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Original Article

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Meta-analysis of the role of zooplankton faecal pellets in ocean carbon export flux

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Abstract

Faecal pellets of marine zooplankton play a key role in the biological carbon pump, i.e. all biologically mediated processes by which organic carbon produced by photosynthesis is stored in the ocean's interior. Numerous factors (size and biomass of faecal pellets, composition and abundance of zooplankton, etc.) can affect the sinking rate of zooplankton faecal pellets and thus the efficiency of their export at depth. A number of quantitative studies of the role of zooplankton faecal pellets in the biological carbon pump have been conducted, focusing either on a region or a type of faecal pellets. These studies highlighted the large variability in the contribution of faecal pellets to carbon fluxes, ranging from 0% to 100%. Here, we used a meta-analysis approach to extract quantitative data on the size, biomass, and role of marine zooplankton faecal pellets in ocean carbon export from 197 scientific articles. Our study focused on the six most studied faecal pellet types (mixed, cylindrical, ellipsoidal, tabular, spherical, and drop-shaped). We showed that abundance and biomass fluxes of faecal pellets, as well as their contribution to particulate organic carbon fluxes, increased with ecosystem productivity, here approximated by surface chlorophyll-*a* concentration. Furthermore, the fluxes of marine zooplankton faecal pellets (both by abundance and biomass) were positively correlated, and the sampling location, rather than the type of faecal pellet, better explained this correlation. Additionally, sinking rates were strongly correlated with volume, length, and width of faecal pellets, for all faecal pellet types. Sinking rates did not vary with depth, although measurements become scarcer with depth. Our literature review highlights the crucial role of faecal pellets in the biological carbon pump and the need to study less known types of faecal pellets, such as ellipsoidal faecal pellets, and to measure multiple variables on the same samples. Finally, we recommend that modellers wishing to represent faecal pellets in global biogeochemical models choose a constant sinking rate with depth within the range of the quantitative values reported here.

Keywords: carbon export; faecal pellets; marine zooplankton; modelling; sinking rate

Introduction

Marine zooplankton contribute considerably to the global carbon cycle within the Biological Carbon Pump (BCP). The BCP refers to all the biologically mediated processes that enable organic carbon created by photosynthesis in the euphotic layer to be transferred to the depths of the oceans. Three main pathways are usually distinguished: the gravitational pump, the migrant pump, and the mixing pump (Buesseler et al. 2008, Siegel et al. 2023). The gravitational pump is the sinking of organic matter (faecal pellets, phytodetritus, carcasses, etc.) out of the euphotic layer under the effect of gravity (Boyd et al. 2019). The migrant pump transports organic carbon throughout the migration of some zooplankton species to depth on diel and seasonal timescales (Steinberg and Landry 2017). Finally, the mixing pump is the export of organic carbon due to physical mixing (Stukel et al. 2017). The BCP is estimated to transfer ~10 PgC every year to the interior of the ocean (Siegel et al. 2023) limiting the increase in carbon dioxide concentration in the atmosphere. In the climate change context, it is particularly important to better understand how the BCP works and how it may evolve in the future (Ratnarajah et al. 2023). Among these pathways, the most important one is the gravitational pump contributing to ~60% of the total carbon export (Boyd et al. 2019). In this study, we will focus on the zooplankton faecal pellets that are the main contributors to the gravitational pump (Bisson et al. 2020, Nowicki et al. 2022) and whose contribution to POC fluxes has been reported to be highly variable (from 0% to 100%, reviewed in Turner 2015).

Since the first studies on zooplankton faecal pellets, one central question remains: why is the faecal pellet contribution to POC flux so variable? (Pilskaln and Honjo 1987). Many studies tried to answer this issue and several factors have been proposed to explain such variations. In particular, faecal pellet roles in carbon fluxes can vary with space (Wilson et al. 2008, Steinberg and Landry 2017) and time (Wexels Riser et al. 2002, Wilson et al. 2013, Cao et al. 2024). These variations may be the results of varying phytoplankton (Bienfang 1980, Frangoulis et al. 2001, Liu and Wu 2016a, White et al. 2018) or zooplankton (Grunewald et al. 2002, Frangoulis et al. 2005, Liszka et al. 2019) community structure and composition. Moreover, some zooplankton species feed on faecal pellets, either altering them (coprohexy: fragmenta-

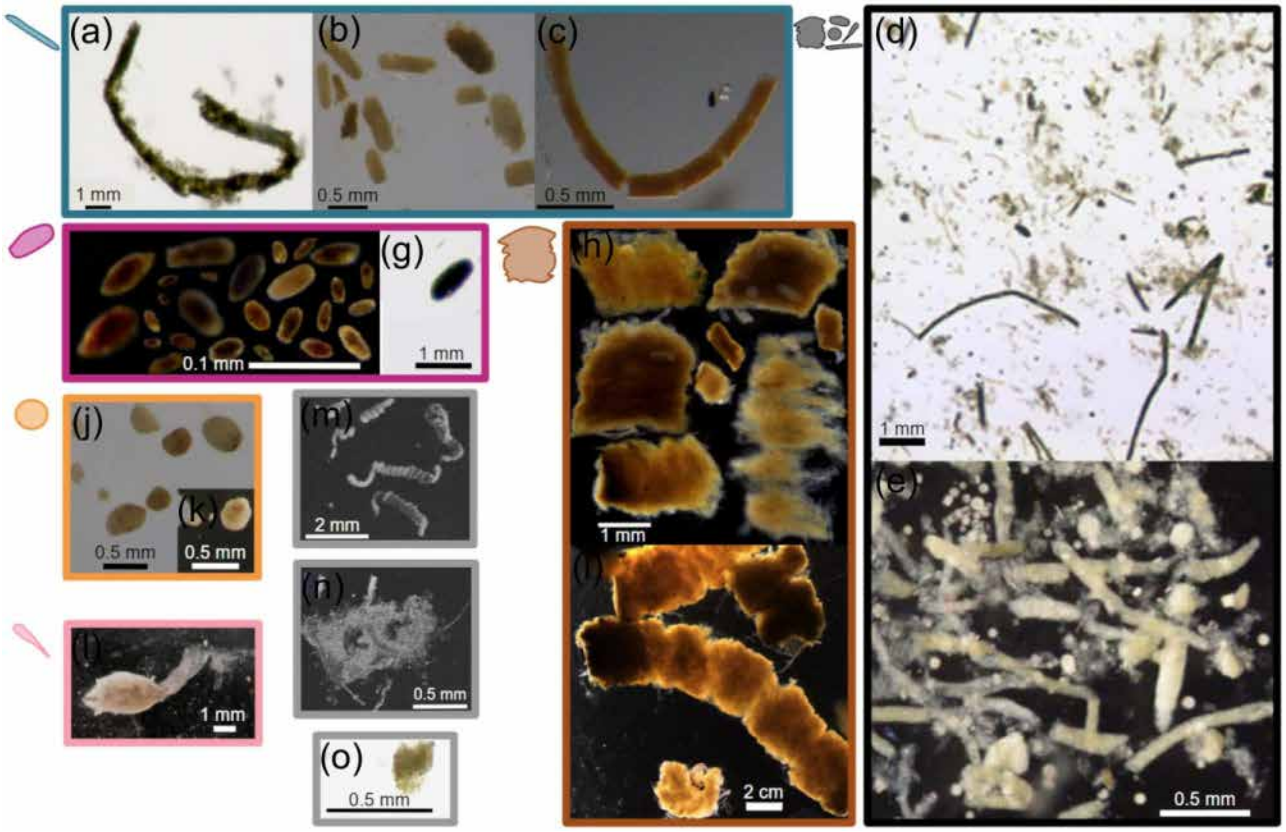

Figure 1. Examples of images of zooplankton faecal pellets from the literature. The images are classified and framed by type of faecal pellet as defined in Table 1. The colours and icons correspond to those used throughout the study: blue for cylindrical, black for mixed, dark pink for ellipsoidal, orange for spherical, brown for tabular, pale pink for drop-shaped, and grey for irregular, spiral, and amorphous faecal pellets. Each image has its own scale bar. a, d, and g from Laurenceau-Cornec et al. (2015); b, j, and k from Belcher et al. (2017); c from Cavan et al. (2015); e from Wilson et al. (2008); f and h from Durkin et al. (2021); i from Steinberg et al. (2023); l from M. Perhirin; m and n from Bruland and Silver (1981) and o from Wang et al. (2023).

tion in smaller/slower sinking particles; coprochaly: altering the faecal pellet volume and density after the disruption of the peritrophic membrane) or consuming them (coprophagy) (Lampitt et al. 1990, Noji et al. 1991). Increased interception and recycling of faecal pellets reduce the efficiency of the carbon pump, leading to a decreased faecal pellet abundance with depth (Sampei et al. 2004, Durkin et al. 2021), and hence a decreased contribution to carbon export. In the idealized framework of a model, Mayor et al. (2020) found that particle-associated copepods were even responsible for 81% of the annual flux attenuation of fast-sinking detritus, the particle class representing zooplankton faecal pellets.

