate and divergence from your model output from the well-graphed results is probably appropriate and currently missing from either LN 410-419 or LN 484-492.

Response: As noted above, we have added additional text to make it clearer that our 'turnover time' represents the e-folding time of the system (these additions mostly occur in Section 2.3.1 or section 3.1). While we appreciate that it may be helpful at times to discuss the structure of a model in a Methods section, this reviewer does not seem to provide specific rationale for why they want to include the model equation in the Methods for this manuscript. We do agree strongly that it would be helpful to explain the underlying assumptions and structure of this model in more detail to be accessible to a broad audience, and we have now done so in the Results section. However, we feel that it is difficult to understand the model without first discussing the results that the model is being used to contextualize. Therefore, we think the manuscript flows more naturally if the model is only presented as an analysis/evaluation tool after the presentation of our culture dataset. We have, however, also provided some additional text in the methods section (Section 2.3.1) that describes the general behavior of isotope turnover.

Discussion:

LN 407: make this statement more clear, incorporate the data supporting your point into actual sentences and not a jumble of somewhat disjointed text in sub brackets. It is one of your main points, so presenting it clearly here serves both the authors and the readers best interests.

Response: Done

LN 419-425: The authors confirmed that the diets were of equal quality, so take this background information and find a place in the intro for it where you discuss diet quality effects, it is quite unnecessary here as it is not directly relevant to the conditions in your study.

Response: We feel that it is appropriate, in the discussion, to evaluate the merits and shortcomings of our model as it relates to our data, and so we have retained the paragraph where we assess the assumptions inherent to our isotope mixing model. However, we agree that it is unnecessary to say that we verified this composition here. Instead, we reference the sections in the methods and results above.

LN 428: some discussion and some clear indications as to why your model indicates turnover in about half the time that your feeding study data does would be appropriate. IMO, the model

results are the weakest part of your feeding study here, as at 490 days your CWCs are 3, 3, 2, and 1 per mil greater than their corresponding diets… This model output needs to be revisited, IMO.

Response. We hope that our edits to the results now clarify this point of concern.

LN 526-532: This number of references are not required to demonstrate this point, IMO.

Response: We have edited down this number of references

LN 537: might define relative pore size for GFFs that define the cutoff of SPOM.

Response: We have added the cutoff (0.7 micron nominal pore size) noted above in the methods to this section as well.

LN 544-547: Seems redundant from the introduction where you set up the background that was necessary for this study, please edit for brevity.

Response: We agree that this line is redundant from the introduction and background. However, we feel that by deleting this sentence, we would be unable to fully discuss our results in the context of the existing literature. We think it is natural to reference questions or hypotheses noted in the introduction in our discussion section, as long as we explain how our study has moved the readers understanding forward. We have tried to do this appropriately in lines 547-549 of the original manuscript.

LN 566: This is lengthy enough again to feel like more broad review of literature that feels more appropriate in the introduction than at length in the discussion. A comparison against two to three studies of similar spp is adequate, IMO. LN 573-575 would suffice. Please edit for brevity.

Response: We appreciate this reviewer's goal of making the paper more readable. However, we are a bit hesitant to remove parts of this paragraph. We are motivated to include this detail to make the work more broadly accessible to geochemists (rather than just ecologists) who may not be as familiar with the ecological literature on coral diet, but who may be interests in applying this proxy to learn about past nutrient cycling. During the preparation stages of this manuscript, conversations with geochemist colleagues suggested to us that it is important to provide copious evidence that cold-water corals can feed on zooplankton in the deep ocean and that zooplankton indeed do live very deep in the water column, since in much of the geochemistry literature it is assumed that the most abundant and available food source in the deep ocean is SPOM. Indeed, this concern was also noted by Reviewer #2 and the editor. As a result, we have retained most of this text but have rewritten this section substantially to address the concerns of the others who have provided constructive criticism on this manuscript.

LN 586: Your study spp was sampled shallowly, I do not find the the extensive discussion of circulation in cold water reefs here as particularly relevant to this study. You have nicely

demonstrated size dependent usage of zoops in this setting, but I would stick to a tighter discussion of AA evidence of zoop use and not stray into deep circulation on cold water reefs, the lengthy speculation distracts from the author's solid results.

