RC2' comments

The manuscript by Toullec provides a comprehensive analysis supported by global ocean sediment traps data, ocean color satellite measurements and models to understand PIC fluxes, its export and transfer efficiency in the global ocean, and the role of plankton phenology in determining the PIC fluxes and standing stock. The analysis is strong and well structured and demonstrates a high level of knowledge also supported by relevant literature in the field.

I found the study an important and timely contribution in the understanding of global ocean carbon fluxes, the biological carbon pump and the carbonate pump, under fast-changing global ocean scenarios due to anthropogenic CO2 rise. The study is also very relevant in ocean-atmosphere interactions processes and CO2 balance.

While highlighting important processes in a very complete and comprehensive way, with appropriate methodology and statistical tools, I found the overall manuscript hard to read , encountering difficulties in following the argumentations for the way the manuscript is structured, for the long sentences, at times truncated (verbs missing), and for the variety of concepts and arguments introduced several times at different points. Therefore I suggest a thorough revision of the language and of the sections for clarity and smoothness of the text and a re-organization of the discussion sections with less sub-headings and with more highlights on novel concepts and differences to what has been known so far in the field (that I found hard to identify in the overall text). In particular, I suggest organizing the introduction and discussion section with clear parts on how the present study addresses the discrepancies in the field and how it advances the knowledge or proposes new pathways and hypotheses. I honestly find it difficult to follow PIC/POC standing stock, Teff, PEeff argumentations and the taxa or processes responsible behind these estimates as these concepts are introduced several times but rather in an unstructured way. I suggest major revisions for this reason, but the underlying concepts in my opinion are there.

AC: I thank RC2 for the constructive feedback. I have thoroughly revised the manuscript to improve readability and clarity. Long sentences were simplified, missing verbs corrected, and the overall flow enhanced. The Introduction and Discussion have been reorganized to clearly highlight how the study addresses knowledge gaps and to emphasize novel findings. Key concepts are now presented in a coherent and structured manner, reducing repetition and improving the logical progression of the argument. I believe these changes significantly improve clarity while preserving the scientific rigor of the work. These aspects are also highlighted by RC1.

I appreciate RC2 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.

Specific comments (with line numbers):

45-48: incomplete sentence

AC: The sentence has been clarified separated into 2 sentences

"The transfer efficiency (Teff,) corresponds to the proportion of exported organic matter that reaches the deep ocean. Teff, is lower at high latitudes and higher at low latitudes (Henson et al., 2012)."

48-57: unclear text. I suggest revisiting. Why the BCP is boosted?

AC: Ballast hypothesis postulates that biominerals (e.g. calcite, biogenic silica) may increase aggregates sinking velocity (excess of density) thus increasing the BCP.

This paragraph has been revised (implemented and nuanced), with clearer structure:

"Satellite-based estimates of net primary production (NPP) at low latitudes carry substantial uncertainties, potentially biasing PE_{eff} calculations (Henson et al., 2019; Ryan-Keogh et al., 2023; Weber et al., 2016). Recent AI-based models improve the link between deep-ocean particle flux measurements and satellite observations (Picard et al., 2024, 2025). While T_{eff} is not consistently correlated with $CaCO_3$ export flux (Henson et al., 2012), sediment trap data show that coccoliths and coccospheres are more efficiently transported when incorporated into fecal pellets or marine snow (Honjo, 1976; Pilskaln and Honjo, 1987; Guerreiro et al., 2021; Liu et al., 2022; Toullec et al., 2022). The "ballast effect," postulates that biominerals like $CaCO_3$ and biogenic silica are expected to increase particle density and sinking velocity (Iversen and Ploug, 2010; Laurenceau-Cornec et al., 2020). Hence, BCP is expected to be enhanced by biomineralizing plankton (coccolithophores, diatoms). Nonetheless, the ballast effect remains debated because upper-ocean $CaCO_3$ export flux is not always linked to particle transfer efficiency, leaving the ballast hypothesis controversial (Henson et al., 2012)."

58-60: greater lability of organic matter is associated with higher degradation rates, therefore I expect that this labile fraction is not exported to the deep ocean.

AC: I agree with RC2, greater lability and greater degradation rates should be associated with smaller export efficiency. To remove any confusion, the text has been modified accordingly:

"Seasonal influence is an important factor affecting Teff of carbon to the deep sea. During phytoplankton blooms, the exported organic matter is more labile, which likely expect to reduce its transfer efficiency."

