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Cascading effects of calanoid copepod functional groups on the biological carbon pump in the subtropical South Atlantic

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Life strategies, ecophysiological performances and diel vertical migration (DVM) of zooplankton key species affect the efficiency and strength of the biological carbon pump (BCP). However, it is unclear to what extent different functional groups affect the BCP. Depth-stratified day and night samples (0–800 m) from the subtropical South Atlantic were analyzed focusing on the calanoid copepod community. Calanoid abundance, biomass distribution and species-specific impact on the passive (fecal pellets) and active (via DVM) vertical flux of carbon were determined. Species were assigned to different migrant groups where, their contributions were estimated by using the proportion of the migratory community instead of simple day-night differences in biomass. This novel approach leads to more robust flux estimates, particularly for small sample sizes. According to migration ranges and day/night residence depth, functional groups were characterized, i.e. small- and large-scale epipelagic and mesopelagic migrants. Epipelagic small-scale migrants transported respiratory ($1.5 \text{ mg C m}^{-2} \text{ d}^{-1}$) and fecal pellet ($1.1 \text{ mg C m}^{-2} \text{ d}^{-1}$) carbon from the upper to the lower epipelagic zone, where the latter can fuel the microbial loop, and thus deep chlorophyll maxima, or be ingested by other zooplankton. Large-scale migrants actively transported up to $10.5 \text{ mg C m}^{-2} \text{ d}^{-1}$ of respiratory carbon from the epipelagic layer into the twilight zone. The majority was transported by *Pleuromamma borealis* ($5.7 \text{ mg C m}^{-2} \text{ d}^{-1}$) into the upper mesopelagic. In addition, up to $8.0 \text{ mg C m}^{-2} \text{ d}^{-1}$ was potentially egested as fecal material by large-scale zone shifters. Mesopelagic migrants transported respiratory ($0.2 \text{ mg C m}^{-2} \text{ d}^{-1}$) and fecal pellet carbon ($0.1 \text{ mg C m}^{-2} \text{ d}^{-1}$) even deeper into the ocean. Community consumption of migrants in the epipelagic layer during the night was $98 \text{ mg C m}^{-2} \text{ d}^{-1}$, while non-migrants consumed $98\text{--}208 \text{ mg C m}^{-2} \text{ d}^{-1}$ in the epipelagic zone, with a potential subsequent egestion of $29\text{--}62 \text{ mg C m}^{-2} \text{ d}^{-1}$. This carbon may fuel omnivorous-detritivorous feeding, the microbial loop and/or may sink as fecal pellets. This case study shows how calanoid functional groups mediate carbon fluxes in the subtropical South Atlantic Ocean and demonstrates how detailed community analyses can elucidate the complexity of pelagic carbon budgets.

KEYWORDS

diel vertical migration (DVM), carbon cycle, active carbon flux, zooplankton ingestion, zooplankton respiration, biological carbon pump, zooplankton functional groups, twilight zone

1 Introduction

The biological carbon pump (BCP) is a key mechanism within the global carbon cycle, and the transfer of organic carbon derived from primary production into the deep sea is strongly mediated by the zooplankton link. The BCP removes 5–16 Gt C y^{-1} from surface waters into the oceans' interior, ultimately reducing atmospheric CO₂ levels. Approximately 1% of this organic carbon reaches the deep-sea sediments (Falkowski et al., 1998; Henson et al., 2011; Sigman and Hain, 2012; Archibald et al., 2019b). Marine food webs play an essential role in mediating the CO₂ exchange and transformation between the atmosphere and the oceans (Steinberg and Landry, 2017), with 21–65% of marine primary production (PP) channeled through mesozooplankton to higher trophic levels (Hernández-León et al., 2001; Hernández-León and Ikeda, 2005; Bode et al., 2018b).

Zooplankton modifies organic carbon via ingestion, sloppy feeding, incorporation into body tissue (growth, reproduction), egestion, i.e. repackaging into fecal pellets, excretion and respiration (Iversen et al., 2010; Steinberg and Landry, 2017; Maas et al., 2020; Pauli et al., 2021). In terms of passive carbon fluxes, these processes affect aggregate size spectra, biochemical composition, and consequently, sinking speed of particulate organic carbon on its way to the deep sea (Kjørboe, 2000; Iversen and Ploug, 2010). Fecal pellets can be degraded by the microbial loop, re-ingested by zooplankton and/or they may sink further to deeper layers forming larger, rapidly sinking aggregates (Stamieszkin et al., 2015; Steinberg and Landry, 2017; Pauli et al., 2021). Fecal pellet flux usually accounts for ≤40% of total passive POC flux. However, it is highly variable and strongly influenced by sporadic events, e.g. salp “blooms” (Bruland and Silver, 1981; Perissinotto and Pakhomov, 1998). In a recent global model, it was estimated that the passive carbon flux (= gravitational pump) is responsible for 70% of total global carbon export, of which 85% were zooplankton pellets, 15% sinking phytoplankton aggregates, while migrating zooplankton accounted for ~10% of total export (Nowicki et al. 2022). Pellet size, density and the abundance of key zooplankton taxa are critical determinants of passive POC fluxes. Pellets of copepods and euphausiids are able to sink tens to hundreds of meters per day, while larger and denser salp fecal pellets cover a daily

distance of more than one thousand meters (Thor et al., 2003; Turner, 2015; Steinberg and Landry, 2017; Karakuş et al., 2021; Pauli et al., 2021). In the Southern Ocean, for instance, feeding behavior and vertical distribution of the zooplankton community directly impacted the amount of carbon exported to the deep ocean (Manno et al., 2015). Therefore, the strength (surface processes of carbon uptake) and efficiency (subsurface processes of carbon transport to the deep sea) of the BCP depend heavily on biological components, e.g. microbial activity, zooplankton composition, grazing and particle aggregation, which may change regionally and/or seasonally (De La Rocha and Passow, 2007; Buesseler and Boyd, 2009; Turner, 2015; Armengol et al., 2019).

Active vertical carbon transport by diel migrants can represent a considerable portion of total carbon export (Al-Mutairi and Landry, 2001; Kobari et al., 2013; Stukel et al., 2013; Kwong et al., 2020), depending on the size, taxonomic structure of the associated zooplankton community and also hydrographic conditions (Al-Mutairi and Landry, 2001; Steinberg et al., 2008; Kiko and Hauss, 2019; Tutasi and Escrivano, 2020). In the Sargasso Sea, active carbon flux comprised 5–33% of the passive POC flux, and an increase in migrant mesozooplankton biomass caused a significant increase in the mean annual active carbon transport from the epi- to the mesopelagic zone (Steinberg et al., 2012). Shifts in the zooplankton community composition induced by climate change directly affect the global carbon cycle by impacting the transport of organic material from the surface ocean to great depths (Brun et al., 2019). Via vertical migration, organisms can transport biomass to deeper layers, where they respire, produce fecal pellets and/or they can be ingested by deeper-dwelling predators or are exposed to natural mortality. It is recognized that zooplankton body size, feeding strategies and DVM behavior affect the efficiency of the BCP (Steinberg et al., 2000; Al-Mutairi and Landry, 2001; Isla et al., 2015; Cavan et al., 2017; Brun et al., 2019; Hernández-León et al., 2019).

Copepod communities are characterized by high taxonomic and functional diversity (Steinberg and Landry, 2017) and they comprise 50–95% of total mesozooplankton biomass, playing a crucial role in marine food webs, biogeochemical cycles and consequently, in the BCP (Longhurst and Harrison, 1989; Turner, 2004; Brun et al., 2019). DVM is usually characterized by an ascent of certain zooplankton species to surface waters at

dusk/night, where they feed, followed by a descent at dawn/day, after which they reside at depth until the next ascent (Pearre, 2003; Isla et al., 2015). In contrast to this regular DVM, other migration patterns have been described, such as inverse DVM (iDVM) with a reversed movement pattern (Ohman et al., 1983) and ontogenetic vertical migration (OVM), where vertical movement is related to developmental stages (Hays, 1995; Holliland et al., 2012). Inverse diel migrants feed in the upper layers during the day and migrate to deeper layers during the night, presumably to maximize feeding while avoiding competition and/or predation by regular migrants (Bosch and Rowland Taylor, 1973; Ohman et al., 1983a; Pinti et al., 2019). Timing and distances traveled via DVM vary among species and regions, and the impact of this behavior on the active carbon flux critically depends on the biomass and metabolic demands of migrants and their respective DVM ranges. Grouping zooplankton communities by their key traits such as size, metabolic demand, feeding strategy and DVM behavior will help to understand their role in the BCP (Hays et al., 1994; Cavan et al., 2017; Brun et al., 2019; Teuber et al., 2019; Tutasi and Escribano, 2020).

Data on copepod distribution with high taxonomic resolution and their impact on the BCP in the subtropical South Atlantic are scarce. The present case study investigated vertical migration behavior of calanoid copepods and how they potentially affect the BCP in this area. In particular, we 1) describe the calanoid community structure and composition with a high taxonomic and vertical resolution; 2) identify diel vertical migrants; 3) determine key species involved in the removal of organic matter (ingestion) and active transfer of carbon out of the epipelagic zone and; 4) identify and compare different calanoid groups and elucidate their role in active and passive carbon fluxes via respiration and fecal pellet production (egestion). We discuss how the different calanoid functional groups impact the ocean's carbon cycle focusing on major traits such as body size, energetic demands, feeding strategies and DVM behavior. Finally, the high taxonomic and vertical resolution allowed us to develop a new method of estimating carbon fluxes by using the proportion of the taxon-specific migratory community instead of simple day-night differences in biomass. This new approach leads to more robust flux estimates, being less prone to errors, particularly for small sample sizes. Ultimately, this new approach provides a better framework to understand the importance of community composition and species-specific traits for the carbon flux mediated by calanoid copepods in the subtropical South Atlantic.

2 Material and methods

2.1 Study area and sampling

Mesozooplankton samples were collected in the southeastern Atlantic Ocean during the research cruise ANT

XXIX/1 with RV *Polarstern* in November 2012. Stratified vertical hauls were carried out within 24 h with a Hydro-Bios Multinet Maxi (0.5 m² net opening, 9 nets, 150 µm mesh size) from 800 m depth to the surface (strata: 800-700-600-500-400-300-200-100-50-0 m). The filtered water volume was measured with a flowmeter attached to the net opening. After retrieval, samples were preserved in a 4% borax-buffered formaldehyde in seawater solution. Abundance and community structure of calanoid copepods of one day (stn. 16; bottom depth 5,433 m) and one night station (stn. 15; bottom depth 5,462 m) were analyzed (Figure 1). Simultaneous profiles of temperature, salinity, and dissolved oxygen content were obtained with a conductivity temperature depth sensor (CTD) attached to a rosette water sampler (Fahrbach and Rohardt, 2008). Primary production rates were measured at each station via ¹³C bicarbonate tracer incubations, for details consult Fonseca-Batista et al. (2017).

