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Fecal Pellet Production by North Atlantic Zooplankton

A thesis submitted in partial fulfillment of the requirement
for the degree of Bachelor of Science in Biology from William & Mary

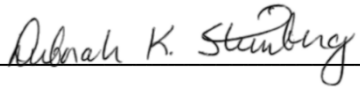
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Abstract

Fecal pellet carbon (FPC) production by zooplankton is a significant component of the ocean's biological carbon pump: the suite of biological processes that mediate export of carbon to the deep ocean, ultimately leading to the sequestration of atmospheric carbon dioxide in the ocean. In this study, mesozooplankton (zooplankton 0.2 mm to ~2 cm) were collected from the epipelagic zone in the temperate North Atlantic Ocean during day and night in May 2021. Zooplankton were live separated into five size fractions and incubated on board ship in natural surface seawater to measure fecal pellet production rate of the mixed mesozooplankton community. Individual animals in each size class used in experiments were counted and identified by major taxonomic groups, and fecal pellets were counted, measured, and analyzed by CHN analysis to determine amount of particulate organic carbon and nitrogen produced as fecal pellets. Despite having a small contribution to dry-weight biomass relative to individual abundance, zooplankton in the smallest size class (200-500 μm) contributed the most to FPC production. When normalized for total dry weight biomass of animals collected throughout the May 2021 cruise, FPC production was higher during the night than day, but this difference was not significant. This research is important to our understanding of the ocean's biological pump, allowing us to more accurately model the impact of the open oceans – the largest ecosystem on earth – on long-term climate regulation.

Introduction

The export of organic matter from the surface waters to the deep ocean is an extremely important process that fuels pelagic and benthic ecosystems worldwide, and is a major component of global carbon and nitrogen cycling. The oceans' biological pump, the suite of biological processes that mediate export of carbon to the deep ocean, is one of the largest carbon sequestration processes in the world and is driven by biological activity across many trophic levels. Without the carbon export carried out by the oceanic biological pump, ~50% more CO₂ would be present in Earth's atmosphere (Sanders et al. 2014). One of the most important ways by which organic matter reaches deeper into the water column is by zooplankton fecal pellet production and export. Zooplankton of many types graze on phytoplankton and egest fecal pellets that sink and become a major component of 'marine snow,' as deep-sea sediment trap studies demonstrate (reviewed in Turner, 2015). The biological pump is also enhanced by the diel-vertical migration behavior of many zooplankton, by which mesopelagic zooplankton feed on primary producers near the surface during the night, and then return to the deep during the day to metabolize their food and egest fecal pellets (Steinberg & Landry, 2017). The carbon and nitrogen in fecal pellets exported below the surface or mixed-layer zones is less likely to be returned to the atmosphere and is thus 'sequestered' at depth.

The amount of fecal pellet production, and carbon/nitrogen export to the deep ocean is determined by the size, abundance, and type of zooplankton present in an ecosystem

(Steinberg and Landry 2017, Stamieszkin et al., 2021). For example, zooplankton size affects how much fecal matter and total carbon are being produced in an ecosystem, as smaller zooplankton produce smaller fecal pellets, which sink at a slower rate and are thus more likely to be fragmented and consumed by other organisms (Liszka et al. 2019).

Remineralization of fecal pellets by bacteria in the water column also decreases carbon export to the deep ocean, although to a lesser extent than fragmentation and consumption (Belcher et al. 2016). In the subarctic North Pacific Ocean, fecal pellets produced by small zooplankton were abundant in the upper epipelagic zone, but quickly attenuated as depth increased (Stamieszkin et al., 2021). Sediment trap studies found that, on average, about 86% of small fecal pellets are attenuated upon reaching a depth of 100m, thus pellets contributed relatively little to flux of particulate organic carbon (POC) to the mesopelagic zone and deeper (Stamieszkin et al., 2021; Durkin et al., 2021).

In this study, I analyze fecal pellet carbon (FPC) produced by mesozooplankton in the North Atlantic Ocean during late May. This research is part of the EXport Processes in the Ocean from RemoTe Sensing (EXPORTS) project; a large, interdisciplinary study comparing the ocean biological carbon pump in the North Pacific and Atlantic Ocean (Siegel et al. 2016). I compare my North Atlantic results to those from a similar analysis in the North Pacific Ocean to better understand how zooplankton community structure affects carbon export.

Methods

Zooplankton Collection and Live Experiments

The sampling and experiments on live plankton examined in this study took place during the EXPORTS research cruise, May 1st to June 1st, 2021, in the North Atlantic Ocean west of the British Isles. (I was not present for live zooplankton collection and experimentation; these were conducted by members of the Steinberg laboratory at sea during the EXPORTS cruise.)