Response. We thank the reviewer for this important comment. In Section 2.1 (Collection of live coral specimens) we now motivate why B. elegans was chosen as a study subject. Specifically, we note the range of depths over which it lives include the 'deep sea'. While this species (and the genus more generally) isn't a reef-building coral, it can co-occur with D. dianthus. As noted in the previous response to the comment on Line 566, we are hesitant to remove all of this discussion because we want to demonstrate that there is an existing body of literature supporting the idea that deep corals live in environments where zooplankton can also be found. However, we have edited the text so that we more clearly describe the limitations of our study and to be clear that we are discussing possible implications rather than making speculative conclusions.

LN 613 to 628: edit for brevity.

Response. We have concerns about editing this section for brevity because this is a hydrographically complex region, and it is important to understand the dynamics in order to explain the d15N of suspended particles. Additionally, we note that Reviewer #2 wanted more detail about tidal mixing (They suggest: "Maybe quickly introduce the tidal regime and hydrodynamics if you want to explain the well mixed water column (might be out of the scope of this manuscript)." We have shortened the text in this section as suggested, but have also modified it to increase clarity based on the comments offered by Reviewer #2 (see additional responses to reviewer comments below).

Reviewer 2: Ulrike Hanz

The author conducted a very thought through study in order to understand the trophic ecology of a non-symbiotic, shallow, cold-water coral. The study is well performed and took also place over a reasonable timescale. The study organism could have been chosen more carefully (a deeper species) but overall it gives valuable knowledge about the trophic ecology of cold-water corals.

Response. We appreciate the positive feedback offered by Reviewer #2. We agree that a species like Desmophyllum dianthus would have been more directly applicable given most of the existing paleoenvironmental work on this species. However, we chose B. elegans because its depth range overlaps with that of D. dianthus, it is much easier to sample (doesn't require ROV or large boat time),there are no potential complications of growing it under different pressure conditions and because it too has a robust fossil record and has been used for paleoenvironmental study. We have amended the text to make our choice of species clearer by adding a few lines of text to Section 2.1.

My main concern is the overall goal of the study. Cold-water corals are supposed to be used as a proxy for the marine N cycle and trophic ecology, which should "help to illuminate drivers of past climate". Many cold-water corals depend on such a wide range of food sources, as also

mentioned in the manuscript, which do not all have to be related to the surface ocean N concentration or the main N cycling processes. Especially, the fact that corals can switch their food source depending on the actual food conditions will mask environmental changes by the uptake of a different food source. This makes it nearly impossible to allocate the nitrogen isotopic composition to the actual food sources, since some can increase and some can decrease the delta ratio. A proxy should have a very limited number of possible interdependencies.

Response: We appreciate the thoughtful comments given by this reviewer and strongly agree that a proxy should indeed have a very limited number of possible interdependencies. However, given the complexity of the Earth system, this is rarely possible. A good example of an existing, well-established proxy that is also complex is the coral proxy for d18O of seawater, in which a measurement of coral carbonate d18O is temperature-corrected by a measurement of coral Sr/Ca (which is itself temperature sensitive). The goal of our study is to illuminate the conditions under which the d15N CBON proxy works well, and the conditions under which it will not work well, so that geochemists don't apply it indiscriminately. We believe that despite the complex nature of food sources for cold-water corals, this proxy is still promising under certain conditions, especially given an overall robust global correlation between $\delta^{15}N$ *of corals and exported OM (Wang et al., 2014 cited in the manuscript) and some existing applications showing that cold-water coral d15N CBON agrees with other proxies, such as diatom- and foraminifera-bound* $\delta^{15}N$ *from the same region (e.g. Wang et al. 2017, cited in our main text).*

A downside of this study is also that a proxy should be relatively universal, whereas *Balanophyllia elegans* is (to my knowledge) restricted to western North America and lives in a rather unstable shallow environment. A better choice for a proxy coral in that regard would be a deep, cosmopolite coral in oligotrophic conditions with only one obvious food source, as also suggested by Robinson et al. 2023 and Wang et al. 2017, like for example Desmophyllum dianthus or *Lophelia pertusa*. Additionally, I am missing a comment if *B. elegans* skeletons are found (abundantly) as fossils, which would be important for the use as a proxy. I would therefore suggest removing the proxy suggestion (especially in regard to the climate) from the (title and) manuscript, since it is anyway only very briefly mentioned. I am aware that it is suggested by many authors to use CWCs as a proxy, whereas, despite my general doubts, corals chosen by other authors were in much fewer variable environments.

