

# RC1' comments

Reviewer comments – egusphere-2025-4395 – Evaluation of the Particulate Inorganic Carbon Export Efficiency in the Global Ocean

Overview:

The research article by Jordan Toullec, entitled “Evaluation of the Particulate Inorganic Carbon Export Efficiency in the Global Ocean”, explores particulate inorganic carbon export in the global ocean and discusses the role of various planktonic groups, differences between oceanic regions, and correlation with net primary production of particulate organic carbon.

Overall, the manuscript is interesting as it combines available data collected in the field, using sediment traps, for example, and satellite imaging. The amount of work transpires from all the data compiled, which is presented in the “Results” section. The discussion also targets a variety of processes, making it relevant. The “Materials and Methods” and “Results” sections are somewhat rich in information but not overly long, which is good, and the results also report on a variety of data that are well compiled together.

However, the reviewer believes that major revisions are required on the writing itself. The manuscript would benefit significantly from a deep review of the text. In numerous instances, sentence formulations are not appropriate, and missing words or repetitions make the text unnecessarily complicated to read in some parts. Consistency and flow are lacking, especially in the introduction and discussion, where the reader quickly gets lost in the amount of information. Similarly, verbs are missing in some instances, and sentences are not properly formulated. Nevertheless, the reviewer believes that a careful re-reading and re-writing of the above-mentioned sections of the manuscript by the author would decrease these issues significantly. The reviewer will then consider assessing the second version of the manuscript once these comments have been implemented. The reviewer also acknowledges that the author may not be a native speaker, but believes that with care given to the grammar and once all point-by-point comments added below have been implemented, another round of review will lead to a quality paper suitable for publishing.

**AC:** I sincerely thank RC1 for the careful reading of our manuscript and for the constructive feedback regarding the clarity and quality of the writing (Also highlighted by RC2). I fully acknowledge the concerns raised about sentence structure, consistency, and overall flow, particularly in the Introduction and Discussion sections. In response, I have thoroughly revised the entire discussion with particular attention to clarity, coherence, and readability. I have carefully reformulated sentences where wording was inappropriate, corrected grammatical issues, removed repetitions, and ensured that all

statements are complete and syntactically correct. I believe that these revisions have significantly improved the overall readability and scientific clarity of the manuscript.

I appreciate RC1 understanding and constructive guidance, and I hope that the revised version now meets the standards required for publication in Biogeosciences. Please find below my justification and responses to comments.

Comments:

Line 8: I believe this should read “calcifying” rather than “calcified” (same throughout the text).

**AC:** The term has been modified, throughout the text

Line 9: same as above.

**AC:** The term has been modified

Line 24: instead of “due to”, I would advise using “through”.

**AC:** The sentence has been modified

Line 25: same as first comment.

**AC:** The term has been modified

Line 26: word missing, it should read “referred to as”.

**AC:** The sentence has been modified

Line 24-27: sentence is a bit overloaded, it would benefit from a rewrite, likely in 2 distinct sentences.

**AC:** The sentence has been separated into 2 distinct sentences:

*“Phytoplankton, through photosynthesis, uptake CO<sub>2</sub> and produce particulate organic carbon (POC). On the other hand, calcifying phytoplankton (such as coccolithophores), produce both POC and inorganic carbon (particulate inorganic carbon, PIC). Calcification process, often referred to as calcium carbonate (CaCO<sub>3</sub>) production, releases CO<sub>2</sub>, this is the counter pump effect.*

Line 30-31: statement of “to estimate a particle/sinking flux” made twice, consider deleting one.

**AC:** The sentence has been modified

*“To measure a particle flux, the sediment traps and Thorium-234 activity ( $^{234}\text{Th}$  activity) are the most widespread techniques, both in terms of time and geography (Savoye et al., 2006, Le Moigne et al., 2014).”*

Line 40: I would slightly edit this sentence, as technically speaking, the calcification process removes alkalinity and releases  $\text{CO}_2$ . Later, once  $\text{CaCO}_3$  has dissolved, I agree that alkalinity increases, as well as the uptake of  $\text{CO}_2$ . However, given that it is a “loop”, I think stating that it increases alkalinity and  $\text{CO}_2$  uptake may be misleading. This would be up to the author to edit, but it should be considered.

**AC:** I agree with RC1 comment; to consider a “net” uptake of  $\text{CO}_2$  from the atmosphere thanks to this process, the depth of dissolution should be implemented in the statement. I have deleted this part of the sentence.

Line 41: this should read “associated with”.

**AC:** The sentence has been modified

Lines 45-47: this sentence has no verb.

**AC:** My apologies for this absence. The sentence has been modified and separated into 2 distinct sentences:

*“The transfer efficiency ( $T_{\text{eff}}$ ) corresponds to the proportion of exported organic matter that reaches the deep ocean.  $T_{\text{eff}}$  is lower at high latitudes and higher at low latitudes (Henson et al., 2012).”*

Line 64: this should read either “with a complex food web” or “with complex food webs”.

