Reviewer Nina Keul:

The manuscript “The contributions of various calcifying plankton to the South Atlantic calcium carbonate stock” (https://doi.org/10.5194/egusphere-2025-4234) by Anne Kruijt and colleagues investigates how the three main calcifying plankton groups — coccolithophores, foraminifera, and planktonic gastropods (heteropods and pteropods) — contribute to particulate inorganic carbon (PIC) stocks and export in the South Atlantic Ocean. The authors present data from a sampling campaign, quantifying the depth-integrated PIC standing stock, production, and export for all three groups.

The research is original and addresses a critical question in the field of marine biogeochemistry, providing a more holistic understanding of how the major calcifying plankton groups contribute to carbon cycling and export in the South Atlantic. The study is conceptually strong, clearly written, and presents complex results in a way that is accessible to the reader.

Reply: We thank Dr. Keul for her compliments and her critical but constructive review.

However, certain sections, particularly the Materials and Methods section, require clarification and reorganization to improve readability and ensure that methods and assumptions are clearly linked to the presented data. While I understand that the authors use previously published values of turnover time, I see this as highly critical, as it does not take into account the fact that gastropods are, in fact, multicellular organisms that have a more complex life cycle than single-celled foraminifera and coccolithophores (e.g., seasonality, stagnant growth). Therefore, using the same equation for turnover time as for coccolithophores and foraminifera will lead to a drastic overestimation of pteropod contribution, which in fact is seen here (citing from abstract) — “implying that not only coccolithophores but also gastropods may be more important PIC producers than foraminifera.” That is the main shortcoming of the paper, in my opinion. I know this method has been used before, but the issue surrounding turnover time needs to be addressed here.

Reply: We agree that much uncertainty regards the lifestyle of gastropods. We will include text outlining their more complex ecology, including aspects of seasonality and stagnant growth, although constraints on such aspects are insufficient to adapt our general approach. To accommodate this comment by the reviewer, we will adapt our estimate of turnover time, which in our approach is the tuneable parameter. We originally limited our analyses to the approach presented in Ziveri et al. (2023), which enabled us to directly compare our results with theirs. For the revised version we will include calculations using longer turnover time estimates from the literature, resulting in a range of plausible pteropod contributions.

Furthermore, the manuscript, while very well written, needs to be checked very carefully for consistency (in used terms, layout, etc.) and formatting of figures needs to improved.

Reply: We thank Dr. Keul for her compliments and critical reading. We will check the revised manuscript very carefully and correct all remaining errors and inconsistencies.

Despite these issues, the manuscript provides valuable insights for the community

and is well-positioned to advance our understanding of PIC production and export across multiple plankton groups. I would recommend publication after the authors address the points raised in the review.

I wish the authors success with the revisions and remain available for further feedback.

Best wishes,
Nina Keul

Here is a detailed list of comments:

Reply: A numbered reply is added to each comment.

l. 38 “haptophyte”: I let the authors be the judge if it is reasonable to assume that the community of BGD all know that term.

1) *We understand the concern. We will add this reference: Jordan, 2009. (https://doi.org/10.1016/B978-012373944-5.00249-2), so that readers who do not know the term can find more information.*

• l. 87: The order in which the three groups are addressed should always be the same; here it is GFC, but in section 2.4 it is F (2.4.1), G (2.4.2), C (2.4.3).

2) *We will change this to the order in section 2.4 (f, g, c).*

• Fig. 1:

o “Multinetting” — is this indeed a verb?

3) *We will change it to ‘MultiNet sampling’.*

o Formatting: in some boxes there is an extra space before the unit (e.g., for PIC), in some not (e.g., counts # for F).

4) *We will check and correct this.*

• l. 117: How do you know that the Benguela Current was too remote to influence the study site? Consider rephrasing “remote”

5) *We will rephrase to: ‘Waters at our study location at the time of sampling were low in nutrient concentrations (see section 3.1) so plankton concentrations were expected to be low. Our study location is assumed to lie outside the reach of the Benguela upwelling system. The extent of this system is commonly reported to reach only approximately 100 – 200 m offshore (Siddiqui et al., 2023; Hagen et al., 2001; Lutjeharms et al., 1987) although we do note that filaments shedding off the boundary current can reach much further offshore (Rogerson et al., 2025; Lutjeharms et al. 1987).*

• l. 119: “Samples from station 39 (further northwest; Figure 2) and stations 6 and 9 were used to reconstruct the PIC/POC ratio of Limacina bulimoides and Heliconoides inflatus, two abundant and cosmopolitan pteropod species.” This sentence should go to another section.