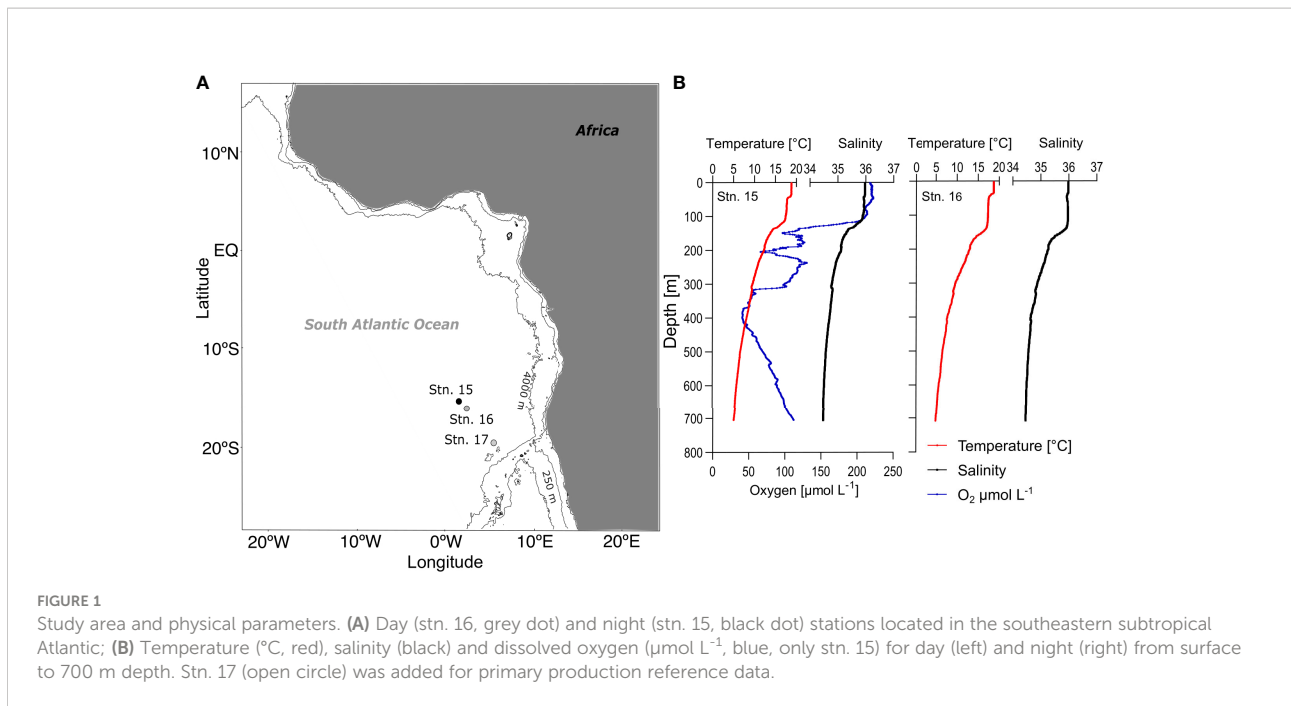
2.2 Abundance and biomass

In the home laboratory, formalin-preserved mesozooplankton samples were split (Motoda, 1959) and transferred to a sorting solution (0.5% propylene-phenoxetol, 5% propylene glycol and 94.5% deionized freshwater; Steedman, 1976). Calanoid copepods were sorted according to their developmental stages (copepodids C1-3 and C4/5, adult females and males), counted and identified to genus or, if possible, to species level under a dissecting microscope (Leica MZ12) (Bradford-Grieve et al., 1999; Razouls et al., 2005). Rare species (<100 individuals per sample) were counted from the entire sample. Total length (TL, mm) of up to 100 calanoid individuals per taxonomic category (i.e. family/genus/species) and stage was measured (~6,600 specimens in total). Abundance and size measurements data for all species found here are available from the data publisher PANGAEA via the persistent identifier <https://doi.pangaea.de/10.1594/PANGAEA.946061>. Dry mass (mg, DM) of calanoids [1] was calculated based on the median TL of each taxonomic category (Chisholm and Roff, 1990; Homma et al., 2011).

$$[1] \quad \ln DM = 2.74 \times \ln TL - 16.41$$

2.3 Carbon budget

Individual respiration rates (µl O₂ ind⁻¹ h⁻¹) for slow- [2, R_s] and fast-moving [3, R_f] calanoids were calculated by applying regression models based on ~300 *in situ* respiration measurements using a 10-Channel Fiber Optic Oxygen Meter (OXY-10, PreSens, Precision Sensing GmbH) during two research cruises in this area (Bode et al., 2013; Bode et al., 2018b). According to Bode et al. (2013) and Teuber et al. (2019), slow-moving copepods belong to the copepod families Eucalanidae, Subeucalanidae and Rhincalanidae, while all



other copepods represented fast-moving species. Individual respiration rates were calculated from individual DM (mg) and *in situ* temperatures (T), i.e. the median temperature ($^{\circ}\text{C}$) at the respective sampling depth, applying the equations from [Bode et al. \(2018b\)](#):

$$[2] \quad \ln R_s (\mu\text{l O}_2 \text{ ind}^{-1} \text{ h}^{-1}) \\ = -2.18 + 0.787 \times \ln(\text{DM}) + 0.131T$$

$$[3] \quad \ln R_f (\mu\text{l O}_2 \text{ ind}^{-1} \text{ h}^{-1}) \\ = -0.890 + 0.646 \times \ln(\text{DM}) + 0.094T$$

For non-migrating copepods, daily R_s and R_f were calculated for 24 h at their residence depth. For migrating copepods, a residence time of 12 h each was assumed in the upper and lower layers, respectively, and thus respiration and finally carbon demand were calculated for 12 h each at the two residence depths with the two respective *in situ* temperatures.

Since respiration rates from laboratory experiments usually reflect the copepods' routine or standard metabolism, they can be converted to carbon units to calculate the copepods' minimum energy requirements ([Ikeda et al., 2001](#)). For the calculation of respiratory carbon loss, oxygen consumption rates (R , $\mu\text{l O}_2 \text{ ind}^{-1} \text{ d}^{-1}$) were converted to respiratory carbon losses [4] (RC , $\mu\text{g C ind}^{-1} \text{ d}^{-1}$) assuming that 1 ml O_2 equals 0.44 mg organic carbon using a respiratory quotient (RQ) of 0.82 for a mixed diet consisting of proteins, carbohydrates and lipids ([Winberg, 1956](#); [Gnaiger, 1983](#); [Schukat et al., 2013](#)). MMC is the molar mass of carbon (12 g mol^{-1}) and MV the molar volume

of an ideal gas (22.4 L mol^{-1}):

$$[4] \quad RC = (\mu\text{g C ind}^{-1} \text{ d}^{-1}) = R \times \text{RQ} \times \frac{\text{MMC}}{\text{MV}}$$

Ingestion rates [5] (I , $\mu\text{g C ind}^{-1} \text{ d}^{-1}$) were calculated after [Ikeda and Motoda \(1978\)](#), using an absorption efficiency (U) of 0.7 and a gross growth efficiency (K_1) of 0.3. Egestion rates (E ; $\mu\text{g C ind}^{-1} \text{ d}^{-1}$) were assumed to be 30% of ingestion ($E = 0.3 \times I$) ([Ikeda and Motoda, 1978](#)).

$$[5] \quad I (\mu\text{g C ind}^{-1} \text{ d}^{-1}) = RC \times \frac{1}{U - K_1}$$

Total community ingestion and egestion for each taxon and copepodite stage was calculated based on their abundances per m^2 in the respective depth interval.

Particulate organic carbon (POC) flux to each underlying depth layer was assessed based on average primary production rates (C_{prod} , $\text{mg C m}^{-2} \text{ d}^{-1}$) in this region as determined by [Fonseca-Batista et al. \(2017\)](#) during the research cruise, and applying the equation after [Suess \(1980\)](#) [6], where C_{flux} is the POC flux ($\text{mg C m}^{-2} \text{ d}^{-1}$) at water depth $Z \geq 50 \text{ m}$.

$$[6] \quad C_{\text{flux}} (\text{mg C m}^{-2} \text{ d}^{-1}) = \frac{C_{\text{prod}}}{(0.0238 \times Z) + 0.212}$$

To assess the potential impact of calanoids on the POC flux, we used a box model after [Homma et al. \(2011\)](#) and modified after [Bode et al. \(2018b\)](#). Model parameters and assumptions were as follows: (i) the amount of organic carbon (OC) that enters the system (POC_{in}) is provided by primary production (PP) for the surface layer (0-50 m) and it can be calculated for

the subsequent strata according to [6] depending on water depth Z. (ii) The amount of OC that is lost within a layer can be consumed by calanoids; whatever is lost and is not directly consumed by calanoids, is accessible to other organisms within the same layer or will become available as suspended POC. (iii) The absorption efficiency ($U = 0.7$) is constant throughout the water column and the egestion of calanoids, i.e. fecal pellet production, contributes to the POC reaching the depth layer below. (iv) Remaining POC that is not ingested or is egested by others in the same layer, directly sinks. Lastly, (v) the RQ is constant throughout the water column and RC is lost as dissolved inorganic carbon (DIC) in the respective depth layer.

2.3.1 Diel vertical migration and active carbon transport

Based on differences in vertical distribution, species were assigned to four different types of migrant groups, switching between different depth zones with specific migration ranges, i.e. small-scale epipelagic migrants, large-scale DVM zone shifters, small- or large-scale migrants at the epi- and mesopelagic interface as well as large-scale mesopelagic migrants. To determine DVM distances, weighted mean depths (WMD) of taxa for both day and night stations [7] and migration ranges ΔZ (defined as WMD_{day} minus WMD_{night}) were calculated after Andersen et al. (2001).

$$[7] \quad WMD = \frac{\sum(n_i * z_i * d_i)}{\sum(n_i * z_i)}$$

where n_i is abundance per m^3 , z_i is the depth range of the respective sampling interval and d_i is the mid-depth of the sampling interval. Copepod species were identified and classified as non-migrants ($\Delta Z < 25$ m), small-scale migrants ($25 < \Delta Z < 100$ m), large-scale migrants ($\Delta Z > 100$ m), while inverse migrants were characterized by negative ΔZ .

Migrant biomass ($mg DM m^{-2}$) was estimated across different reference water depths, i.e. across 50 m depth (within the epipelagic zone), 200 m (across the upper mesopelagic boundary), 300 m (within the upper mesopelagic layer) and 400 m (across the lower mesopelagic boundary). Given the similarities between hydrographic regime and community composition among the sampled stations, we assume the migrants' habitat distribution did not change substantially. Due to currents and changes in water masses, species composition varies naturally in marine pelagic ecosystems. To compensate for these irregularities in day/night biomass, migrant biomass was calculated based on the migratory portion (MP) of a respective taxon instead of the simple difference in biomass between day and night. To determine the MP crossing a certain depth layer, the MP of biomass was calculated based on the absolute biomass of the night-time station and the relative changes in biomass vertical distribution between day and night. Albeit net avoidance is

not a concern for copepods, we propose this method to be applied for zooplankton carbon flux calculations in general. Therefore, to account for bias of net avoidance, the night-time biomass was determined as the final community to calculate the migrant's population proportion.