62: Are there more recent studies with respect to Lima et al 2014? I would expect a lower Teff for higher turnover at low latitudes for a variety of other biological processes also temperature mediated. Are there more in-situ observations? Or do you imply that in CaCO3 productive regions despite a fast turnover and high lability or organic matter, this organic matter is fast removed by the ballast effect?

AC: I suggested that in annually $CaCO_3$-productive regions (low latitudes), despite the rapid turnover and high lability of organic matter (associated with higher temperatures and an active microbial loop), organic matter may be transported thanks to the ballast effect.

"In low latitudes, which are annually $CaCO_3$ -productive regions, some modelling and observational syntheses have demonstrated that PE_{eff} tends to be lower while T_{eff} is relatively higher (Henson et al., 2012; Lima et al., 2014)."

AC: In the next paragraph, I suggested that in annually $CaCO_3$ productive regions (lower latitude), the ballast effect could attenuate the apparent high turnover rate and high particles lability due to faster sinking rate (as a result, the particles would settle more quickly and have less time to be dissolved and remineralized) and so increase T_{eff}.

"The 'packaging factor' theory suggests that CaCO3-dominated ecosystems (subtropics and equatorial area) are associated with a complex food web, and CaCO3 would be more tightly packaged in fast-sinking fecal pellets, associated with potential ballast effect on the POC (Laurenceau-Cornec et al., 2020)"

AC: Hence, the associated organic matter should be more rapidly removed by the ballast effect.

AC: A more recent study (Henson et al., 2019), suggests that the whole ecosystem structure, rather than just the latitude, is important in setting export efficiency. Huang & Fassbender (2024) observed latitudinal variation in PE_{eff} based on BGC-Argo float observations in the Southern Ocean, supporting the concept of latitudinal influence.

Henson, S., Le Moigne, F., & Giering, S. (2019). Drivers of carbon export efficiency in the global ocean. Global biogeochemical cycles, 33(7), 891-903.

Huang, Y., & Fassbender, A. J. (2024). Biological production of distinct carbon pools drives particle export efficiency in the Southern Ocean. *Geophysical Research Letters*, *51*(12), e2023GL107511.

AC: These more recent studies can be implemented in the revised manuscript:

"In low latitudes, which are annually $CaCO_3$ -productive regions, some modelling and observational syntheses have demonstrated that PE_{eff} tends to be lower while T_{eff} is relatively higher (Henson et al., 2012; Lima et al., 2014, Huang & Fassbender, 2024). However, the most recent studies agree that the structure of the ecosystem is a major driver of PE_{eff} and T_{eff}, even more so than latitude (Henson et al., 2019)."

72: PCB = BCP?

AC: My apologies, the acronym has been changed

90: the depth of reference? I think 100-200 m (as in the methods section?) but I would clarify it here too.

AC: I indicated the depth (Euphotic zone, which depends of PAR & Kd_{490nm}).

"This study examines the variability of euphotic zone PIC production and deep PIC flux"

95: how deep do ocean color sensors go?

AC: In general, most of the satellite ocean color signal (Modis, SeaWifs…) comes from the upper surface to 20–40 m of the ocean (Up to ~80–100 m in extremely clear oligotrophic waters). Not even 10m for very turbid waters. I added text about it:

"Satellite ocean color observations are representative the near-surface optical properties (upper 20–40 m in open ocean conditions)."

Eq. 1: can acidification and rising temperature effects be included in the growth rate calculation for coccolitophores?

AC: The effect of temperature is already incorporated into the model formulation. Specifically, growth rates of *Gephyrocapsa huxleyi* increase with temperature up to an optimal maximum, as described in A New Approach to Estimating Coccolithophore Calcification Rates From Space (Hopkins and Balch, 2018). https://onlinelibrary.wiley.com/doi/abs/10.1002/2017JG004235

Regarding ocean acidification (OA), I agree that this is an important consideration. However, OA is not explicitly included in the model used in the present study, as this was beyond its intended scope. However, several modeling studies have incorporated OA effects explicitly. For example, Carbonate Chemistry and Coccolithophore Calcification in CMIP5 Models (Krumhardt et al., 2020, https://onlinelibrary.wiley.com/doi/abs/10.1029/2020GB006727) examined the response of coccolithophore calcification to increasing CO_2 concentrations. Their results indicate that most ocean regions exhibit reduced calcification as CO_2 increases and acidification intensifies. They project an approximately 11% decline in global oceanic calcification by the end of the century relative to preindustrial CO_2 levels. Notably, while coccolithophore abundance may increase in certain regions, cells tend to become more lightly calcified under elevated CO_2 conditions.

If the RC2's question is whether temperature and OA can, in principle, be used to model $CaCO_3$ production, then the answer is yes. Both factors are mechanistically linked to coccolithophore growth and calcification and have been incorporated into other modeling frameworks.