6) *We agree but also need to mention station 39 here. We shall proceed as follows:*
   - *We will tackle this in the second sentence:*
     - *‘All data presented in this paper were collected within 48 hours at stations 3, 4, 6, and 9. The stations were less than 2 km apart and water column characteristics were similar. An exception is station 39, located further north (Figure 2). Data collected at this station are not included in the main analysis of this paper, but will be addressed in section 2.2.1 and Appendix B.’*
   - *In section 2.2.1 we will add a line explaining that samples from station 39, station 6 and station 9 were used to reconstruct the PIC/POC ratio of Limacina bulimoides and Heliconoides inflatus, and explain why we included station 39 (in short: we assumed no latitude related difference in the Limacina bulimoides and Heliconoides inflatus PIC/POC ratios, so in order to obtain a higher number of measured individuals we added the specimen from station 39 to our analysis.)*

• Fig. 2 caption: The methodology (Copernicus data extraction) should also be

described in the text, not just in the figure caption.

7) *We will include the data extraction in the main text.*

• Fig. 2c: Station 39 is not readable. What does “Station with number” mean (upper right corner)?

8) *Agreed, we will change the accompanying text and the colour of the points and numbers in the map.*

• l. 135: How were station 39 samples collected? Also via oblique multinet tows? Please add.

9) *Station 39 samples were collected in the same manner as samples at station 6 and 9. We will clarify this in the text.*

• l. 140: Was this splitting performed on the ship? If yes, how did you ensure a 50:50 split on a moving ship (as the splitter should be level when using)?

10) *Splitting was indeed performed on the ship but weather conditions were good enough to keep the splitter level. This is now included in the manuscript.*

• l. 142: What about pteropods? How big is the bias here by using a 200 µm net? Do you have estimates? The smallest pteropods we find are usually 80 µm in diameter.

11) *We used a 200 µm mesh for several reasons. First, we had to prevent reported clogging and breaking of nets with smaller mesh-sizes and active escape of larger pteropods from fine meshed nets towed at a low speed. This would lead to undersampling of adult pteropods. Moreover, our 100 µm nets broke during a stormy haul and two of the five nets were severely damaged. So ultimately, we use a 200 µm mesh based on the study by Bednaršek et al. (2012), who report that the peak of the biomass lies around 300 µm. However, we realise many studies report that small pteropods are undersampled when using these nets (Bednaršek et al., 2012; Manno et al. 2017; Anglada-Ortiz et al., 2021). We will address this in the revised manuscript as follows:*

- *In the methods section, we will mention that smaller pteropods, especially juveniles, will also be underrepresented by using a 200 µm mesh, and that our pteropod biomass estimates should be interpreted as a conservative estimate.*
- *We will come back to this in the discussion section and point out that the planktonic gastropod biomass is likely higher than our results suggest.*

• l. 175: Stored in polyethylene (jars)? Krantz vials? Were they dried before storing? Were they washed (e.g., quick DI bath)?

12) *These lines refer to the way samples were stored after sorting. We stored them in 1 mL polyethylene vials, in 96% ethanol. We will add this information to the manuscript.*

• l. 182: Add a datatable (can be in supplement) to list the n of each category (full, empty, adult, juvenile).

13) *We made our complete dataset, containing counts for each identified species and category, available on Zenodo as well as a datasheet containing the calculations and conversions from counts and measured weights to PIC concentrations.*

• l. 187: I am a bit puzzled by this comment (in relation to unweighed

pteropods). I have weighed individual pteropods before; in the case of H. inflatus, the shells of the smaller specimens were still 20+ µg, which could be weighed without problem on an ultramicrobalance.

14) *In case of very low yields, we did not want to risk losing (juvenile) individuals while transferring sample from vial to petri-dish to weighing cups. We therefore chose to not attempt at weighing these samples, but instead use the counts, and reconstruct the weights.*

• General comment: Please specify in which institute the analyses were performed (e.g., l. 201 — the automated microscope system).

15) *We will add the institutes for each of the analyses*

• l. 222: "Unlike the shells containing living plankton" — rephrase.

16) This will be changed to:
'We also calculated the export concentration (Cexp, mg m-3), which refers to the concentration of empty shells or shells that contain dead specimens.'

• Equation 4: You mention that cups were split — was that taken into account in the calculations?

17) *It was. We will add a short line here to clarify this*.

• l. 289: The same turnover times as Ziveri et al. are used (5–16 days), which I have a hard time with. While the calculations per se are correct, I feel this is far from reality, where stagnant growth is common, especially in temperate areas as in your study location. Since turnover time is a crucial parameter in flux calculations, using these low turnover times might overestimate pteropod fluxes. Furthermore, in the case of planktonic foraminifera, this is more reasonable; here, values are in agreement with lifespan, as there is no stagnant growth phase for forams.