Response: We have now added text to Section 2.1 to better motivate B. elegans as a study subject. The genus Balanophyllia is cosmopolitan and fossil samples as old as Eocene in age have been used as proxies. This work is now cited in the main text. Also, again, we are very hesitant to remove the discussion of coral skeletal d15N as a proxy from both the title and the entire manuscript as investigating the potential of CWC as the N cycle proxy is the main motivation of this work. We appreciate the concern of the reviewer, which appears to be grounded in the idea that the marine N cycle dynamics at Friday Harbor would be too complicated to reconstruct with B. elegans skeletal d15N. However, the marine N cycle is typically comprised of many components which are well represented in Friday Harbor (e.g. uptake of nitrate by phytoplankton, uptake of OM by zooplankton, etc). Thus, we l think many of the results in this manuscript have implications for the application of cold-water coral skeletal d15N more generally. One of the things we hope that we are able to do in this paper is show that coral skeletal d15N may be sensitive to food-web structure. This result certainly has implications

for studies that rely on coral skeletal d15N to reconstruct marine N cycling. In the paleoproxy community, we feel it is important to both publish studies that show how proxies work well, and the conditions under which they may be complicated to apply. One implication of our work in the coastal settings is the $\delta^{15}N$ of corals might be sensitive to the food web structure. This finding bears implication for the open ocean (deep) settings, where the proxy has been originally developed and applied (e.g. Wang et al., 2014 and 2017) that potential changes in the trophic ecology need to be considered when such studies are attempted.

Nevertheless, I think that the study is very valuable for trophic ecology studies since there are still many knowledge gaps in the ecology of CWCs and this study fills many of them. For example, the study proofs very well that there is only a small difference in tissue and skeleton $d^{15}N$ values of the coral and also that there is no unexpected trophic isotope effect, if corals feed on zooplankton.

Additional investigations of fatty acids could have confirmed the preference of zooplankton as a food source for this coral.

Response: We are glad to hear that the reviewer thinks this study will be valuable for trophic ecology studies! We are unsure whether the comment about fatty acids is a suggestion to include more references on this topic. However, we have cited many previous studies in Section 4.4 of the main text (e.g. Dodds et al., 2009; Kiriakoulakis et al., 2005; Naumann et al. 2015) that have used lipid biomarkers to suggest that CWCs feed on metazoan zooplankton.

Comments:

Line 32 to 37: I think this is out of the scope of this study.

Response: This comment seems to stem from this reviewer's concerns about the utility of coral N isotopes as a paleoproxy. However, because we are specifically asking a question about the origin of the coral carbonate-bound d15N value in this study, rather than tissue d15N, we feel that it is important to motivate why one might care about the carbonate-bound d15N composition in the first place. It is of interest to understand coral carbonate-bound d15N composition in large part because this composition is being actively used as a proxy in the community for marine N cycling.

Line 41-42: Sentence does not fit there. Could be mentioned in the method part.

Response: As noted in our response to Reviewer 1, we feel it is important to define delta notation before using it extensively in the introduction. From a brief survey of the literature, the definition of delta notation is commonly offered in the introduction section of papers, for example in Wang et al. (2017) which is already cited in our reference list.

L58-59 repetition (maybe remove from L41)

Response: We completely agree that this sounds repetitive. We meant to make the difference between L41 and L58-59 more nuanced. Specifically, there are some d15N proxies for marine N

cycling from sediments that are subject to diagenesis and bioturbation, and a newer class of d15N that are 'biological' and less subject to post-depositional processes. We have removed the mention of biological archives from the original manuscript's Line 41 (now Line 47) as suggested.

L73 check sentence and replace "are" by "can". Bioturbation has nevertheless nothing to do with the ability of using radiometric methods.

Response: We agree that the language here was confusing initially. We have edited this line to read: 'CWC skeletons are not subject to bioturbation and thus absolute ages can be determined with decadal precision on the time scales of glacial-interglacial climate variability through U-Th series dating'.

L78 Only deep CWCs have the ability to reconstruct deep-sea environmental conditions, not the shallow ones that were used in this study.