**AC:** The sentence has been modified:

*“are associated with a complex food web”*

Line 78-79: the sentence is confusing; consider rephrasing.

**AC:** The sentence has been rephrased and separated into 2 distinct sentences:

*“Blooms of coccolithophores (e.g., *Gephyrocapsa (Emiliana) huxleyi*) can produce highly reflective patches at the ocean surface and exhibit distinctive optical properties (Balch et al., 1996, 2005; Balch and Mitchell, 2023). These optical signatures can be*

*used to estimate particulate inorganic carbon (PIC) concentrations and production rates at the global scale (Hopkins & Balch, 2018; Hopkins et al., 2019)."*

Lines 84-85: the paper from Kwon et al., 2024 states that 20% more CO<sub>2</sub> would be emitted to the atmosphere if CaCO<sub>3</sub> dissolution in the upper ocean did not occur. This does not necessarily mean that 20% more CO<sub>2</sub> is captured. The formulation used here is misleading.

**AC:** The sentence has been reformulated:

*"Kwon et al. (2024) showed that without CaCO<sub>3</sub> dissolution in the upper ocean, approximately 20 % more CO<sub>2</sub> would be released to the atmosphere."*

Line 86: while the research article from Renforth and Henderson, 2017, is an important piece of work for carbon sequestration research, the reviewer expresses some concerns as to why it is used here. Aren't there more suitable references? Please justify the use here.

**AC:** I agree with RC1's comment that the two cited articles (Renforth & Henderson, 2017; Planchat et al., 2023) are not directly related to the specific processes of calcifying plankton production and dissolution fluxes, but rather to the role of alkalinity in controlling oceanic CO<sub>2</sub> sequestration and balance. Although these references do not specifically focus on calcifying plankton, they were included to acknowledge relevant studies addressing the broader role of PIC dynamics and alkalinity balance in regulating air-sea carbon exchange.

*"In addition, processes such as PIC production, sinking flux, and dissolution are key components of the ocean alkalinity balance, which in turn regulates atmospheric carbon uptake in surface waters (Renforth and Henderson, 2017; Planchat et al., 2023)."*

Line 105: this should read "such as that PIC...".

**AC:** The sentence has been modified:

Line 114: there is one too many "to", it should read "integrated to 100 m using...".

**AC:** The sentence has been modified:

Line 122: the link provided did not work at the time of the review. Please review and make sure that the data are accessible.

**AC:** Indeed, the web site has changed and is now referred as Hermes Globcolour (<https://hermes.acri.fr/>). The link has been changed in the text.

Lines 125-128: I do not fully understand the use of semicolons here. Commas would be more appropriate, and there is no need for capitalised words after the colon and semicolons.

**AC:** Thank you for pointing out my mistake, I modified the semicolons and changed the capitalised words, after the commas.

Line 130: please review the citation. I believe Biogesociences has specific formats for referencing websites, such as the date of access and further details. Please review.

**AC:** The website referencing has been reviewed. The date of last access has been added to the referencing (... , last access: 2 February 2024)

Line 137: why consider the first 200m for foraminifers and pteropods, while only considering the first 100m for coccolithophores?

**AC:** This discrepancy primarily reflects a technical limitation in the comparison between datasets. The global distribution of calcifying zooplankton taxa (foraminifers and pteropods) reported by Knecht et al. (2023) provides PIC standing stock estimates integrated over the upper 200 m, whereas global coccolithophore PIC standing stock is typically computed over the upper 100 m (Eq. 3; Balch et al., 2018). However, this difference in integration depth is unlikely to substantially affect the interpretation of our results. Coccolithophore abundance generally decreases markedly below 100 m depth, often becoming negligible or absent; therefore, PIC standing stock integrated over 100 m versus 200 m is expected to differ only marginally. Moreover, our discussion of global PIC standing stocks across taxa focuses primarily on their monthly climatology and seasonal variability, rather than on a strict quantitative comparison.

Line 158: I do not understand where the value of 388 comes from. Please elaborate.

**AC:** The value corresponds to the sum of sediment traps used in the dataset independently of the number of flux observations (i.e. multiple flux observations with the same sediment trap), this value differs of the 262 sediment trap locations because Multiple sediment traps may have been deployed on the same mooring line.

My apologies, the sum is 391 not 388. The value has been modified; the sentence has been clarified.

Line 189: “deployment” should be plural

**AC:** The sentence has been corrected

Line 202: I believe “coverage” should be used instead of “covering”, but this might need to be double checked.