Zooplankton communities are highly diverse, which also implies the production of a large variety of faecal pellets (Fig. 1). These different morphological characteristics can help to distinguish faecal pellets in sediment traps or nets and infer potential producers (Pasternak et al. 2000, Wilson et al. 2013, Manno et al. 2015). Another common method to study faecal pellets is to incubate organisms in the lab and collect their faecal pellets. Only a few studies have attempted to compile information on faecal pellets and their role in the BCP (Turner 2002, 2015, Steinberg and Landry 2017). From a more quantitative point of view, some studies gathered data for specific regions only or a specific type of faecal pellets (Phillips et al. 2009, Atkinson et al. 2012, Kim et al. 2024). More recently, Li et al. (2024) combined data on faecal pellet contribution to POC flux from 18 locations in the global ocean. They found a good correlation between marine primary production and faecal pellet contribution to carbon export.

Surprisingly, despite their diversity and potential role in carbon export, zooplankton faecal pellets have received little attention in modelling studies. Still, few modelling studies have quantified faecal pellet role at the global scale and estimated global budgets. For example, Clerc et al. (2023) and Luo et al. (2024) included large faecal pellets produced, respectively, by filter-feeding gelatinous macrozooplankton, and fish and tunicates, in global biogeochemical models. Serra-Pompei et al. (2022) highlighted the major role of faecal pellets from large zooplankton at 1080 m, emphasizing their key role in sequestering carbon rather than only exporting it. At a more local scale, Andersen and Nival (1988) modelled a Mediterranean ecosystem using data from one sediment trap. They highlighted the role of faecal pellets of copepods and salps in the vertical flux of organic matter. Other modelling studies focused on specific behaviour of copepods and inferred their impact on carbon fluxes through the release of faecal pellets at depth (Wallace et al. 2013) or via coprohexy/coprochaly (Mayor et al. 2020). Finally, using an individual-based model, Stamieszkin et al. (2015) studied the links between copepod size and community composition and faecal pellet export.

In this context, the objectives of this study were to (1) exhaustively compile quantitative data related to the morphology of zooplankton faecal pellets (length, width, volume) and their role in carbon export (biomass and abundance flux, contribution to POC flux, sinking rate), and to (2) explore potential global trends. Thanks to this meta-analysis, we wanted to (1) identify knowledge gaps and/or biases in literature, (2) refine their role in global carbon export and eventually identify global patterns, and (3) inform modellers, especially on faecal pellet sinking rate.

Materials and methods

Zooplankton faecal pellet scientific research database

The research protocol of this study was inspired by the systematic review guidelines (Collaboration for Environmental Evidence 2022) and focused on the contribution of recognizable zooplankton faecal pellets to carbon export.

Articles were extracted from the literature July 4 of 2024 because they contained either ('zooplankton' or 'mesozooplankton' or 'copepod∗' or 'salp∗' or 'appendicularian∗' or 'larvacean∗' or 'krill∗' or 'amphipod∗') and ('pellet∗' and ('flux' or "export' or "POC' or "length' or 'size' or 'volume' or 'sinking' or 'faecal' or 'fecal')) in their title or ('zooplankton' or 'mesozooplankton" or 'copepod∗' or 'salp∗' or appendicularian∗' or 'larvacean∗' or 'krill∗' or "amphipod∗') and ('pellet∗' and ('flux' or 'export' or 'POC' or 'length' or 'size' or 'volume' or 'sinking' or 'faecal' or "fecal')) and ('ocean' or 'marine')) in their abstract from BibCNRS (a portal of the French National Center of Scientific Research for electronic documentary resources, https://bib.cnrs.fr/) ($n = 530$). A personal database of scientific literature compiled by the first author was also used and 64 articles were added to the database. The resultant global database ($n = 594$) included mostly scientific articles and a few book chapters. Titles and abstracts of this database were manually screened and classified as ≪ Good ≫ ($n = 222$) or ≪ Bad ≫ ($n = 372$). ≪ Good ≫ was assigned if the study focused on marine zooplankton faecal pellets and contained quantitative values on either the carbon content, the size, the sinking rate of the faecal pellets, or their contribution to carbon flux. If there was any doubt about the presence of quantitative data, the rest of the text was briefly reviewed. The focus was made on identifiable or recognizable zooplankton faecal pellets and not on the faecal aggregates or other types of sinking particles.

Using BibCNRS as a research database gives access to the vast majority of scientific literature. Some articles may still be missing following this search. However, we believe that the extensive screening we did and the addition of our personal database of scientific articles have made it possible to study the vast majority of scientific articles dealing with zooplankton faecal pellet data.

Among the 222 ≪ Good ≫ articles, 3 were reviews and 11 modelling studies without novel measured data. For 11 articles, the full manuscripts were not available online (grey literature or articles published before 1990), and were then discarded for the analyses. We checked that scientific articles used in the reviews were in our database. Modelling studies were analysed separately, see section *Modelling studies* below. Hence, quantitative data were extracted from 197 studies, either digitized from figures (using the online application *Plot Digitizer* https://plotdigitizer.com/app), from tables (using the online tool *Docsumo* https://www.docsumo.com/free-tools/extract-tables-from-pdf-images), or from the text itself.

Two types of data were gathered. Data measured at one time and one place (for variables related to faecal pellet role in POC flux) or measured on one faecal pellet (for variables related to morphology and biomass) are thereafter referred to as individual faecal pellet records. Averaged data (over time and/or space for variables related to faecal pellet role in POC fluxes, or over multiple faecal pellets for variables related to their morphology and biomass) are thereafter referred to aggregated faecal pellet records. The sample size for the aggregated faecal pellet records was not often available; hence, the sample size was not saved in the final dataset.

Additional variables

In order to standardize the database and to be able to take into account the information retrieved either on the shape of the faecal pellets or on the taxa that produced them, a subset of 37 studies, which already categorized faecal pellets and used to build the faecal pellet database, were reviewed to associate the faecal shape with zooplankton taxa (Table 1). Some scientific articles also took into account the size (e.g. Ayukai and Hattori 1992), the colour (e.g. Wilson et al. 2008), or the state of deterioration (e.g. González et al. 1994a) of zooplankton faecal pellets. However, since this information was not available in all articles, we focused our standardization on shape only (mixed, cylindrical, ellipsoidal, spherical, tabular, drop-shaped, irregular, spiral, amorphous, large, conical). Given the great diversity in the morphology of faecal pellets and the numerous factors that can affect it (Werner 2000, Wilson et al. 2008), this homogenization probably implies compromises in methodologies, as faecal pellets produced by the same taxa under different conditions may belong to different types of faecal pellet. For example, faecal pellets produced by amphipods were described as brown (Matsuno et al. 2016), ellipsoidal (Carroll et al. 1998), or cylindrical (Wassmann et al. 2000, Werner 2000, Wexels Riser et al. 2007). Brown type was not retained in the standardization process. The cylindrical shape was still the most common description in the database, but the ellipsoidal shape might still be representative of amphipod faecal pellets as written in Table 1. Similarly, chaetognath faecal pellets were described as ellipsoidal (Giesecke et al. 2010) or drop-shaped (Dilling and Alldredge 1993).