The total respiratory carbon flux (RC_{flux}) across the reference depths was calculated based on species-specific migrant biomass and energy requirement [8], indicating the daily downward RC_{flux} ($mg C m^{-2} d^{-1}$) calculated for 12 h at *in situ* temperatures at the respective resident depth:

$$[8] \quad RC_{\text{flux}} (mg C m^{-2} d^{-1}) = MRC_{\text{deep}} * B_{\text{tn}} * MP_z * 12hd^{-1}$$

where MRC_{deep} is the mass-specific respiration rate converted to carbon ($mg C mg DM^{-1} h^{-1}$), respired at depth during day (DVM) or during night (iDVM) calculated at *in situ* temperatures, B_{tn} is the integrated biomass of the respective migratory taxa at night ($mg DM m^{-2}$), and MP_z is the migrating portion of the population across the reference depth, i.e. the depth above or below which the largest MP was found.

3 Results

3.1 Hydrography

Both stations were located at the margin of the subtropical South Atlantic gyre, under the influence of the Benguela Current (BC) upwelling system. Sea surface temperature (SST) was relatively low at 18–19°C compared to other subtropical open-ocean regions. The mixed layer reached down to approx. 40 m, with another subsurface mixed layer down to approx. 105 m (0–38 m: 18.8°C, 49–105 m: 17.8–17.4°C; Figure 1). Below that, temperature and salinity decreased steadily with depth, reaching 5°C at 700 m. An oxygen minimum zone ($<60 \mu\text{mol O}_2 L^{-1}$) was present at the day station 16 between 320 and 450 m (minimum of $41 \mu\text{mol O}_2 L^{-1}$ at 386 m). For the night station, no oxygen profile is available due to technical problems. Chlorophyll *a* concentration was high compared to other oceanic regions in the eastern Atlantic Ocean during the research cruise. Primary production rates averaged $1012 mg C m^{-2} d^{-1}$ in this region during the cruise, which was used for our carbon budget calculations ($1429 mg C m^{-2} d^{-1}$ at stn. 15, $676 mg C m^{-2} d^{-1}$ at stn. 16 and $930 mg C m^{-2} d^{-1}$ at stn. 17 in Fonseca-Batista et al., (2017). The hydrography has been described in detail in Bode et al., (2015); Bode et al., (2018a); Bode et al., (2018b) and Fonseca-Batista et al. (2017).

3.2 Abundance and biomass

In total, 25 calanoid copepod families and 57 genera were identified, comprising at least 117 species. The mean total length

of the calanoids varied widely, ranging from 0.4 mm for copepodids of *Disco* spp. to 6.7 mm for *Eucalanus hyalinus* adult females. The calanoid copepod community showed pronounced vertical changes and depth zones could be divided into upper and lower epipelagic (UEL = 0-100 m, LEL = 100-200 m) as well as upper and lower mesopelagic layer (UML = 200-400 m, LML = 400-800 m).

In general, abundance and biomass decreased with depth, with maxima in the surface layer during night and day and a bimodal distribution during the day (Figure 2). Total calanoid abundance (TCA) decreased from max. 1289 ind m⁻³ during the night and 508 ind m⁻³ during the day in the surface layer to 203 ind m⁻³ (night) and 94 ind m⁻³ (day) in the 50-100 m layer and further to 35 ind m⁻³ (night) and 24 ind m⁻³ (day) in the 100-200 m layer. TCA increased again in the 200-300 m layer with 45 ind m⁻³ during the night and 147 ind m⁻³ during the day. Minimum TCA occurred in the deepest layer (700-800 m) with 8 ind m⁻³ at night and 6 ind m⁻³ during the day (Figure 2). TCA averaged for each the UML and LML yielded higher abundances during the day (UML = 113 ind m⁻³; LML = 16 ind m⁻³) as compared to the night (UML = 51 ind m⁻³; LML = 12 ind m⁻³).

Correspondingly, total calanoid biomass (TCB) was higher during the night with 33 mg DM m⁻³ in the upper 50 m compared to 14 mg DM m⁻³ during the day (Figure 2). TCB decreased strikingly with depth and was similar for both day and night in the 50-100 m layer (night-day = 4.4-4.3 mg DM m⁻³) and in the 100-200 m layer (night = 1.6 mg DM m⁻³; day = 1.1 mg DM m⁻³). TCB increased again in the 200-300 m layer with 4.8 mg DM m⁻³ during the night and 3.1 mg DM m⁻³ during the day. Minimum TCB occurred in the deepest layer (700-800 m) with 0.2 mg DM m⁻³ at night and 0.5 mg DM m⁻³ during the day (Figure 2). In accordance to abundance, TCB averaged for each the UML and LML yielded higher biomass at depth during the day (UML = 3.9 mg DM m⁻³; LML = 1.5 mg

DM m⁻³) as opposed to the night (UML = 2.5 mg DM m⁻³; LML = 0.7 mg DM m⁻³).

3.3 Community composition

Due to different roles in passive and active carbon fluxes, the calanoid community was divided into a non-migrant community at the respective residence depths and a migrant one between different depths, based on their species- and stage-specific weighted mean depths (WMDs) and migration ranges (ΔZ). If developmental stages showed different migration behavior within one species or genus, they were assigned to different groups. Non-migrant species of the families Eucalanidae, Subeucalanidae and Rhincalanidae were assigned to a separate group, the so-called “thrifty floater” community, since they are slow-moving copepods with low metabolic rates and potential bimodal vertical distribution. If ΔZ was >25 m but abundances were very low (≤ 0.5 ind/m⁻³), or rare species occurred only during day or night, their migration behavior could not be characterized, taxa were placed in an undetermined group. For details on WMDs see [Supplementary Material](#).

3.3.1 Non-migrants

In this study, around 42 calanoid taxa were identified as non-migrants ([Supplementary Figure 1](#)), as the difference between their day and night WMDs was <25 m. The non-migrant epipelagic community (0-200 m) consisted mostly of all copepodite and adult stages of *Acartia* spp., *Nannocalanus minor*, *Scolecithrix danae* and *Centropages bradyi*, and furthermore of *Calocalanus* C4/5 copepodids, *Clausocalanus* males and C1-3 stages, females and C4/5 copepodids of *Ctenocalanus* spp., *Neocalanus gracilis* C1-5 copepodids as well as females and copepodids C1-5 of *Euchirella* spp., *Lucicutia*

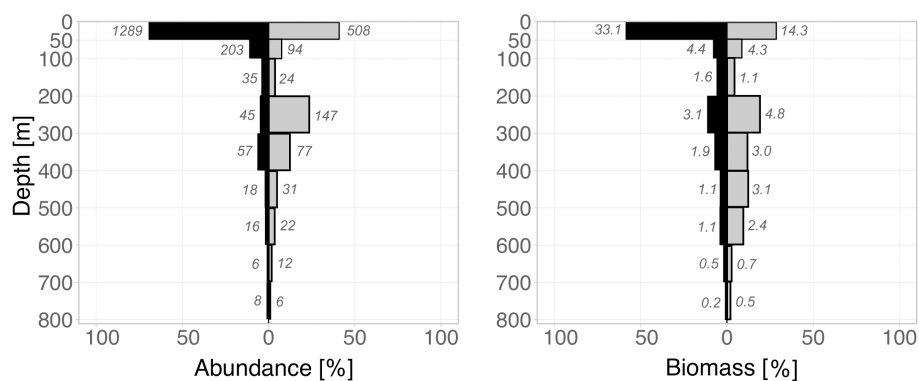


FIGURE 2

Vertical distribution of total calanoid copepod abundance (left) and biomass (right) from the surface to 800 m depth during day (grey bars) and night (black bars). The x-axis depicts the relative total calanoid abundance and respective biomass per station; the numbers beside each bar indicate absolute abundance (ind m⁻³) and biomass (mg DM m⁻³) in that specific depth layer.

gaussae and *Mecynocera clausi*. In addition, adult females and copepodids C1-5 of Paracalanidae (*Delibus*, *Paracalanus*) also had an important contribution to the energetic demands in the EL. In the upper and lower mesopelagic layers (200-800 m), the most important non-migrant taxa regarding the metabolic demands of the community were adult females and males of *Metridia effusa*, and *Spinocalanus* spp., all copepodite stages of *Metridia venusta*, *Scaphocalanus* and *Temoropia* spp., copepodids C1-5 of *Pleuromamma quadrungulata* and copepodids C4/C5 of *Scolecithricella*.

3.3.2 “Thrifty-floaters” and undetermined community

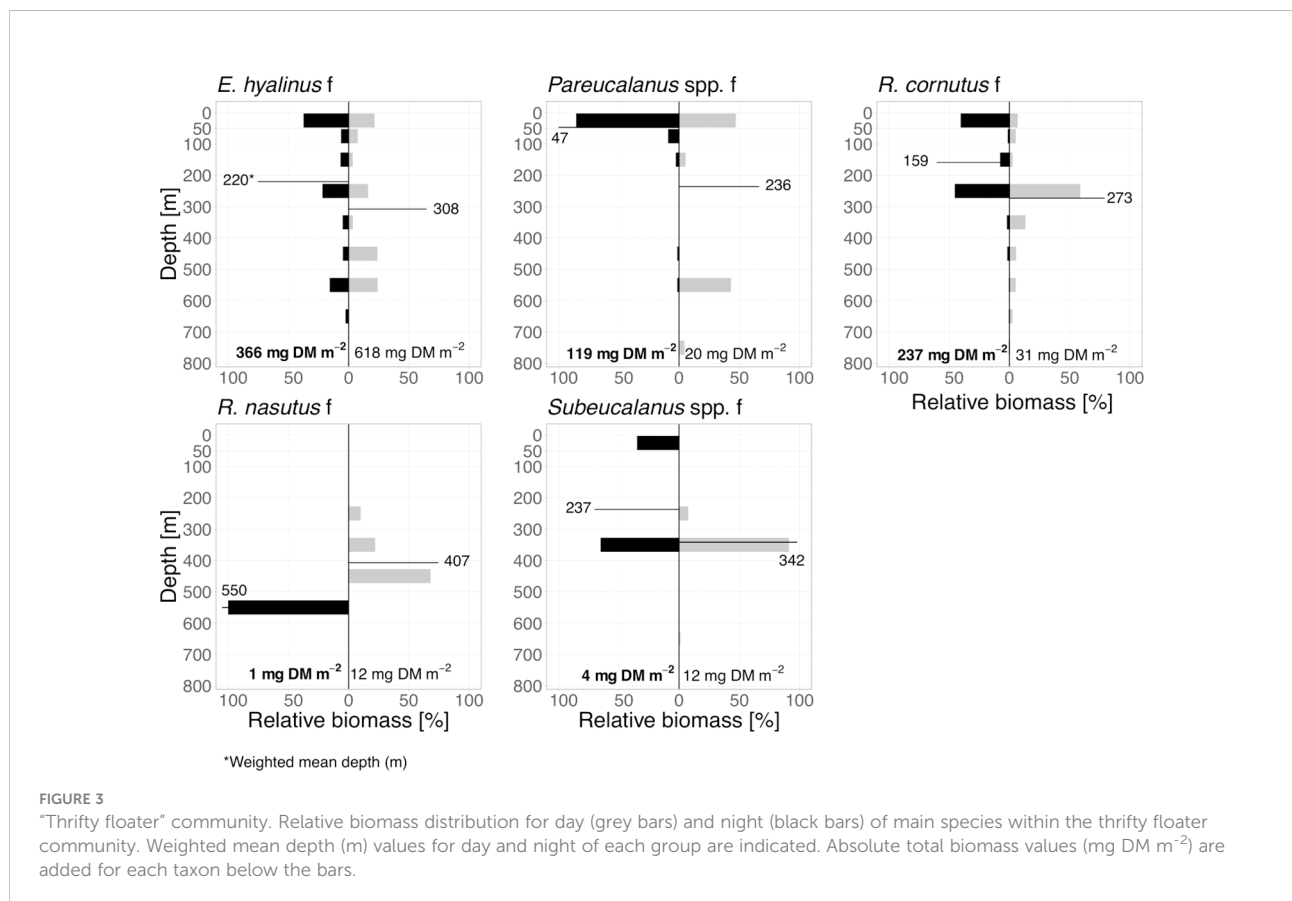
As mentioned above, within the non-migrants, we further characterized certain taxa based on their metabolic strategies. The “thrifty floater” term was coined by Teuber et al. (2019) and here referred to the group that consisted of *E. hyalinus*, *Rhincalanus cornutus*, *Rhincalanus nasutus*, *Subeucalanus* spp. (mostly *Subeucalanus mochachus/pileatus* and/or *subtenuis*) and *Pareucalanus* spp. (mostly *Pareucalanus sewelli* and/or *langae*) (Figure 3). Rather than undergoing DVM, these groups are assumed to have bimodal distribution patterns due to their special life cycle adaptations including opportunistic dormancy stages. Females of *E. hyalinus* and *R. cornutus* were dominant in