**AC:** To avoid any ambiguity, the sentence has been revised.

*“EZ PIC production values  $< 0.1 \text{ mg m}^{-2} \text{ d}^{-1}$  were removed from the dataset to exclude values close to zero or below the detection limit, which may result from a lack of satellite coverage.”*

Line 204: “fecal pellet” should be plural.

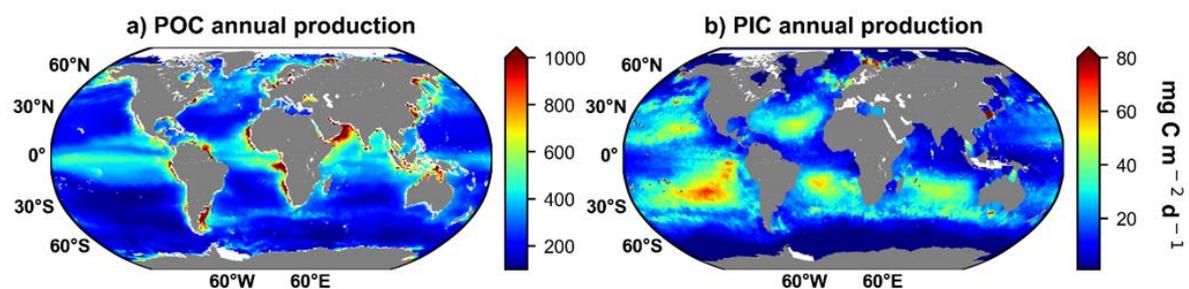
**AC:** The grammatical agreement has been corrected, and this change has been applied to all other occurrences of the term “fecal pellet”.

Line 223: “regions” is missing.

**AC:** The words has been implemented

Line 224: in figure 2, could the tiles “a” and “b” be set on the same y-axis scale? The use of a logarithmic scale in “b” makes the direct comparison trickier. Please review whether it makes sense to put it on the same scale as “a” for easier comparison. If not, please provide the comparison in the response to reviewers.

**AC:** The logarithmic scale has been removed. Given that PIC production is much lower than POC production, the colorbars require different ranges to reflect the respective magnitudes (e.g., 100–1000 for POC and 1–80 for PIC production).



Line 253: this should read “gives us” and consider a full stop after “event” to separate the two trains of thought.

**AC:** The sentence has been rephrased:

*“This study highlights the importance of rapid calcification events. Satellite observations of coccolithophore blooms, which typically last less than 30 days, suggest that PIC fluxes from sediment traps should be integrated over short deployments rather than longer periods.”*

Line 281: the sentence “NPP compared as compared to PIC” is misleading. Please edit accordingly.

**AC:** The sentence has been clarified

“The correlation between PIC flux and NPP yields higher  $R^2$  values compared to the correlation between PIC flux and PIC production (Fig. 5).”

Line 285-287: the caption would benefit from some details as to what “n.s.” means (which I believe is “no significant”) and especially what value is considered “n.s.”

**AC:** The caption has been implemented:

*“Non-significant correlations ( $p$ -value > 0.5, Pearson test) are indicated by “n.s.””*

Lines 295-296: given that the 6 depths have already been discussed and introduced before, there is no need to add them here again (same as line 300). Only saying “at all depths” for the North Atlantic and “between 500 and 4000m in the North Indian Ocean” would lighten the text from numbers, making it more reader-friendly.

**AC:** The text has been modified accordingly

*“EZ PIC production and deep PIC flux are observed in the North Atlantic (100 to >4000m) and the Southern Ocean (100-500m and 1000-2000m). North Indian Ocean regions (subtropical areas) are also characterized by PIC production positively correlated with deep PIC flux (500 to 4000m, Fig. 6).”*

Line 313-314: the start of the sentence is a bit awkward. Please revise.

**AC:** The sentence has been modified.

*“When mapped onto a  $1^\circ \times 1^\circ$  grid, the contributions of zooplankton fecal pellets and sinking phytoplankton aggregates exhibit a significant latitudinal pattern (Fig. 7 in Nowicki et al., 2022).”*

Line 333: duplicate “in”.

**AC:** The duplicate has been removed

Line 340: the formulation “and follow the pattern than zooplankton” does not make sense. Please revise.

**AC:** The sentence has been revised as:

*“and exhibit a pattern similar to that of zooplankton fecal pellet contributions to the gravitational pump (Fig. 7).”*

Line 356: “demonstrates” should not take an s here, and please review the sentence as it does not sound correct.

**AC:** The sentence has been revised

*“At the global scale, our results indicate that EZ PIC production is not correlated with PIC flux in the upper ocean.”*

Line 365: this should either read “there is a large uncertainty in the...” or “there are large uncertainties in the...”.

