

Zooplankton fecal pellet flux in the abyssal northeast Pacific: A 15 year time-series study

S. E. Wilson,^{a,*} H. A. Ruhl,^b and K. L. Smith, Jr.^c

^aSchool of Ocean Sciences, Bangor University, Anglesey, United Kingdom

^bNational Oceanography Centre, University of Southampton Waterfront Campus, Southampton, United Kingdom

^cMonterey Bay Aquarium Research Institute, Moss Landing, California

Abstract

Sinking particulate material collected in sequencing sediment traps moored at 3500 m depth (600 m above bottom) from 1993 to 2008 at the abyssal time-series Sta. M in the northeast Pacific was analyzed via microscopy and digital imaging. Intact zooplankton fecal pellets were quantified and size, shape, and carbon content were measured. The most common identifiable fecal pellets were from larvaceans, which feed on small particles. Other abundant fecal pellets were likely produced by large copepods and euphausiids. The proportion of identifiable fecal pellet carbon to total particulate organic carbon (POC) flux varied and ranged from 3.3% to 47.7%. Fecal pellet flux and fecal pellet-derived carbon flux was lowest in February, and highest in May, August, and November samples. The proportion of total POC in identifiable fecal pellets was negatively correlated to overall POC flux and to indicators of climate variability. The North Pacific Gyre Oscillation and Northern Oscillation Index climate indices were negatively correlated to the dominance of fecal pellets in POC flux, with changes in fecal pellet fluxes temporally lagging climate-related changes by about 3 and 5 months, respectively. Variations in zooplankton distribution and abundance affect biogeochemical cycling to abyssal depths, further demonstrating how a changing climate may affect deep-sea ecology. The dominance of zooplankton fecal pellets can shift proportionally, providing new insight into the processes controlling marine carbon sequestration in the deep sea.

Zooplankton are key contributors to the ocean's biological pump as they can consume sinking and suspended material and then repackage this material into relatively dense sinking fecal pellets which can accelerate downward movement of particulate organic carbon (POC) (Lampitt et al. 1990; Silver and Gowing 1991; Turner 2002). Changes in the characteristics of zooplankton fecal pellets with depth have been used to indicate the importance of zooplankton repackaging of particles to the downward flux of POC (Carroll et al. 1998; Turner 2002; Wilson et al. 2008). Variations in zooplankton size, vertical migration patterns, mode of nutrition, and community structure can differentially alter the transfer efficiency of sinking POC (Noji 1991; Legendre 1999; Schnetzer and Steinberg 2002). Fecal pellet export can also depend on seasonal food availability, grazing, coprophagous behavior, and microbial remineralization (González and Smetacek 1994; Stukel et al. 2011). However, only a few temporal studies have been conducted on how zooplankton affect the efficiency of carbon transport to the deep sea. Questions that persist include: What is the contribution of zooplankton to POC fluxes in the deep ocean? Does the quality and quantity of sinking zooplankton fecal pellets vary with changing climate?

In the deep sea, sinking fecal pellets can be an important source of organic material and variations in pellet flux will ultimately affect benthic communities (Pilskaln and Honjo 1987; Smith et al. 2002). Although many of the fecal pellets produced within the euphotic and mesopelagic zones may succumb to bacterial remineralization and/or grazing and disruption via other zooplankton, larger pellets and pellets produced by vertical migrators have a greater chance of

reaching bathypelagic depths (Fowler and Knauer 1986; Noji et al. 1991; Dagg et al. 2003). Fragmented pellets may then be ingested by microzooplankton or become incorporated into sinking marine snow particles, becoming unrecognizable as fecal pellets (Noji et al. 1991). Additionally, the pellets and marine snow particles ingested and repackaged by deep resident zooplankton sink further still (Urrère and Knauer 1981; Noji 1991; Conte et al. 2001). Zooplankton residing within the deeper layers of the ocean cyclically consume, break apart, and repackage particles and once on the deep seafloor, a fecal pellet is likely to have been altered and repackaged several times (Urrère and Knauer 1981; Conte et al. 2001; Wilson et al. 2008).

A large amount of the recognizable material collected in sediment traps are fecal pellets produced by zooplankton, and this proportion can vary with depth, season, and location (Carroll et al. 1998; Wilson et al. 2008). Positive correlations have also been made linking fluctuations in POC flux at abyssal depths with variations in epipelagic zooplankton biomass (Smith et al. 2008). Temporal changes of fecal pellet flux in deep-sea sediment traps can give further indication of how seasonal and natural climate variation may affect zooplankton assemblages and the sinking POC flux. Investigating the long-term contribution of pelagic zooplankton to deep-sea carbon flux is warranted as variations in climate have also been shown to affect abyssal ecosystems (Ruhl et al. 2008; Smith et al. 2008, 2009).

Long time-series studies have demonstrated that zooplankton communities are sensitive to environmental changes on various temporal scales (Ohman et al. 2012; Steinberg et al. 2012). As part of the Bermuda Atlantic Time-series Study (BATS), Steinberg et al. (2012) showed an increase in zooplankton biomass from 1994 to 2010,

* Corresponding author: stephanie.wilson@bangor.ac.uk

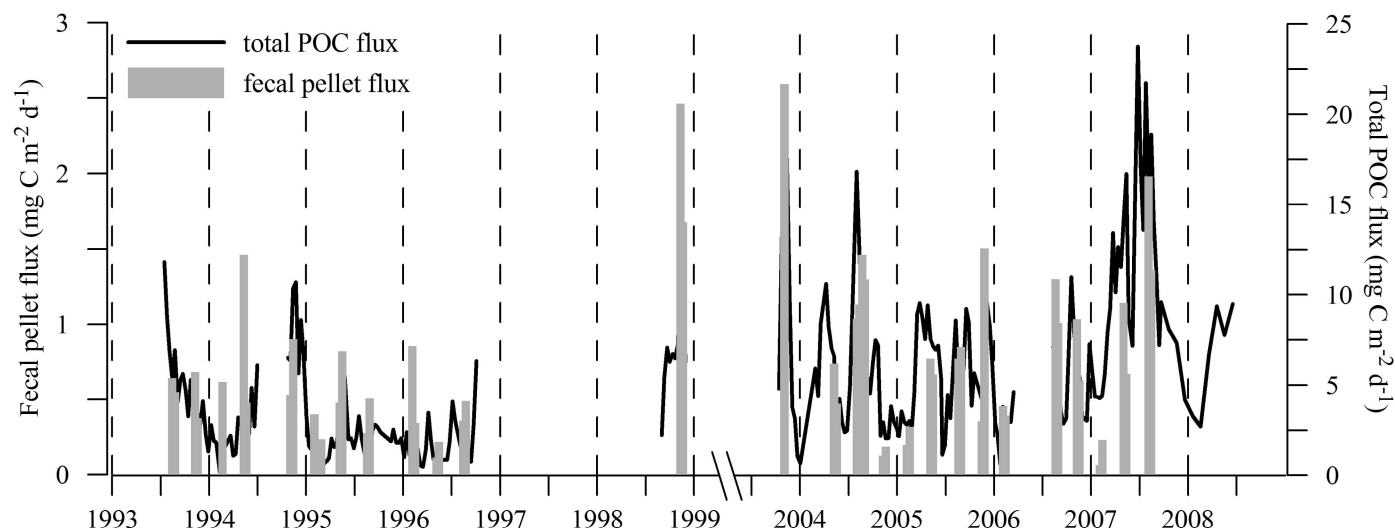


Fig. 1. Total intact fecal pellet flux from 1993 to 2008 within the February, May, August, and November Sta. M 600 mab sediment trap samples (left axis, gray bars) and POC flux (right axis, black line). Blank spaces between lines and bars indicate where samples were unavailable or missing.