210: Can you specify the difference in estimation? How many months were used in the model?

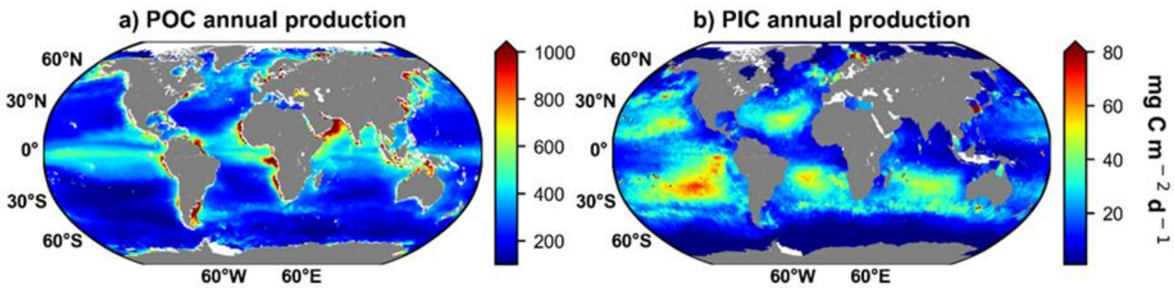
AC: I used 302 months into the model (sept 1997 to oct 2023), while Hopkins & Balch, 2018 integrated 144 months. Moreover, I used satellite merged products (AV-SWF, AVW-MERSWF, AVW-MERMODSWF, MODVIR, MODIS, see Table S1). Using the merged product, I expected broader ocean coverage: I implemented the sentence:

"At the global scale, annual EZ PIC production of 1.65 ± 0.36 Pg C y-1 was estimated (monthly mean ± σ, 1997-2023 annual mean, 302 months of observation)"

"The difference between the global estimates reported by Hopkins & Balch (2018) and those obtained in this study may be explained by the use of a merged satellite product (see table S1), which provides broader ocean coverage"

210-215: Can you add why NPP and PIC production are not concentrated in the same regions? Is it entirely due to plankton phenology?

AC: The discrepancy is mostly due to the favorable calcification conditions induced by the model (Temperature and EZ depth), there are characteristics of annually $CaCO_3$ productive regions.



NPP (POC production) is driven by nutrient availability (nitrate, phosphate, iron). Regions like upwelling zones or high-latitude oceans have high nutrient supply, so phytoplankton biomass and NPP are high (as you can see on the left Map). Whereases PIC production, especially by coccolithophores, is favored in nutrient-poor, stable waters (oligotrophic subtropical gyres), where coccolithophores can thrive and calcify efficiently.

The phenology also explains such patterns. In nutrient-rich regions, fast-growing diatoms dominate phytoplankton biomass and drive NPP, outcompeting coccolithophores (that can bloom later).

AC: I implemented the text:

"NPP (POC production, Fig 2) is driven by nutrient availability (nitrate, phosphate, iron). Upwelling zones or high-latitude oceans have high nutrient supply, so phytoplankton production is high. Whereases PIC production, especially by G. huxleyi, is favored in nutrient-poor, stable waters (oligotrophic subtropical gyres), where coccolithophores can thrive and calcify efficiently"

220: Can you add why the difference in residence time between POC and PIC?

AC: Both PIC and POC residence time can result in a balance between dissolution/remineralization and sinking. To sink, both PIC and POC need to be aggregated (marine snow or fecal pellet). PIC can be attributed to abundance of free-floating coccoliths, that can be more accumulated at the surface than POC.

AC: POC can be readily consumed by bacteria, zooplankton, leading to rapid remineralization. PIC ($CaCO_3$) is chemically more resistant to biological degradation in the surface waters. It dissolves only under specific conditions (undersaturated carbonate waters, deep ocean or by biology).

AC: The text has been implemented:

"Both PIC and POC residence times reflect a balance between sinking and removal processes such as dissolution or remineralization. For either to sink efficiently, aggregation into marine snow or incorporation into fecal pellets is generally required. PIC observation (ocean colors based) results mainly from free-floating coccoliths, which can accumulate at the surface to a greater extent than POC. In contrast, POC is readily consumed by bacteria and zooplankton, leading to rapid remineralization in the upper ocean. PIC ($CaCO_3$), however, is chemically more resistant to biological degradation in surface waters and typically dissolves only under specific conditions, such as in undersaturated carbonate waters, in the deep ocean."

250-255: unclear sentence/statement, suggest to revise.