**AC:** The sentence has been revised:

*“Total CaCO<sub>3</sub> production in the water column remains highly uncertain, with current estimates ranging from 0.7 to 4.7 Pg C yr<sup>-1</sup> (Berelson et al., 2007; Buitenhuis et al., 2019; Lee, 2001).”*

Lines 376, 377, 380: “coccolithophore” should be plural (check throughout the text)

**AC:** The plural has been checked throughout the text, when ‘coccolithophore(s)’ where used.

Line 385: “fecal pellet” should be plural (check throughout the text)

**AC:** The plural has been checked throughout the text, when ‘fecal pellets’ where used.

Line 392: the sentence is not correct. Please review.

**AC:** The entire paragraph has been revised:

*The “packaging factor” theory proposed by François et al. (2002) suggests that subtropical and equatorial regions characterized by CaCO<sub>3</sub>-dominated ecosystems produce fast-sinking fecal pellets, leading to high PIC export flux. According to the particle-dependent export model of Nowicki et al. (2022) (Fig. 7), the relative contribution of fecal pellets to carbon export is indeed higher in these regions compared to aggregates. However, in our dataset, both PIC export flux and deeper flux are globally lower in subtropical and equatorial areas, despite higher PIC production (see Fig. 7). This contradicts the idea that CaCO<sub>3</sub> packaged into fecal pellets is protected from dissolution. Regarding aggregate contributions to carbon export (Fig. 7), opal-dominated systems (temperate and sub-polar ecosystems) are associated with high PIC flux, which also appears inconsistent with the “packaging theory,” as these aggregates are considered highly labile and susceptible to disaggregation and remineralization. Such aggregates may have higher PIC turnover rates, enhancing PIC export efficiency ( $E_{eff}$ ). Overall, PIC production in the euphotic layer is decoupled from both PIC export efficiency ( $E_{eff}$ ) and the effective transit through the mesopelagic layer ( $T_{eff}$ ). Upper-ocean*

*PIC loss is generally attributed to biologically mediated dissolution (Morse et al., 2006; Friis et al., 2006; Buitenhuis et al., 2019; Sulpis et al., 2021; Dean et al., 2024). Zooplankton and bacterial activity decrease with depth (Hernández-León et al., 2020), so intense grazing and potential biologically mediated PIC dissolution are expected in the epipelagic and mesopelagic layers. Once CaCO<sub>3</sub> is packaged into aggregates or fecal pellets, it is expected to be protected from surrounding seawater and associated dissolution processes. Consequently, CaCO<sub>3</sub> may avoid dissolution controlled by the saturation depths of calcite and aragonite. In principle, packaged CaCO<sub>3</sub> settling below the saturation depth should remain protected. However, zooplankton grazing can fragment aggregates in the epipelagic and mesopelagic layers, potentially explaining PIC loss in shallow waters (Toullec et al., 2019 and references in there).*

Line 396: “layer” should be plural.

**AC:** Layers is plural now

Line 397: “regardless of the respective depths of calcite and aragonite saturation” does not make sense. While I understand the idea, the sentence is not correct. Please edit.

**AC:** The entire paragraph has been revised (see my answer above):

*“Once CaCO<sub>3</sub> is packaged into aggregates or fecal pellets, it is expected to be protected from surrounding seawater and associated dissolution processes. Consequently, CaCO<sub>3</sub> may avoid dissolution controlled by the saturation depths of calcite and aragonite.”*

Line 400: change “in there” to “therein”.

**AC:** The entire paragraph has been revised (see my answer above):

line 420: here “suggest” should take an s.

**AC:** An s has been added to “suggest’

line 424: here it should read either “microzooplankton vacuoles induce PIC dissolution” or “microzooplankton vacuole induces PIC dissolution”.

**AC:** The sentence has been revised (‘microzooplankton vacuole induces PIC dissolution’)

Lines 429-431: the sentence is misleading, consider separating into 2 distinct sentences.

**AC:** The sentence has been split into 2 sentences:

*“However, ecosystem differences in microzooplankton grazing, particle export flux, and trophic structure have been largely underestimated. This limitation affects biogeochemical models that aim to predict the role of microbial communities in oceanic carbon flux.”*

Line 443-445: I am not fully sure I agree that blooming is an avoidance mechanism. Please argue your thoughts, but consider editing the sentence.

**AC:** I edited the sentence to precise my thoughts

*“Irigoien et al. (2005) suggested that blooming species (e.g., *Phaeocystis*, *G. huxleyi*) might partially escape microzooplankton grazing at the onset of the bloom, potentially due to predation-avoidance traits such as forming colonies, larger cell size, spines, or the production of toxic compounds. Blooming may temporarily exceed grazing capacity, leading to apparent escape from predation, but this is a population-level outcome rather than an evolved avoidance “strategy.”*

Line 445-447: this sentence is not correct. It should read “could produce so much biomass that...”, “won’t” should be edited to “will not” ... Please review.