this group from EL to LML, while females of *R. nasutus* were also dominant at depth. Females of *Pareucalanus* spp. were less abundant, occurring mostly in the EL. In addition to *E. hyalinus* and *R. cornutus*, adult females and copepodids C1-3 and C4/5 of *Subeucalanus* spp. as well as C1-3 and C4/5 stages of *Pareucalanus* spp. were also abundant at depths during the day (Figure 3).

The undetermined group was mainly composed of Metridinidae C1-3. Due to the low taxonomic resolution, their migration behavior could not be resolved. Copepodids C1-3 of *Scolecithricella* spp., copepodids C4/5 of *Pseudoamallothrix* spp. and *Metridia curticauda/brevicauda* contributed to total calanoid ingestion but, their migratory behavior was also unclear (Supplementary Figure 1).

3.3.3 Diel vertical migrants

In total, 25 calanoid taxa performed large- ($\Delta Z > 100$, m) and small-scale (ΔZ between 25 and 100 m) regular DVM and inverse DVM (iDVM). Calanoids were separated into four migrant functional groups containing a regular (r) and inverse (i) DVM subgroup according to their WMDs during night and day, migration behavior (large-/small-scale) and their association with specific depth zones (EL, UML, LML) (see also Tables 1, 2 and Figure 4 for DVM, Figure 5 for iDVM).



Metridia lucens was treated separately, as it is a known large-scale migrant. However, it was absent at our night station, but highly abundant at 200–800 m during the day (38 ind m^{-3}). It was classified as a large-scale zone shifter, since copepodids C4/5 had a WMD of 440 m and females of 320 m during the day, assuming that 100% of the population migrated into the 0–50 m layer during night (Table 1).

Group 1 - Small-scale epipelagic migrants: *Small-scale migrants in the EL, migrating within 0–200 m, never leaving this depth zone.*

1_r: Copepodids C1–3, adult females of *Calocalanus* spp. were classified as small-scale migrants within the upper EL with WMDs of 80 and 72 m for the day and 30 and 45 m for the night, respectively. *Mesocalanus tenuicornis* females migrated within the entire EL, with WMD of 150 m during the day and 92 m at night (Figure 4 and Table 1).

1_i: iDVM in the upper 100 m was performed by copepodids C1–3 and C4/5 of *M. tenuicornis*. WMDs for these stages were 34 and 36 m during the day, while at night WMDs were 63 and 64 m, respectively. *N. gracilis* females migrated within the entire EL with WMDs of 75 m during day and 156 m during night (Figure 5 and Table 1).

Group 2 - Large-scale DVM zone shifters: *Large-scale migrants moving across the EL (200 m) to the UML and/or LML.*

2_r: *Pleuromamma borealis* had a large migration distance of >200 m with day WMDs of 247–257 m and night WMDs of 25–33 m for copepodids C1–5 and adult females. Day WMDs of females and C4/5 of *Clausocalanus* spp. (263 and 302 m, resp.) and *Pleuromamma abdominalis* (344 and 302 m, resp.) were similar to those of *P. borealis*. However, these two species were scattered in multiple upper water layers during the night, while a small part of the population seemed to stay at depth. Males of small *Pleuromamma* spp. (*P. borealis/gracilis/piseki*) were summarized in one category, as they are morphologically difficult to identify to species level. They had a WMD of 450 m during the day and 101 m at night. Other species were also large-scale zone shifters, however, with much lower abundances: *Pleuromamma xiphias* females (WMD day: 650 m, WMD night: 174 m), *P. quadrangulata* males (WMD day: 568 m, WMD night: 176 m), *Pleuromamma robusta* females (WMD day: 367 m, WMD night: 150 m), *Scottocalanus securifrons* females (WMD day: 450 m, WMD night: 150 m), *Lucicutia* c.f. *ovalis* females, males and C1–5 copepodids (WMDs day: 50–75 m, WMDs night: 750 m) (Figure 4 and Table 1).

2_i: Large-scale iDVM was performed by *Aetideus armatus* (C1–3) and *Aetideus giesbrechti* females, exhibiting day WMDs of 75 m and 150 m, respectively, and night WMDs of 303–350 m (Figure 5 and Table 1). However, only a small part of the populations seemed to migrate (24% and 10% migratory portion, respectively).

Group 3 - Small- or large-scale DVM at the epi- and mesopelagic interface: *Small- or large-scale migrants within the UML; the majority of the populations always remained below 200 m.*

3_r: Females of *P. quadrangulata* occurred with a daytime WMD of 350 m and a nighttime WMD of 228 m. Yet, a smaller part of the population also migrated into the LEL connecting this zone to the UML (Figure 4 and Table 1).

3_i: Small-scale iDVM was performed by *M. effusa* (C1–5) and *Scolecithricella* spp. (males) with similar day and night WMDs of ~265/272 m and 313/354 m, respectively (Figure 5 and Table 1).

Group 4 - Large-scale DVM mesopelagic zone shifters: *Large-scale migrants within the mesopelagic zone, switching between UML and LML.*

4_r: This category comprised typical deep-sea species including copepodids C4/5 of *Scottocalanus* and adult females of *Augaptilus longicaudatus*, *Haloptilus paralongicirrus*, *Metridia venusta* and *Spinocalanus* c.f. *magnus*. Daytime WMDs ranged between 431 to 650 m in this group, while nighttime WMDs were between 250 and 412 m (Figure 4 and Table 1).

4_i: Females of *Euchirella pulchra* and *Haloptilus* c.f. *oxycephalus* comprised this group, with daytime WMDs of 485 and 546 m, respectively. At night, WMD was 650 m for both (Figure 5 and Table 1).

3.4 Carbon budget and active carbon fluxes

Total calanoid community ingestion (TCI) of the non-migrant group including the “thrifty floater” and undetermined groups in the EL (0–200 m) ranged from 98 mg C m⁻² d⁻¹ at the day stn. 16 to 208 mg C m⁻² d⁻¹ at the night (stn. 15), while migrants (G1_r, G2_r and *M. lucens*) consumed 98 mg C m⁻² d⁻¹, i.e. only nighttime feeding in the EL (Figure 6). Within the UML, 17 to 24 mg C m⁻² d⁻¹ were ingested by the non-migrant group and only 0.9 mg C m⁻² d⁻¹ by deeper migrant groups (G3_r, G4_r). Thus, the non-migrating community had the largest impact on carbon fluxes in the respective depth ranges. Non-migrant calanoids were responsible for the potential consumption of 10–21% of primary production in the EL, whereas another 10% could be attributed to migrant species. In the mesopelagic layers, rather low fractions of incoming POC were potentially consumed by calanoid copepods, with the majority of POC_{in} consumed by non-migrants in the UML (8.3–12.0%) and in the LML (7.1–9.0%) (Figure 6).

Among the non-migrating taxa, *N. minor* females and C1–3 (9–35 mg C m⁻² d⁻¹), *Acartia* spp. females and C1–3 (28–36 mg C m⁻² d⁻¹) and *M. clausi* females (2–20 mg C m⁻² d⁻¹) contributed most to EL community consumption. Altogether, non-migrants consumed a total of 56–153 mg C m⁻² d⁻¹ in the upper 50 m, and the largest fraction was ingested by adult females with 34–75 mg C m⁻² d⁻¹. Overall, the undetermined DVM group ingested 5–9 mg C m⁻² d⁻¹ in the EL (0–200 m). The “thrifty floater” group ingested a total of 18–21 mg C m⁻² d⁻¹ in the EL, with the large *E. hyalinus* (8–14 mg C m⁻² d⁻¹) and *R. cornutus* (3–6 mg C m⁻² d⁻¹) showing highest community consumption rates. Since

TABLE 1 Respiratory carbon (RC flux) and egestive carbon (EC flux) flux of the dominant diel vertical migrating copepods.