AC: This paragraph has been reformulated:

"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"

265-270: calcified taxa PIC stock does not correlate with PIC export flux on a global scale. This concept is repeated twice. However, here it is stated that coccolitophores dominate at high latitudes, previously it is stated that coccolitophores dominate the PIC standing stock, but it is also stated that PIC standing stock or production is higher at lower latitudes. So if not coccolitophores, who is dominating PIC standing stock at low latitudes?

AC: Coccolithophores always dominate the PIC standing stock (Fig. 3b). Coccolithophore can be co-dominant with pteropods at low latitude close to the equator (Fig. 4). In Fig. 4, any calcifying taxa standing stock demonstrates correlations with PIC export flux.

AC: The paragraph has been reformulated (the repetition has been deleted):

The estimate of calcified taxa PIC stock, including coccolithophores, pteropods, and foraminifera, is not correlated with annual PIC export flux on a global scale (Fig. 4a). These estimates show that coccolithophores dominate the PIC standing stock, followed by pteropods and then foraminifera (Fig. 4). The latitudinal variation in PIC standing stock indicates an overlap between coccolithophore and pteropod PIC standing stock at the equator (Fig. 3b, 3e & Fig. 4b). *Coccolithophores and pteropods can contribute roughly equally to the PIC standing stock, but coccolithophores dominate at latitudes above 40°.*

279-283: unclear statement with some repetitions, can you rephrase?

AC: The paragraph has been reformulated:

"No significant correlation is observed between log-transformed PIC flux and log-transformed NPP in the upper 100 m (Fig. 5). On average, although Pearson's correlation coefficients are low ($R^2 < 0.25$), the correlation between PIC flux and NPP is generally higher than that between PIC flux and PIC production (Fig. 5). At the deepest layer (>4000 m), however, the correlation between PIC flux and PIC production ($R^2 = 0.104$) exceeds that between PIC flux and NPP ($R^2 = 0.089$)."

Discussion Section: as already indicated, I strongly suggest to revise the structure of the whole section.

AC: The discussion structure has been entirely revised, also considering RC1 comments/suggestions. Please consider the new version of the discussion at the end of my responses to RC2 (below)

409-410: I find this sentence contrasting, to me very slight losses would agree with well-preserved coccoliths in fecal pellets.

AC: I agree with RC2 comment, this phrasing is confusing, I reformulated the sentence:

"Several studies indicate that calcite is largely preserved during zooplankton gut passage, as evidenced by well-preserved coccoliths in fecal pellets (Harris, 1994; Honjo, 1976; Honjo and Roman, 1978; Roth et al., 1975; Samtleben and Bickert, 1990)."

Figure 8: what are the highlights and major findings of the present study, and its novelty? I think the results are not clearly evidenced as they are kind of hidden between different argumentations and references to previous works. I think it would be important to clearly describe Figure 8 that resumes the present study results and advancements in a sub-paragraph per-se.

AC: I agree with RC2. To highlight the novelty of this study, I have simplified Figure 8 and dedicated a specific paragraph to its discussion (4.4. Ecosystem control on PIC flux, see the updated text below).

The discussion structure has been entirely revised, also considering RC1 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 every concept known so far in the field to explain my results and build this story. Variability of PIC flux efficiency and biological mediated $CaCO_3$ 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 $CaCO_3$) in deep sediment traps (Klaas and Archer, 2002). However, $CaCO_3$ export flux in the upper ocean does not correlate with transfer efficiency (Henson et al., 2012), suggesting that $CaCO_3$ does not significantly protect POC from degradation at mesopelagic depths. Ecosystem structure, rather than mineral ballast, might be the primarily controls the biological carbon pump. François et al. (2002) proposed the "packaging factor" theory, suggesting that high $CaCO_3$ 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 suggests that ecosystem structure and phenology are more important than the ballast effect in controlling PIC E_{eff} and T_{eff}.

4.2. Taxa Contribution to Global PIC Stock and Production

Global $CaCO_3$ production estimates remain uncertain, ranging from 0.7 to 4.7 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 Pg C yr^{-1}, 20–89% of global CaCO3 (Gangstø et al., 2008; Lebrato et al., 2010; Buitenhuis et al., 2019). Foraminifers: 0.036–0.14 Pg C yr^{-1}, 2–4% of global CaCO3 (Schiebel, 2002; Lebrato et al., 2010; Buitenhuis et al., 2019). Coccolithophores: ~90% of $CaCO_3$ 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_{eff}). In this study, the PIC E_{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_{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_{eff}, while zooplankton fecal pellets could enhance PIC T_{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 $CaCO_3$-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 $CaCO_3$-rich ecosystems (subtropics and equatorial). However, observed PIC fluxes are lower in subtropical and equatorial areas despite higher production, challenging the idea that $CaCO_3$ 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_{eff}. Overall, PIC production in the euphotic layer is decoupled from PIC E_{eff} and T_{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 $CaCO_3$ 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_{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.