In the end, each data point was linked to a type of faecal pellet (represented hereafter by icons and colours) and, when possible, their most likely producers. Irregular, spiral, amorphous, large, and conical zooplankton faecal pellets appeared in less than 5 scientific articles (Table 1). Due to this low amount of data, these five types were not considered in the rest of the study.

In situ chlorophyll-a concentration ([Chl-a]) was measured in only 86 scientific articles (including 8 incubations or cultures data) out of the 197 in the database. Hence, to approximate the productivity of all sampled ecosystems at the global scale, monthly climatology of surface chlorophyll-a concentration (L3 mapped product, 4 km, MODIS-Aqua Ocean Colour Data, https://oceandata.sci.gsfc.nasa.gov/l3/) was used. For data sampled during a month or less, the sampling month and the location (latitude, longitude) were used to retrieve the chlorophyll-a concentration. For data sampled during more than a month, averaged chlorophyll-a concentration values at the location (latitude, longitude) were computed. For 218 pairs of location and month out of 824, chlorophyll-a concentration values were not available. All of

Table 1. Types of zooplankton faecal pellets used in this study, a list of most likely zooplankton producers based on the literature, synonyms that can be found in literature, references defining such shapes of zooplankton faecal pellets and number of scientific articles mentioning them.

Type of faecal pellet	Most likely producers	Synonyms found in literature	# of scientific articles mentioning it
Cylindrical 	Large copepoda (Honjo and Roman 1978, Bathmann et al. 1991, Noji et al. 1991, Accornero and Gowing 2003, Sampei et al. 2009, Kobari et al. 2010, Cole et al. 2016) Euphausiaceae (González et al. 1994a, Belcher et al. 2017, Yang et al. 2019) Decapoda larvae (Matsuno et al. 2016) Amphipoda (Werner 2000, Wexels Riser et al. 2007)	Long, filiform, strings	131
Mixed 	Unidentified zooplankton	NA	99
Ellipsoidal 	Small and medium-sized copepoda (Nöthig and von Bodungen 1989, González et al. 1994b) Larvacea (González et al. 1994a, Matsuno et al. 2016, Durkin et al. 2021) Barnacle larvae (Matsuno et al. 2016) Amphipoda (Carroll et al. 1998) Chaetognatha (Giesecke et al. 2010)	Ovoid, oval, elliptical	59
Spherical 	Microzooplankton (Gowing and Silver 1985) Rhizaria (Gowing and Silver, 1985) Nauplii larvae (Pasternak et al. 2000, Yoon et al. 2001) Protozoans (Gowing and Silver 1985, Nöthig and von Bodungen 1989, González 1992)	Round	25
Tabular 	Salpa (Caron et al. 1989, Accornero et al. 2003, Steinberg et al. 2023)	Rectangular flakes, flakes	22
Drop-shaped 	Chaetognatha (Dilling and Alldredge 1993) Pyrosoma (Drits et al. 1992) *Limacina helicina* (Manno et al. 2010)	NA	6
Irregular	Doliolida (Bruland and Silver 1981, Koster et al. 2011)	NA	4
Spiral	*Carinaria* sp. (Wilson et al. 2008) Pteropoda (Bruland and Silver 1981)	NA	4
Amorphous	Unknown (Kobari et al. 2010, Wang et al. 2023)	NA	3
Large	Fishes (Accornero and Gowing 2003, Durkin et al. 2021)	NA	2
Conical	*Clio* sp. (Yoon et al. 2001)	NA	1

Shapes are ordered from the most frequently studied to the least. The colours and icons correspond to those used throughout the study: blue for cylindrical, black for mixed, dark pink for ellipsoidal, orange for spherical, brown for tabular, pale pink for drop-shaped, and grey for irregular, spiral, and amorphous faecal pellets, as in Fig. 1

them were located close to the coast or in polar regions and were not considered in the study. Chlorophyll-a concentration values were then discretized into three categories: low productive regions ([Chl-a] < 0.1 mg m^{-3}), moderate productive regions (0.1 mg m^{-3} $<$ [Chl-a] $<$ 1 mg m^{-3}) and high productive regions (1 mg m^{-3} $<$ [Chl-a]).

The exact same procedure was applied to sea surface temperature (SST, L3 mapped product, 4 km, MODIS-

Aqua Sea Surface Temperature Data, https://oceandata.sci.gsfc.nasa.gov/l3/). SST data was not available for 93 locations. Three categories were created: cold (SST $< 5°C$), medium (SST between 5°C and 15°C), and warm (SST $> 15°C$) waters.

To standardize sampling locations, an ocean basin (Arctic, Northern Atlantic, Southern Atlantic, Indian, Pacific, and Southern Oceans and Mediterranean Sea) was assigned to each location based on latitudes and longitudes. The Arctic Ocean borders were defined by the 10°C isotherm in July. The northern limit of the Southern Ocean was defined as 60°S. The Atlantic Ocean was separated into the Northern (latitude $> 0°$) and the Southern (latitude $< 0°$) Atlantic Ocean.

Modelling studies

In the database, 11 articles used models to compute faecal pellet fluxes, contribution to POC flux and/or abundances. The parameters related to faecal pellets (e.g. sinking rate, volume, production rate) were retrieved from these studies. For each parameter, a type of faecal pellet was assigned.

To supplement the model literature and focus on faecal pellet sinking rates, a second query was done in *Elicit: The AI Research Assistant* (https://elicit.com/). We asked 'What is the sinking rate of detritus produced by zooplankton in biogeochemical models?' and the 24 most pertinent scientific articles were screened. Two were already present in our database. Among the 22 others, most of them did not explicitly represent zooplankton faecal pellets but large detritus or fast-sinking particles. This search therefore mainly contributed to the discussion on the representation of faecal pellets in models.

Final datasets

The final dataset contained data about faecal pellet morphology and biomass (length in µm, width in µm, volume in μm^3, carbon content in $\mu gC\ pellet^{-1}$ or in $mgC\ mm^{-3}$, density in $gC\ cm^{-3}$) and their role in POC flux (abundance fluxes in # $m^{-2}\ d^{-1}$ and biomass fluxes in $mgC\ m^{-2}\ d^{-1}$, contribution to POC flux in %), along with their metadata (month, year, latitude in °N, longitude in °E, depth in m, type of faecal pellet, ocean sampled, surface chlorophyll-a concentration in $mgC\ m^{-3}$, productivity level, sea surface temperature in °C, temperature category, sampling method, reference, DOI). Data were aggregated or individual faecal pellet records. This database was then filtered to extract samples for which several variables had been measured (e.g. abundance and biomass flux, sinking rate, and length).

Model parameters related to faecal pellets were stored in another dataset containing parameter names, values, and units, and the reference from which they were extracted.

The different datasets used in this study are available on Seanoe (Perhirin et al. 2025a).

Data analyses

A Kruskal–Wallis analysis (Kruskal and Wallis 1952) was used to test for the impact of the productivity level on the faecal pellet contribution to POC flux and abundance/biomass fluxes. It was followed by a Dunn pairwise test (Dunn 1961) with Bonferroni p-values correction for multiple comparisons, to assess the significance of the observed patterns (Dunn 1961). The same procedure was applied to test the impact of the SST categories.

The correlation between aggregated faecal pellet records of faecal abundance and biomass fluxes was tested using Spearman's correlation coefficients, with Bonferroni P-values correction for multiple comparisons (Dunn 1961). The same methodology was applied to aggregated faecal pellet records of faecal pellet sinking rates and volumes or lengths or widths. The effect of faecal pellet type and the ocean basin on the relation between faecal pellet abundance and biomass fluxes was evaluated using linear models fitted to the individual records. In the analyses, patterns were considered significant if P-values were lower than 0.01.