Functional group	Stage	WMD		ΔZ	MC depth		Reference depth	MP	MB	RC flux	EC flux
		[m]			[m]						
		Day	Night	Day	Night						
1_r Small-scale DVM surface residents											
<i>Calocalanus</i> spp.	F	72	45	27	50-100	0-50	50	65	6	0.6	0.4
	C1-3	80	30	50	50-100	0-50	50	93	8	0.8	0.6
<i>M. tenuicornis</i>	f	150	92	58	100-200	50-100	100	77	6	0.1	0.1
1_i Small-scale iDVM surface residents											
<i>N. gracilis</i>	f	75	156	81	50-100	0-50	100	38	7	0.1	0.1
<i>M. tenuicornis</i>	C1-3	34	86	52	0-50	50-100	50	88	1	<0.1	<0.1
	C4/5	36	87	51	0-50	50-100	50	85	1	<0.1	<0.1
2_r Large-scale DVM zone shifters											
<i>Clausocalanus</i> spp.	f	263	142	121	200-300	0-50	200	60	17	0.4	0.3
	C4/5	222	81	141	200-300	50-100	200	59	7	0.2	0.1
<i>P. abdominalis</i>	f	344	179	165	200-300	50-100	200	67	15	0.1	0.1
	C4/5	302	164	138	200-300	0-50	200	53	10	0.1	0.1
<i>P. borealis</i>	f	256	33	223	200-300	0-50	200	94	178	2.6	2.0
	C1-3	247	25	222	200-300	0-50	200	98	25	0.7	0.5
	C4/5	257	25	227	200-300	0-50	200	99	119	2.4	1.8
<i>Pleuromamma</i> spp.	m	450	101	349	500	0-50	200	79	135	0.9	0.7
<i>M. lucens</i> *	f	322	-	-	-	-	200	-	12	0.1	0.1
	C4/5	440	-	-	-	-	200	-	179	2.5	1.9
Others**	-	-	-	-	-	-	-	-	-	0.5	0.4
2_i Large-scale iDVM zone shifters											
<i>A. armatus</i>	C1-3	150	350	200	100-200	300-400	200	24	0.2	<0.1	<0.1
<i>A. giesbrechti</i>	f	150	303	153	100-200	200-300	200	10	0.1	<0.1	<0.1
3_r Large-scale DVM mesopelagic residents											
<i>P. quadrangulata</i>	f	350	228	122	300-400	200-300	300	78	12	0.1	0.1
3_i Small-scale iDVM mesopelagic residents											
<i>M. effusa</i>	C1-3	250	313	63	200-300	200-300	300	15	<0.1	<0.1	<0.1
	C4/5	272	353	81	200-300	300-400	300	75	2	<0.1	<0.1
<i>Scolecithricella</i> spp.	m	265	354	89	200-300	300-400	300	38	2	<0.1	<0.1
4_r Large-scale DVM mesopelagic zone shifters											
<i>A. longicaudatus</i>	f	452	250	202	400-500	200-300	400	93	1	<0.1	<0.1
<i>H. paralongicirrus</i>	f	442	302	140	200-300	200-300	400	21	2	<0.1	<0.1
<i>M. venusta</i>	f	546	412	134	400-500	200-400	400	79	2	<0.1	<0.1
<i>Scottocalanus</i> spp.	C4/5	650	380	270	500-600	300-400	400	100	2	<0.1	<0.1
<i>Spino. c.f. magnus</i>	f	431	328	103	400-500	300-400	400	28	4	<0.1	<0.1
4_i Large-scale iDVM mesopelagic zone shifters											
<i>E. pulchra</i>	f	485	650	165	200-300	600-700	400	58	1	<0.1	<0.1
<i>H. c.f. oxycephalus</i>	f	546	650	104	400-500	700-800	500	52	0.2	<0.1	<0.1

**M. lucens* was absent in the night station but assumed to be a large-scale DVM zone shifter. Estimates refer to total mesopelagic biomasses, carbon respiration and egestion for 12 h down (MP assumed to be 100%).

**Other migrant species with particularly low contributions to the RC flux, such as: *Lucicutia c.f. ovalis* f, m and C1-5; *Scottocalanus securifrons* f; *Pleuromamma robusta* f; *Pleuromamma xiphias* f and C4/5; *Pleuromamma quadrangulata* m.

Small-scale (25-100 m), large-scale (>100 m), regular and inverse migrants within and between the EL (0-200 m), UML (200-400 m) and LML (400-800 m) are listed in their respective functional group. Weighted mean depth (WMD) for day and night of each functional group are given. DZ is the mean distance migrated (m). MC depth (m) is the layer where the majority of the community (MC) resided during the day and night. Reference depth (m) is the layer taken as the threshold to calculate RC flux, above or below which the majority of the population resided, the respective migrant biomass (MB, mg DM m⁻²) and finally the respiratory carbon (RC) and egestive carbon (EC) fluxes were calculated. F, female; m, male; C, copepodids.

TABLE 2 Percentage contribution of most important (>5% FG flux) regular migrants within respective functional groups to total respiratory carbon (RC) flux across reference depths.

FG	FG RC flux [mg C m ⁻² d ⁻¹]	Depth [m]	Components	% FG flux
G1 _r	1.5	50	<i>Calocalanus</i> spp. C1-3	53
			<i>Calocalanus</i> spp. f	39
			<i>M. tenuicornis</i> f	8
G2 _r	10.5*	200	<i>P. borealis</i> f	25
			<i>M. lucens</i> f	24
			<i>P. borealis</i> C4-5	23
			<i>Pleuromamma</i> spp. m	9
			<i>P. borealis</i> C1-3	6
G3 _r	0.1	400	<i>P. quadrangulata</i> f	49
G4 _r	0.1	400	<i>Spino. c.f. magnus</i> f	21
			<i>H. paralongicirrus</i> f	11
			<i>Scottocalanus</i> spp. C4-5	9
			<i>M. venusta</i> f	7

*This includes *M. lucens*. FG, functional group.

community ingestion decreased with depth while diversity increased, taxon-specific community ingestion was generally ≤ 10 mg C m⁻² d⁻¹ in the UML and ≤ 4 mg C m⁻² d⁻¹ in the LML.

Among the migrants, highest ingestion rate in the EL was observed for G2_r (62 mg C m⁻² d⁻¹). Most of this carbon was consumed in the upper 0-50 m by *P. borealis* (44 mg C m⁻² d⁻¹). Within G1_r migrants, a total of 7.6 mg C m⁻² d⁻¹ was ingested in the EL (Figure 6), with *Calocalanus* spp. being the main consumer (7.3 mg C m⁻² d⁻¹). Young copepodids C1-3 and adult females of small *Calocalanus* spp. and *M. tenuicornis* (migrant group G1_r) transported up to 1.5 mg C m⁻² d⁻¹ as respiratory carbon (RC) and 1.1 mg C m⁻² d⁻¹ as egestive carbon (EC) from the 0-50 m into the 50-100 m layer. Migrant group G2_r actively transported 7.9 mg RC m⁻² d⁻¹ and 6.0 mg EC m⁻² d⁻¹ from the EL down into upper mesopelagic layers, with *P. borealis* (5.7 mg RC m⁻² d⁻¹) as main contributor (C1-6 stages, Tables 1, 2). *M. lucens* was assumed to be a large-scale zone shifter. *M. lucens* copepodids C4/5 had a WMD of 440 m and females of 320 m during day, but the species was completely absent in the night samples. As known migrants, they potentially transported 2.6 mg RC m⁻² d⁻¹ and 2.0 mg EC m⁻² d⁻¹ from the surface layers into the UML and even LML. Assuming a migratory portion of 100% into the 0-50 m, *M. lucens* potentially added a maximum of 28 mg C m⁻² d⁻¹ to TCI in the surface layer (Figure 6 and Table 2).

Due to the very low abundances of mesopelagic migrants (G3_r and G4_r), active transport of carbon within the UML and into the LML was present but low (Table 1). Adult females of *P. quadrangulata* (G3_r) actively transported 0.1 mg C m⁻² d⁻¹ as each, RC and EC across 300 m within the UML, while *M. effusa* (G3_i) transported <0.1 mg C m⁻² d⁻¹ of RC and EC across that depth (Tables 1, 2). Likewise, low values were observed across 400 m for deeper LML migrants G4_r (Table 1 and Figure 2).

Inverse migrants made a very small contribution to the community fluxes. G1_i and G3_i were the most important groups, ingesting around 0.9 mg C m⁻² d⁻¹ in the upper 0-100 m and 0.4 mg C m⁻² d⁻¹ in the UML, respectively. Active transport by inverse migrants was very low with overall 0.2 mg C m⁻² d⁻¹ of both RC and EC (Table 1; G1_i – G4_i).

4 Discussion

Comparing active versus passive carbon fluxes of depth-stratified calanoid copepod communities and identifying the key players involved in each community helps to disentangle carbon pathways and better understand the ocean carbon cycle. We identified different functional groups of calanoid communities with specific roles in export and recycling processes and consequently in the biological carbon pump (BCP) in the subtropical Southeast Atlantic, an area largely understudied.

The limited number of stations analyzed here represent large uncertainties in our flux estimates and functional groupings. Yet, to the best of our knowledge, no other studies within this particular region of the South Atlantic attempted to estimate export fluxes and migration patterns of the calanoid community, let alone in such detail. Despite the lack of replication, our results fit well to previous studies discussed below (see also Table 3). The calanoid community composition in this area corroborates the composition of our functional groups (Bode et al., 2018a; Bode et al., 2018b; Teuber et al., 2019). Mesotrophic conditions with high abundances of small- to medium-sized calanoids have been reported for the eastern subtropical South Atlantic influenced by the Benguela Current, i.e. upwelling filaments can extend up to 600 km offshore (~72-93 species found;

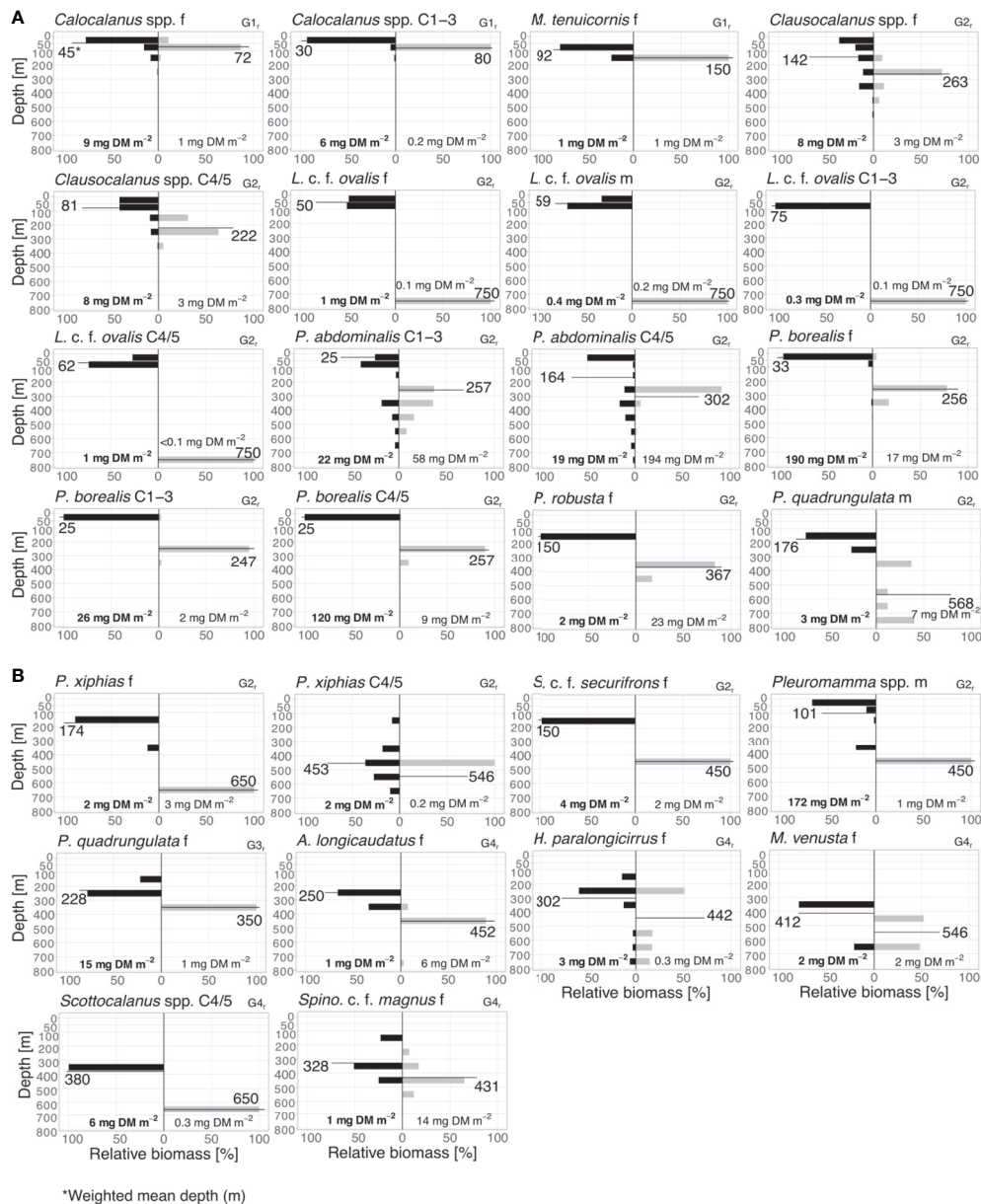


FIGURE 4
 Diel vertical migrants. **(A)** Biomass distribution of main regular diel vertical migrants (G₁ – 2₁) and **(B)** biomass distribution of main regular diel vertical migrants (G₂ – 4₁). Absolute total biomass values (mg DM m⁻²) are given for day (grey bars) and night (black bars) for each taxon. Weighted mean depths (m) for day and night for each group are indicated.