Response: As noted above, some of this concern may stem from us not appropriately motivating why B. elegans is an appropriate species to study. While it can be collected from shallow depths, individuals of B. elegans live up to 500 m water depth (and therefore are deep-sea dwelling since they live below ~200 m water depth) and their habitat can overlap with D. dianthus. As such, these corals still do have the potential to reconstruct both deep and surface properties. As mentioned above, and we argue in the manuscript, we think that our findings in this shallow water settings bear implications for the deep water CWC.

L83-84 Why is it mentioned that they feed predominantly on algal material when further down it is stated that they are considered generalists. I would make that clear from the beginning.

Response: We agree that the citations used here are confusing. We have removed them and just describe the assumptions/rationale employed by Wang et al. (2014) in this discussion.

L92 8-9 ‰ is still one trophic level higher than 2 x 3 ‰

Response: We agree we should make this clearer. We have changed this sentence to read: 'A zooplankton diet should result in an approximate two-level trophic transfer between surface PON and coral tissue (e.g., Sherwood et al. 2008), closer but still not equal to the observed 8-9 ‰ offset'.

L102 deep-ocean environments

I would also be careful stressing the importance of deep CWCs when they were not studied.

Response: We changed this to deep-ocean. As noted above, this coral species does indeed live in the deep ocean.

L103 cold-water reef

Response: Done

L121 suddenly no space between lines, which happens more often.

Response: We apologize for this formatting issue! We have fixed it throughout the text.

Figure 1 Do not use a screenshot with buttons and (looks like) hyperlinks on it. Geographical position should be indicated by a raster or similar on the border of the map. A wider overview would help the (non-American/Canadian) reader to locate the area. Add a picture of the corals in their natural environment, that gives additional information to the reader and nicely illustrates the manuscript.

Response: We have edited Figure 1 as suggested.

L126 I am not sure about it, but can the position on a vertical rock walls also have an influence on the available food sources? Suspended material will sink down and cannot be resuspended and be far less available than for example zooplankton.

Response: This is a good point! We have incorporated this general idea (i.e. that corals live in locations of relatively high food supply) into our discussion of food supply to corals in Section 4.4. However, we do think suspended material could theoretically still be a source of food if entrained in water, even if it has low potential to be resuspended along rocky walls.

L129 Potential encrusting sponges could also influence the $d^{15}N$. Maybe briefly mention associated fauna.

Response: We are unsure of how encrusting sponges could influence the d15N unless they were a source of contamination (which we note we removed) or unless the corals consumed the sponges as part of their diet, or unless the sponges altered local N dynamics. Given the reviewers expertise in this area, we think the latter may be what's suggested. We have added a line to the discussion on CWC diets noting that extensive recycling in deep sea coral reef environments by associated fauna may also influence d15N. Specifically, this line reads: "Maier et al. 2023 suggest that the biodiversity and productivity of CWC reefs in the deep sea are supported by a number of processes such as CWC's ability to consume a range of dietary components (DOM, bacterioplankton, inorganic resources), efficient resource recycling, and their ability to align their activity and growth with fluctuations in food availability."

L167 Remove since color name not used in manuscript.

Response: Done

L185 Were the corals not stressed by taking them out of the water?

Response: We did not include a detailed account of how this was done, but briefly: Corals were transferred from their incubation bottles to feeding dishes in small cups of seawater which were then flushed with newly prepared fresh seawater after the corals had eaten. This approach

minimized exposure to air. In some cases, the corals did get briefly exposed to air (stress was visible by corals retracting their tentacles) in which case they were allowed to recover for a few minutes prior to feeding. We have edited the sentence flagged by this reviewer to read: 'Corals were fed their respective nauplii diets by transferring coral individuals from their incubation bottle to a small dish filled with artificial seawater with minimal exposure to air so as not to stress the corals.'

L186 A µL unit is not really informative since we do not know the concentration of the suspension. I would use a carbon or nitrogen concentration as a unit.

*Response: This is a good point. We do not have the data on carbonate or nitrogen concentration of this suspension. However, to give a better idea of what the artemia suspension looks like, we have edited line 177 above to read: "*Fresh batches of nauplii were hatched from *Artemia* cysts at approximately monthly intervals, filtered into a concentrated suspension, stored frozen at -18ºC…". *The goal here in reporting the volume is to indicate that all corals across treatments were fed the same volume of a concentrated suspension. Our Table S3 shows that the C:N ratios across all Artemia types are very similar.*

L203 Why name them "short" and "long"? Its confusing for the reader and easier if just named starved or non-starved (like in the text).