Numerical tools

All statistical analyses were conducted in the programming environment R 4.3.1 (R Core Team 2021). The package *tidyverse* (Wickham et al. 2019) was used for data manipulations. The packages *sp* (Pebesma and Bivand 2005) and *lubridate* (Grolemund and Wickham 2011) were used to manipulate coordinates and dates data, respectively. The packages *RColorBrewer* (Neuwirth 2022), *ggplot2* (Wickham et al. 2021), *cowplot* (Wilke 2020), and *ggimage* (Yu 2023) were used to produce general graphics. The packages *sf* (Pebesma and Bivand 2023), *rnaturalearth* (Massicotte et al. 2023), and *rnaturalearthdata* (South et al. 2024) were used to produce the maps. The package *corrplot* (Wei et al. 2021) was used to compute correlation coefficients.

Results

Database presentation

Data gathered in this meta-analysis covered almost the entire global ocean (78.00°S to 88.83°N and 177.61°W to 179.80°E). Data were sampled between November 1967 and May 2022. Summer, spring, and autumn were the most studied seasons (with data in 125, 98, and 87 scientific articles, respectively), while winter was the least studied (49 scientific articles).

A majority of the scientific studies used sediment traps data (56%) and one-third (34%) incubation data. Among the other methods, it is worth mentioning the use of imagery to study faecal pellets (McDonnell and Buesseler 2010, Katija et al. 2017, Fragoso et al. 2022, Giménez et al. 2023) and an echosounder (Røstad and Kaartvedt 2013).

On average, 2.5 ± 1.4 (ranging from 1 to 6) variables were measured in each study. Zooplankton faecal pellet flux (abundance and biomass together) was the most studied variable, while density was the least studied (Fig. 2). Cylindrical faecal pellets were the most studied type, with a minimum of 15 scientific articles per variable (Fig. 2) reflecting the domination of crustacean zooplankton at the global scale (Table 1) (Drago et al. 2022). On average, 1.7 (± 1.1, between 1 and 6) types of faecal pellets and 2.7 (± 2.7, between 1 and 22) taxa were studied per scientific article.

Carbon fluxes of zooplankton faecal pellets

The contribution of zooplankton faecal pellets to POC flux spanned the entire range from 0% to 100% and the median contribution was between 5% and 22%, depending on the productivity of the ecosystem (Fig. 3b). Flux of zooplankton faecal pellets was on average about 1000–10 000 faecal pellets $m^{-2}\ d^{-1}$ (Fig. 3c) and represented between 0.1 and 8 $mgC\ m^{-2}\ d^{-1}$ (Fig. 3d). These values increased significantly with the productivity of the ecosystem ($P < 0.0001$ between each box-

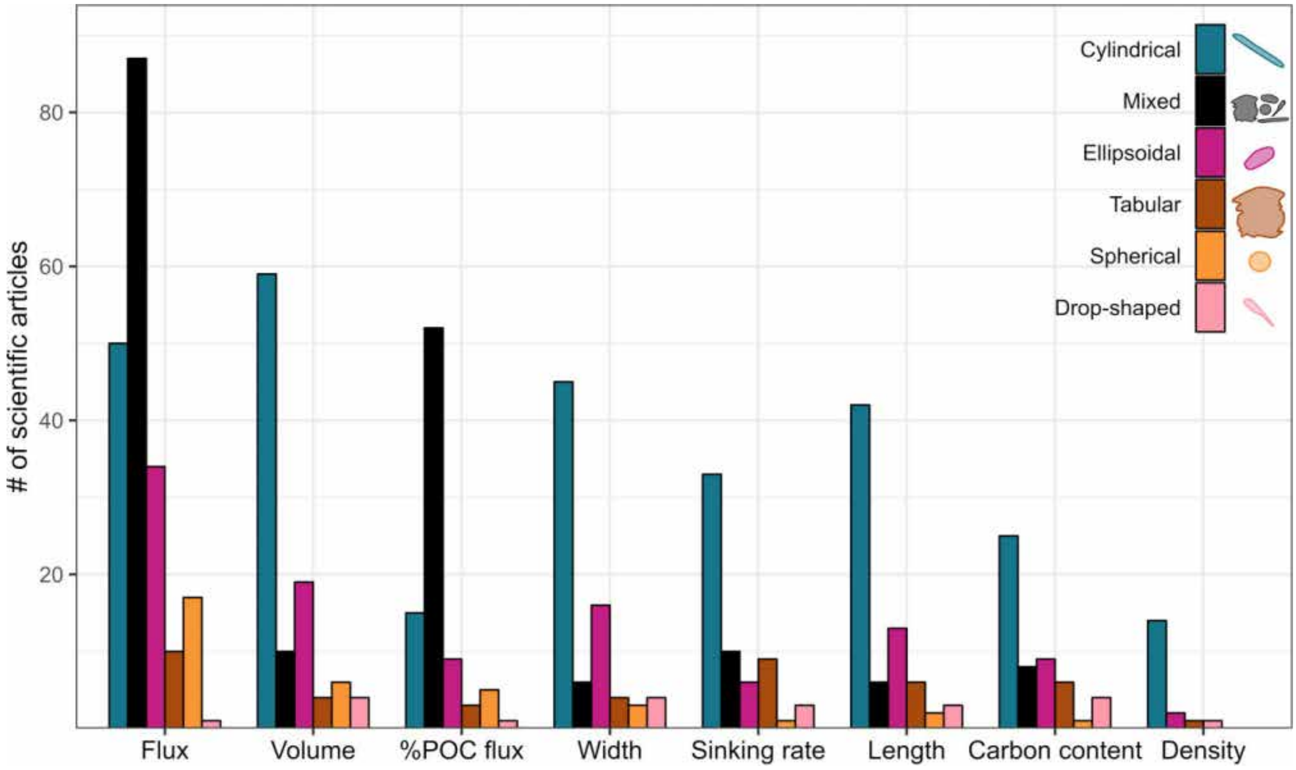

Figure 2. Number of scientific articles containing data among the 8 quantitative variables used in this study. Colours represented the type of faecal pellets concerned: cylindrical (131 articles), mixed (99), ellipsoidal (59), tabular (25), spherical (22), and drop-shaped (6).

plot, except between low- and medium-productive regions in faecal pellet abundance flux).

For both aggregated and individual records, there were positive and strong correlations between the abundance and biomass of the zooplankton faecal pellet fluxes ($P < 0.0001$; Fig. 4b, c, and d). The two linear models tested here on individual faecal pellet records were significant (Fig. 4a and c). However, the types of zooplankton faecal pellets explained almost nothing ($R^2 = 0.04$, $P < 0.001$; Fig. 4a), while the sampling location explained more of the relationship between abundance and biomass zooplankton faecal pellet fluxes ($R^2 = 0.430$, $P < 0.001$; Fig. 4c). This was not the case for aggregated faecal pellet records (Fig. 4b and d).

The contribution of zooplankton faecal pellets to POC fluxes was slightly more correlated to biomass fluxes than to abundance fluxes (Supplementary Fig. S2). For individual records, contribution to POC fluxes were low (<20%) when faecal pellet abundance fluxes were below 500 # m^{-2} d^{-1} (Supplementary Fig. S2A) or faecal pellet biomass fluxes were below 0.1 mgC m^{-2} d^{-1} (Supplementary Fig. S2C). However, for aggregated records, data was lacking.

Morphology of zooplankton faecal pellets and sinking rates

There were strong positive correlations between the sinking rate and the size of zooplankton faecal pellets (Fig. 5), in agreement with previous studies who reported a relationship between volume and sinking rate of zooplankton faecal pellets (Smayda 1969, Bruland and Silver 1981). The sinking rates and the density of faecal pellets were also correlated (Supplementary Fig. S3). It was not possible to compute the correlation between the sinking rate and the carbon content of zooplankton faecal pellets because not enough studies measured both variables ($n = 3$).

Vertical profiles of zooplankton faecal pellet sinking rate

Sinking rates reached an average of 100 m d^{-1} for all types of faecal pellets, except for tabular ones that sank one order of magnitude faster (Fig. 6). There was almost no variation of the sinking rate with depth.