Woodd-Walker, 2001; Woodd-Walker et al., 2002; Schnack-Schiel et al., 2010; Bode et al., 2018a; Bode et al., 2018b). Zooplankton biomass values in the upper 200 m have been reported to display rather weak seasonal and interannual signals in open ocean regions (Martin et al., 2015).

Generally, studies focusing on carbon fluxes are restricted to the epipelagic layer (<200 m), with differences in biomass being only attributed to the presence of diel vertical migrants, disregarding other possible causes (e.g. currents/changes in

water masses, species composition, patchiness). However, biomass and abundance mismatches have been observed in studies even when replication was possible. For instance, in the coastal upwelling system off northern Chile, total zooplankton biomass integrated over 600 m was ~1.7 times higher during the night than during the day (Escribano et al., 2009). Additionally, biomass of the copepod *Eucalanus inermis* integrated for the upper 600 m also varied 1.9-4.3 times between the same stations sampled during day and night off northern

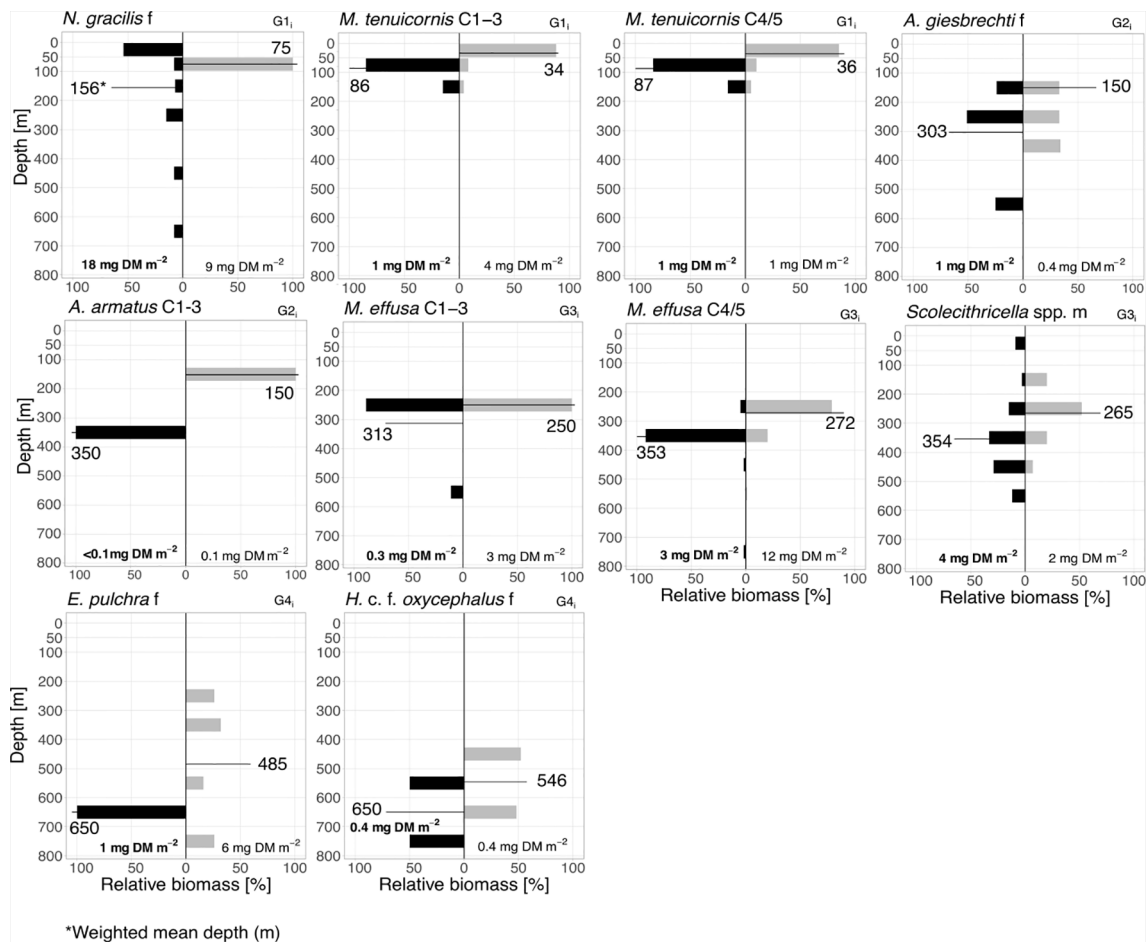


FIGURE 5

Inverse diel vertical migrants. Biomass distribution of main inverse diel vertical migrants (G1-4). Absolute total biomass values (mg DM m⁻²) are given for day (grey bars) and night (black bars) for each taxon. Weighted mean depths (m) for day and night of each group are indicated.

Chile (Hidalgo et al., 2005). Schukat et al. (2021) also observed a ~1.2-1.9 times difference in abundance (0-100 m) within the same stations during day and night (two 24 h stations, sampled at 6 h intervals) for the surface-concentrated species, *Calanus chilensis*, from the northern Humboldt Current off Peru. As such, differences in biomass/abundance between day and night (here, ~1.8 times higher biomass in the night sample) may not necessarily be a consequence of small sample size and/or too dissimilar oceanographic stations but appears to be a natural phenomenon of marine pelagic copepod communities. Consequently, our approach to calculate active flux based on the proportion of the taxon-specific migratory community to a given depth bypasses this issue and should be considered in future studies.

The processes on how migrant copepod communities affect export fluxes in the pelagic realm can vary according to seasonality (high migrant biomass leading to high carbon removal in post-bloom conditions, Isla et al., 2015), environmental parameters and

region (Cavan et al., 2017; Archibald et al., 2019b; Kiko and Hauss, 2019), community composition (Yamaguchi et al., 2002; Wassmann et al., 2003; Brun et al., 2019; Soviadan et al., 2021) and size (Iversen et al., 2010; Turner, 2015; Ohman and Romagnan, 2016). The total active respiratory carbon (RC) flux of calanoid copepods across 200 m added up to 10.5 mg C m⁻² d⁻¹, which equals 3.8 g C m⁻² y⁻¹. This was about twice as high as the annual mean for the Bermuda Atlantic Time-Series study (BATS) area in the oligotrophic subtropical North Atlantic gyre with 1.5 ± 0.5 g C m⁻² y⁻¹ actively transported across 150 m (Table 3; Steinberg et al., 2012). Our study area was still affected by the highly productive Benguela Current (Bode et al., 2018a; Bode et al., 2018b), which may have caused higher abundances of migrant species, and as such, a higher RC flux compared to the one in the oligotrophic region from the BATS site. To compare our study with existing literature, we assumed a 12 h residence time at any given depth during the day or night to calculate the RC flux of migrants, which may lead to an overestimation (Dam et al.,