**AC:** The sentence has been corrected:

*” By this way, blooming coccolithophores such as *G. huxleyi* could produce so much biomass that microzooplankton grazing pressure will not be significantly sufficient to dissolve the  $\text{CaCO}_3$  coccoliths in their acid vacuole.”*

Line 448: the use of “regarding” does not make much sense here. Similarly, the sentence is confusing. Please edit.

**AC:** The sentence has been edited:

*“In contrast, in subtropical and equatorial ecosystems, where coccolithophore biomass remains relatively constant throughout the year (low seasonal variability, see Fig. 7) and microzooplankton grazing pressure is also consistently high, coccoliths may not provide sufficient protection from predation, and can therefore be continuously dissolved within microzooplankton acidic vacuoles (Antia et al., 2008; Dean et al., 2024). »*

Line 453: this should read “a mesocosm” study. Otherwise, “the mesocosm study from XXX”.

**AC:** The sentence has been modified

*“a mesocosm study demonstrated...”*

Line 455-456: why is “E. huxleyi” used here, while throughout the author used G. huxleyi? Please edit for consistency.

**AC:** My apologies for this confusion. The genus has been modified (*G. huxleyi*)

Line 461: the end of the sentence does not make sense. Consider changing “more” to “higher” or equivalent. Please edit.

**AC:** Higher has been implemented (instead of ‘more’)

Line 462: I am not sure how phytoplankton phenology is a time-dependent concept, why saying “During [...] phytoplankton bloom phenology”? Please edit.

**AC:** I agree with RC1, ‘phenology’ should not be included here. The sentence has been revised

*“During North Atlantic phytoplankton bloom, grazing by microzooplankton increased”*

Line 477: here, “that” should be added after “showed”. Please edit.

**AC:** The term has been added after ‘showed’

Line 489: duplicate of “In subtropical areas” from the previous sentence. Consider deleting.

The duplicate has been deleted

Line 507: please edit to maintain consistency in abbreviation, especially regarding PIC E<sub>eff</sub> and PIC T<sub>eff</sub>.

**AC:** Abbreviations (PIC E<sub>eff</sub> et PIC T<sub>eff</sub>) have been standardized

Line 512: duplicate of “effect”. Please edit.

**AC:** The sentence has been rephrased:

*“However, only a few experimental studies have directly demonstrated the effect of zooplankton functional diversity on CaCO<sub>3</sub> dissolution.”*

Line 520: this should read “result in”. Please review.

**AC:** “Result in” have been implemented

**AC:** The discussion structure has been entirely revised, also considering RC2 comments/suggestions. The new version of the discussion is more concise; subsection

has been merged to reduce redundancies as much as possible. The ideas follow a logical order, until the conclusion. The highlights of this study raised by the results are summarized in Fig. 8, which highlights the novelty of this study (the figure also has been simplified).

The discussion is now shorter, and the highlight of this study is now a significant part of the discussion. I must mention that I use specific concepts known so far in the field to explain my results and build this story. Variability of PIC flux efficiency and biological mediated  $\text{CaCO}_3$  dissolution is still underestimated at present and is in desperate need of new proof-of-concept studies. This is why my study matters, given that our understanding of the subject is still incomplete.

## 4. Revised discussion

### 4.1. Mesopelagic PIC Flux and Ballast Effect Hypothesis

The ballast hypothesis originates from correlations between POC flux and mineral fluxes (opal and  $\text{CaCO}_3$ ) in deep sediment traps (Klaas and Archer, 2002). However,  $\text{CaCO}_3$  export flux in the upper ocean does not correlate with transfer efficiency (Henson et al., 2012), suggesting that  $\text{CaCO}_3$  does not significantly protect POC from degradation at mesopelagic depths. Ecosystem structure, rather than mineral ballast, might be the primary controls the biological carbon pump. François et al. (2002) proposed the “packaging factor” theory, suggesting that high  $\text{CaCO}_3$  productive systems also contain organisms producing sinking fecal pellets that efficiently deliver organic carbon to deep waters (e.g., Nowicki et al., 2022). In subtropical and equatorial upwelling regions, export flux is not always associated with mineral ballast (Le Moigne et al., 2014), highlighting spatial variability in biomineral inclusion and supporting the role of ecosystem structure and phytoplankton phenology. On a global scale, our results demonstrate that EZ PIC production is not correlated with PIC flux in the upper ocean. However, in specific bioregions (RECCAP2), significant correlations exist between EZ PIC production and deep PIC flux (North Atlantic, Southern Ocean, and North Indian Ocean, Fig. 6, Table S4). These observations suggest that ecosystem structure and phenology are more important than the ballast effect in controlling PIC  $E_{\text{eff}}$  and  $T_{\text{eff}}$ .