Response: We agree that this is confusing. We now refer to these groups as starved and not-starved throughout.

L222 Maybe briefly mention why this complicated method was used.

Response: We added a line at the beginning of this paragraph reading: 'It is necessary to separate organic matter from the coral carbonate matrix in advance of the N isotope measurement methods used here (see Section 2.6 below).' The small amount of nitrogen (~2-5 nanomole/mg of coral material) did not allow for a more conventional "combustion" method. We did not specify this in the text as the use of dissolution/oxidation/"denitrifier" methodolgy for coral-bound organic nitrogen $\delta^{15}N$ is described in detail in the original Wang et al (2014) paper about the method.

L264f If this is an established method, it doesn't need to be explained again.

Response. See response to Reviewer #1 above.

Figure 3 Add some more y-tick mark labels on the y-axis, then it is easier to read.

Response: See Response to Reviewer #1's comments above.

L315 So the model gives a trophic offset of 3 ‰ for all Artemia strains? For me, it looks very much like a logarithmically decreasing offset with increasing $d^{15}N$ of the diet at the last time point. Maybe check that. Where is the model output?

Response: We have revised the results to hopefully make this point clearer. It is clear from our data that the coral tissue at the end of the experiment did not reach an isotopic equilibrium with the new diet (hence, the observation that d15N of the tissue is increasing near the last time point as this reviewer points out). However, we can still use the model in Equation 1 to extract an estimate of the turnover time and trophic isotope effect from our results, despite not yet reaching an equilibrium. This application of this model requires that we fit all of the data simultaneously, which results in a single trophic offset and single turnover time for all of the corals across our four treatments. The model output are the fits plotted on Figure 3, as well as the values reported for our apparent trophic offset (3 ‰) and turnover or e-folding time. We have more clearly referenced the presence of this output on Fig. 3 at the end of Section 3.1 in the Results.

L316 How is that the isotopic turnover time when the regressions did not reach an equilibrium yet? Also, one value for all experiments seems not right.

Response. See responses above, including responses to Reviewer 1 regarding the model and turnover time

L323 Figure 4 should be referenced in the sentence before (no statistics in the figure).

Response: Done

Figure 4 Some more y-axis tick marks would be nice. What happened to the starved coral at the time point between 100 and 200 days? Is it just an outlier, or did something go wrong?

Response: See response to Reviewer #1's comments. The starved coral data point between 100 and 200 days was an outlier and is now removed from the figure.

Figure 5a Would be nice to know when the phytoplankton bloom happened in these years. B) Not really informative for me. I think it's much better visible in figure 5a.

Response: Unfortunately, we don't have data on the timing of the phytoplankton blooms locally. We felt like panel (B) could be useful in that it more concisely shows the average offset between tissue and skeleton. Given the suggested edits from Reviewer #1 which will compress the y-axis scale in panel (A), we have decided to leave Figure 5B as-is.

L350 Is this not an indication of riverine input, which would also introduce terrestrial matter, that can influence the isotopic compositions? Additionally, the sampling region is very close to a city/village. Are there no anthropogenic effects to be expected?

Response: We agree that this is important to discuss. We do not discuss the implications of the vertical profiles in the result section, but do discuss this indication of riverine input in the discussion (the paragraph starting at line 613 in the original manuscript). The Juan de Fuca Straight exhibits estuarine mixing, and we note that fresher and warmer water observed is likely sourced from the Georgia Strait which has lower salinity due to the outflow of the Fraser River. There is indeed a small city at Friday Harbor, but it is not industrial. We are not aware of any published data on anthropogenic N in the San Juan Channel. There is indeed some agriculture

on San Juan Island. However, we think it should be sufficient to document the d15N of nitrate, which accounts for any possible anthropogenic inputs, found to be not significant ($\delta^{15}N$ of nitrate in our field area is very similar to the regional nitrate offshore).

Figure 6 Is this indicating N fixation within the water column? Otherwise, how do you explain that SPOM has a lower $d^{15}N$ than NO_3^-?