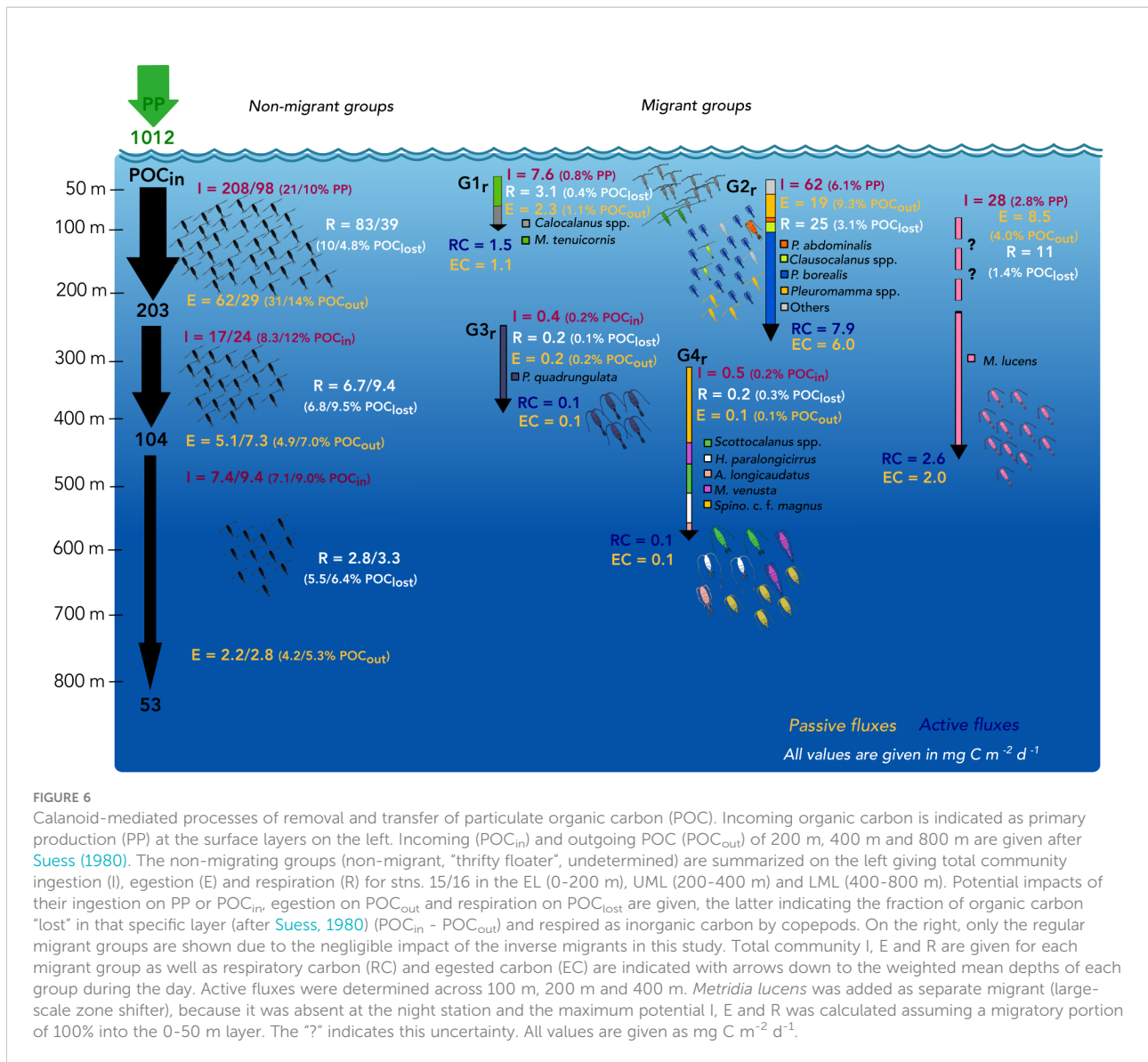


FIGURE 6

Calanoid-mediated processes of removal and transfer of particulate organic carbon (POC). Incoming organic carbon is indicated as primary production (PP) at the surface layers on the left. Incoming (POC_{in}) and outgoing POC (POC_{out}) of 200 m, 400 m and 800 m are given after Suess (1980). The non-migrating groups (non-migrant, “thrifty floater”, undetermined) are summarized on the left giving total community ingestion (I), egestion (E) and respiration (R) for stns. 15/16 in the EL (0–200 m), UML (200–400 m) and LML (400–800 m). Potential impacts of their ingestion on PP or POC_{in}, egestion on POC_{out} and respiration on POC_{lost} are given, the latter indicating the fraction of organic carbon “lost” in that specific layer (after Suess, 1980) (POC_{in} - POC_{out}) and respired as inorganic carbon by copepods. On the right, only the regular migrant groups are shown due to the negligible impact of the inverse migrants in this study. Total community I, E and R are given for each migrant group as well as respiratory carbon (RC) and egested carbon (EC) are indicated with arrows down to the weighted mean depths of each group during the day. Active fluxes were determined across 100 m, 200 m and 400 m. *Metridia lucens* was added as separate migrant (large-scale zone shifter), because it was absent at the night station and the maximum potential I, E and R was calculated assuming a migratory portion of 100% into the 0–50 m layer. The “?” indicates this uncertainty. All values are given as mg C m⁻² d⁻¹.

1995; Zhang and Dam, 1997; Steinberg et al., 2012; Ariza et al., 2015). Nevertheless, according to the newest quantification of the biological carbon pump, the total carbon export for a respective “tropical” region, where our stations were located, was 30 g C m⁻² y⁻¹, of which 11% (equals 3.3 g C m⁻² y⁻¹) could be assigned to migrating zooplankton (Nowicki et al., 2022), thus, fitting well to the estimated values in the present study.

Considering that the South Atlantic has an area of ~40 million km² (https://www.ngdc.noaa.gov), the active carbon flux of calanoid copepods from the epi- to the mesopelagic zone, mostly caused by small- to medium-sized *P. borealis* and *M. lucens*, yielded an estimate of 1.5 Mt C y⁻¹ in the present study. This flux was actively transported down as respiratory carbon via DVM and may represent an important source of carbon removal in the oceans. In the Southern Ocean, macrozooplankton was

estimated to contribute 0.12 Gt C y⁻¹ to total modeled carbon export across 150 m (Karakuş et al., 2021) and zooplankton-mediated processes accounted for up to 80% of salp fecal pellet flux (Pauli et al., 2021). Altogether, a mean global carbon export of ~10.2 Gt C y⁻¹ was recently estimated, still containing high uncertainties, especially due to high spatial and seasonal variability. This suggests a weakening of the ocean’s carbon storage capacities due to climate-change-induced stratification and expansion of the subtropical gyres (Nowicki et al., 2022). In contrast, in the northern North Atlantic, for instance, carbon export increased due to shifting distributions of abundant, large-sized copepods (Brun et al., 2019).

For macrozooplankton, e.g pelagic decapods, within the northern Benguela upwelling system, the potential RC flux out of the EL was 4.4 mg C m⁻² d⁻¹ and 2.6 mg C m⁻² d⁻¹ within the

TABLE 3 Literature data of active carbon fluxes (respiratory carbon) from epi- to mesopelagic depths mediated by mesozooplankton in different areas/regions of the world ocean in comparison with our study.

Active carbon flux		Study Area	Reference
mg C m ⁻² d ⁻¹	g C m ⁻² y ⁻¹		
10.5		Subtropical (eastern) South Atlantic	Present study
	1.5	North Atlantic subtropical gyre (BATS)	Steinberg et al., 2012
2.0-9.9		North Atlantic subtropical gyre region	Steinberg et al., 2000
6.2-40.6		North Atlantic subtropical gyre region	Dam et al., 1995
1.13-4.45		Canary Island region	Ariza et al., 2015
1.92-4.29		Canary Island region	Hernández-León et al., 2001
1.85-8.28		Canary Island region	Yebera et al., 2005
0.9-83.3		Subtropical Atlantic	Hernández-León et al., 2019a
2.8-8.8		Eastern tropical Pacific, subtropical (northwest) Atlantic, Sargasso Sea	Longhurst and Harrison, 1989
4.9		ALOHA	Hannides et al., 2009
1.4-35.1		ALOHA and K2	Steinberg et al., 2008
3.6		ALOHA	Al-Mutairi and Landry., 2001
7.3-19.05		Equatorial Pacific	Hidaka et al., 2001
20.4		Equatorial Pacific	Zhang and Dam., 1997
49		NW Mediterranean	Isla et al., 2015
1.1		Subarctic (K2) and subtropical (S1) North Pacific	Kobari et al., 2013

BATS, Bermuda Atlantic Time-Series study; ALOHA, A Long-term Oligotrophic Habitat Assessment, North Pacific subtropical gyre.

UML and LML between 200 and 600 m, respectively (Schukat et al., 2013). Species-specific migration behaviors are evident for the decapods, as also shown for the copepods in our study, emphasizing that migration patterns and distances vary across species. However, highly variable standard deviations for the species-specific WMDs (0 to 124 m) of the decapod species (Schukat et al., 2013) indicate the importance of further research on migration amplitudes for copepods in the Benguela Current and adjacent regions. Patchiness and net avoidance of macrozooplankton and micronekton can have a crucial impact on abundance and thus subsequent estimates such as RC flux, highly depending on the sampling efficiency of the net used (Schukat et al., 2013 and references therein). For copepod sampling, however, net avoidance is not a concerning factor (Pillar, 1984). In this study, biomass of non-migrants within 0-200 m did not show a considerable difference between day and night biomass (430 versus 578 mg C m⁻², resp.), also indicating a minor potential effect of the sampling gear.

In the present study, the majority of organic carbon was consumed by the non-migrant groups, while their abundance and biomass decreased with depth, which is the typical pattern seen for pelagic ecosystems with decreasing food availability (Yamaguchi et al., 2002; Kosobokova et al., 2011). Overall, the potential impact of calanoid community ingestion on primary production (PP) in the epipelagic layer (EL) was relatively low (10-21% of PP for non-migrant and 10% of PP for migrant groups). These values are reasonable considering the high primary production due to the influence of the Benguela Current (Bode et al., 2018b) and that, especially in (sub)

tropical open-ocean regions, microzooplankton (<200 μm) are major phytoplankton consumers resulting in more complex and potentially less efficient food chains (Dam et al., 1995; Hernández-León et al., 2002; Calbet and Landry, 2004). The importance of smaller-sized calanoids, not only in terms of abundance but also in terms of grazing, and their role in ecosystem functioning has been recognized since the 1990s (Morales et al., 1991; Turner, 2004). However, distribution studies on a high taxonomic level are extremely time-consuming and therefore rare, ultimately limiting our understanding of the carbon pathways and flux dynamics between the epi- and mesopelagic realms, and the role of smaller-sized calanoids in it. It has been estimated that small copepods (<2 mm total length) ingest 1.8-27.2 Gt C y⁻¹ globally, suggesting that this ignored metazoan-copepod link could increase current estimates of biogeochemical fluxes and export to higher trophic levels and cannot be neglected in global models (Roura et al., 2018).

4.1 Export versus recycling calanoid communities

Copepod size has been appointed as a key trait responsible in determining the amount of fecal pellets (FP) that reach the deep sea, with community composition playing a major role in the variability of this flux (Steinberg et al., 2012; Stamieszkin et al., 2015; Steinberg and Landry, 2017). Small FP have reduced aggregation potential and sinking rates, and as such they are

more exposed to coprophagy, coprophagy and/or microbial remineralization processes, reducing sinking FP flux and increasing retention processes (Kjørboe, 2000; Kjørboe, 2001; Iversen and Poulsen, 2007; Steinberg et al., 2012; Stamieszkin et al., 2015). Species >2 mm total length (TL) may already contribute substantially to sinking POC fluxes (Stamieszkin et al., 2015; respective prosome lengths (PL) were converted to TL with a mean copepod PL:TL ratio of 0.8). Hence, copepods of ≤ 1.3 mm TL mostly contribute to the recycling of carbon and nutrients in their respective depth layer, while fecal pellets of medium-sized species (~ 1.3 – 2.0 mm TL) may partly sink out and contribute to export processes. Major consumers in the present study were small species of *Paracalanus*, *Delibus*, *Ctenocalanus*, *Mecynocera*, *Calocalanus* (max. mean TL 0.8 mm) and *Acartia* (max. mean TL 1.2 mm), as well as medium-sized *N. minor* (max. mean TL 2.1 mm), *P. borealis* (max. mean TL 2.0 mm) and *M. lucens* (max. mean TL 2.3 mm). Of these dominant species, the latter three may partly contribute to the vertical POC fluxes in a given layer due to their sizes. *P. borealis* and *M. lucens* also transport respiratory and egestive carbon down to mesopelagic layers via DVM, linking the surface layer to the twilight zone (Kelly et al., 2019). Bode et al. 2018a, b described similar results of small copepod species dominating total copepod ingestion in the epipelagic zone in this area.

Epipelagic small-scale regular migrants such as *Calocalanus* spp. also transport respiratory and egestive carbon from the upper into the lower epipelagic zone, where it can fuel the microbial loop, deep chlorophyll maxima or, in terms of organic carbon, be potentially ingested by other migrant or non-migrant zooplankton. $G1_i$ was the group with the largest contribution to the active flux among inverse migrants. Yet, they had a much lower impact on the overall active RC carbon across 50 m ($0.2 \text{ mg C m}^{-2} \text{ d}^{-1}$) when, compared to regular migrants, with *N. gracilis* females being the most important taxon. Small (sub) tropical epipelagic calanoids are characterized by constantly high metabolic rates (Kattner and Hagen, 2009; Teuber et al., 2013), thus, they may be continuously feeding, egesting, producing molts etc. High fecal pellet production rates will greatly support the epipelagic and mesopelagic microbial communities (Thor et al., 2003).