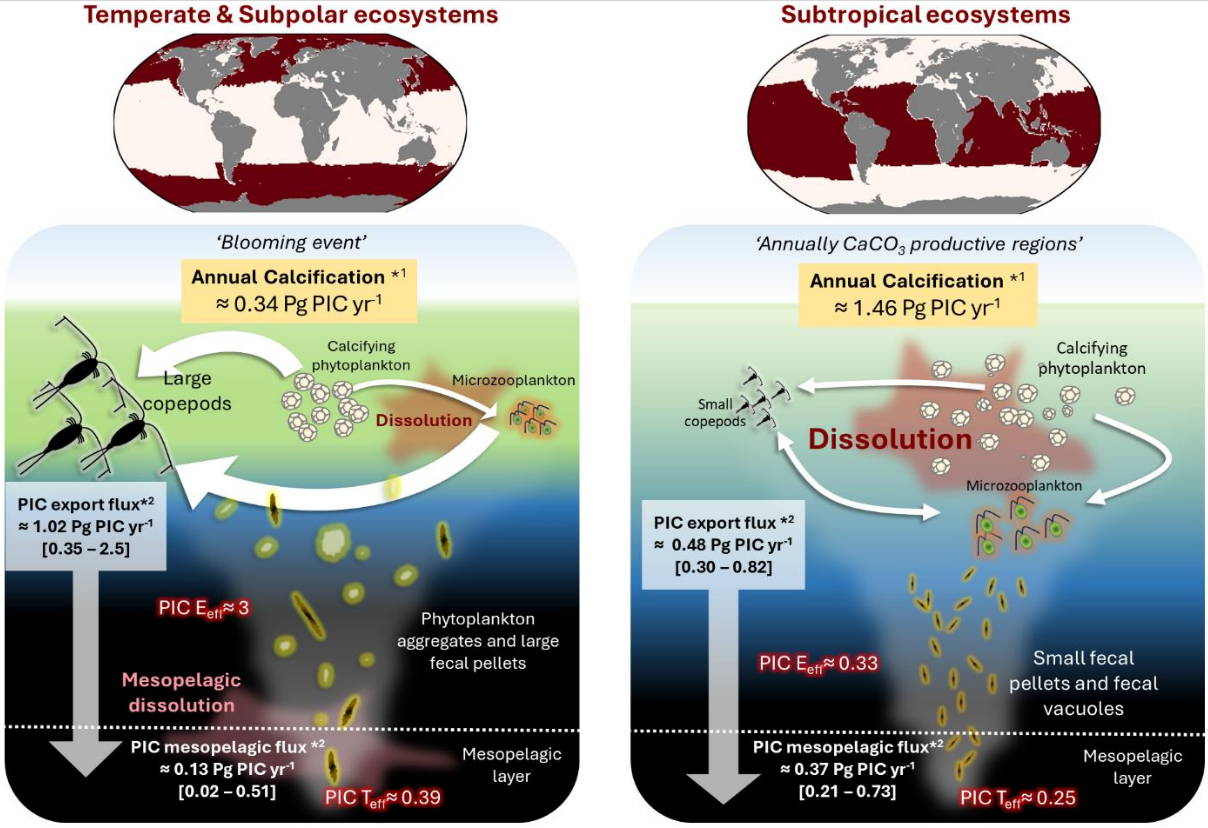
4.5. Ecosystem control on PIC flux

Microzooplankton (<200 μm) 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_{eff} and PIC T_{eff} across latitudes (Fig. 7). In the North Atlantic, microzooplankton consume 288–589 mg C m^{-2} 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 $CaCO_3$-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 PIC E_{eff} to PIC T_{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 $CaCO_3$-mediated dissolution by microzooplankton (Fig. 8) that may affect PIC E_{eff}.



*1 Satellite based NPP, excluding continental margin (200m depth) and interior sea

*2 Estimates based on the sediment trap annual PIC flux (g C m^{-2} yr^{-1}) extended to the total surface area. Results are expressed by the median and interquartile [q25 – q75]

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 µm to 2 mm; Microzooplankton (mostly protists, < 200 µm) 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_{eff} and biologically mediated $CaCO_3$ dissolution. Our results highlight that the variability of PIC E_{eff} and the mechanisms regulating $CaCO_3$ 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.