which positively correlated to sea-surface temperature, primary production, water column stratification, and several multi-decadal climate indices such as the North Atlantic Oscillation (NAO). Lavaniegos and Ohman (2007) found there was a decrease in displacement volume of zooplankton from 1951 to 2005 within the California Current Ecosystem (CCE) region, which also correlated with increased water column stratification. Also within the CCE, Ohman et al. (2012) used stable nitrogen isotopes to reveal the sensitivity and resilience of zooplankton to climate forcing over interannual, decadal, and multi-decadal timescales.

In this study we quantified zooplankton fecal pellets from sediment trap samples at a long time-series station in the eastern North Pacific Ocean to determine their contribution to POC flux in the region. We measured the fraction of sinking POC flux that is comprised of particles recognizable as zooplankton fecal pellets within sediment trap material at 3500 m depth from 1993 to 2008 to quantify (1) how zooplankton fecal pellet fluxes change on seasonal and annual timescales, (2) whether fecal pellet type and quantity correlate with surface-ocean conditions and regional climate indices, and (3) if the percent contribution of fecal pellets to POC flux is correlated to overall POC fluxes.

Methods

Sta. M (34°50'N, 123°0'W; 4100 m depth, ~ 220 km west of Point Conception off of the central California coast) is an abyssal time-series site in the California Current upwelling region of the eastern North Pacific Ocean that has been ongoing since 1989 (Smith and Druffel 1998). Sta. M is also near several of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) and California Current Ecosystems Long-Term Ecological Research program (CCE-LTER) stations (Ohman and Venrick 2003). This region experiences high seasonal variability in surface-water primary productivity (Smith et al. 2008).

Two sediment traps, which are sequenced to collect sinking particulate matter at 10 d intervals, have been moored at 4050 m (50 m above the bottom [mab]) and 3500 m (600 mab) since the beginning of the time-series in 1989 (Baldwin et al. 1998). Gaps in sampling are apparent in Fig. 1. This study focused on the fecal material from the sediment trap moored at 3500 m, which is above the benthic boundary layer and should not include resuspended particles (Baldwin et al. 1998). Here we present data on intact zooplankton fecal pellets that were collected in sediment traps from 1993 to 2008. Material before 1993 was unavailable. A detailed description of the sediment traps and sample processing at Sta. M can be found in Baldwin et al. (1998).

Upon recovery of the sediment traps aboard ship, collection cup material was gently poured into small trays where large, fragile fecal pellets (e.g., salp pellets) were counted when present, and pelagic animals believed to have swum into the traps were recorded and removed. After this procedure, the trap material was carefully poured back into the collection cups and frozen. In the laboratory, the samples were thawed, split, and 1/8 of the total sample was then refrozen for microscopic analysis. Given this processing, it is likely that some of the more fragile fecal pellet material was fragmented further. This study therefore focuses on the particles recognizable as fecal pellets observed in the sediment trap samples, and results are likely an underestimate of the total contribution of some fecal pellets to POC flux.

Due to the large quantity of samples and length of time required to sort and analyze, a total of 52 sample cups were selected and analyzed within the months of February (11 samples), May (12), August (16), and November (13) from 1993–1999 and 2003–2007, with each cup having a 10 d integrated sample resolution. Using the selected samples, the material from the 600 mab sediment traps was gently poured onto a gridded petri dish, and fecal pellets, as well as other identifiable items, were counted and photographed

Table 1. Mean monthly data showing fecal pellet flux, total particulate organic carbon (POC), and proportion of POC flux consisting of fecal pellets ± 1 standard error of the mean.

	Fecal pellet flux (mg C m ⁻² d ⁻¹)	Total POC flux (mg C m ⁻² d ⁻¹)	% POC flux
Feb	0.36 \pm 0.07	2.52 \pm 0.39	20.09 \pm 5.0
May	0.67 \pm 0.11	6.18 \pm 1.42	16.73 \pm 4.0
Aug	0.91 \pm 0.12	7.44 \pm 1.56	21.40 \pm 4.5
Nov	1.00 \pm 0.23	7.50 \pm 1.44	12.54 \pm 1.4
Total	0.79 \pm 0.10	6.07 \pm 0.84	18.08 \pm 2.3

on a Big Catch Microscope Digital Camera 560. Identifiable items in the sediment trap material included both intact and partially degraded fecal pellets, fragments of larger zooplankton, as well as foraminiferans, acantharians, radiolarians, and diatom tests.

Fecal pellets from five randomly selected grids were counted, and pellet length and width were measured using ImagePro software (Wilson et al. 2008). Color, shape, and appearance (e.g., fully intact or partially degraded—both of which were quantified as “intact” fecal pellets) were also noted. Pellet shape was used to determine general zooplankton group. Cylindrical pellets are generally produced by crustacean zooplankton such as large calanoid copepods, decapods, mysids, and euphausiids (Martens 1978; González 1992; Yoon et al. 2001). Ellipsoid pellets are produced by larvaceans, ovoid pellets by various groups including pteropods, chaetognaths, and copepods, and spherical pellets by small copepods and crustacean nauplii (González 1992; Gorsky and Fenaux 1998; Yoon et al. 2001).

The fecal pellets produced by salps are tabular in shape and sink rapidly (Madin et al. 2006). Salp fecal pellet abundance data were obtained for all trap samples from 1993 to 2008 with the exception of the abovementioned gaps, via direct observations of the trap material once onboard the ship due to the fragile nature of these fecal pellets.

Volumes of the fecal pellets were calculated from the length and width measurements and formulas for a sphere, cylinder, and ovoid shapes. The ellipsoid pellets were differentiated from ovoid in that they were slightly pointed on both ends and are readily recognizable as larvacean fecal pellets, although the volume equations were the same. Volumes were then converted to carbon using a conversion factor of 0.08 $\mu\text{g C mm}^{-3}$ (as in Wilson et al. 2008). Carbon flux values were then calculated using the total pellet carbon in each sample divided by the area of the sediment trap opening, and the length of time the trap was open. For salp pellets, which in the time-series database were only counted and not measured, a midrange value of 119 $\mu\text{g C pellet}^{-1}$ (Madin 1982) was used in order to incorporate salp pellet carbon into the analysis.