“Thrifty floater” taxa such as *E. hyalinus*, *R. cornutus*, *Pareucalanus* spp. (max. mean TL 3.6–6.7 mm) and larger migrants such as *P. abdominalis* (max. mean TL 3.5 mm) can have a major impact on the export POC fluxes at epi- and mesopelagic depths, as they produce larger, rapidly sinking fecal pellets. The ‘thrifty floater’ species are able to retrieve into oxygen minimum zones (Auel and Verheye, 2007). They may actively reduce their metabolic rates and enter event-driven dormancy at copepodid C5 or adult females, when resource conditions are unfavorable (Teuber et al., 2014; Teuber et al., 2019). These species typically show bimodal vertical distribution patterns, as seen in the present study, and likely contribute to the export via fecal pellet flux throughout the entire water column.

In contrast, large DVM species such as *P. abdominalis* were present only in low abundances in this subtropical oceanic region. Yet, in colder, more productive regions large DVM key species have a high impact on both passive and active carbon fluxes and such play an important role in terms of global biological carbon pump efficiencies (Steinberg and Landry, 2017; Karakuş et al., 2021; Pauli et al., 2021).

In total, the large-scale zone shifters ($G2_r$) alone ingested approximately 6% of surface PP and transferred up to $7.9 \text{ mg C m}^{-2} \text{ d}^{-1}$ into the upper mesopelagic zone, representing the most important group regarding the active transfer of carbon into the twilight zone. *M. lucens* can likely be added to this group (Timonin et al., 1992; Atkinson et al., 1996; Timonin, 1997), but with an even deeper day-time residence depth transporting up to $2.5 \text{ mg C m}^{-2} \text{ d}^{-1}$ into the lower mesopelagic zone (Figure 6). Few reports exist of *Clausocalanus* migrating in large numbers (Roe, 1984; Wishner et al., 2008) and about diel changes of *P. borealis* (Roe, 1972; Roe, 1984; Andersen et al., 2004). Little is known about the movement of smaller taxa (e.g., *Microcalanus*) despite their acknowledged significant ecological and biogeochemical roles (Roura et al., 2018). Besides larger-sized *P. abdominalis* and *P. xiphias*, the small congeners of *Pleuromamma gracilis* undergo similar DVM in the North Pacific subtropical gyre (Ambler and Miller, 1987). Interestingly, active ambush-feeders (carnivores) such as *A. armatus* and *A. giesbrechti* were performing iDVM with very small RC flux contributions ($< 0.01 \text{ mg C m}^{-2} \text{ d}^{-1}$). However, reports describing species that display iDVM are scarce (Roe, 1984) and insight into the ecological feedback is still limited (Pinti et al., 2019). Due to the few reports on taxa performing inverse migration and the low biomass found in our study, their contribution to the active transfer of carbon was reasonably small. Avoiding the competition of regular migrants and finding better feeding opportunities appear to be vital drivers of iDVM (Ohman et al., 1983), but this behavior is not yet fully understood. Overall, studies on the species-specific DVM behavior of abundant organisms in the oceans are still lacking and focusing on their traits will have a significant impact on how we model global carbon cycles. New camera systems used to collect distributional data in the field could help to better understand and integrate these different behaviors into Earth's system models (Giering et al., 2020; Kiko et al., 2020; Maas et al., 2021).

It is not well understood if epi- and mesopelagic smaller-scale migrants are continuously feeding and egesting (Ambler and Miller, 1987). The extent to which migrant copepods defecate their gut contents during non-feeding residence times at depths is still not known. Gut passage times of copepods are highly variable among species and difficult to assess (Morales et al., 1991). For instance, sub-Antarctic *M. lucens* and *Pleuromamma robusta* were feeding mainly during the night in upper layers with rather long gut evacuation times leading to potential defecation of some of the food ingested in surface layers at depth (Atkinson et al., 1996). Mean gut passage times of

migrating *P. xiphias* and *Euchirella messinensis* from the BATS site (Bermuda) were 191 and 114 min., respectively (Schnitzer and Steinberg, 2002). Longer gut evacuation times were observed among large-scale DVM species and are likely due to lower temperatures at depth depressing their metabolism (Atkinson et al., 1996; Schnitzer and Steinberg, 2002). Furthermore, high metabolic rates and continuous food availability may argue for constant feeding of epipelagic active converters (Kattner and Hagen, 2009; Teuber et al., 2019) such as *Calocalanus*, but for the mesopelagic zone this is still largely unknown. Several species have been observed to adapt their DVM behavior to food availability in highly variable ecosystems such as the southern Benguela upwelling system with calanid copepods remaining in the more productive upper layers for the entire 24 h and stopping DVM, if food availability is low (Huggett et al., 2007). *M. tenuicornis*, also a calanid copepod, did not perform such small-scale DVM in the oligotrophic North Pacific Central gyre (Ambler and Miller, 1987), exemplifying how much this behavior can vary. Mesopelagic migrants may take advantage of higher food concentrations in the epi- and mesopelagic interface, i.e. increased POC fluxes below the euphotic zone (Buesseler and Boyd, 2009; Sano et al., 2013; Le Mézo and Galbraith, 2021), but may have to feed continuously due to generally lower food availabilities at depth. This may depend on the feeding strategy and trophic preferences of respective species, e.g. predatory cruising vs. detritivorous scavenging.

4.2 Cascading effects on the carbon export mediated by diel vertical migrants

Both retention and export processes can be greatly enhanced by the activities of diel vertical migrants, essentially “feeding” the mesopelagic realm (Wassmann, 1998; Isla et al., 2015; Gorgues et al., 2019; Stukel et al., 2019; Hernández-León et al., 2020). There are different potential cascading effects depending on how different calanoid species or groups can successively transport carbon even deeper into the ocean’s interior via DVM, following the so-called Vinogradov’s ladder of migration (Vinogradov, 1962; Hernández-León et al., 2020). The different migration depths and occurrence ranges (100–600 m) of decapods (Schukat et al., 2013) and calanoid copepods (this study, Supplementary Figure 2) indicate that Vinogradov’s ladder of migration applies within zooplankton orders. The carbon transport along this ladder has been described for zooplankton biomass in general (Hernández-León et al., 2020), but the processes how carbon is successively passed on are not well understood. In our study, for instance, large non-migrants (e.g. *E. hyalinus*) produce large fecal pellets in EL which can sink out into and enrich the UML. Here, omnivorous-detritivorous mesopelagic migrants, (e.g. *Scottocalanus*) may readily feed on this carbon material once ascending to the UML and then returning to the LML for the rest of the day (Sano et al., 2013; Le Mézo and Galbraith, 2021). Small-scale epipelagic inverse and regular migrants of group 1 (G1_r: *Calocalanus*; G1_i: *M.*

tenuicornis, *N. gracilis*) transport carbon ingested at the surface to subsurface layers, where subsurface phytoplankton can be fueled by the CO₂ respired or by the nutrients made available via the microbial loop from their fecal pellets (Turner, 2002; Steinberg and Landry, 2017). In G1_i, *M. tenuicornis* (max. mean TL 2.2 mm) and *N. gracilis* also produce fecal pellets large enough to sink out into the LEL or UML.

In the twilight zone, sinking materials become increasingly important as food source and omnivorous-detritivorous and carnivorous feeding strategies are advantageous (Vinogradov, 1962; Kiørboe, 2000; Kiørboe, 2001; Koppelman and Frost, 2008; Sano et al., 2013; Bode et al., 2018b; Teuber et al., 2019; Maas et al., 2020). For instance, dissolved organic matter excreted by migrating *P. xiphias* has been identified to enrich and support growth of the mesopelagic microbial communities (Maas et al., 2020), further creating pathways between the upper and lower layers of the ocean. Although in our study, biomass of iDVM groups was low and therefore, their cascading effects appear weak, inverse mesopelagic migrants (e.g. G3_i and G4_i) can effectively repack organic matter from the layer below the epipelagic zone. Much like regular migrants, this can be achieved by transporting carbon further into the ocean’s interior, where it can either be respired, egested (with subsequent recycling or sinking out) or ingested (as prey). They can prey upon regular migrants of G2 calanoids, their fecal pellets or organic matter derived from the microbial loop (Turner, 2002; Iversen and Ploug, 2010; van der Jagt et al., 2020). For example, in G3_i, medium-sized *M. effusa* and *Scolecithricella* spp. (max. mean TL 1.6 mm) produce intermediate-sized fecal pellets, which may partly sink out and partly be immediately remineralized (Thor et al., 2003; Iversen et al., 2010; van der Jagt et al., 2020), constituting an important component of the processes maintaining the BCP. In the northern Benguela upwelling system, mesopelagic migrant decapods transported organic carbon ingested in upper mesopelagic layers deeper into lower mesopelagic depths (Schukat et al., 2013). As such, DVM can be a significant gateway for nutrients to reach the upper mesopelagic community, where active input of organic matter can provide enough energy to sustain the deeper-living organisms’ demands (Stukel et al., 2019; Hernández-León et al., 2020).

5 Concluding remarks

In the light of current anthropogenic emissions of 36.6 Gt CO₂ y⁻¹ (2018; <https://de.statista.com>), our estimates of copepod active carbon fluxes in the eastern South Atlantic may appear depressingly low. High uncertainties still exist in global carbon export models and their predictions for the future ocean, especially due to high regional and seasonal variability. Our case study in the subtropical South Atlantic emphasizes the complexity of the copepods’ role in the biological carbon pump

in subtropical oceanic regions, demonstrating how the identification of different calanoid functional groups may disentangle mechanisms of carbon recycling and export processes. Applying this approach with higher spatial coverage and in regions with higher migrant biomass, will elucidate the different mechanisms, in which carbon is transported along Vinogradov's ladder of migration into the deep ocean, particularly if considering also other zooplankton key taxa such as salps, euphausiids or decapods. Hence, the pieces of the puzzle still need to be resolved and put together. Identifying key plankton functional types will help us to better quantify and accurately model the mechanisms and pathways involved in the ocean's carbon cycle.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: <https://doi.pangaea.de/10.1594/PANGAEA.946058>, PDI-31522.

Author contributions

LDFO sorted and identified the specimens, conducted the morphological and data analyses and wrote the manuscript. MBD supervised the abundance and data analyses and contributed significantly to writing the manuscript. AS supervised the active flux calculations and together with HA and WH contributed to the supervision and finalization of the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be constructed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.920483/full#supplementary-material>

SUPPLEMENTARY FIGURE 1

Biomass distribution of species with undetermined diel vertical migration behavior. Absolute total biomass values (mg DM m^{-2}) are given for day (grey bars) and night (black bars) for each taxon. Weighted mean depths (m) for day and night of each group are indicated.

SUPPLEMENTARY FIGURE 2

Average day (open circles) and night (closed circles) weighted mean depths of calanoid functional groups. Range of migrations among groupings demonstrate Vinogradov's ladder of migrations, with overlapping communities transporting and potentially exchanging resources into deeper waters from surface layers.

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