18) *We agree that much uncertainty regards the lifestyle of gastropods. We will include text outlining their more complex ecology, including aspects of seasonality and stagnant growth, although constraints on such aspects are insufficient to adapt our general approach. To accommodate this comment by the reviewer, we will adapt our estimate of turnover time, which in our approach is the tuneable parameter. We originally limited our analyses to the approach presented in Ziveri et al. 2023, which enabled us to directly compare our results with theirs. For the revised version we will include calculations using longer turnover times, resulting in a range of plausible pteropod contributions.*

• Table 2: Add references to all values, not just V.

19) *We will add a row to the table containing the references for the turnover time estimates.*

• l. 330: I value that you try to assess turnover time differently, but again, we know from sediment trap studies that pteropod flux is not the same over the year, so we cannot make these calculations and extrapolate them into a full year, even in a medium-seasonality region such as yours. February, I would imagine, is post-bloom (after summer); I would assume differences in winter. See for instance Oakes et al. 2021, where they only found pteropods in 17/36 sediment trap samples (Oakes RL, Davis CV, and Sessa JA, 2021. Using the

Stable Isotopic Composition of Heliconoides inflatus Pteropod Shells to Determine Calcification Depth in the Cariaco Basin. Front. Mar. Sci. 7:553104. doi: 10.3389/fmars.2020.55310).

20) *In lines 329-332, we stressed that our calculations are based on the steady state assumption. For any organism, particularly gastropods, this may not be valid. This introduces some uncertainty but in the absence of detailed time series, taking the simplest assumption here is the best solution.*

• Figure 3: Should be prepared more carefully. For example, the X-axis line is barely visible, and the second Y-axis line is shown incorrectly.

21) *This will be fixed.*

• l. 398 / 299: Does this apply to F and P, or only P? How was full versus empty assessed in foraminifera (staining?)? In Materials and Methods, it gives the impression that only P were assessed in this regard (species or sometimes genus type, organic matter content (full or empty), and in the case of gastropods, life-stage (juvenile or adult)).

22) *Will clarify the Materials and Methods section 2.2.1. To answer your question, we assed full versus empty for both foraminifera and gastropods.*

- *For gastropods, we could see clearly through the microscope weather a shell contained body tissue or not. If it contained body tissue, it was regarded as 'full', if not, it was regarded as 'empty'*
- *For foraminifera, the same approach was taken. We classified foraminifera tests as 'full' when there was a significant amount of white/green tissue visible within the shell.*

All foraminifera in our samples, as well as the foraminifera in the reconstructed 125-200 µg size fraction were considered 'adult'. The distinction between adult and juvenile was thus only made for the gastropods.

• l. 402: Add (SE) after "Standard error = 0.08."

23) *Agreed; we will add this*.

• Fig. 5: I am not sure whether this needs to be plotted or can be better represented in a datatable. If the authors decide to keep the figure, its visual appeal needs improvement (remove helper lines, format consistently, include corresponding p-values).

24) *As suggested, we will change this figure into a table containing, for H. inflatus adult and juvenile and L. bulimoides adult and juvenile:*

- *the size of each sample (number of specimens within the sample),*
- *PIC:POC ratios measured for each sample*
- *The slope of the trendline fitted to the three samples*
- *The R^2 value of each slope*

• Section 3.3: Species names in italics; Syracosphaera needs capitalization.

25) *We will correct this.*

• Fig. 6: Remove grid lines; make lines and symbols the same size and thickness.

26) *We will update it accordingly.*

• Table 3: Explain acronyms (SS); check digits and only list significant amounts based on the error associated with the calculations/initial measurements. If in doubt, perform error propagation.

27) *We will explain all acronyms in the table caption. We also corrected Table 3, adding the 25% uncertainty adopted around the reported standing sock, living concentration and export concentration. We will explain this in the main text and the caption. The corrected table is added below.*

