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Response of deep-sea deposit-feeders to detrital inputs: A comparison of two abyssal time-series sites

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ABSTRACT

Biological communities on the abyssal plain are largely dependent on detritus from the surface ocean as their main source of energy. Seasonal fluctuations in the deposition of that detritus cause temporal variations in the quantity and quality of food available to these communities, altering their structure and the activity of the taxa present. However, direct observations of energy acquisition in relation to detritus availability across megafaunal taxa in abyssal communities are few. We used time-lapse photography and coincident measurement of organic matter flux from water column sediment traps to examine the impact of seasonal detrital inputs on resource acquisition by the deposit feeding megafauna assemblages at two sites: Station M (Northeast Pacific, 4000 m water depth) and the Porcupine Abyssal Plain Sustained Observatory (PAP-SO, Northeast Atlantic 4850 m water depth). At Station M, studied over 18-months, the seasonal particle flux was followed by a salp deposition event. At that site, diversity in types of deposit feeding was related to seabed cover by detritus. At PAP-SO, studied over 30 months, the seasonal particle flux consisted of two peaks annually. While the two study sites were similar in mean flux (~8.0 mgC m^{-2} d^{-1}), the seasonality in the flux was greater at PAP-SO. The mean overall tracking at PAP-SO was five times that of Station M (1.9 and 0.4 cm^2 h^{-1}, respectively); both are likely underestimated because tracking by some common taxa at both sites could not be quantified. At both sites, responses of deposit-feeding megafauna to the input of detritus were not consistent across the taxa studied. The numerically-dominant megafauna (e.g. echinoids, large holothurians and asteroids) did not alter their deposit feeding in relation to the seasonality in detrital supply. Taxa for which deposit feeding occurrence or rate were correlated to seasonality in particle flux were relatively uncommon (e.g. enteropneusta), known to cache food (e.g. echiurans), or to be highly selective for fresh detritus (e.g. the holothurian *Oneirophanta mutabilis*). Thus, the degree of seasonality in deposit feeding appeared to be taxon-specific and related to natural history characteristics such as feeding and foraging modes.

1. Introduction

Communities on the abyssal plain are largely dependent on detritus from the surface ocean as their main source of energy. These particles form the base of the food web, where it is partitioned between all size classes of organisms (e.g. Durden et al., 2017; van Oevelen et al., 2012). Seasonal fluctuations in the deposition of detritus to the deep-sea floor (Billett et al., 1983; Rice et al., 1986) cause temporal variation in both the quantity and quality of food available to benthic communities (Kiriakoulakis et al., 2001; Lampitt et al., 2001). Inter- and intra-annual variations in this food supply alter the structure of sediment communities (e.g. Drazen et al., 1998; Pfannkuche, 1993; Ruhl et al., 2008), both epibenthic and infaunal communities, and the partitioning of this resource amongst the community (Dunlop et al., 2016). Mobile deposit-feeding megafauna play a major role in the cycling of carbon through abyssal benthic communities (Durden et al., 2017), and the inter-annual abundance and composition of this group is altered with variations in this carbon input (Billett et al., 2001, 2010; Kuhnz et al., 2014; Ruhl and Smith, 2004; Smith et al., 2014).

Seasonal variation in food supply has also been linked to seasonality

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in the biological functions of individual megafauna, such as growth rates in some deep-sea echinoderms and fish (Gage, 1987; Tyler, 1988), and reproduction and recruitment in some echinoderms (Benitez-Villalobos and Diaz-Martinez, 2010; Booth et al., 2008; FitzGeorge-Balfour et al., 2010; Tyler, 1986; Tyler et al., 1982; Wigham et al., 2003). Such biological functions require energetic reserves above the basic energetic needs for survival, suggesting temporal variations in energy use. Increased deposit-feeding in parallel with detrital deposition, followed by increased reproduction has been observed for the echinoid *Echinocrepis rostrata* (Vardaro et al., 2009); this pattern suggests the coupling of energy availability, acquisition and use. Decoupling of acquisition and use is achieved via energy reserves or 'storage', as modelled in the dynamic energy budget (Sousa et al., 2010). Different lifestyles result in different energy reserves, so the coupling of variations in energy availability, acquisition and use are not uniform across taxa; however, direct observations of energy acquisition in relation to availability across taxa in abyssal communities are few.