Several monthly climate indices were compared to the pellet flux data: the Northern Oscillation Index (NOI; Schwing et al. 2002), North Pacific Gyre Oscillation (NPGO; Di Lorenzo et al. 2008), and the Bakun Upwelling Index (BUI; Bakun 1973). The NOI is an index of sea-level air pressure anomalies indicative of El Niño Southern Oscillation influences in the northeast Pacific. The NPGO is indicative of changes in North Pacific sea-surface gyre

circulation and has interannual to decadal variability, and the BUI relates to changes in wind-driven coastal upwelling in an area to the northeast of Sta. M. at 36°N, 122°W. Surface-ocean net primary production as well as export flux of POC out of the euphotic zone estimates from satellite were also examined in relation to pellet fluxes. These satellite data were created using methods outlined in Smith et al. (2008) for an area of 50 km radius around the study site for the period November 1996 through 2007, when ocean color data are available.

POC flux, climate, and surface-ocean data were correlated to fecal pellet data, taking into account any statistically significant time lags (where fluxes lag behind the climate indices), if appropriate, using nonparametric Spearman rank cross correlations (as in Smith et al. 2006). Differences between the major fecal pellet shapes, fluxes, and months sampled were statistically tested using nonparametric Mann–Whitney tests (MW) at a 95% confidence interval.

Results

Identifiable fecal pellet–derived POC fluxes from 1993 to 2008 (excluding notable gaps, 1997–1998 and 1999–2003) were highly variable, ranging from 0.062 (February 2007) to 2.6 (November 2003) $\text{mgC m}^{-2} \text{d}^{-1}$ with other large fecal pellet POC fluxes recorded in November 1998 and August 2007 (Table 1; Fig. 1). Total pellet POC flux was positively correlated to overall POC flux (Spearman rank, $r_s = 0.78$, $p < 0.001$) on a monthly basis as well as several of the constituent pellet fluxes including the cylindrical, ellipsoid, ovoid, and spherical shapes ($r_s \geq 0.57$, $p \leq 0.001$). MW results showed no significance between individual years (MW, $p > 0.05$), although there was marginal significance between the year groups 1993–1997 and 2003–2008 (MW, $p = 0.07$).

When the fecal pellet flux data were averaged by month, there was a slight but nonsignificant difference in total pellet POC flux between May and August (MW, $p = 0.08$) and February pellet POC fluxes were significantly lower than the other months (MW, $p \leq 0.05$). The lowest fecal pellet fluxes were predominantly in the February samples and the highest in November (Fig. 2). The identifiable fecal pellet material generally constituted a small portion of the total POC flux. However, this proportion is regarded as a lower bound of the actual values (Fig. 2). These proportions of fecal pellet to total POC flux ranged from an average of 12.5% for November samples to 21.4% for August samples, with a total mean of 18.08% for all samples on a monthly basis (Table 1; Fig. 2).

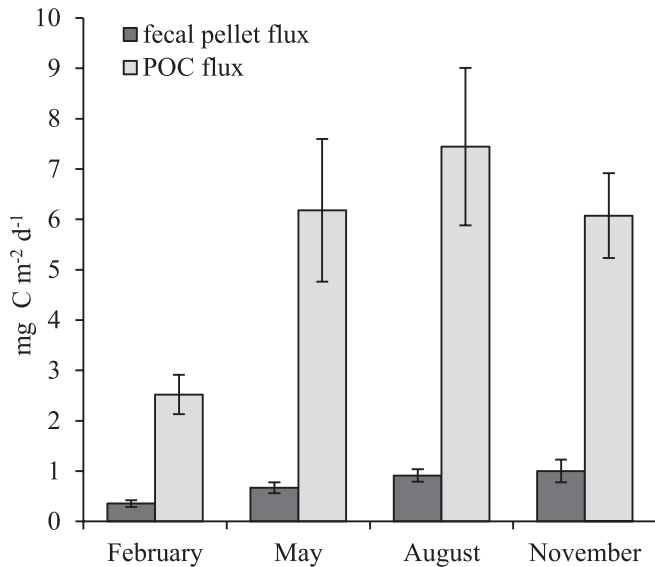


Fig. 2. Mean monthly POC and intact fecal pellet flux values for all February, May, August, and November Sta. M 600 mab sediment trap samples counted. Error bars = ± 1 standard error of the mean.

Many of the dominant fecal pellet shapes varied significantly between and within February, May, August, and November (MW tests, Table 2). Ellipsoid (larvacean) pellets had highest fluxes in November and lowest in February and cylindrical (crustacean) pellets slightly higher in August (Fig. 3). Mean ellipsoid pellet flux increased from February to November (Fig. 3). Spherical pellet flux was lowest in all sediment trap samples and the pellets were generally the smallest in size (Fig. 3).

The larvacean and crustacean fecal pellets (ellipsoid and cylindrical pellets, respectively) together dominated the samples throughout the time series. Larvacean fecal pellets had the highest pellet fluxes in November 1998, 2003, and 2005 (Fig. 4), which correlated significantly with the POC and total pellet flux ($r_s = 0.80$, $p < 0.001$). Crustacean fecal pellets in Sta. M sediment trap samples had the highest pellet fluxes in August 2004 and 2007 and correlated with POC and total pellet flux as well (Fig. 4, $r_s \geq 0.78$, $p = 0.001$).

Tabular-shaped salp pellets were no longer identifiable in the preserved sediment trap samples; however, the quantity of salp pellets had been recorded during initial collection (counts were made while removing swimmers during processing of the trap material immediately upon recovery and carbon content was estimated) throughout most of the time series (Fig. 5). Salp pellet carbon flux did not correlate with POC flux or any climate indices as these pellets were rare in traps ($> 3/4$ of all samples from the time-series did not contain any salp pellets). Highest salp pellet fluxes occurred in the spring, and there were significant seasonal differences between summer and fall, and fall and winter (Fig. 6, MW $p \leq 0.01$).

The majority of the fecal pellets in the traps were either light brown or dark brown in color, with no statistical differences between the traps by season. In samples with high fluxes, there were slightly more light brown pellets. The smallest contribution to total POC flux were red and

white pellets; however, there were also no statistical differences between months. The fraction of recognizable fecal pellets that were partially degraded or damaged decreased marginally with increasing POC flux.

The proportion of fecal pellet POC flux was negatively correlated to total POC flux ($r_s = -0.52$, $p = 0.001$) on a per-sample basis. The proportion of pellet POC flux to overall POC flux, though, was not correlated to total pellet POC flux. Higher fluxes of POC had proportionally less identifiable pellet POC. The relationship between total POC flux and percent pellet POC flux can be described by the following equation determined by regression:

$$y = 9.30 + (22.79/x) \text{ (Fig. 7, } r^2 = 0.55 \text{ } p < 0.001) \quad (1)$$

where y = the proportion of pellet POC flux (%) and x = the total POC flux ($\text{mg C m}^{-2} \text{ d}^{-1}$). This shows that at Sta. M, during higher POC fluxes, percent pellet flux did not get much above $\sim 9\%$, but percent pellet flux could be higher when POC fluxes are lower than that. We point out, however, that this relationship is derived from one place and one depth, but over many years, and that as x approaches values below ~ 0.2 the material reaches a theoretical limit of 100% pellet material.