Response. We have now modified the text in Section 4.5 to clarify which factors contribute to the slightly lower d15N of SPOM (i.e. Rayleigh fractionation of nitrate and/or assimilation of regenerated N). N_2 fixation would not be a significant contributor to the surface (euphotic) N inventory at this high NO3- site as the N mass balance requires.

Figure 7 Maybe use seasons to describe sampling times (autumn-winter-spring- summer-autumn)? Would make it look a bit nicer. Or give information about the phytoplankton bloom, then certain months are important and they can make big differences.

Response. We don't have frequent enough sampling to represent each season and we sometimes don't have paired samples from within a single campaign, so we chose to make our sampling timing more transparent. We also replaced the words 'autumn' and 'spring' in the main text that we used to refer to some field campaigns with the exact months associated with sampling.

Figure 8 How do you argue that this assimilation effect is true, when actually the $d^{15}N$ of NO_3 is lower than the $d^{15}N$ of the SPOM?

Response. Actually, the $\delta^{15}N$ of SPOM is either lower (~4 ‰) or similar to or converges on the incident nitrate of 6-7 ‰. As discussed in Section 4.5, the lower $\delta^{15}N$ of SPOM points to some influence of incomplete consumption and/or some recycling (largely in spring months) See comments above and edits to Section 4.5.

Figure 9 Why is this figure in the discussion?

Response: We have moved this figure to above the start of the discussion section. It was originally included right after the discussion because it did not fit on the previous page with Figure 8, but we have decreased the sizes for readability. Figure 9 is indeed cited in the Results section first (line 378 of the original manuscript).

L425 It's good that the quality in the experiments stayed the same, but in nature corals will take up what is available. This can be phytoplankton or zooplankton or other material. The availability of plankton depends also on the climate and would explain the isotopic difference of 1-2 ‰, that was argued to be produced by different N cycling in surface water by Wang et al. 2017.

Response: We note that cold-water corals have been observed to be generalists in terms of feeding. However, they could still derive the majority of their nutrition from one source. We think our results suggest that this source is likely zooplankton, which we try to show is supported by other studies as well (in our discussion of the published literature in Section 4.4., for example).

With regard of the reviewer's comment on phytoplankton being one of the possible sources, the typically reported 6-9‰ offset between phytoplankton OM and CWC tissue/skeleton OM $\delta^{15}N$ exclude the possibility that POM comprises a dietary component for CWC, this is offset is a factor 2 to 3 larger than the universal 3‰ one level trophic also demonstrated in our incubation experiment. Also, while this reviewer seems to be concerned that the results from Wang et al. (2017) may indicate a change in diet rather than a change in N cycling, we still think the results of Wang et al. are fairly robust given that their coral records agree strongly with diatom and foraminifera-based records from the same region. Similarly, the strong regression of Wang et al. 2014 of coral d15N with the d15N material exported from the surface globally suggests that regional differences in specific components of coral diet (e.g. types of zooplankton, other possible forms of OM) have a relatively small influence in the coral's d15N. In any case, we appreciate that this reviewer is worried about us overinterpreting our results. Therefore, we have re-written Section 4.4 extensively with this concern in mind. The two paragraphs below capture an example of how we've tried to rewrite this section:

"Despite evidence for zooplankton as the main dietary source for B. elegans at Friday Harbor, we acknowledge that this feeding strategy may not apply for corals living in habitats that are hundreds to thousands of meters deep. As pointed out in a recent review (Maier et al. 2023), the presence of CWC reefs in the food-limited deep ocean appears paradoxical, and it is not likely that the food available to corals at Friday Harbor looks identical to food available to corals living at >1000 m water depth. Indeed, Maier et al. 2023 suggest that the biodiversity and productivity of CWC reefs in the deep sea are supported by a number of processes such as CWC's ability to consume a range of dietary components (DOM, bacterioplankton, inorganic resources), efficient resource recycling, and their ability to align their activity and growth with fluctuations in food availability.