### 4.2. Taxa Contribution to Global PIC Stock and Production

Global  $\text{CaCO}_3$  production estimates remain uncertain, ranging from 0.7 to 4.7  $\text{Pg C yr}^{-1}$  (Berelson et al., 2007; Buitenhuis et al., 2019; Lee, 2001). Contributions from coccolithophores, foraminifers, and pteropods vary widely. Pteropods: 0.87–4.2  $\text{Pg C yr}^{-1}$ , 20–89% of global  $\text{CaCO}_3$  (Gangstø et al., 2008; Lebrato et al., 2010; Buitenhuis et al., 2019). Foraminifers: 0.036–0.14  $\text{Pg C yr}^{-1}$ , 2–4% of global  $\text{CaCO}_3$  (Schiebel, 2002; Lebrato et al., 2010; Buitenhuis et al., 2019). Coccolithophores: ~90% of  $\text{CaCO}_3$  production in North Pacific (Ziveri et al., 2023). Deep sediment traps recover significant amounts of

foraminifers and pteropods (Table 1, Fig. 3 in Neukermans et al., 2023), whereas coccolithophores dominate surface stocks and production. These observations remain poorly understood regarding taxon-specific contribution and require more proof-of-concept and process-based studies to better quantify ecosystem-specific controls on PIC production and export.

### **4.3. Influence of Ecosystem Structure on PIC Export**

The fraction of phytoplankton exported production that is remineralized is mainly influenced by ecosystem structure, which is linked to the seasonal amplitude of NPP (Fig. 7a). Blooms of diatoms and coccolithophores (e.g., *G. huxleyi*), which are expected to cause intense particle sedimentation, occur mostly in areas with high annual mean and amplitude of NPP (Fig. 7a). In contrast, nanoplankton/picoplankton dominate global production in oligotrophic areas (low latitudes) with low annual NPP amplitude (Lima et al., 2014). The ballast effect hypothesis, induced by biomineral inclusion (calcite and biogenic silica), has long been considered a mechanism to enhance particle export efficiency ( $PE_{\text{eff}}$ ). In this study, the PIC  $E_{\text{eff}}$  (proportion of PIC production exported from the surface) is generally higher above 40°N and below 40°S (temperate and subpolar regions). The PIC  $T_{\text{eff}}$  (proportion of exported PIC reaching the deep ocean) is higher between 40°N and 40°S (subtropics) and exhibits a pattern like zooplankton fecal pellet contributions to the gravitational pump (Fig. 7b). Considering particle types in the gravitational pump (Nowicki et al., 2022), phytoplankton aggregates could enhance PIC  $E_{\text{eff}}$ , while zooplankton fecal pellets could enhance PIC  $T_{\text{eff}}$ . The following sections explore the mechanisms behind these patterns.

### **4.4. “Biological Gatekeeper” of the mesopelagic PIC Flux**

#### **4.4.1. Packaging Factor and Aggregate Contribution**

The packaging factor theory (François et al., 2002) suggests subtropical and equatorial  $\text{CaCO}_3$ -rich ecosystems produce fast-sinking fecal pellets, enhancing PIC export. In this study, the particle-dependent export model (Nowicki et al., 2022, Fig. 7b) demonstrated that fecal pellet contributions are higher in these  $\text{CaCO}_3$ -rich ecosystems (subtropics and equatorial). However, observed PIC fluxes are lower in subtropical and equatorial areas despite higher production, challenging the idea that  $\text{CaCO}_3$  packaged in fecal pellets is protected from dissolution. Opal-dominated systems (temperate/subpolar) exhibit high PIC flux, suggesting that labile aggregates can still enhance PIC turnover and PIC export  $E_{\text{eff}}$ . Overall, PIC production in the euphotic layer is decoupled from PIC  $E_{\text{eff}}$  and  $T_{\text{eff}}$ . Upper-ocean PIC loss is primarily attributed to biologically mediated dissolution (Morse et al., 2006; Friis et al., 2006; Buitenhuis et al., 2019; Sulpis et al., 2021; Dean et al., 2024). Zooplankton and bacterial activity decrease with depth (Hernández-León et al., 2020); however, epipelagic and mesopelagic grazing still appears to affect PIC loss.

#### 4.4.2. Hypothetical Processes of Biological-Mediated PIC Dissolution

Heterotrophic bacteria colonizing  $\text{CaCO}_3$  particles appear to induce minimal dissolution, suggesting a limited role in PIC loss during sinking (Bissett et al., 2011). Similarly, the increase in hydrostatic pressure experienced by *G. huxleyi* aggregates during sedimentation does not significantly enhance calcite dissolution (Tamburini et al., 2021). Experimental and modeling studies also show that calcite is largely preserved during zooplankton gut passage, with dissolution generally low or negligible across various species and conditions (Harris, 1994; Honjo, 1976; Roth et al., 1975; Langer et al., 2007; Jansen and Wolf-Gladrow, 2001; Antia et al., 2008; Toullec et al., 2022; Dean et al., 2024). Despite lower contributions of fecal pellets to the gravitational pump at high latitudes (Fig. 7b), PIC  $E_{\text{eff}}$  remains elevated in these areas (temperate and subpolar regions), suggesting that additional factors likely related to plankton community composition and phenology play an important role in controlling PIC preservation and export.