We then examined the relationships between POC flux and the percent pellet POC flux from a set of data gathered from other studies and sites (*see* references in Fig. 7B,C legend). We found that, across a range of separate depths and locations, these two quantities were not significantly correlated for the available epi- and bathypelagic studies (Fig. 7A). However, there was a significant correlation relationship with other bathy- and abyssopelagic studies ($r_s = -0.41$, $p = 0.02$) (Fig. 7B). The correlation of bathy- and abyssopelagic samples between POC flux and percent pellet POC flux was driven by the Sargasso Sea time-series data (BATS; Shatova et al. 2012) and is insignificant without that data. A regression equation for that Sargasso Sea data, similar to the one for Sta. M (Eq. 1), was also found (Eq. 2) but with different coefficients (Fig. 7B).

$$y = 1.67 + (12.16/x) \text{ (Fig. 7, } r^2 = 0.49 \text{ } p < 0.001) \quad (2)$$

When examined on a monthly basis, total fecal pellet POC flux had correlations suggesting seasonal and interannual variation. Indeed, pellet POC flux was positively correlated to the highly seasonal BUI upwelling index when pellet fluxes lag the BUI index by 3 months ($r_s = 0.48$, $p = 0.01$, Fig. 8). Total pellet POC flux was also correlated to the NPGO index, which has interannual variation, with a 3 month time lag between changes in gyre physical parameters and total pellet POC fluxes ($r_s = 0.38$, $p = 0.05$, Fig. 8). Correlations between total pellet POC and the NOI were not significant, but peaked at 4 and 6 months ($r_s = 0.29$ – 0.32 , $p \leq 0.14$).

The proportion of fecal pellet to overall POC flux correlated negatively to the NPGO with a 3–6 month time lag (max $r_s = -0.48$, $p = 0.01$) and NOI with a 5 month time lag ($r_s = -0.5$, $p < 0.001$). Positive values in the BUI, NPGO, and NOI are also linked to increased total POC flux and peaks in correlations where fluxes lag behind the climate indices by 2 months ($r_s = 0.49$, $p < 0.008$), 3 months

Table 2. Results of Mann–Whitney nonparametric statistical tests to determine if the median fecal pellet fluxes ($\text{mg C m}^{-2} \text{d}^{-1}$) were significantly different (A) between shapes for each month and (B) between months for each shape. Bold print denotes significant differences with a confidence interval of 95%. cyl. = cylindrical, ell. = ellipsoid, ovo. = ovoid, sph. = spherical.

A					
Month	Shape	Median	<i>n</i>	<i>p</i>	
Feb	cyl.	0.1099	11		
	ell.	0.0501	11	0.0418	
	cyl.	0.1099	11		
	ovo.	0.0914	11	0.6458	
	cyl.	0.1099	11		
	sph.	0.0043	11	0.0001	
	ell.	0.0501	11		
	ovo.	0.0914	11	0.0878	
	ell.	0.0501	11		
	sph.	0.0043	11	0.0003	
	ovo.	0.0914	11		
	sph.	0.0043	11	0.0001	
	May	cyl.	0.2227	12	
		ell.	0.1362	12	0.2145
cyl.		0.2227	12		
ovo.		0.2209	12	0.5834	
cyl.		0.2227	12		
sph.		0.0047	12	0.0000	
ell.		0.2209	12	0.0051	
ovo.		0.1362	12		
sph.		0.0047	12	0.0002	
Aug		cyl.	0.2652	16	
		ell.	0.1894	16	0.3964
		cyl.	0.2652	16	
		ovo.	0.3176	16	0.5847
		cyl.	0.2652	16	
	sph.	0.0215	16	0.0000	
	ell.	0.1894	16	0.0050	
	ovo.	0.3176	16		
	ell.	0.1894	16		
	sph.	0.0215	16	0.0000	
	ovo.	0.3176	16	0.0000	
	Nov	cyl.	0.1824	13	
		ell.	0.2787	13	0.5383
		cyl.	0.1824	13	
ovo.		0.2162	13	0.8375	
cyl.		0.1824	13		
sph.		0.0052	13	0.0000	
ell.		0.2787	13		
ovo.		0.2162	13	0.6816	
ell.		0.2787	13		
sph.		0.0052	13	0.0000	
ovo.		0.2162	13		
sph.		0.0052	13	0.0000	

($r_s = 0.51$, $p < 0.007$), and 6 months, respectively ($r_s = 0.4$, $p < 0.04$). The percent pellet POC was not, however, correlated to either net primary production or export flux from November 1996 through 2007.

Table 2. Continued.

B					
Shape	Month	Median	<i>n</i>	<i>p</i>	
cyl.	Aug	0.2652	16		
	Feb	0.1099	11	0.0717	
	Feb	0.1099	11		
	May	0.2227	12	0.1166	
	Feb	0.1099	11		
	Nov	0.1824	13	0.1048	
	May	0.2227	12		
	Aug	0.2652	16	0.5934	
	Aug	0.2652	16		
	Nov	0.1824	13	0.6452	
	May	0.2227	12		
	Nov	0.1824	13	1.0000	
	ell.	Aug	0.1894	16	
		Feb	0.0501	11	0.0003
Feb		0.0501	11		
May		0.1362	12	0.0392	
Feb		0.0501	11		
Nov		0.2787	13	0.0031	
May		0.1362	12		
Aug		0.1894	16	0.0148	
Aug		0.1894	16		
Nov		0.2787	13	0.5836	
May		0.1362	12		
Nov		0.2787	13	0.1495	
ovo.		Aug	0.3176	16	
		Feb	0.0914	11	0.0001
	Feb	0.0914	11		
	May	0.2209	12	0.0042	
	Feb	0.0914	11		
	Nov	0.2162	13	0.0127	
	May	0.2209	12		
	Aug	0.3176	16	0.0902	
	Aug	0.3176	16		
	Nov	0.2162	13	0.0913	
	May	0.2209	13		
	Nov	0.2162	12	0.6833	
	sph.	Aug	0.0214	16	
		Feb	0.0043	11	0.0012
Feb		0.0043	11		
May		0.0047	12	0.7350	
Feb		0.0043	11		
Nov		0.0052	13	0.4173	
May		0.0047	12		
Aug		0.0215	16	0.0032	
Aug		0.0215	16		
Nov		0.0052	13	0.0027	
May		0.0047	12		
Nov		0.0052	13	0.5316	

Discussion

Community structure influences POC flux—There is currently little information on the deep-sea mesozooplankton community structure in the waters above the Sta. M mooring, and here we speculate as to the depth at which pellets found in the sediment traps were produced. The origin of the observed pellets and their “trophic position” are likely from detritivorous zooplankton repackaging suspended and sinking particles at depth. Some of the