Zooplankton collection and experiments followed the protocols explained in Stamieszkin et al. (2021) for the North Pacific. Briefly, live zooplankton for experiments were collected at a depth of 15m during the day and night with a 1-m diameter, 200 μm plankton net.

Zooplankton were live sorted into five size fractions using nested mesh-bottomed buckets (200, 500, 1000, 2000, and 5000 μm) with each size fraction placed into incubation testing chambers containing natural surface seawater and incubated on board ship at in situ sea surface temperature. The zooplankton were above the mesh (200 μm), with the intent to allow fecal pellets to sink through and prevent zooplankton from feeding on, or breaking up, the sinking pellets (Stamieszkin et al. 2021) (Fig. 1). At the end of the experiment fecal pellets were collected and frozen for future analysis. I analyzed one of these experiments for my thesis, with samples taken during the night (21:45-23:40 local time) on May 28, and during the day (09:13-09:59 local time) on May 29, 2021. For both day and night, two replicate containers were prepared for each zooplankton size class, resulting in four samples

to analyze for each size fraction (two animal samples and two fecal pellet samples), plus two controls.

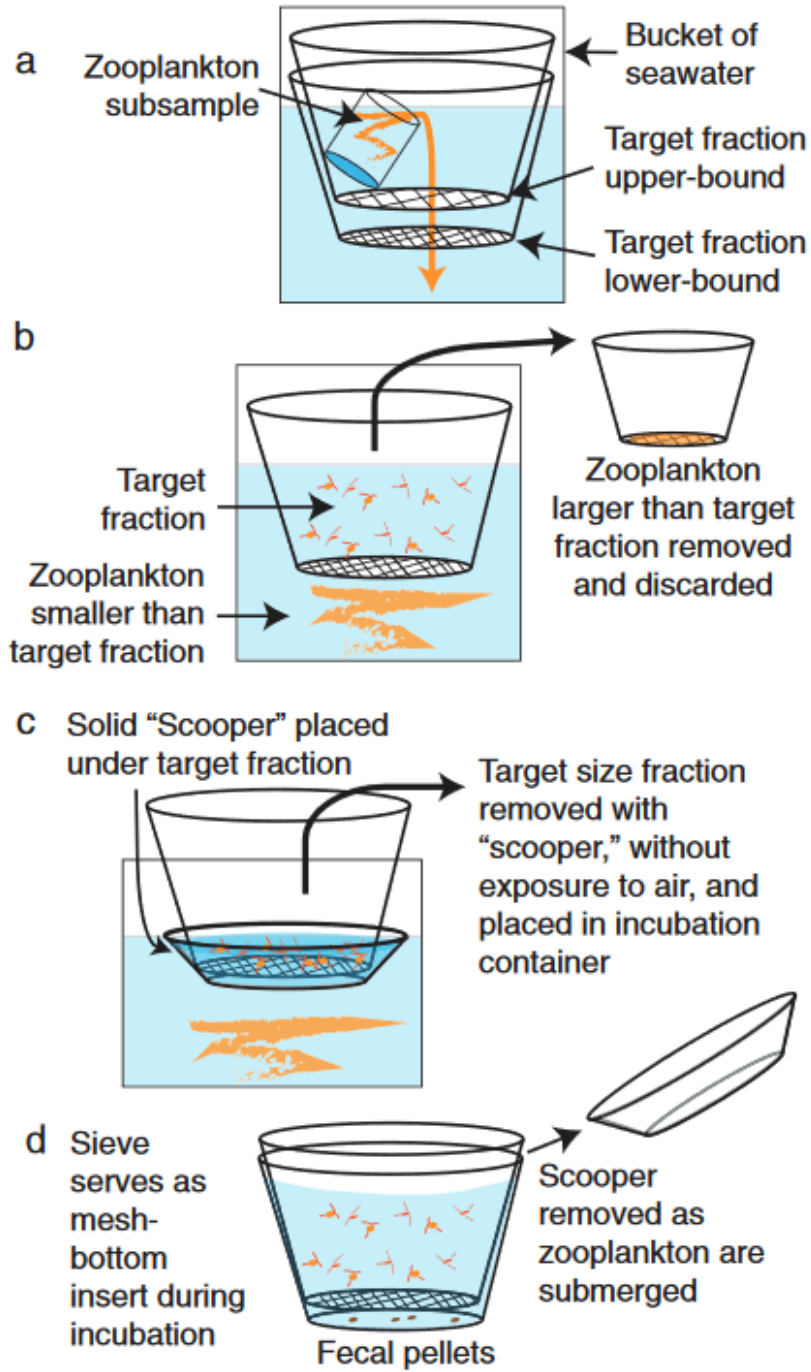


Figure 1. Illustration of live zooplankton experimental procedure carried out during the May 2021 cruise. Taken from Stamieszkin et al. (2021).