Studies attempting to assess whether deep-sea deposit feeding varies in response to the detrital input have been limited in temporal resolution, overall study duration (e.g. Smith et al., 1993b), in the availability of concurrent detrital flux data (e.g. Bett et al., 2001), or have focused on particular taxa (e.g. echiurans, Bett and Rice, 1993; enteropneusts, Smith et al., 2005). These studies have estimated deposit-feeding activity using time-lapse photography by assessing lebensspuren ('life traces') visible on the soft sediment as an indicator of feeding. By this method, the movement in some deep-sea holothurians was observed to be altered by the presence of detrital aggregates on the seabed (Kaufmann and Smith, 1997). Lebensspuren have also been used to determine that the deposit-feeding activity of an echinoid (Vardaro et al., 2009) and the total deposit-feeding community (Bett et al., 2001) vary with food input on intra-annual timescales.

We use time-lapse photography and coincident measurement of organic matter supply to examine the impact of seasonal inputs of detritus on its acquisition by the deposit feeding megafauna across taxonomic groups in a single assemblage. We compare two long-term abyssal sites with different megafaunal communities, Station M in the northeastern Pacific and the Porcupine Abyssal Plain Sustained Observatory (PAP-SO) in the Northeast Atlantic. First, we establish the seasonality in organic matter supply at each site. Then we examine the potential relationships between this seasonality in food availability and the occurrence and rates of deposit-feeding by mobile megafauna via quantification of lebensspuren. From these data, we consider how this temporal variation in food supply may influence megafaunal community function, and more generally carbon cycling in the abyss.

2. Method

2.1. Study sites

The megabenthic assemblages of both Station M (34°50′N 123°06′W, 3950–4000 m water depth) and PAP-SO (48°50′N 16°30′W, 4850 m water depth) and have been studied for more than 25 years (Hartman et al., 2012; Smith et al., 2013; Smith et al., this issue). At Station M, there is a seasonal signal in particulate organic carbon (POC) flux that was augmented by the deposition of salp carcasses to the abyssal seafloor in 2012 (Smith et al., 2014). At PAP-SO, a strong seasonal variation in POC flux has been observed (Lampitt et al., 2010), along with seasonal change in the composition of deposited detritus (Kiriakoulakis et al., 2001).

2.2. Measuring detrital inputs and seasonality

Detrital input at the both sites was quantified by two methods: (i) sediment traps, and (ii) visually assessed seabed cover in images. At Station M, settling particles were collected with a McLane Parflux sediment trap (Honjo and Doherty, 1988) set at 600 m above bottom (mab), with collecting cups typically open for 10 days. Organic carbon was calculated as measured total carbon less measured inorganic carbon content of freeze-dried samples. Time gaps in the 600 mab data time series were infilled with data from a sediment trap set at 50 mab, based on a linear regression of data between traps over the entire time series. Details of the Station M POC flux data collection are provided in Smith et al. (2018) and Smith et al. (2013). Water column particle flux to the seabed at PAP-SO was captured using Mc Lane Parflux sediment traps set at 100 mab and 1850 mab (Lampitt et al., 2010), with collection cups typically open for periods of 14 days. Sample POC was analyzed using the methods described in Salter (2007); in brief, samples were freeze dried, acidified and pelletized before being analyzed using an HCN–S elemental analyzer.

The fraction of seabed covered by detritus was measured by estimating the area of detrital aggregates in oblique time-lapse images (Fig. A.1). Detrital aggregates and salp carcasses were quantified in portions of seabed photographs at Station M (Table 1; see below for image annotation method; Sherman and Smith, 2009). At both sites, aggregates were measured in a quantified area of one photo per day. Seabed percentage cover was calculated for each image assessed (see below), and mean values determined to match sediment trap time periods (Station M 10-day; PAP-SO 14-day).

Typical seasonality in detrital flux to the seafloor was established by creating a composite year from all available sediment trap data at each site: 1989–2017 at Station M (data from Smith et al., 2018) and 1989–2014 at PAP-SO. This was based on the 600 mab data from at Station M and 1850 mab water depth at PAP-SO, binned at 10-day intervals at Station M and 14-day intervals at PAP-SO. Similarly, seasonality in near-seabed particle flux during the period of seabed photography was examined in 600 mab at Station M and 100 mab data at PAP-SO. Seasonality in the detrital flux was tested with ANOVA, while Spearman's rank correlations between the composited detrital flux data from different depths at each site, and with seabed cover in photographs, were calculated.