Nevertheless, Maier et al. (2023) and references therein highlight that most deep CWC reefs occur in regions with higher-than-average annual primary productivity, indicating that these CWC reefs are sustained by inputs of high energy to the system, where there is also evidence for the presence of vertically migrating zooplankton. The vertically migrating zooplankton have been found near both relatively shallow (<200 m, Duineveld et al. 2007, Garcia-Herrera et al., 2022) and deep (~1000 m, e.g. Carlier et al. 2009) CWC reefs. Moreover, there are a number of other independent studies that reveal a single trophic level offset between the $\delta^{15}N$ of zooplankton prey and the $\delta^{15}N$ soft tissue of asymbiotic scleractinian corals at specific sites (Duineveld et al., 2004, Sherwood et al. 2005; 2008; 2009; Carlier et al., 2009; Hill et al., 2014; Maier et al., 2020). Given the 'normal' trophic level offset reported for CWCs in our laboratory culture experiment, these published observations underscore that zooplankton could be a dominant dietary component of corals other than B. elegans as well."

L437 Microbial symbionts will change depending on the environmental conditions. I think its difficult to argue an influence of microbial symbionts in an artificial environment.

Response: This is a fair assessment. We had just hoped to provide some thoughts as to the potential role of microbial symbionts, given that they have been implicated in N assimilation of cold-water corals previously (Middelburg et al. 2016). We have now cited Middelburg et al. in this section and changed the words 'argues for' to the gentler word 'suggests'.

L457 There is a lot of literature about seasonal differences/decrease in food supply.

Response: We have removed the sentence noted in this line. We cite a sampling of the relevant literature in Section 4.4.

L457 Deep-sea corals

I think the consensus is that deep-sea environments are limited in particulate food sources. Also, be careful with describing deep-sea corals too much, since you worked with shallow corals.

Response: We have edited this and the following lines slightly so as to make sure we don't suggest the opposite of what the reviewer is communicating here. We want to suggest, as described in the recent review of Maier et al. (2023), that there seem to be periods of feast and famine conditions for most deep-sea coral reefs and have explicitly noted the paradox of CWCs living in the resource-limited deep sea in Section 4.4. See comments above about our B. elegans species actually falling into the group of deep-water corals.

L466ff Please check if the turnover time is right. Visually, it looked much longer.

Response: See comments regarding the definition of turnover time in our response to the comments given by Reviewer #1. We do not expect the turnover time to equal the time that it takes for the tissue to reach equilibrium with the food source. We have changed wording across the text to make this definition more accessible to the general reader.

L526-533 Repetition of the introduction. I would remove it from the discussion.

Response: Done.

L538 Not glass fiber filters in general. They exist in different mesh sizes.

Response: Clarified

L540 Subsurface is everything below water level. Here underneath the photic zone is meant if I understand this right.

Response. In oceanography, it is common to use 'subsurface' to refer to 'below the euphotic zone'. We have clarified this in the main text.

L543 shouldn't be the deeper SPOM isotopically more enriched?

Response: Correct. This is noted in line 542.

L547 Again, I would be careful with comparing the deep sea to shallow environments.

Response. See comments above.

L551 If you still have material, you could consider measuring fatty acids to support your argument and proof that they feed on zooplankton.

Response: Unfortunately, we don't have this material any longer, but we agree that this would be a nice complement.

L565 This seems like a stress response. That might also have an effect on the feeding behavior and therefore maybe also isotopic composition.

Response: Yes – it definitely is! We have now added a line to the methods do show that we tried to avoid exposing the coral to air during the experiment. We have also now removed this line because it is distracting. We had observed this behavior in interactions with this coral informally, outside of the actual lab experiments (or only when we were sacrificing the corals).

L586-598 Most of this paragraph is considering deep-sea environments on the seafloor and not shallow corals.

Response: Again, see comments above about the depth range of B. elegans.

L608 HNLC abbreviation not explained.

Response: replaced with 'high nutrient low chlorophyll'.

L613 Replace the word ostensibly.

Response: replaced with 'appeared to be'

Why is nitrate assimilation incomplete? There are no nitrate measurements from the surface ocean, where nitrate might be much more depleted. Data starts at around 5 m depth.

Response: As noted in the main text, nitrate is still abundant in the upper water column (euphotic zone/surface) in the San Juan Channel, indicating incomplete nitrate assimilation. Additionally, 5m water depth is considered to be the surface ocean for oceanographic purposes (for instance, this is much shallower than the typical depth of the surface mixed layer depth, typically 10-25 m in the coastal settings)

L620 Rivers can also introduce nitrate.

Response: Already noted in Line 626.

L638 Maybe quickly introduce the tidal regime and hydrodynamics if you want to explain the well mixed water column (might be out of the scope of this manuscript).