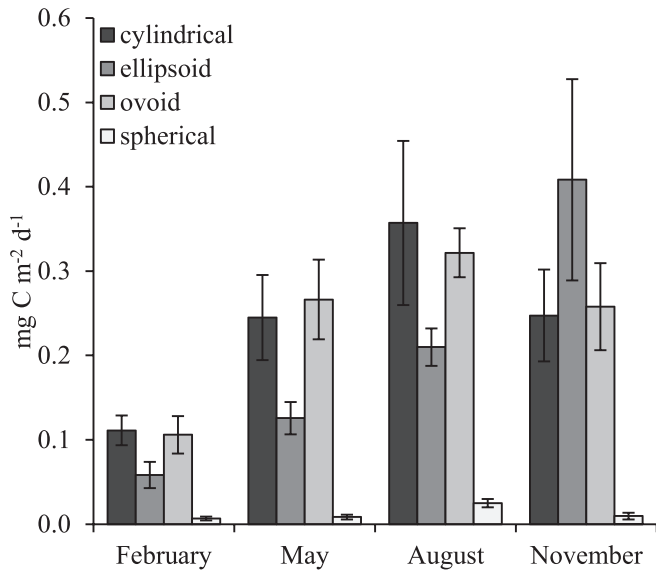


Fig. 3. Seasonal pellet flux ($\mu\text{g C m}^{-2} \text{d}^{-1}$) for cylindrical, ellipsoid, ovoid, spherical for all February, May, August, and November samples counted. Error bars = ± 1 standard error of the mean.

larger fecal pellets, such as those produced by salps and euphausiids, may sink from the euphotic and upper mesopelagic zones to 3500 m intact. However, it is also likely that the material in the pellets were consumed and repackaged multiple times before reaching their final destination (Carroll et al. 1998; Conte et al. 2001). These speculations are the subject of future and ongoing work in the field.

Zooplankton community structure can have an effect on POC flux to the deep sea. The dominant pelagic taxa, in terms of abundance, in the eastern North Pacific Ocean at 3500 m depth near the Monterey Bay (~ 445 km north of Sta. M) are larvaceans, medusae, and crustaceans (Robison

et al. 2010). The most common identifiable fecal pellets in the traps from this study were ellipsoid-shaped pellets presumed to be produced by larvaceans. Larvaceans filter small-sized plankton and detrital aggregates and repackage this material into larger fecal pellets (Deibel and Turner 1985; Gorsky and Fenaux 1998). These larvaceans, which generally contribute less to the export flux of carbon than copepods, are nonetheless significant contributors to POC flux via their dense, fast-sinking fecal pellets and abandoned mucus houses, more so than previously thought (Robison et al. 2005; Berline et al. 2010; Lombard and Kjørboe 2010). A significant long-term increase in larvacean biomass, where other pelagic tunicate biomass has been decreasing (accompanied by an increase in stratification), is already evident between 1951 and 2005 in the Southern California region of the CCE, which includes the area around Sta. M (Lavaniegos and Ohman 2007). We hypothesize that larvaceans at the site currently provide an important transport mechanism for conveying organic matter to the deep ocean through sinking fecal material and that as their numbers rise, their importance will increase with surface-ocean warming and water column stratification.

Due to their rapid degradation rates and variable sinking speeds (Turner 2002), both larvacean pellets and crustacean pellets in the Sta. M sediment traps are presumed to have been produced mainly within the bathypelagic zone. A comprehensive survey of the vertical distribution and abundance of zooplankton from the nearby Monterey Canyon using remotely operated vehicle observations showed that although the highest abundances of larvaceans were found to be above 500 m (Robison et al. 2005), there was also an increase in larvacean abundance from 2500 m to the seafloor at 3500 m depth (Robison et al. 2010). Abandoned larvacean houses, or “sinkers,” were also prevalent throughout the water column to 3500 m (Robison et al. 2005, 2010). Within the mesopelagic, an increase

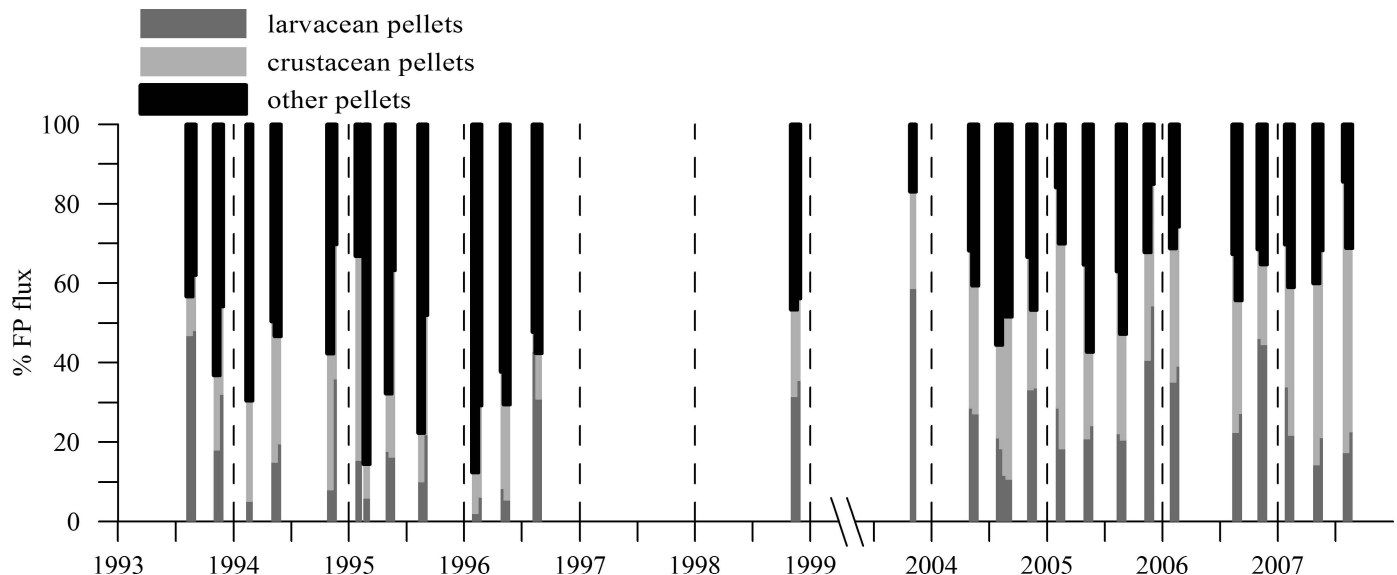


Fig. 4. Contribution of larvacean (ellipsoid-shaped) and crustacean (cylindrical-shaped) fecal pellet flux to total pellet flux over the course of the time series. Note: overlapping bars where time points are close.