Finally, a Multiple Opening Closing Net and Environmental Sensing System (MOCNESS) was used to collect zooplankton within the upper 0-100m of water throughout the entire research cruise. Data for these tows was used to 'scale up' FPC production per dry weight of zooplankton in each size fraction to FPC production per square meter in the top 0-100m of ocean (epipelagic zone) for each size fraction, during day and night for all zooplankton size fractions combined.

Zooplankton and Fecal Pellet Analysis

Analysis of the zooplankton and fecal pellet samples at the VIMS zooplankton ecology lab began in Fall 2022. Frozen zooplankton and fecal pellets were analyzed from experiments conducted during day and night. Samples of zooplankton and fecal pellets were thawed and poured into petri dishes with marked quadrants for ease of counting under an Olympus SZX12 dissecting microscope. The zooplankton were counted and identified based on major taxonomic groupings (e.g., copepod, amphipod, cladocera, gastropod, etc.) rather than by species level, and were deposited into a smaller petri dish to isolate them from debris in the water (including occasional fecal pellets, which were removed and added to the fecal pellet fraction – see below). The animals were emptied onto filter discs of predetermined mass, and rinsed in ammonium-formate solution to remove residual salts left on the animals from their storage in seawater. Filters were weighed immediately after animals were transferred for wet weight measurements (not used in any analysis) and then left in a 60°C

drying oven for >24 hours before re-weighing for dry weights. All weight measurements were taken on a Sartorius BP211D digital balance.

Fecal pellet samples were similarly thawed and poured into a petri dish with marked quadrants. Any animals found in the fecal pellet samples were added to the same petri dish where animals were isolated. Fecal pellets were pipetted out of the sample dish into a rotating acrylic counting wheel. Using an Infinity3-3UR camera, attached to the same dissecting microscope, pellets were imaged at a consistent 250x magnification using Infinity Analyze software. Settings within the software were changed as needed for clarity of the images, but only small adjustments were made. Afterwards, images of fecal pellets were opened in CellSens for measurement. Fecal pellets were measured individually for length & width in CellSens using the polyline tool, and values were entered manually into an excel spreadsheet. Using a calibration slide with a line of known length, pixel length-measurements given by Cellsens were converted into millimeters. The equation for an ovoid $V = (4/3) \pi (\text{length})(\text{width}^2)$ subsequently was applied to pellet dimensions, assuming length as the greater value measured on each pellet, to calculate volumes. Pellet volumes were converted to mg carbon using the equation $0.041 (1 \text{ Stdev} = \pm 0.019) \text{ mgC} * V (\text{in mm}^3) = \text{mg Carbon mm}^{-3}$ (Gleiber et al. 2012). After imaging, pellets were poured using a funnel onto 25mm GF/F filter disks and vacuum filtered. Pellets were then transferred to small tubes, labeled, and re-frozen for CHN analysis at a later time (CHN Data not included in my analysis).

Statistical Analysis

This study replicated the statistical analysis performed in Stamieszkin et al. (2021). A Wilcoxon ranked-sum test was applied to data on fecal pellet volumes during day vs night to determine any significant diel differences in pellet size. Similarly, a one-way ANOVA was applied to FPC data for zooplankton size classes to determine any significant difference in average FPC between plankton size classes. The standard deviation of the pellet volume to carbon equation from Gleiber et al. (2012) was carried forward throughout all data and used to calculate standard errors. All statistical tests were performed in R-studio, and all data was manipulated and graphed in Excel.

Results

Environmental Context

During the daytime sampling for this experiment, temperature at depth of collection (0-15 meters) was 12.8°C, salinity was 35.56 PSU, chlorophyll *a* fluorescence 1.75 mg/m³, and oxygen 263 µmol/kg. The mixed layer depth during the day was ~35 meters. During the nighttime sampling, temperature at 15 meters was 12.7°C, salinity was 35.55 PSU, chlorophyll *a* fluorescence 2.0 mg/m³, and oxygen 265 µmol/kg. The mixed layer depth during the night was ~20 meters.

Zooplankton Community Structure

The highest abundance of animals occurred in the smallest (200-500 µm) size fractions, but despite their abundance, their total dry weight biomass often was less than that of animals in larger size classes. Cladocera made up the majority of individuals in smaller size fraction samples, and small copepods and gastropods were more abundant at night than during the day (Table 1). Larger animals like amphipods and polychaetes were more abundant during the night. Foraminifera and Acantheria were abundant in many samples but are not further considered in this study as they are single-celled organisms that do not produce fecal pellets. Note that controls still contain some zooplankton, as whole/unfiltered seawater was used for experiments (Table 1).