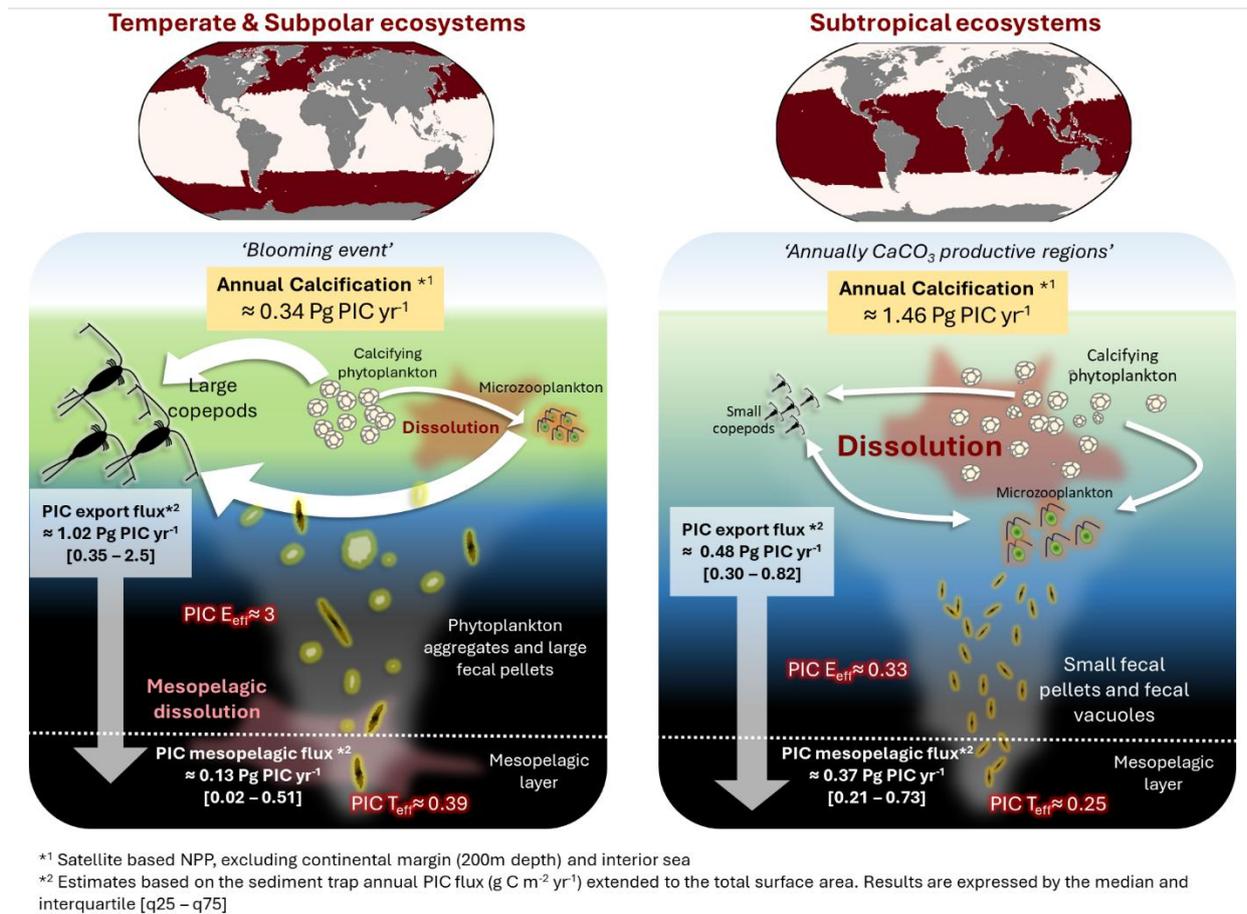
#### 4.5. Ecosystem control on PIC flux

Microzooplankton (<200  $\mu\text{m}$ ) play a central role in regulating primary producer biomass and facilitating carbon export via fecal vacuoles or aggregates (McNair et al., 2021; Calbet and Landry, 2004). Their grazing intensity exhibits strong latitudinal variation, from 59% of annual primary production in temperate–polar regions to 75% in tropical–subtropical regions (Calbet and Landry, 2004), patterns that align with the observed PIC  $E_{\text{eff}}$  and PIC  $T_{\text{eff}}$  across latitudes (Fig. 7). In the North Atlantic, microzooplankton consume 288–589  $\text{mg C m}^{-2} \text{ day}^{-1}$  in the mixed layer during mid-summer, representing 39–115% of local phytoplankton production (Burkill et al., 1993), highlighting their substantial contribution to particle processing and carbon flux. Blooming coccolithophores, such as *G. huxleyi*, can temporarily escape microzooplankton grazing during bloom onset through predation-avoidance traits like colony formation, larger cell size, spines, or toxin production (Irigoien et al., 2005; Monteiro et al., 2016). Conversely, subtropical and equatorial regions, characterized by low seasonal variability in coccolithophore biomass and continuous grazing pressure, experience ongoing PIC loss, possibly due to dissolution within microzooplankton vacuoles (Antia et al., 2008; Dean et al., 2024). Large zooplankton can indirectly preserve PIC by suppressing microzooplankton biomass and repackaging coccoliths into fast-sinking fecal pellets (Nejstgaard et al., 1994). Indeed, a mesocosm study demonstrated that large copepod (*Calanus finmarchicus*) ingestion rates were similar during blooms of diatoms and *G. huxleyi* (Nejstgaard et al., 1994). However, *C. finmarchicus* biomass increased 3 times more in mesocosms dominated by *G. huxleyi* compared to mesocosms with diatom blooms at similar algal biomass (Nejstgaard et al., 1994). The authors suggested that during bloom conditions, copepods “preferentially” graze on the microzooplankton. The incorporation of coccoliths inside large fecal pellets (from mesozooplankton) is the result of passive non-selective feeding behavior (e.g. current feeding, see detail below), and not necessarily selective grazing on coccolithophores.

Our dataset reveals a positive correlation between PIC production and PIC flux in the North Atlantic across all depth layers (Fig. 6), emphasizing the role of zooplankton-mediated carbon transfer (Hernández-León et al., 2020). Zooplankton functional traits vary by bioregion (Benedetti et al., 2023): temperate and subpolar regions are dominated by large, detritivorous or omnivorous copepods that feed passively (current- or cruise-feeders; Fig. 5 in Benedetti et al., 2023), whereas subtropical and equatorial regions are dominated by smaller, carnivorous copepods that feed actively (ambush- or current-ambush-feeders). Grazing by these distinct functional groups' shapes phytoplankton biomass and community structure, ultimately influencing the efficiency and depth of PIC export (Le Quéré et al., 2016; Vallina et al., 2014; Fig. 8).