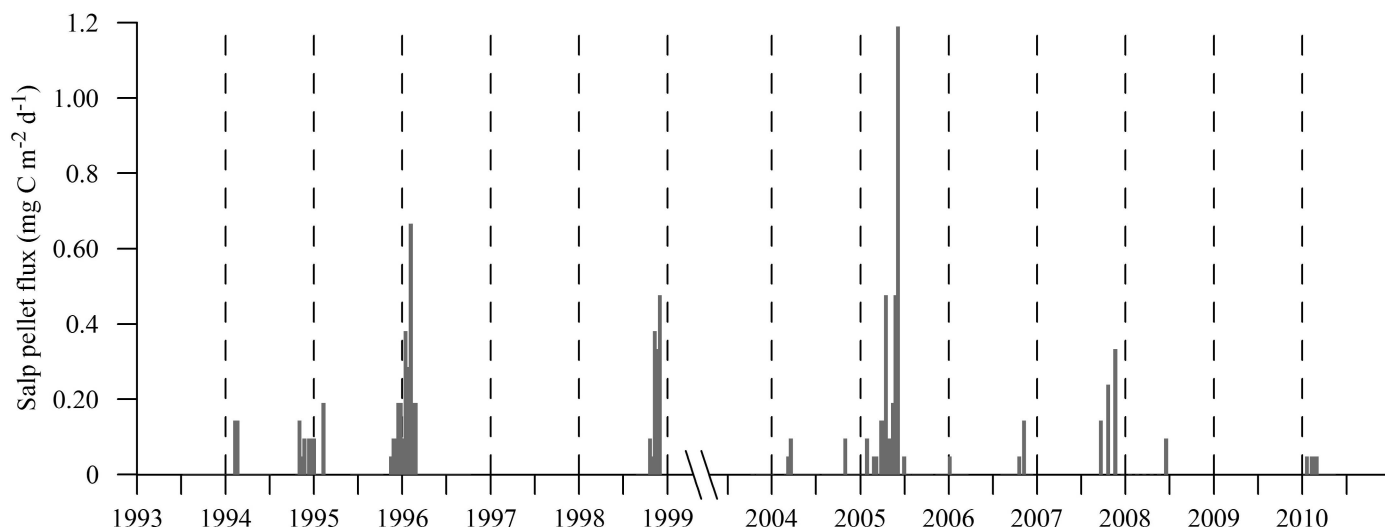


Fig. 5. Total salp pellet flux from all cruises between 1993 and 2008. With the exception of gaps from 1997–1998 and 1999–2003, blank spaces indicate zero salp pellets present in the sediment traps.

with depth in larvacean fecal pellets was also observed in sediment traps from 150 to 500 m deployed within the subtropical North Pacific Ocean at Hawaii Ocean Time-series Sta. ALOHA (Wilson et al. 2008). Although not increasing with depth as were larvaceans, there was a more steady distribution of crustaceans observed from 1800 m in the nearby Monterey Canyon throughout the bathypelagic (Robison et al. 2010). Larvacean fecal pellets were more prominent than cylindrical pellets in the 600 mab Sta. M trap, possibly as a result of the more fragile nature of cylindrical pellets (Honjo 1978; Turner 2002). A large proportion of the ovoid pellets are also produced by crustaceans, such as smaller copepods and amphipods, and there were numerous crustacean swimmers in the sediment trap samples, many amphipods of which were new species

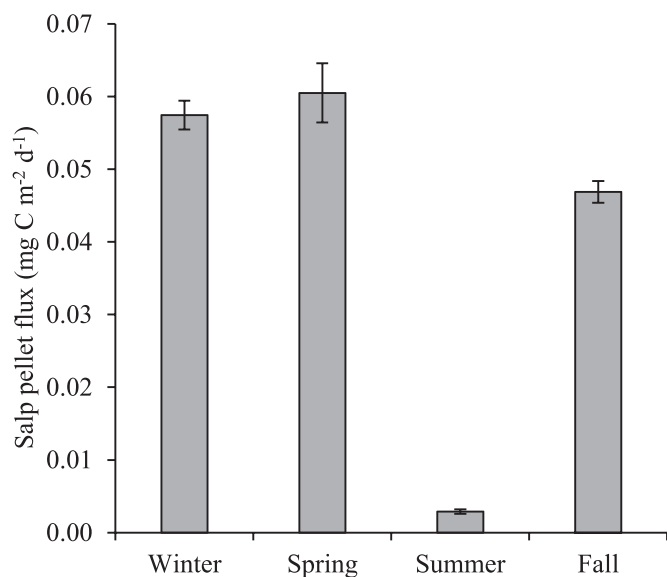


Fig. 6. Seasonal salp fecal pellet flux. Error bars = ± 1 standard error of the mean. As salp pellets have a more complete time series, note that x-axis is by season and not month.

(Hendrycks and Conlan 2003). Like larvaceans at this depth, these deep-sea crustaceans are generally detritivores but there may also be carnivorous crustacean zooplankton.

Salp pellets can contribute to deep POC flux from upper layers of the ocean and occurred occasionally in the 3500 m trap (Fig. 5). Salps are efficient filter feeders residing in the upper 1000 m that can feed upon particles 0.1 to 10 μm in size and produce large, rapidly sinking fecal pellets (Sutherland et al. 2010). These pellets can sink from the epipelagic and mesopelagic zones to bathypelagic depths in 1–2 d (Wiebe et al. 1979; Phillips et al. 2009). Lavanigos and Ohman (2007) reported an overall decrease in pelagic tunicate biomass in the CCE from 1951 to 2005, although there was a small increase from the late 1990s to the early 2000s. Neither trend was observable in the salp fecal pellet flux time-series data from this study, and this may be because salp blooms are patchy and pellets sink very fast (Phillips et al. 2009). Salp contribution to the carbon pump near Sta. M is likely very high but difficult to ascertain from sediment traps alone. Salp pellets are also fragile and therefore were not observed intact within the frozen sediment trap samples; however, as these pellets, when present, were always noted and counted immediately upon trap collection, we were able to incorporate these counts, using estimates of salp pellet carbon into the total pellet analysis (Madin 1982), as well as a separate time-series that is inclusive of all available salp pellet count data from 1993 to 2010 (Fig. 5).

It is key to note that fecal pellets recognizable in this study were intact or mostly intact particles. Although no sediment trap sample would contain a complete collection of fecal pellets from the entire deep-sea zooplankton community, we can get a snapshot of the contribution of those species that produce intact sinking fecal pellets. Pellets more likely to break apart into smaller or unrecognizable fragments include scyphozoans, ctenophores, and doliolids, many of which do not produce solid fecal pellets. Fecal fluff and partially degraded fecal pellets were also observed in the sediment trap samples. Fecal fluff