Model parameter values were within the range of observed faecal pellet sinking rates. Sinking rates of tabular pellets were fixed at around 1000 m d^{-1}, matching with observed values (Fig. 6) (Andersen and Nival 1988, Clerc et al. 2023). For other types of faecal pellets, parameters representing sinking rate were around 50–100 m d^{-1} (Andersen and Nival 1988, Mayor et al. 2020, Countryman et al. 2022, Clerc et al. 2023), hence in the range of observed values for these types (Fig. 6). Here, in the model representing ellipsoidal faecal pellets, producers were small copepods (Countryman et al. 2022). However, no study in our dataset measured the sinking rate of ellipsoidal faecal pellets.

Discussion

This meta-analysis clarified the significant role of zooplankton faecal pellets in carbon fluxes. Their contribution to POC fluxes, as well as the intensity of their abundance and biomass fluxes, increased with the ecosystem productivity. We highlight biases in data related to zooplankton faecal pellets and

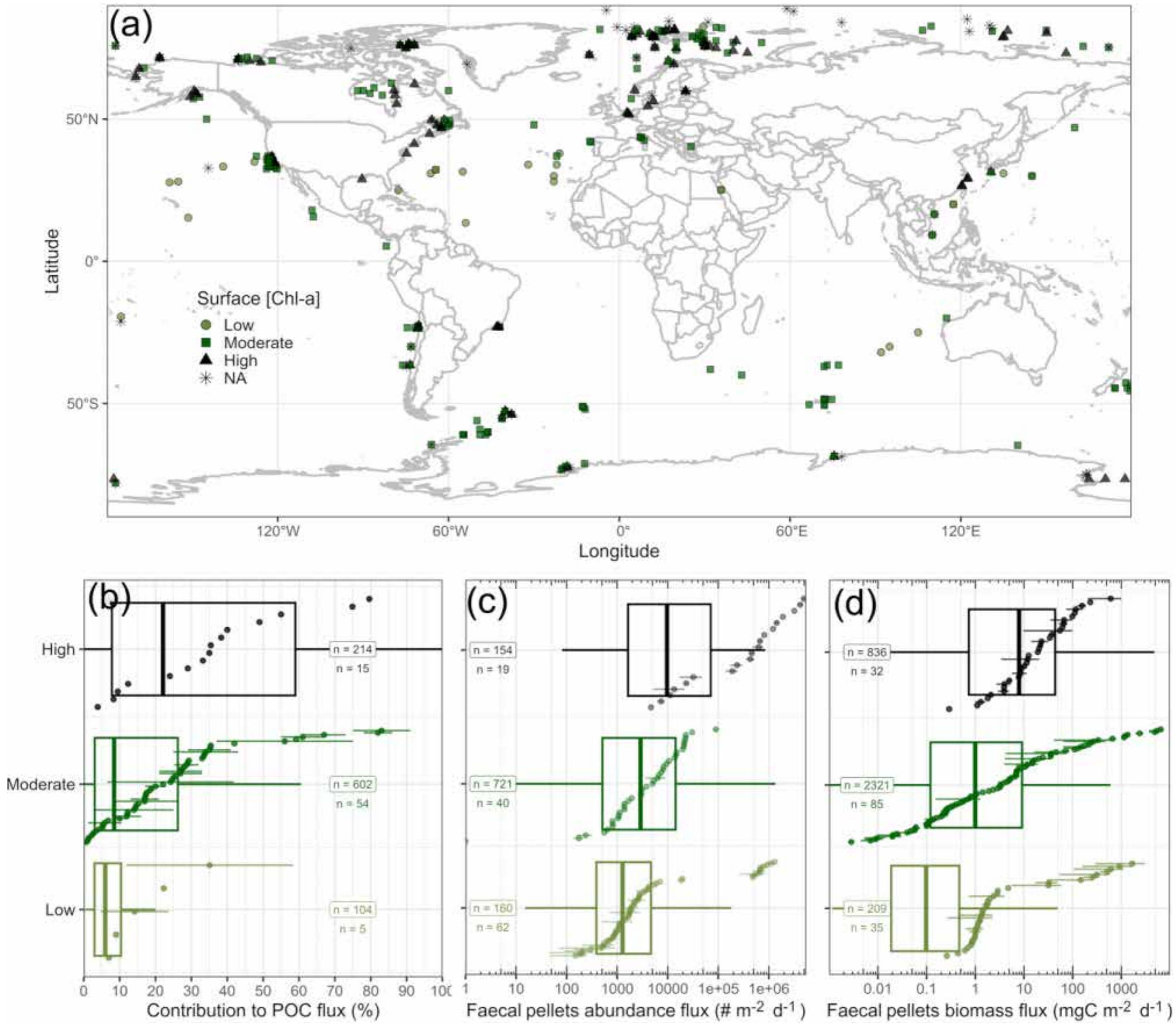

Figure 3. Geographical distribution of the contribution and flux data in the faecal pellet dataset (a). Surface chlorophyll-a concentration at each location was retrieved from the monthly climatology AquaMODIS Chl-a L3 product (4 km) and discretized in three productivity classes. Colours and shapes represent the three productivity classes, no data are represented by a star. Distribution of zooplankton faecal pellet contribution to POC flux (%, b), of zooplankton faecal pellet abundance flux (# m^{-2} d^{-1}, c) and biomass flux (mgC m^{-2} d^{-1}, d) for all locations and depending on the productivity class. Box-plots represented the distribution of individual faecal pellet records retrieved from figures and/or tables. Numbers of values used per box-plot are indicated in boxed text. Aggregated faecal pellets records obtained from the literature are shown as dots in the background, their numbers are indicated below the boxed text. Note the x-log10 axis in c and d.

make recommendations for experimentalists and modellers who wish to study zooplankton faecal pellets and their role in the carbon export.

Faecal pellet database caveats

Despite the extended spatial coverage of the sampling locations, data were still scarce for the gyres and at deep oceanic waters. There was a clear imbalance between the Northern and Southern hemispheres (shown for Flux and %POC flux data in Fig. 3a). Winter was the least studied season, due to the difficulty to access some regions of the global ocean. Finally, it is important to note that most of the studies measuring individual characteristics and sinking rates of zooplankton faecal pellets were published more than 20 years ago.

Although most of the data gathered here came from sediment traps, they have several biases. Because of the way they are deployed, they do not allow for significant spatio-temporal resolution but this is counterbalanced by the large amount of data that has been gathered. They also might miss rare but important export events such as the ones following blooms (Miquel et al. 2015) and be affected by hydrodynamics, especially at shallow depths (Siegel et al. 2024, Yu et al. 2001). They tend to underestimate flux and they have a bias towards intermediate-size particles (Buesseler et al. 2007). Moreover, in high productivity environments, actively feeding zooplankton organisms (called swimmers) can enter the traps and disaggregate the captured particles or produce new ones, thus affecting the measured flux (Knauer et al. 1979, Karl and Knauer 1984). For all these reasons, it is important to keep in mind that data