Table 1. Mesozooplankton abundance in incubation experimental containers (volume ~4-liters) classified by general taxonomic group.

Experiment	Size Class	Cladocera	Copepod	Gastropod	Foram	Acantheria	Krill	Polychaete	Medusa	Pteropod	Amphipod	Cliopyramidata	Chaetognath
18 (Day)	200	431	93	17	3						1		
18 (Day)	200	376	76	9	1								1
18 (Day)	500	89	68			9	3	1		18			
18 (Day)	500	73	60	2	5				2	10			
18 (Day)	1000	19	43	4	6	3		1					
18 (Day)	1000	15	33	4	3	9							
18 (Day)	2000	19	8	4	2	6							
18 (Day)	2000	21	24	15	6	5							
18 (Day)	5000											2	
18 (Day)	5000											2	
18 (Day)	200 (ctrl)		4										
18 (Day)	200 (ctrl)		55		2								
16 (Night)	200	108	23	10	3	3							
16 (Night)	200	295	59	10	4	3					1		
16 (Night)	500	69	140	8	5	2					6		
16 (Night)	500	28	44	3	4	1					1		
16 (Night)	1000	4	42	9	5		1						1
16 (Night)	1000	4	42	3	2	5							
16 (Night)	2000	2	42	1	10	14		1					
16 (Night)	2000	13	41	8	10	6		3					
16 (Night)	5000	9	16	7	9	2		1			6		
16 (Night)	5000	29	48	1	2			11			3		1
16 (Night)	200 (ctrl)		14	1	1								
16 (Night)	200 (ctrl)	1	37	2	4	1							

Fecal pellet size and carbon content

There was no statistically significant difference between fecal pellet size (volume) during the day vs during the night (Wilcoxon Ranked-Sum test $p = .5283$). In addition, there was no statistically significant difference in average FPC between plankton size classes (one-way ANOVA $p = .342$).

FPC production normalized for zooplankton biomass and time

FPC production (normalized for zooplankton biomass and incubation time; FPC/DW*hr) decreased as size class increased for both day and night experiments (Fig. 2). The 200-500 μm size class made up >50% of the mesozooplankton community FPC production (Fig. 3), and was significantly higher than any other size class. FPC production decreased in each

subsequent larger size class, however, due to high variability, the only statistically significant difference between any two size fractions was between 200 and 500 μm . FPC production was higher during the day vs night in all but the 2000 and 5000 μm size classes (Fig. 2), and larger size classes made up a higher proportion of community FPC at night (Fig. 3). Overall, FPC production per experimental dry weight biomass was about 2-fold higher during the day (0.051 mgC/mgDW*hr) versus at night (0.023 mgC/mgDW*hr).

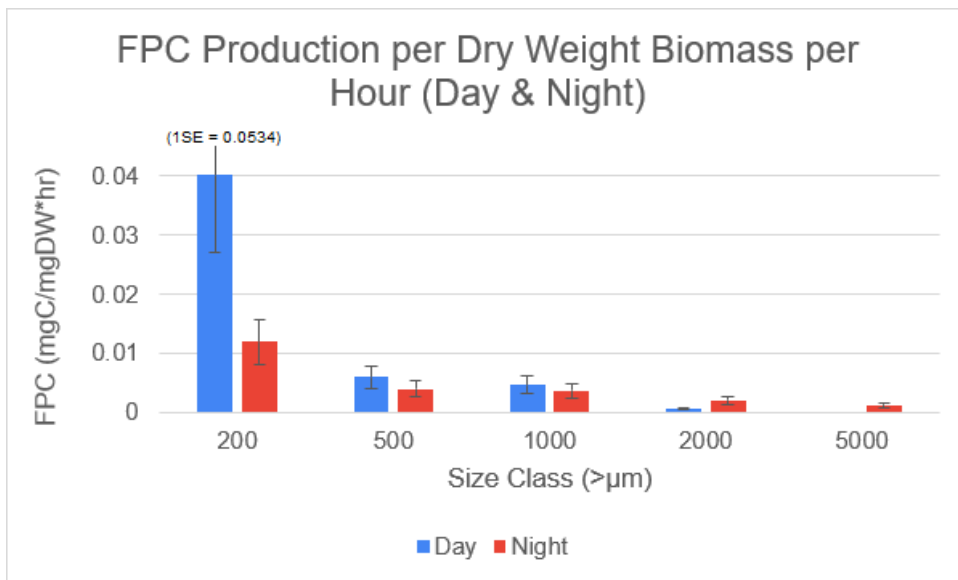


Figure 2. FPC production normalized per dry weight zooplankton biomass in each size class. Each bar represents mean of n=2 replicates. Error bars are 1 Standard Error.