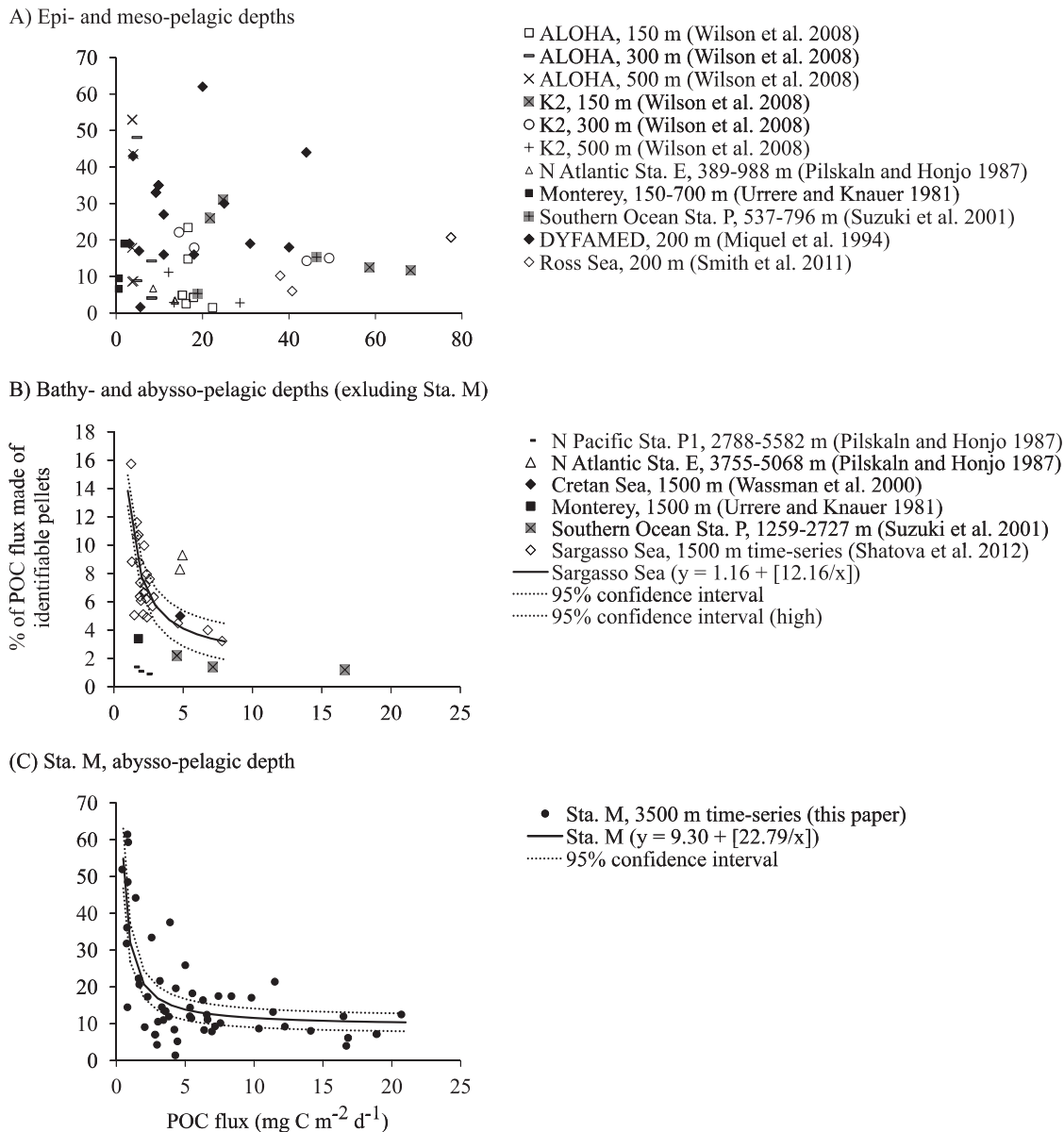


Fig. 7. Scatterplot showing total POC flux vs. the percent contribution of identifiable pellet POC to total POC flux for (A) epi- and mesopelagic depths and (B) bathy- and abyssopelagic (both from other deep and mid-water flux studies), and (C) the Sta. M time series.

was not quantifiable due to the amorphous and loosely packaged nature of the particles (Stemmann and Boss 2012). The proportion of fecal pellets that were partially degraded however, was slightly, although not significantly, lower during periods of high flux. This could potentially mean that zooplankton were not necessarily food limited at times and did not consume many fecal pellets or that most of the partially degraded pellets were already so degraded as to be unrecognizable as fecal pellets. Further study is required to elucidate the relationships between fecal fluff and POC flux.

Proportion of fecal pellets to total POC flux and correlation to natural climate variation—Fecal pellet-derived carbon flux varied seasonally and correlated with POC flux. Greater pellet fluxes are, not surprisingly, related to overall POC flux. However, the general decline in the proportion of pellet

POC as overall POC flux increased suggests that during higher deep sea fluxes, non-pellet-oriented mechanisms, such as aggregation and sinking of moderately labile material, may be relatively more important (Fig. 7). Conversely, when overall POC fluxes are lower within the deep sea, the dominance of pellets in fluxes increases.

One potential hypothesis to explain our observations is that the higher proportion of non-identifiable pellet material in higher fluxes is related to a lesser role of pellet production and/or greater importance of lower trophic-level organic matter production, aggregation, and/or sinking. The factors which lead to reduced dominance of pellet POC during higher POC fluxes could be related to primary production exceeding zooplankton consumption, but primary production and export flux were not correlated to percent pellet POC. Thus, we speculate that the balance

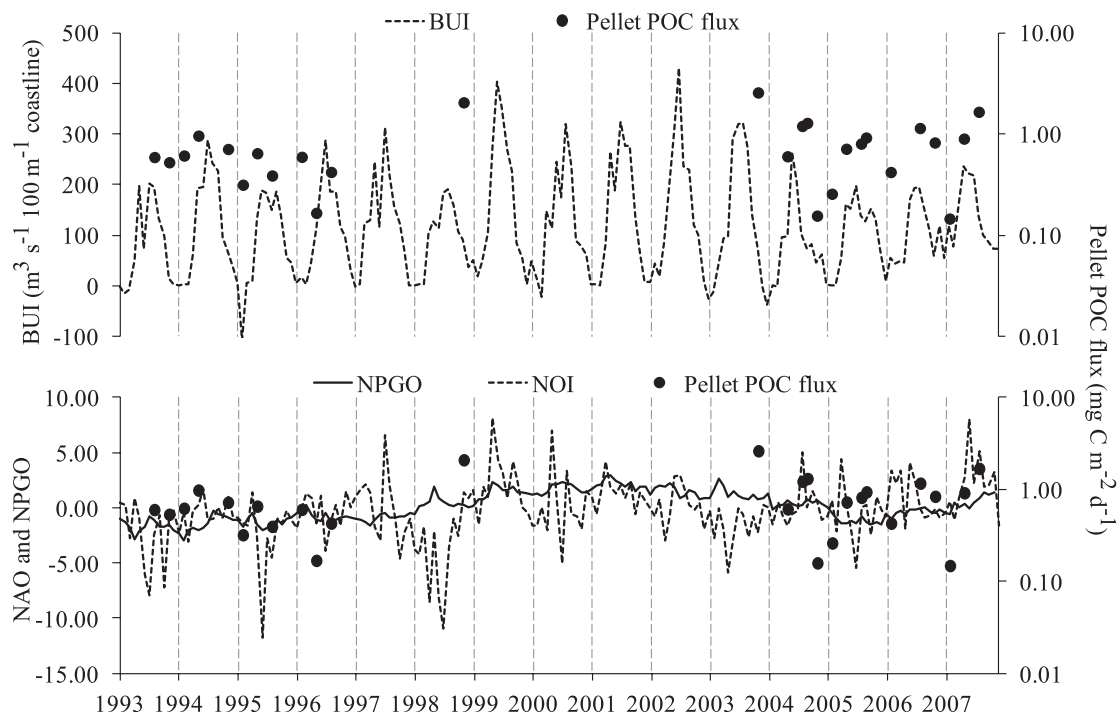


Fig. 8. Climate indices Bakun Upwelling Index (BUI), North Pacific Gyre Oscillation (NPGO), and Northern Oscillation Index (NOI) with total pellet flux over available time-series samples. Data plotted are inclusive of the time lags from when the variations occurred. Pellet fluxes lag the BUI and NPGO indexes by 3 months and the NOI at 4 (and 6) months.