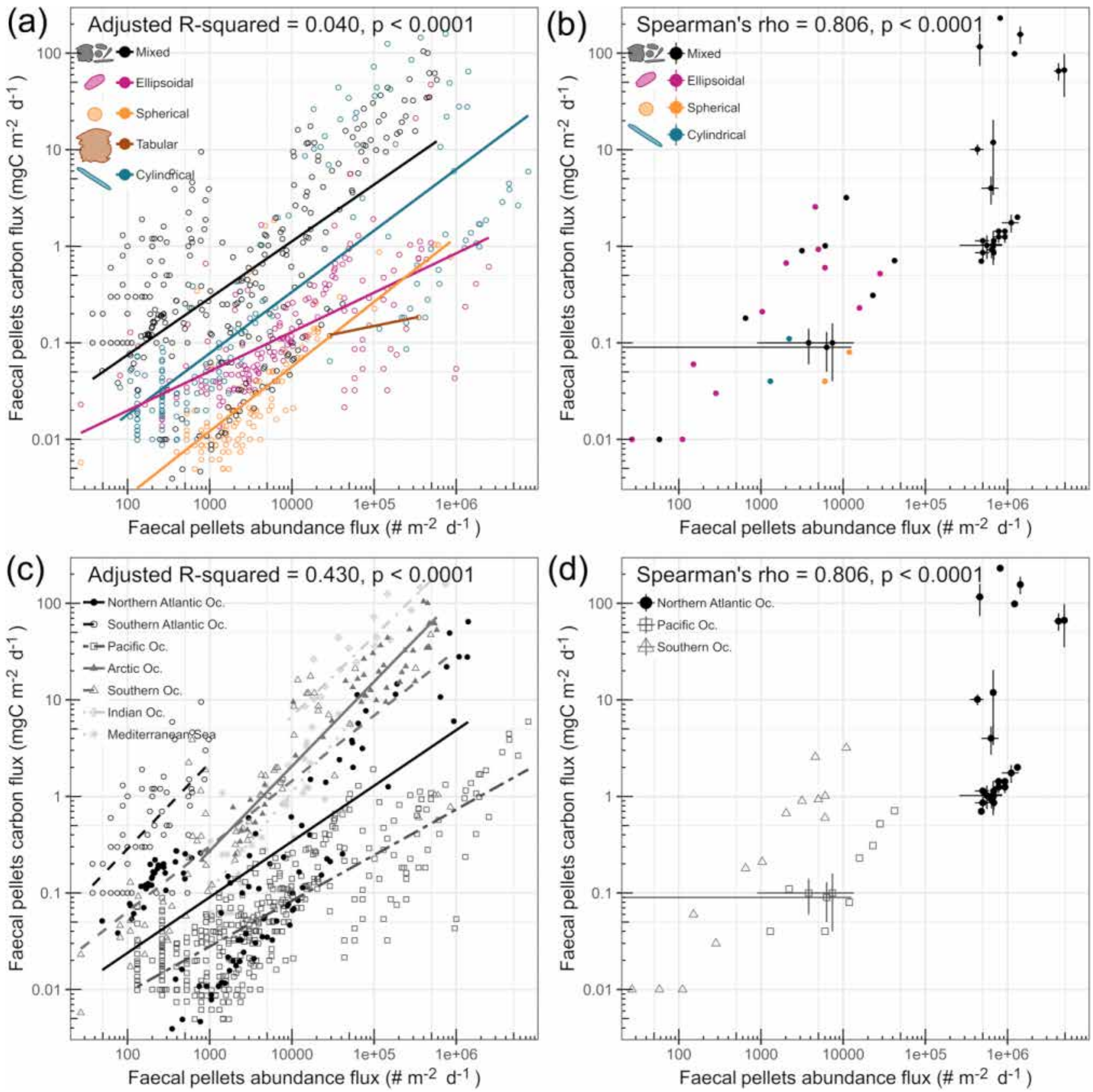

Figure 4. Relations between zooplankton faecal pellet abundance flux (# m^{-2} d^{-1}) and carbon flux (mgC m^{-2} d^{-1}). Individual faecal pellet records retrieved from figures and/or tables are shown in a and c. Aggregated faecal pellet records (mean ± standard deviation) obtained from the literature are shown in b and d. In the first row, points are coloured based on the type of zooplankton faecal pellets. In the second row, points are coloured based on the sampling location of zooplankton faecal pellets. Adjusted r-squared coefficients were computed to test the overall fit of the linear models with either the type of faecal pellets (a, adjusted R2 = 0.04, $P < 0.0001$) or the sampling location (c, adjusted R2 = 0.430, $P < 0.0001$) as explanatory categorical variables. Spearman correlation coefficients rho (computed only on aggregated faecal pellet records, standard deviations were not taken into account) are indicated in the top left corner of b/d. Note the log10 axes.

from sediment traps might represent the lower range of flux values.

Variability in faecal pellets contribution to POC fluxes

Surface chlorophyll-a concentration explained part of the faecal pellets dynamics and their contribution to POC flux. This process was already observed at a smaller scale in the Pacific Ocean along the California coast (Dagg et al. 2014) and in the Southern Atlantic Ocean (Giménez et al. 2023). In an Arctic system, Darnis et al. (2024) also showed that faecal pellet export had increased following zooplankton-enhanced feeding activity. Nevertheless, some ecosystems in low productivity regions were characterized by high abundance fluxes of zooplankton faecal pellets ($>5.10^5$ # m^{-2} d^{-1}, Fig. 3c). These data were sampled at BATS in the Sargasso Sea. This increased faecal pellet flux was attributed to the arrival of planktonic organisms from higher trophic levels following a physico-chemical disturbance on the mesoscale (Goldthwait and Steinberg 2008). Similarly, there was a group of elevated

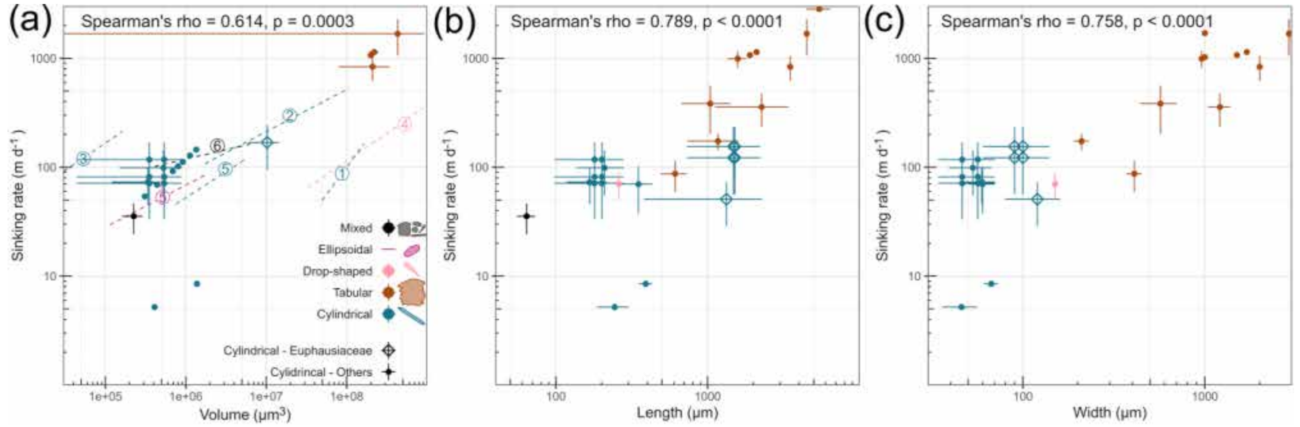

Figure 5. Zooplankton faecal pellet sinking rate (mean ± standard deviation, m d^{-1}) depending on zooplankton faecal pellet volume (mean ± standard deviation, $n = 25$, μm^3; a), length (mean ± standard deviation, $n = 29$, µm; b), and width (mean ± standard deviation, $n = 29$, µm; c). Data are coloured based on the type of the faecal pellets. Spearman correlation coefficients rho (computed only on aggregated faecal pellet records, standard deviations were not taken into account) are respectively indicated in the top left corner of each subplot. In A, dashed lines represented linear published relationships between faecal pellet sinking rate and their volume (#1 = Coppock et al. (2019), #2 = Fowler and Small (1972), #3 = Frangoulis et al. (2001), #4 = Giesecke et al. (2010), #5 = Small et al. (), #6 = Wiebe et al. (1976)). Diamonds indicated cylindrical pellets produced by euphausiids. Note the log10 axes.

biomass fluxes of zooplankton faecal pellets in low productive regions (>100 mgC m^{-2} d^{-1}, Fig. 3d). These data were sampled at ALOHA in the Pacific Ocean. This was attributed to the presence of detritivorous and carnivorous species in the mesozooplankton community (Wilson et al. 2008). Likewise, data from South Georgia sampled in a high productivity region presented low abundance flux of zooplankton faecal pellets (Belcher et al. 2017). These mismatches between productivity and faecal pellet fluxes may result from a temporal decoupling between primary production and the production of particles, especially because the faecal pellet producers considered in this study are not always primary consumers (e.g. chaetognatha, copepoda, etc.) as in Wilson et al. (2008). These mismatches might also result from discrepancies between chlorophyll-a concentration estimates from remote sensing and productivity. Moreover, surface chlorophyll-a concentration cannot reveal any potential high sub-surface chlorophyll-a maxima.