The present study suggests that in temperate and subpolar ecosystems, large copepods could increase the PIC export flux efficiency in 2 different ways: 1) Repackage coccoliths into fecal pellet (passive current feeding). 2) Apply a strong enough grazing pressure on microzooplankton, which could indirectly reduce  $\text{CaCO}_3$ -mediated dissolution by microzooplankton (Dean et al., 2024, Fig. 8). In contrast, marine snow aggregates may create microenvironments that promote PIC dissolution in the mesopelagic layer, potentially explaining the observed decrease from  $\text{PIC } E_{\text{eff}}$  to  $\text{PIC } T_{\text{eff}}$  in temperate ecosystems (Fig. 8).

On the other hand, subtropical regions exhibit continuous grazing and efficient nutrient recycling, but more complex food webs. Microzooplankton strongly regulate primary producer biomass and particulate organic carbon transfer, a fraction of which can then be exported as fecal pellets or aggregates (McNair et al., 2021). This ecological context can be favorable to  $\text{CaCO}_3$ -mediated dissolution by microzooplankton (Fig. 8) that may affect  $\text{PIC } E_{\text{eff}}$ .



**Figure 8:** Synthesis of the potential PIC pathway through the water column, in two distinct ecosystems: a) Subtropical ecosystems (subtropical gyres and equatorial upwellings). b) Temperate zone (North Atlantic, North Pacific and subpolar regions). The white arrows represent the trophic transfer between the different planktonic compartments (Predator prey), and double arrow means that both compartments could be both prey and predator each other. Small copepods correspond to individual body sizes ranging from 200  $\mu\text{m}$  to 2 mm; Microzooplankton (mostly protists, < 200  $\mu\text{m}$ ) represent the flagellates and ciliates community; Large copepods correspond to individual body sizes larger than 2 mm (mostly large calanoid). Note that microzooplankton could be heterotrophic, autotrophic or mixotrophic.

This study integrates the main conceptual frameworks currently proposed in the field to interpret the observed patterns in PIC  $E_{\text{eff}}$  and biologically mediated  $\text{CaCO}_3$  dissolution. Our results highlight that the variability of PIC  $E_{\text{eff}}$  and the mechanisms regulating  $\text{CaCO}_3$  dissolution remain insufficiently constrained, particularly across contrasting biogeographical regimes. These findings underscore the need for targeted proof-of-concept and process-based studies to better quantify ecosystem-specific controls on PIC export. Improving this mechanistic understanding is essential for refining predictions of the oceanic carbon cycle under ongoing environmental changes.