2.3. Quantifying megabenthic community at Station M from Rover photos

The seabed coverage of lebensspuren at Station M was assessed using images from a camera mounted on a seabed-transiting vehicle, the Benthic Rover (Sherman and Smith, 2009) (Table 1). The Benthic Rover was designed to minimize disturbance to the seafloor: it applies minimal down force to the seabed (weight in water 68 kg, including ballast), moves extremely slowly ($\sim$10 m d^{-1}), and produces no continuous light. The camera captured oblique photographs of the seabed as the vehicle advanced along transects of the seabed. The field of view was selected to ensure no overlap between successive images, and large areas obscured by shadows were subtracted. Images obscured by suspended sediment were removed from the analysis. Images were randomized prior to annotation to reduce annotator bias (Durden et al., 2016).

Lebensspuren (Fig. 1) were classified by their morphology, and similarities with previously identified traces (Bell et al., 2013; Bett et al., 1995; Dundas and Przeslawski, 2009; Ewing and Davis, 1967; Heezen and Hollister, 1971; Hollister et al., 1975; Kitchell et al., 1978; Ohta, 1984; Przeslawski et al., 2012; Young et al., 1985). These lebensspuren were identified and their areas measured using Monterey Bay Aquarium Research Institute's Video Annotation and Reference System (VARS; Schlining and Stout, 2006). Image measurements (pixels) were converted to seabed dimension following trigonometric perspective correction (Wakefield and Genin, 1987) using VARS and the camera orientation data (Table 1).

Presence of each lebensspuren type was noted, and total areas of each type per image converted to a percentage of the viewed area (% seabed coverage). Data from individual images were aggregated to provide sufficient seabed area for spatial analysis, over 10-day intervals to coincide with sediment trap collection periods: the mean aggregated field of view per 10-day period was 46.4 m^2 [95% confidence limits of