Sea surface temperature may also account for part of this variability (Supplementary Fig. S1). In warm regions (mostly in the gyres) ecosystems tend to be oligotrophic and dominated by smaller zooplankton (Brun et al. 2016) leading to lower faecal pellet contribution and fluxes. In contrast, cold regions (mostly in the polar regions) host larger zooplankton species (Brun et al. 2016) productivity is restricted to the short polar summer period (Perrette et al. 2011, Daase et al. 2021), leading to intermediate faecal pellet contribution to the POC fluxes and faecal pellet fluxes. The highest faecal pellet contribution to the POC fluxes and faecal pellet fluxes was recorded in temperate regions. The influence of temperature on faecal pellet flux is indirect, acting primarily through temperature-driven changes in individual traits such as size (Brun et al. 2016), which influence faecal pellet production rates (Ayukai and Hattori 1992).

Many other factors, not evaluated in this article, can be responsible for variations of the zooplankton role in carbon export. For example, zooplankton biomass (Gleiber et al. 2012) can impact faecal pellet fluxes. Moreover, zooplankton community composition (Kobari et al. 2010) and the presence of migrators (González 1992, Dagg et al. 2014, Steinberg et al. 2023) might also affect the intensity of faecal pellet fluxes. Sometimes, multiple factors can explain a large range of variations. For example, the presence of sea ice in the environment, as well as the diet and the size of krill, affected the sinking journey of their faecal pellets (Cadée et al. 1993).

Zooplankton faecal pellet biomass and abundance fluxes

The positive relationship between abundance fluxes and biomass fluxes was already reported in regional studies (Carroll et al. 1998, Yang et al. 2019, Li et al. 2024) and is now confirmed at the global scale. The types of faecal pellets defined in this study were mostly related to their shape and to the potential zooplankton producers (Table 1), while sampling locations were defined based on the ocean basin sampled. Thus sampling locations better integrate environmental variability (e.g. temperature, community composition of phytoplankton and zooplankton, etc.) and physical processes such as upwelling or monsoon phenomenon (Li et al. 2024). Hence, the characteristics of faecal pellets possibly impacting flux intensity (e.g. density, size, etc.) might better be captured by the sampling location (Fig. 4c and d) than by the faecal pellet types alone (Fig. 4a and b).

Abundance fluxes do not take into account the carbon content of zooplankton faecal pellets. As mentioned in Durkin et al. (2021), the weaker correlation between abundance fluxes and contribution to POC fluxes might be explained by the abundance of small faecal pellets contributing less than large ones. Hence, abundance fluxes might not be a reliable variable when measured alone.

In addition, zooplankton faecal pellet contribution to POC fluxes might also be affected by variations in the contribution of the other components of the POC such as phytodetritus, carcasses, moults, or other types of marine snow.

Sinking rate of zooplankton faecal pellets

Tabular faecal pellets were the largest, hence sank the fastest. However, only 10 scientific articles measured fluxes from tabular pellets (Fig. 2) and their contribution to POC fluxes was rarely high (Supplementary Fig. S2) (Manno et al. 2015, Décima et al. 2023) and often episodic, with low abundances in the traps (Durkin et al. 2021). This might be explained by two main hypotheses. First, tabular faecal pellets do not have peritrophic membranes compared to the cylindrical faecal pellets produced by crustaceans (Bruland and Silver 1981, Caron et al. 1989, González 1992), hence they might be unrecognizable due to biological and/or physical damage (aggregation and/or disaggregation) before or during sampling (González 1992, Gleiber et al. 2012, Iversen et al. 2017). They can also be a source of food for zooplankton (Doherty et al. 2021). Second, salps, unlike krill, generally do not form groups of organisms dense enough for their faecal pellets to appear in sediment traps (Atkinson et al. 2012), even though such events may seldom be observed (Smith et al. 2014). Their heterogeneous distribution may further hamper their pellets' sampling, as well as their ability to perform extensive diel vertical migrations, a trait shared with other zooplankton such as copepods (Bandara et al. 2021).

Cylindrical faecal pellets can be produced by various zooplankton taxa (Table 1) of very different sizes (from small calanoids to euphausiacea). This appeared in our data with *Centropages typicus* producing the smallest, hence slowest sinking faecal pellets, and krill the largest and fastest, following the relationship between the sizes of the producers and their faecal pellets (Uye and Kaname 1994, Kobari et al. 2010, Stamieszkin et al. 2015). Yet, some copepods produce faecal pellets that sink as fast as the ones produced by krill, despite their size difference. Thus, other factors than size characteristics influenced the sinking rate of faecal pellets. One of them might be the density of the faecal pellets (Supplementary Fig. S3). Phytoplankton community composition might also influence the sinking rate of faecal pellets via their potential effect on density (Bienfang 1980, Frangoulis 2001), known as the ballasting effect (Iversen and Ploug 2010). Furthermore, food quality may impact the sinking rate (Butler and Dam 1994). Effect of diet on the sinking rate of faecal pellets was tested with data gathered in this study. Due to the high variability in sinking rates between faecal pellets produced by different taxa (Wexels Riser et al. 2007, Wang et al. 2023) and the low number of data, analyses were made only on krill and *Acartia tonsa* faecal pellets. It did not reveal a clear pattern on the effect of diet on faecal pellet sinking rate (Supplementary Fig. S4). Finally, the digestion process might affect characteristics of faecal pellets (Atkinson et al. 2012, Liu and Wu 2016b).

Faecal pellet carbon content is highly variable: with latitude (Gleiber et al. 2012), with diet (Urban-Rich et al. 1998, Pauli et al. 2021), and with season (Manno et al. 2015, Li et al. 2022). Atkinson et al. (2012) showed that the sinking rate of krill faecal pellets was negatively correlated to their carbon content. Menschel and González (2019a) and Wang et al. (2023) found an inverse relationship between faecal pellet volumes and carbon content while other studies found a positive relationship (Gleiber et al. 2012, Li et al. 2022, Steinberg et al. 2023). As emphasized in Li et al. (2022), more studies should be done to better understand carbon content variation in various types of faecal pellets and in different temporal and spatial conditions. Furthermore, a better understanding and/or quantification of variations in the carbon content of faecal pellets could clarify the impact of zooplankton in carbon fluxes (Urban-Rich et al. 1998). Further studies must study sinking rates of faecal pellets of zooplankton with a focus on understudied types (ellipsoidal, drop-shaped).

Representing zooplankton faecal pellets in models

Zooplankton faecal pellets are not often explicitly represented in models (Stukel et al. 2014). It is even rarer that their high variability is taken into account. However, when tabular faecal pellets are explicitly represented in global biogeochemical models, they increased carbon fluxes to the deep ocean and in the oligotrophic gyres (Clerc et al. 2023, Luo et al. 2024). Hence, a better representation might be essential to fully understand carbon export variability and efficiency.

The significant positive correlation between sinking rate and size characteristics of zooplankton faecal pellets (Fig. 5) could be of great value to modellers. We recommend modellers to take advantage of it, but in ocean biogeochemical models, this would be useful only when some zooplankton diversity is represented. For example, it would be suitable in size-resolved models such as the one in Serra-Pompei et al. (2020). This model focused on copepods and many faecal pellet size classes were also included each with a sinking rate defined by size. One can imagine a similar model focusing on salps, for which size can correspond to different species (Henschke et al. 2016), or focusing on the entire zooplankton compartment. Some models indirectly take into account the diet of zooplankton by adjusting sinking rate according to the mineral fraction of the particles (Gehlen et al. 2006, Laufkötter et al. 2016, Le Quéré et al. 2016). In individual-based models, following Stamieszkin et al. (2015) could be very promising, i.e. using the prosome length of copepods to predict faecal pellet volume and the resulting sinking rate. Sinking rates were in the range of observed values (between 2.4 m d^{-1} and 221.3 m d^{-1}).

In modelling studies, all model parameters representing sinking rate were constant with depth except in Kvale et al. (2023) (Fig. 6), which assumed that the sinking rate of faecal pellets increases with depth. This assumption is mostly based on Berelson (2001), who studied bulk particles from sediment traps. However, the dataset gathered here for zooplankton faecal pellets did not confirm this assumption. Keeping sinking rate constant might affect a few biogeochemical models that represent large or fast-sinking particles (including zooplankton faecal pellets among other types of particles) with an increasing sinking rate with depth (Gehlen et al. 2006, Karakuş et al. 2021). Better estimates of sinking rates of zooplankton faecal pellets might help to better quantify carbon export and carbon transfer efficiencies (Karakuş et al. 2025).