Station	Group	Living concentration C_{living} [mg m^{-3}]	Standing stock SSm2 [mg m^{-2}]	Export concentration C_{exp} [mg m^{-3}]
6	Planktonic gastropod adult	(5.7 ± 1.4) ×10^{-3}	(1.7 ± 0.4) ×10^{0}	(3.9±1.0) x10^{-5}
6	Planktonic gastropod juvenile	(1.8±0.4) x10^{-3}	(5.3±1.3) x10^{-1}	(3.2±0.8) x10^{-4}
6	Planktonic gastropod total	(7.5±1.9) x10^{-3}	(2.3±0.6) x 10^{0}	(3.6±0.9) x10^{-4}
6	Foraminifera > 200um	(2.1±0.5) x 10^{-3}	(3.2±0.8) x10^{-1}	(6.8±1.7) x10^{-5}
6	Foraminifera 125-200 um	(6.3±1.6) x10^{-7}	(9.5±2.4) x10^{-5}	(2.1±0.5) x10^{-8}
6	Foraminifera total	(2.1±0.5) x10^{-3}	(3.2±0.8) x10^{-1}	(6.8±1.7) x10^{-5}
9	Planktonic gastropod adult	(9.8±2.5) x10^{-4}	(2.9±0.7) x10^{-5}	0
9	Planktonic gastropod juvenile	(1.4±0.4) x10^{-3}	(4.3±1.1) x10^{-1}	(1.1±0.3) x10^{-4}
9	Planktonic gastropod total	(2.4±0.6) x10^{-3}	(7.2±1.8) x10^{-1}	(1.1±0.3) x 10^{-4}
9	Foraminifera > 200um	(1.2±0.3) x 10^{-3}	(1.8±0.5) x10^{-1}	(5.9±1.5) x10^{-5}
9	Foraminifera 125-200 um	(3.6±0.9) x10^{-7}	(5.5 ±1.4) x10^{-5}	(1.8±0.4) x 10^{-8}
9	Foraminifera total	(1.2±0.3) x10^{-3}	(1.8±0.5) x10-1	(5.9±1.5) x10^{-5}
3,4	Coccolith	not relevant	not relevant	(1.8 ± 0.5) x10^{-1}
3,4	Coccosphere	(4.0±1.0) x10^{-2}	(6.9±1.7) x10^{0}	(6.8±1.7) x10^{-3}

Table 3: Living concentration (C_{living}), integrated standing stock (SSm2) and export concentration (C_{exp}) of all plankton groups, separated by station, life stage or size (in case of planktonic gastropods and foraminifera) and shape (in case of coccolithophores). An error of 25% related to measurement uncertainties is assumed around each value.

• Tables (general): Check for consistency, e.g., stdev vs Stdev; check the number of digits (see comment for Table 3); apply consistently across manuscript, tables, and figures.

28) We checked all other tables in the paper for consistency and number of digits. The corrected version of table 4 and table 5 and included below:

Plankton group	Planktonic gastropod	Foraminifera	Coccolith - single	Coccolith - pellet	Coccosphere
Production (mg m^{-2} day^{-1})	0.16 ± 0.07	0.012 ± 0.004	Not relevant	Not relevant	2.0 ± 2.0
F_{exp} (mg m^{-2} day^{-1}	0.18± 0.05	0.019±0.009	0.19±0.08	24.7±11.2	0.03±0.011
production using minimum TT	0.30	0.018			12
TT calculated (small specimen)	4±2.7	67±89	Not relevant	Not relevant	Not relevant
TT calculated (large specimen)	40±33	17 ± 18	Not relevant	Not relevant	Not relevant

Table 4: Results of the Monte Carlo simulations for each plankton group, including the standard deviation. Note that especially the calculated turnover times have a very high uncertainty.

Plankton group	Planktonic gastropod	Foraminifera	Coccolith (single) + coccosphere (single)	Coccolith (pellet) + coccosphere (single)	Coccosphere
Production (%)	7 ± 32	1 ± 6	Not relevant	Not relevant	92 ± 35
Export scenario 1 (%)	44 ± 12	5 ± 3	52 ±12	Not relevant	Not relevant
Export scenario 2 (%)	0.7 ± 9	0.08 ± 1	Not relevant	99 ± 10	Not relevant

Table 5: Relative contribution of each plankton group to the production and export of PIC, based on the mean production and export values and their standard deviations calculated using the Monte Carlo simulations (Table 4). We used an additional Monte Carlo simulation to calculate the standard deviation of the percentual contribution of each group. Uncertainties around the estimated contributions are large, related to the large error associated with the measured values as well as the large uncertainties in the sinking speed and turnover time estimates.

• Table 5: Add explanation of export scenario 1 and 2 in the caption.
29) We will do this.

• Figure 7: Same comment as Figure 6. Chlorophyll-a and chlorophyll are used interchangeably; check consistency throughout manuscript.
30) We will do this.

• Fig. 8: Was, I assume, meant to have a Y-axis.
31) We will correct this.

• l. 507 / 508: m. versus m^{-}. (consistency); check throughout manuscript, tables, and figures.
32) We will do this.

• l. 507: Capitalize March.
33) Thank you for noticing.

• l. 514–516: This shows that turnover time is vastly overestimated in the case

of pteropods.