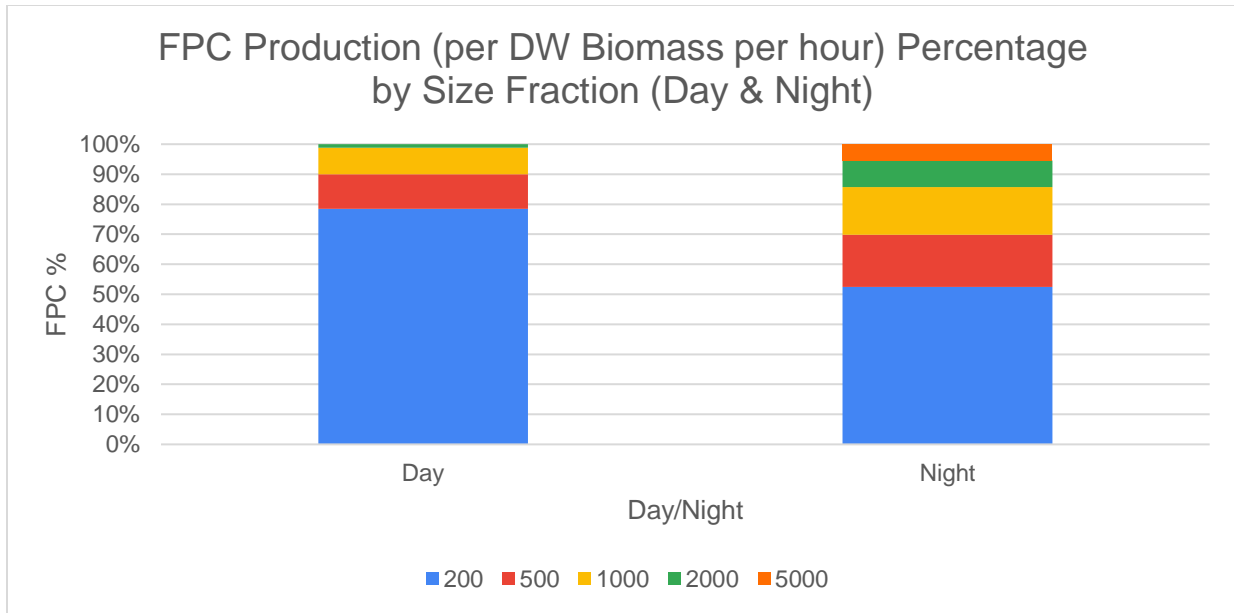
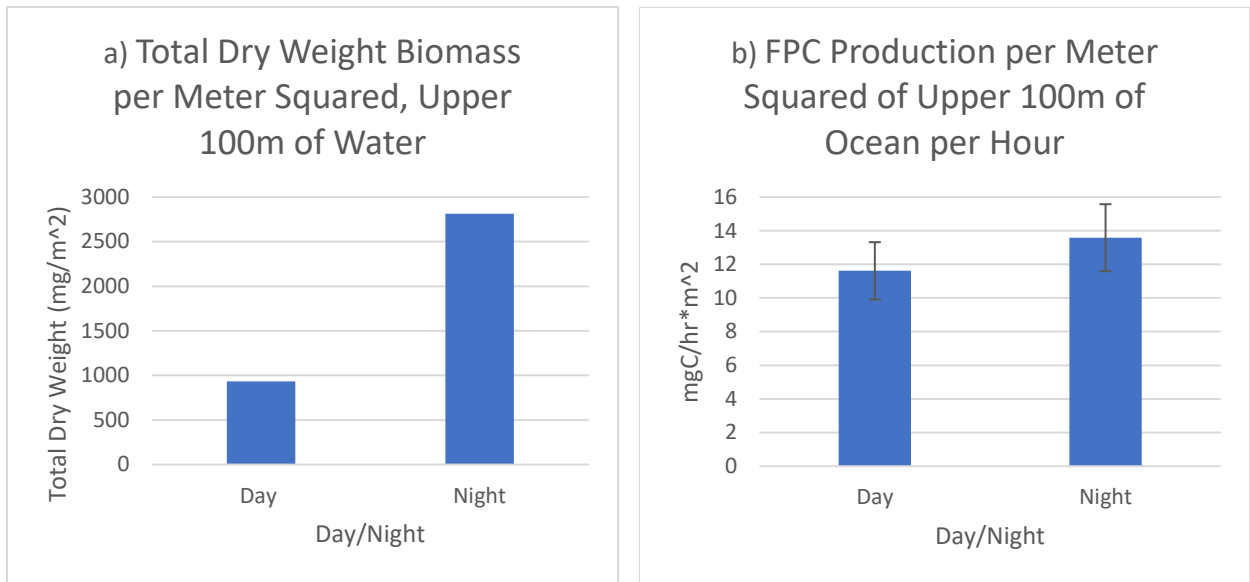


Figure 3. Proportion of FPC production contributed by each zooplankton size class during day and night.