Recommendations for experimentalists and modellers

From our meta-analysis, we suggest the systematic collection of the following variables from a representative subset of sediment trap particles (or all particles, when possible): detailed particle types (including faecal pellet types), individual density and size (at least the major axis of each particle), and total biomass. Efforts should also be made to acquire and make available environmental data to better understand the state of the ecosystem during sampling (e.g. chlorophyll-a concentration, phytoplankton functional groups, quality and quantity of available food for zooplankton, etc.). For laboratory analyses, we recommend concurrent measurement of as many variables as possible on both faecal pellets and their zooplankton producers. Ideally, both faecal pellet flux data (abundance and biomass) and individual-scale data related to both their morphology (length, width, or volume) and their biomass (carbon

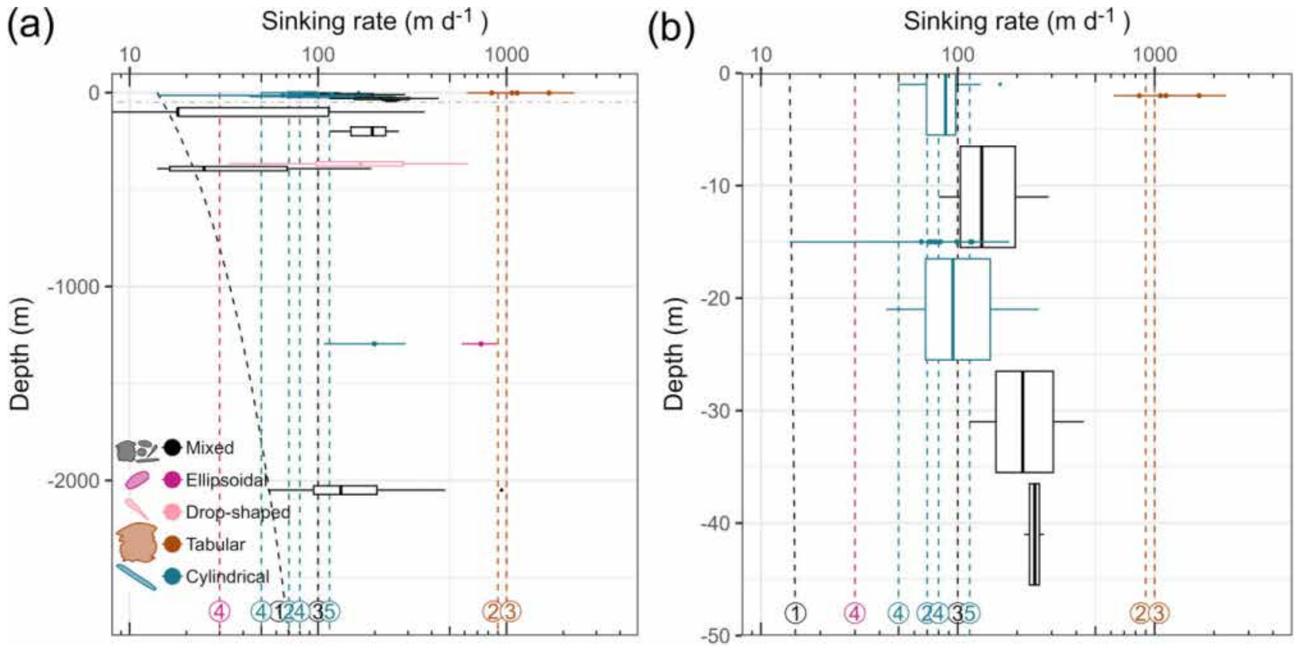

Figure 6. Sinking rate (m d^{-1}) of faecal pellets in function of depth (a) with a zoom in the 0–50 m layer (b). Data are coloured based on the type of faecal pellets. Box-plots represented the distribution of individual faecal pellet records retrieved from figures and/or tables per depth. Points and ranges represented aggregated faecal pellet records (mean ± standard deviation). Dashed lines represented parameters used in models explicitly representing faecal pellets (#1 = Kvale et al. (2023), #2 = Andersen & Nival (1988), #3 = Clerc et al. (2023), #4 = Countryman et al. (2022), #5 = Mayor et al. (2020)). Note the x-log10 axis.

content or density) should be measured on the same faecal pellets, as was done in Gowing et al. (2001), Huskin et al. (2004), and Pauli et al. (2021). Further studies should also acquire data on understudied types of zooplankton faecal pellets (e.g. ellipsoidal, drop-shaped) in order to gain a more comprehensive understanding of their role in carbon export. In addition, efforts should be made to identify at least the type of faecal pellet sampled and avoid the "mixed type" category. This should be facilitated by the use of sediment traps with polyacrylamide gel (Iversen et al. 2017) and the development of image-based methods to classify faecal pellets (Shatova et al. 2012, O'Daly et al. 2024). The different types of faecal pellets should be identifiable in images acquired by recent devices like the Underwater Vision Profiler (UVP) thanks to their size, shape and/or transparency (Steinberg et al. 2023, Perhirin et al. 2025b). Combined with good image resolution, the high acquisition rate of such devices can provide critical insights about the *in situ* morphology, the fine-scale vertical distribution, and the association between the faecal pellets and the communities of zooplankton producers. This will contribute to a better estimation of the biogeochemical role of faecal pellets.

This meta-analysis, and in particular the results reported in Fig. 4, provides modellers with empirically derived benchmarks for parameterizing the range of faecal pellet abundance and biomass fluxes occurring in the global ocean. Figures 5 and 6 also provide information on the best way to set up the model sinking parameter. For biogeochemical models whose role is to represent average behaviours of particles, we recommend a parameter for sinking rate that does not vary with depth and to carefully choose its value depending on the types of zooplankton faecal pellets simulated. Sinking rates influence primary production and surface phytoplankton concentration (Schmittner et al. 2005) when pellets are remineralized in the mixed layer. Thus, a good practice would be to systematically study the sensitivity of primary production, phytoplankton biomass, and carbon export efficiency to prescribed faecal pellet sinking rates (as done in Countryman et al. 2022, Clerc et al. 2023, Luo et al. 2024). Finally, for individual-based models, resolving zooplankton diversity, we recommend a meticulous choice of the sinking rate parameter value depending on the producing taxon or species and taking into account some variability due to zooplankton faecal pellet size variations. As in Stamieszkin et al. (2015), the size of the copepod can help predict the size of the faecal pellet.

Conclusion

Faecal pellet-related data were highly variable in terms of their role in carbon fluxes and their size characteristics, which, in turn, influenced their sinking rates. This variability was partly linked to the productivity of the ecosystem and to the type of faecal pellets but might also be explained by several other factors (phytoplankton community composition, zooplankton size, etc.). The understanding of zooplankton faecal pellet dynamics and their role in POC fluxes will be improved by measuring the recommended set of variables and focusing future studies on understudied types of zooplankton faecal pellets. It will also allow the use of more accurate parameters to represent faecal pellets' dynamics in both biogeochemical and individual-based models.

Conflict of interest

None declared.

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Author contributions

Margaux Perhirin (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Writing – original draft [equal], Writing – review & editing [equal]), Olivier Aumont (Conceptualization [equal], Supervision [equal], Writing – review & editing [equal]), Frédéric Maps (Conceptualization [equal], Funding acquisition [equal], Supervision [equal], Writing – review & editing [equal]), and Sakina-Dorothée Ayata (Conceptualization [equal], Funding acquisition [equal], Supervision [equal], Writing – review & editing [equal])

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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Data availability

Data used in this article were extracted from 212 scientific articles. No new data was produced in these analyses. The data are accessible in SEANOE at https://www.seanoe.org/data/00958/106968/(Perhirin et al. 2025a). All R codes available on GitHub (https://github.com/margauxperhirin/metaanalyseFP).

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