34) As indicated, we will include calculations based on multiple assumptions of turnover in the revised version.

- l. 667: What is an ashed surface water sample?

35) We will include a short section describing the plankton pump sampling and include a reference to other studies making use of this pump system to clarify what we mean by 'ashed sample'.

- Captions of tables in appendix (B2, B3): Species names need italics.

36) We will correct this.

- l. 756: pg μm^{-}. instead of /µm

37) We will correct this and check the manuscript for further inconsistencies.

Cited literature:

Alldredge, A. L., & Cohen, Y. (1987). Can Microscale Chemical Patches Persist in the Sea? Microelectrode Study of Marine Snow, Fecal Pellets. Science, 235, 689–691. https://doi.org/10.1126/science.235.4789.689

Anglada-Ortiz, G., Zamelczyk, K., Meilland, J., Ziveri, P., Chierici, M., Fransson, A., & Rasmussen, T. L. (2021). Planktic Foraminiferal and Pteropod Contributions to Carbon Dynamics in the Arctic Ocean (North Svalbard Margin). Frontiers in Marine Science, 8. https://doi.org/10.3389/fmars.2021.661158

Bednaršek, N., Mozina, J., Vogt, M., O'Brien, C., & Tarling, G. A. (2012). The global distribution of pteropods and their contribution to carbonate and carbon biomass in the modern ocean. Earth System Science Data, 4(1), 167–186. https://doi.org/10.5194/essd-4-167-2012

Dong, S., Berelson, W. M., Rollins, N. E., Subhas, A. V., Naviaux, J. D., Celestian, A. J., Liu, X., Turaga, N., Kemnitz, N. J., Byrne, R. H., & Adkins, J. F. (2019). Aragonite dissolution kinetics and calcite/aragonite ratios in sinking and suspended particles in the North Pacific. Earth and Planetary Science Letters, 515, 1–12. https://doi.org/10.1016/j.epsl.2019.03.016

Hagen, E., Feistel, R., Agenbag, J. J., & Ohde, T. (2001). Seasonal and interannual changes in Intense Benguela Upwelling (1982-1999).

Lutjeharms, J. R. E., & Meeuwis, J. M. (1987). The extent and variability of South-East Atlantic upwelling. South African Journal of Marine Science, 5(1), 51–62. https://doi.org/10.2989/025776187784522621

Manno, C., Bednaršek, N., Tarling, G. A., Peck, V. L., Comeau, S., Adhikari, D., Bakker, D. C. E., Bauerfeind, E., Bergan, A. J., Berning, M. I., Buitenhuis, E., Burridge, A. K., Chierici, M., Flöter, S., Fransson, A., Gardner, J., Howes, E. L., Keul, N., Kimoto, K., … Ziveri, P. (2017). Shelled pteropods in peril: Assessing vulnerability in a high CO2 ocean. In Earth-Science Reviews (Vol. 169, pp. 132–145). Elsevier B.V. https://doi.org/10.1016/j.earscirev.2017.04.005

Rogerson, J., Veitch, J., Siedlecki, S., & Fawcett, S. (2025). Frontal features and mixing regimes along the shelf region of the Southern Benguela upwelling system. Continental Shelf Research, 295. https://doi.org/10.1016/j.csr.2025.105560

Siddiqui, C., Rixen, T., Lahajnar, N., Van der Plas, A. K., Louw, D. C., Lamont, T., & Pillay, K. (2023). Regional and global impact of CO2 uptake in the Benguela Upwelling System through preformed nutrients. Nature Communications, 14(1). https://doi.org/10.1038/s41467-023-38208-y

Subhas, A. V., Dong, S., Naviaux, J. D., Rollins, N. E., Ziveri, P., Gray, W., Rae, J. W. B., Liu, X., Byrne, R. H., Chen, S., Moore, C., Martell-Bonet, L., Steiner, Z., Antler, G., Hu, H., Lunstrum, A., Hou, Y., Kemnitz, N., Stutsman, J., … Adkins, J. F. (2022). Shallow Calcium Carbonate Cycling in the North Pacific Ocean. Global Biogeochemical Cycles, 36(5). https://doi.org/10.1029/2022GB007388

Ziveri, P., Gray, W. R., Anglada-Ortiz, G., Manno, C., Grelaud, M., Incarbona, A., Rae, J. W. B., Subhas, A. V., Pallacks, S., White, A., Adkins, J. F., & Berelson, W. (2023). Pelagic calcium carbonate production and shallow dissolution in the North Pacific Ocean. Nature Communications, 14(1). https://doi.org/10.1038/s41467-023-36177-w