FPC production normalized for total zooplankton biomass in the upper 100m of ocean

Total zooplankton biomass in the upper 100m of ocean was three times greater during the night (2813 mg/m²) versus during the day (934 mg/m²) (Fig. 4a). When normalized to total dry weight biomass per square meter in the upper 100m of the ocean (i.e., integrated 0-100 m), there is no significant difference between FPC production rates during day (11.6 mgC/m²/hr), and night (13.6 mgC/m²/hr) (Fig. 4b). Integrated FPC production in the upper 100m of ocean is still highest for the smallest size classes, with the 200 μm size class accounting for >50% of FPC production (Fig. 5). Integrated FPC production in the upper 100m results in much higher nighttime productivity compared with non-integrated FPC production (Fig. 2), with nighttime integrated FPC production higher than daytime integrated FPC production in all size classes except 200 μm (Fig. 5).



Figures 4. Day vs. night integrated zooplankton biomass and fecal pellet carbon (FPC) production on the May 2021 EXPORTS cruise. a) Total zooplankton dry weight biomass (per m²) in the upper 0-100m of the ocean. b) FPC production normalized per total dry weight biomass in the upper 100m of the ocean.

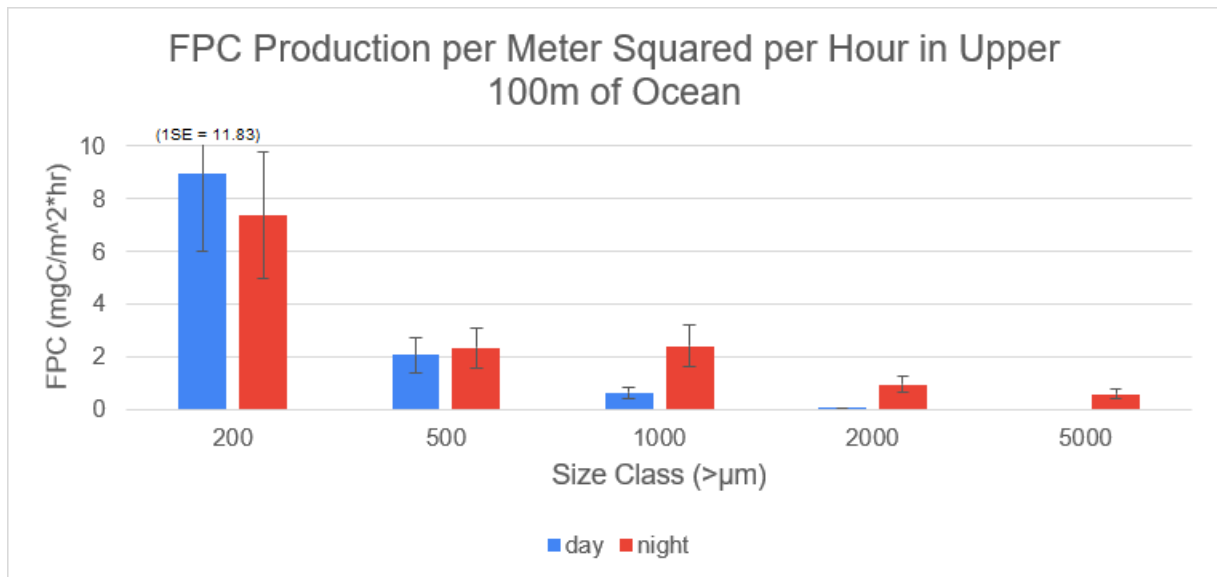


Figure 5. FPC production normalized per total dry weight biomass by size class integrated in the upper 0-100m of ocean.

Discussion

Fecal pellet production is an important contributor to the ocean's biological pump and the export of organic carbon to the deep ocean. Determining the differences in FPC production between day and night, and between zooplankton taxa / size classes aids in quantifying potential carbon export within the open ocean. The findings of this study are consistent with those of similar studies conducted in the North Pacific Ocean and other ecosystems.

Importance of smaller size fraction zooplankton

The smallest zooplankton size fraction examined during this experiment produced the most FPC per dry-weight biomass, which is consistent with the findings of previous studies.

Despite being 2nd largest by total dry weight biomass during day and night in the upper 100 meters of ocean, the 200 μm size class produced the most FPC during both day and night.