Response: We feel that we already do this starting in Line 613 of the original main text (Section 4.5) and starting at Line 921 in the revised text, but we added further clarification in the revised text: "Indeed, nitrate in the San Juan Channel is replete year-round, even at the surface, due to vigorous mixing within the channel (Mackas and Harrison, 1997; Murray et al., 2015). The region experiences tidal mixing, designating it as a well-mixed estuary with minimal density stratification (Banas et al., 1999; Mackas and Harrison, 1997). The strong tidal influence is clearly recognizable from the diurnal patterns of vertical hydrographic structure variability with the salinity/temperature gradients changing in response to the tidal phase (Figure 6a and b). The tidal pumping drives vertical mixing between high nutrient deep water from the Juan de Fuca

Strait and fresher surface water from the Strait of Georgia (Banas et al., 1999; Lewis, 1978; Murray et al., 2015; Mackas and Harrison, 1997)."

L645 Is d15N not supposed to increase when assimilated into phytoplankton?

Response: While we are a bit confused by this reviewer's question, our data do indeed show that the d15N of NO3- increases with greater levels of assimilation (i.e. signified by lower concentrations of nitrate in the water column), but the degree of increase is attenuated by the mixing discussed in detail in Section 4.5.

L666 I don't think that should be the main outcome of this study, since depth was not assessed. This statement is also not true in my opinion. The main food source of corals depends on the availability, not depth.

Response: We agree that depth was not specifically assessed in our study, and so we attempted use language in this paragraph that made it clear we were discussing possible implications of our data (rather than firm conclusions). We have revised this text to make sure this is clearer (e.g. 'may differ', 'warrants further investigations'). It is probably fair to surmise that food availability does depend on depth among other factors, as the amount of OM exponentially decreases with depth in general. We also note that if the reviewer knows of published studies showing that coral d15N and feeding regime varies as a function of food availability, it would be helpful to point us to those specific sources.

In response to the comment, specifically, we have changed the text to read as follows: "for a given $\delta^{15}N$ of sinking PON exiting the surface ocean, the $\delta^{15}N$ recorded by CWC may differ among individuals of the same species feeding on different zooplankton prey, depending on food availability. In fact, Wang et al. (2014), having measured $\delta^{15}N$ of individual septa, did report a "natural variability" of 1-1.5‰ even within a single specimen that might have resulted from some variability of the local food web on a short time scale of few years. Some studies have documented an increase in the degree of carnivory of zooplankton with depth (Dodds et al., 2009; Vinogradov, 1962). For instance, Hannides et al. (2013) recorded a 3.5 ‰ increase in zooplankton $\delta^{15}N$ from 150 m to 1000 m in the Subtropical North Pacific, with the steepest rate of increase from 100 – 300 m. These studies are consistent with previous reports of small but resolvable (1-2 ‰) depth-dependencies of coral $\delta^{15}N$ that could be explained by corals feeding predominantly on zooplankton (Wang et al. 2014). The $\delta^{15}N$ recorded in CWC skeletons also tends to differ among species, as respective species occupy different nutritional niches (Teece et al., 2011). The relationship between CWC species represented in fossil archives to the depth structure of their zooplankton prey warrants further investigation."

L678 In the sentence before it was mentioned that it is not a good proxy because of the low difference in $d^{15}N$ and high variability, that was also shown in this study. Why is it considered a good proxy in this sentence? Corals have, as mentioned, some promising features for being a proxy, but the here presented downsides outweigh/cancel the upsides.

Response: It appears as though the point we are trying to convey in these lines is unclear. First, we do not think we have said anywhere in this paragraph that coral-bound d15N is not a good

proxy. We just note that there are certain scientific questions for which applications of this proxy will be most useful (given the possible dependence on food web structure). Again, the study of Wang et al (2017), as well the study of Studer et al. (2018), now also cited in the manuscript clearly demonstrated strong similarities between coral $\delta^{15}N$ and other biomineral archives (diatoms and forams) variability We have edited these sentences slightly for clarity. We're also not convinced that the concerns we've identified cancel the upsides of this proxy. We are just trying to suggest here that this proxy can be a good choice under certain conditions if it is applied thoughtfully.

Please also check the wording. The text uses some non-standard vocabulary, which disrupts the flow of reading.

Response: Done.