between primary production and grazing may be particularly important in pellet dominance across a range of primary production levels. Other factors linked to increased flux include aggregated algae, the proportion of lithogenic material in POC flux (i.e., the ballast hypothesis), and increases in the amount of non-pellet zooplankton exuviae such as larvacean houses (Armstrong et al. 2002; Robison et al. 2005; Guidi et al. 2008). Additionally, the ratio of carbon to biovolume in the pellets was assumed to be constant, which may indeed vary. Changes in chlorophyll concentrations are known to affect carbon-to-biovolume ratios in fresh fecal pellets (Urban-Rich et al. 1998). While we have no evidence to suggest this is an important bias in terms of the carbon-to-biovolume ratio in our key results, it may also contribute to the outcomes. For example, during lower POC fluxes, bathypelagic zooplankton may have higher assimilation efficiencies, thus reducing this ratio. However, based on studies of assimilation efficiency (Montagnes and Fenton 2012), it seems unlikely that the assimilation efficiencies would systematically vary by 3-fold or more, as would be needed to explain our results.

There is, nonetheless, evidence that whatever the mechanism for controlling pellet dominance, important synchrony in key mechanistic aspects, has been found. The highest fluxes at Sta. M are often associated with visible detrital aggregates on the seafloor (Smith et al. 2008). Such aggregates are known to contain relatively high amounts of organic carbon, including chlorophyll *a*, compared to surrounding sediments (Smith and Druffel 1998). Visible phytodetritus has frequently been observed at the Porcupine Abyssal Plain in the northeast Atlantic during high

POC fluxes (Bett et al. 2001). At times of high pulses of organic matter, there may simply be more food than zooplankton require or there may be a higher quantity of poorly aggregated pellets that disintegrate more readily (both naturally, e.g., from myctophids, doliolids, etc., and/or due to our treatment of the samples) and are therefore not observed intact in our sediment trap samples. Higher abundances of surface zooplankton and export flux have both been correlated to increased water column POC fluxes and coverage of visible detrital aggregates on the seafloor at the site (Smith et al. 2008). The correlation of both pellet POC flux and its proportional dominance in overall POC fluxes to abyssal depths to climatic and oceanic variations such as the NPGO suggest that environmental forcing controls the quantity and quality of fluxes in particular ways. In particular, climate forcing can simultaneously influence several factors such as currents, nutrient availability for primary production, sea-surface temperature, and other variables that could, in turn, relate to variation in zooplankton community dynamics and fecal pellet production with time lags of days to months (Smith et al. 2008).

While studies that have quantified fecal pellet POC are relatively rare, there are studies that provide vertical flux data from both a mesotrophic (Japanese time-series Sta. K2) and an oligotrophic (Hawaii Ocean Time-series Sta. ALOHA) environment in the Pacific Ocean as part of the Vertical Transport in the Global Ocean (VERTIGO) project that were collected during the summer of 2004 and 2005 (Buesseler et al. 2007; Wilson et al. 2008). There are no long time-series records of the relationship between total POC flux and pellet POC flux from VERTIGO or the

other studies that have examined such relationships (*see* references in Fig. 7 legend). Relationships between these variables are not clearly discernible for epi- and mesopelagic depths. However, when combined with our study, these bathy- and abyssopelagic data provide interesting indications that a negative relationship between the proportion of pellet POC flux and total POC flux may be a common feature of deep-sea fluxes (Fig. 7).

The finding that both Sta. M data and a yearlong time series from the Sargasso Sea at 1500 m depth (Shatova et al. 2012) showed significant negative correlation between POC flux and percentage of pellet C comprising that POC flux supports the notion that it may be a widespread phenomenon, but data are still very limited. It is also notable how regression equations differ between Sta. M and the Sargasso Sea (Fig. 7B,C), which may be indicative of differences between productive vs. relatively oligotrophic areas. It is critical to point out that the degree to which this relationship might change from productive to oligotrophic areas or with broad-scale variation in other biogeochemical properties remains to be verified.

Although the proportion of sediment trap material that was indeed fecal pellet in origin is likely higher, and thus the pellet POC fluxes conservative, the variation in identifiable pellets may still be representative of actual variation in pellet POC even if the exact amount is underestimated. It is also possible that many of the observed pellets were produced within the lower bathypelagic and had not yet begun to degrade or be consumed (Carroll et al. 1998). Honjo (1978) concluded that a substantial portion of the smaller particles in their PARTICLE FLUX (PARFLUX) deep-sea traps was due to fragmentation during sinking as well as during the processing and storage of the samples. The samples at Sta. M were also agitated, frozen, and thawed twice before the contents were observed for this study. Our observations do fall within the ranges of other studies dedicated to fecal pellet analysis. In a mesotrophic region of the Atlantic Ocean (Demerara Abyssal Plain, part of PARFLUX; Honjo 1980), fecal pellet fluxes contributed 6.7%, 8.8%, and 9.3% of the total POC flux in November through February at 988, 3755, and 5068 m depths, respectively (Pilskaln and Honjo 1987). In the Canary Basin, Fischer et al. (1996) also observed pulses of sedimentation at 900 m during their 18 month study. There, fecal pellets larger than 100 μm comprised 5% to 26% of the total flux. Like this study, they also noted that these numbers are conservative due to the presence of non-intact fecal pellet fragments.

In summary, the fecal pellets of zooplankton at Sta. M contributed to the flux of POC to the abyssal seafloor throughout the course of the time series, with varying contributions to overall carbon flux. Variations in climate can potentially affect the local zooplankton community and subsequently may be affecting deep-sea ecosystems. This is more apparent when observing changes in the quantity of intact fecal pellets in sediment traps. Higher proportions of identifiable pellets in the POC flux generally occurred at lower fluxes. Fecal pellets, as a food source for deep-sea communities, may be proportionally more important during times of low POC flux. Conversely, these

communities may feed on a proportionally greater amount of lower trophic level POC flux during higher total POC fluxes. Seasonal differences in zooplankton community structure were also apparent from observations of the dominant fecal pellet shapes in sediment traps. Detailed studies looking at the contribution of zooplankton to POC flux may help improve future estimation of how potential climate-related changes in these communities may affect the sequestration of carbon to the deep sea, particularly if such studies can disentangle the potential influences such as phytoplankton aggregation, mineral ballasting, and balances between net primary production and zooplankton feeding.

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