This is consistent with the findings of Stamiezkin et al. (2021) in the North Pacific Ocean and Sharpe (2022) in the York River estuary. Faster weight-specific metabolic rates of smaller zooplankton compared to larger ones most likely contribute to higher FPC production by smaller animals compared to large, as the metabolic theory of ecology predicts that smaller organisms will have a faster metabolism with respect to body size (Brown et al. 2004). However, the high rates of FPC production observed in small size classes of zooplankton may not lead to oceanic carbon sequestration. Small fecal pellets produced by small animals sink more slowly than large, and rarely reach depths beneath the mixed layer

without attenuation (Stamieszkin et al., 2021). Thus these smaller fecal pellets, despite their high abundance, are likely not a significant contributor to organic carbon export to the deep ocean, and much of the carbon they contain is likely remineralized within the epipelagic ecosystem (Stamieszkin et al., 2021; Durkin et al., 2021).

Trends in larger size fraction zooplankton FPC production

Larger size fraction animals contributed less to FPC than the smallest size fraction, but due to their diel vertical migration behavior the larger animals may be more important to carbon export to the deep ocean (Stamieszkin et al., 2021). When normalized for total plankton dry-weight biomass in the upper 0-100m of ocean, FPC rates were higher for larger size fractions during the night (Fig. 5). This is most likely because larger, more motile animals vertically migrate long distances (relative to body length) to surface waters at night to feed (Steinberg & Landry, 2017). As a result, zooplankton biomass in the large size-classes is much higher at night and integrated FPC rates reflect this (Fig 4b). Larger zooplankton tend to produce larger fecal pellets, which sink faster, allowing less opportunity for pellets to be consumed or fragmented by other plankton, or remineralized by bacteria (Liszka et al. 2019; Belcher et al. 2016). In addition, the diel vertical migration behavior of larger zooplankton means that much of their time is spent below the ocean's mixed layer, in which food they consumed in surface waters is 'actively' transported to the deep ocean rather than being recycled to the epipelagic zone (Steinberg & Landry, 2017). However, analysis of experiment data showed that there was no significant difference between individual fecal pellet volumes during the

day and night, nor was there a significant difference in carbon per fecal pellet (a function of size) between size classes. This is possibly because small zooplankton, which in every experiment except one, passed into the fecal pellet collection basin during experiments and may have been contributing to FPC. Nonetheless, the faster sinking of larger fecal pellets and the diel vertical migration behavior of larger zooplankton likely leads to greater contribution towards atmospheric carbon sequestration in the deep ocean.

Diel differences in zooplankton biomass and fecal pellet production

A major component of this study was examining differences between species composition and FPC production during the day and night. A higher proportion of large size fraction animals were sampled during the night due to diel vertical migration into surface waters, and thus FPC production by larger size fractions made up a larger proportion of total FPC during the night vs during the day. The experiments conducted during the cruise had higher total FPC production during the daytime, but when integrated with total dry-weight biomass of zooplankton in the upper 0-100m of ocean, FPC production was higher at night. The slight increase was not statistically significant (Fig. 4b), but demonstrates the impact of diel changes when zooplankton enter surface waters at night to feed.

Small animal contamination and experiment design

Some error may have been introduced in these results by inclusion of some small-size zooplankton in all containers which prevented total isolation of larger size class animals.

These smaller zooplankton potentially could break up and consume some of the fecal pellets produced by target animals in higher size classes. However, many of the small plankton that 'slipped' through the larger size class separation mesh were of a similar type and number found in control experiments, which came from unfiltered surface water. Control experiment animals did not produce any fecal pellets, so the contamination of smaller animals in large size fractions likely had a small effect on FPC production data. Future experiments might revise the methodology or equipment used in separating plankton by size class for FPC production experiments, to reduce this minor source of error.

Comparison with FPC production in the North Pacific Ocean

The experiments in this study were conducted during the spring bloom of the North Atlantic Ocean, at a time and place where primary productivity is very high. The EXPORTS project also involved similar experiments and data collected from the North Pacific Ocean, at a time and in a region where primary productivity is very low (Siegel et al. 2016). Stamieszkin et al. (2021) conducted the exact same experiment as that analyzed in my study in the North Pacific Ocean. I hypothesized that the higher productivity of the North Atlantic Ocean would result in higher FPC production rates compared to the North Pacific Ocean as reported in Stamieszkin et al. (2021). Total zooplankton dry-weight biomass in the upper 100m of ocean was considerably higher in the North Atlantic (Day = 933.6 mg/m², Night = 2812.5 mg/m²) compared to the North Pacific Ocean (Day = ~390 mg/m², Night = ~950 mg/m²). As expected, the case is the same for FPC production per m² of the top 100 meters of

ocean; daytime North Atlantic FPC production was $139 \text{ mgC/m}^2\cdot 12\text{hr}$, while North Pacific FPC production was $\sim 0.9 \text{ mgC/m}^2\cdot 12\text{hr}$, and nighttime North Atlantic FPC production was $163 \text{ mgC/m}^2\cdot 12\text{hr}$, while North Pacific FPC production was $\sim 2.4 \text{ mgC/m}^2\cdot 12\text{hr}$. The results of this North Atlantic study thus differ from those of Stamieszkin et al. (2021) in expected ways, with the region of higher primary productivity leading to higher FPC production and likely ultimately carbon export.

Conclusions

In accordance with similar prior studies conducted in other regions and ecosystems, we find that diel vertical migration plays a major role in determining FPC production, with larger zooplankton rising to the surface to feed upon primary producers, then egest fecal pellets back below the mixed layer, which can become sequestered in the deep sea. We also find that small zooplankton contribute the most to FPC production, though their contribution likely does not result in considerable export of carbon below the mixed layer. Understanding these trends in the ecosystem that interfaces the most with earth's atmosphere is critical to our ability to accurately predict future trends in our changing climate and oceanic processes. Understanding the details of carbon sequestration within the oceans is extremely important to humanity's ability to respond to and mitigate the effects of climate change as the earth's climate continues to pass milestones in CO_2 concentration and annual average temperature.

References

- Al-Mutairi, H., Landry, M.R. (2001). Active export of carbon and nitrogen at station ALOHA by diel migrant zooplankton. *Deep Sea Research Part II: Topical Studies in Oceanography*. 48: 2083–2103. doi:10.1016/S0967-0645(00)00174-0
- Belcher, A., Iversen, M., Manno, C., Henson, S.A., Tarling, G.A., Sanders, R. (2016). The role of particle associated microbes in remineralization of fecal pellets in the upper mesopelagic of the Scotia Sea, Antarctica. *Limnology and Oceanography*. 61: 1049-1064. doi:10.1002/lno.10269
- Brown, J. H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B. (2004). Toward a metabolic theory of ecology. *Ecology*. 85: 1771–1789.
- Durkin, C.A., Buesseler, K.O., Cetinić, I., Estapa, M.L., Kelly, R.P., & Omand, M. (2021). A visual tour of carbon export by sinking particles. *AGU Global Biogeochemical Cycles*. doi: 10.1029/2021GB006985
- Gleiber, M. R., Steinberg, D.K., Ducklow, H.W. (2012). Time series of vertical flux of zooplankton fecal pellets on the continental shelf of the western Antarctic peninsula. *Marine Ecology Progress Series*. 471: 23–36. doi:10.3354/meps10021
- Liszka, C. M., Manno, C., Stowasser, G., Robinson, C., Tarling, G.A. (2019). Mesozooplankton community composition controls fecal pellet flux and remineralization depth in the Southern Ocean. *Frontiers in Marine Science* 6: 230. doi:10.3389/fmars.2019.230

- Sanders, R., Henson, S.A., Koski, M., De La Rocha, C.L., Painter, S.C., Poulton, A.J., Riley, J., Salihoglu, B., Visser, A., Yool, A., Bellerby, R., Martin, A.P. (2014). The biological carbon pump in the North Atlantic. *Progress in Oceanography*. 129: 200–218. doi: 10.1016/j.pocean.2014.05.005
- Sharpe, K.N., (2022). The Role of Zooplankton Community Composition in Fecal Pellet Carbon Production in the York River Estuary, Chesapeake Bay. [Master's thesis, Virginia Institute of Marine Science]
- Siegel, D.A., Buesseler, K.O., Behrenfeld, M.J., Benitez-Nelson, C.R., Boss, E., Brzezinski, M.A., Burd, A., Carlson, C.A., D'Asaro, E.A., Doney, S.C., Perry, M.J., Stanley, R.H.R., Steinberg, D.K. (2016). Prediction of the Export and Fate of Global Ocean Net Primary Production: The EXPORTS Science Plan. *Frontiers in Marine Science*. 3:22. doi: 10.3389/fmars.2016.00022
- Stamieszkin, K., Steinberg, D.K., Maas, A.E. (2021). Fecal pellet production by mesozooplankton in the subarctic Northeast Pacific Ocean. *Limnology and Oceanography*. 1-13. doi: 10.1002/lno.11774
- Steinberg, D.K. and M. R. Landry (2017). Zooplankton and the ocean carbon cycle. *Annual Review of Marine Science* 9: 14.1-14.32. doi: 10.1146/annurev-marine-010814-015924
- Turner, J.T. (2015). Zooplankton fecal pellets, marine snow, phytodetritus and the ocean's biological pump. *Progress in Oceanography*. 130: 205–248. doi:10.1016/j.pocean.2014.08.005