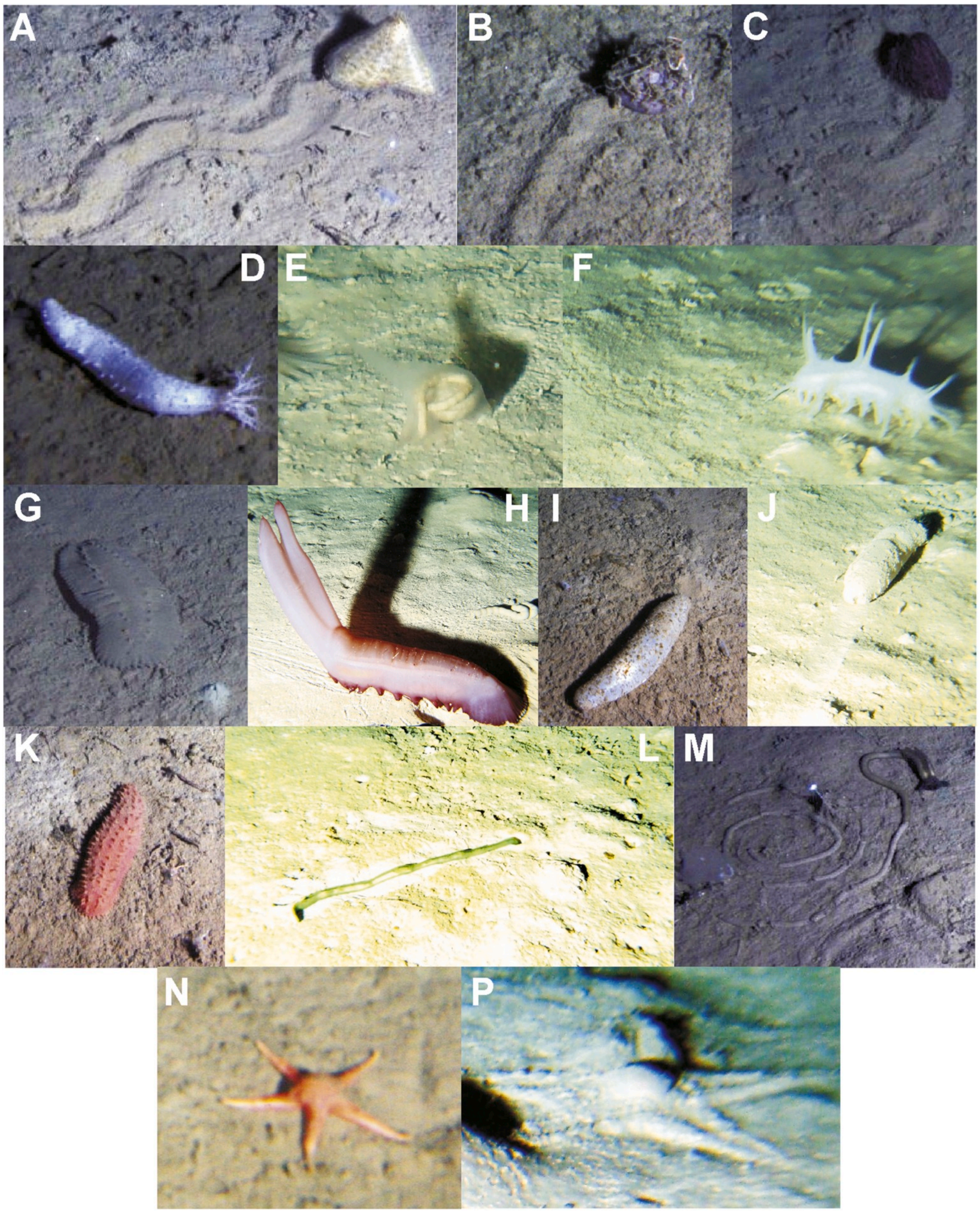

Fig. 1. Select mobile epibenthic-feeding megafauna and lebensspuren (traces) occurring at PAP-SO (*) and Station M (‡), for which tracking rates were estimated: Echinoids and 'w-shaped' tracks A *Echinocrepis* sp. ‡, B *Cystechinus* sp. ‡, C *Cystocrepis* sp. ‡; Holothurians D *Abyssocucumis abyssorum*‡, E Elpidiidae spp.*, F *Oneirophanta mutabilis* leaving 'sparse tube feet impressions', G *Paelopatides* sp. ‡, H *Psychropotes longicauda**‡ leaving 'dense tube feet impressions', I *Pseudostichopus mollis*‡, J *Molpadiodemas villosus** leaving 'smooth wide depression', K Synallactidae gen. et sp. indet. ‡; L Echiuran* and large 'spoke burrow'; M Enteropneust *Tergivelum baldwinae* ‡ with spiral fecal cast over grazed area; Asteroids N *Dytaster gilberti*‡ and P buried *Dytaster grandis grandis** each creating an 'Asteroid feeding impression'.

Table 1
Camera deployment information (T=time-lapse camera; R=Rover-mounted camera); dates listed as dd/mm/yyyy.

Reference number	Porcupine Abyssal Plain			Station M				
	JC062-119 T	JC071-043 T	ME-108-72 T	Pulse 58 T	Pulse 59 T	Pulse 60 T	Pulse 58 R	Pulse 59 R
Deployment start	21/08/2011 12:05	06/05/2012 13:49	17/07/2014 15:39	24/05/2011 19:29	20/11/2011 20:13	13/06/2012 12:59	23/05/2011	22/11/2011
Deployment end	03/04/2012 04:41	19/04/2013 12:30	28/06/2015 08:18	18/11/2011 04:26	11/06/2012 12:25	15/11/2012 11:00	17/06/2011	10/06/2012
Image interval (h)	8	8	8	1	1	1	NA	NA
Usable images	768	1044	1038	4249	4897	3720	84	816
Camera height (m)	0.80	0.80	0.80	2.22	2.22	2.22	1.12	1.12
Vertical field of view (°)	26.6	26.6	26.6	35	35	35	33.6	33.6
Horizontal field of view (°)	35	35	35	49	49	49	42	42
Camera tilt below horizontal (°)	30	30	30	32	32	32	39	39
Field of view assessed (m^2) for fauna/ lebensspuren	0.7262	0.7140	1.1484	9.53	9.53	9.53	2.71	2.71
Field of view assessed (m^2) for detritus	0.7262	0.3287	0.6794	9.779	9.779	9.779	NA	NA

39.1, 50.1].

2.4. Quantifying megabenthic deposit-feeding rates

Deposit-feeding (tracking) rates of megafauna (Fig. 1) were assessed from time-lapse oblique images from both sites (Table 1): the tripod camera (Canon EOS 5D) at Station M (Kaufmann and Smith, 1997; Sherman and Smith, 2009), and Bathysnap camera (Imenco SDS 1210) at PAP-SO (Bett, 2003). To improve comparability in the data from the two camera systems, only a portion of the total seabed area in view was analyzed (Fig. A.1). Lebensspuren were classified and measured as described in section 2.3. Creation (tracking) rates were calculated from estimated area and elapsed time, traces begun and completed between successive images were assigned a time of half the image interval.

In the case of surficial deposit feeders that did not leave a trace (e.g. *Abyssocucumis abyssorum* and *Oneirophanta mutabilis* at Station M, Elpidiidae spp. at PAP-SO), a linear rate of motion was calculated (cm h^{-1}), from which the areal trace creation rate ($cm^2\ h^{-1}$) was estimated using the anterior body width as an assumed track width. Only specimens that appeared in the field of view for a minimum of three successive images

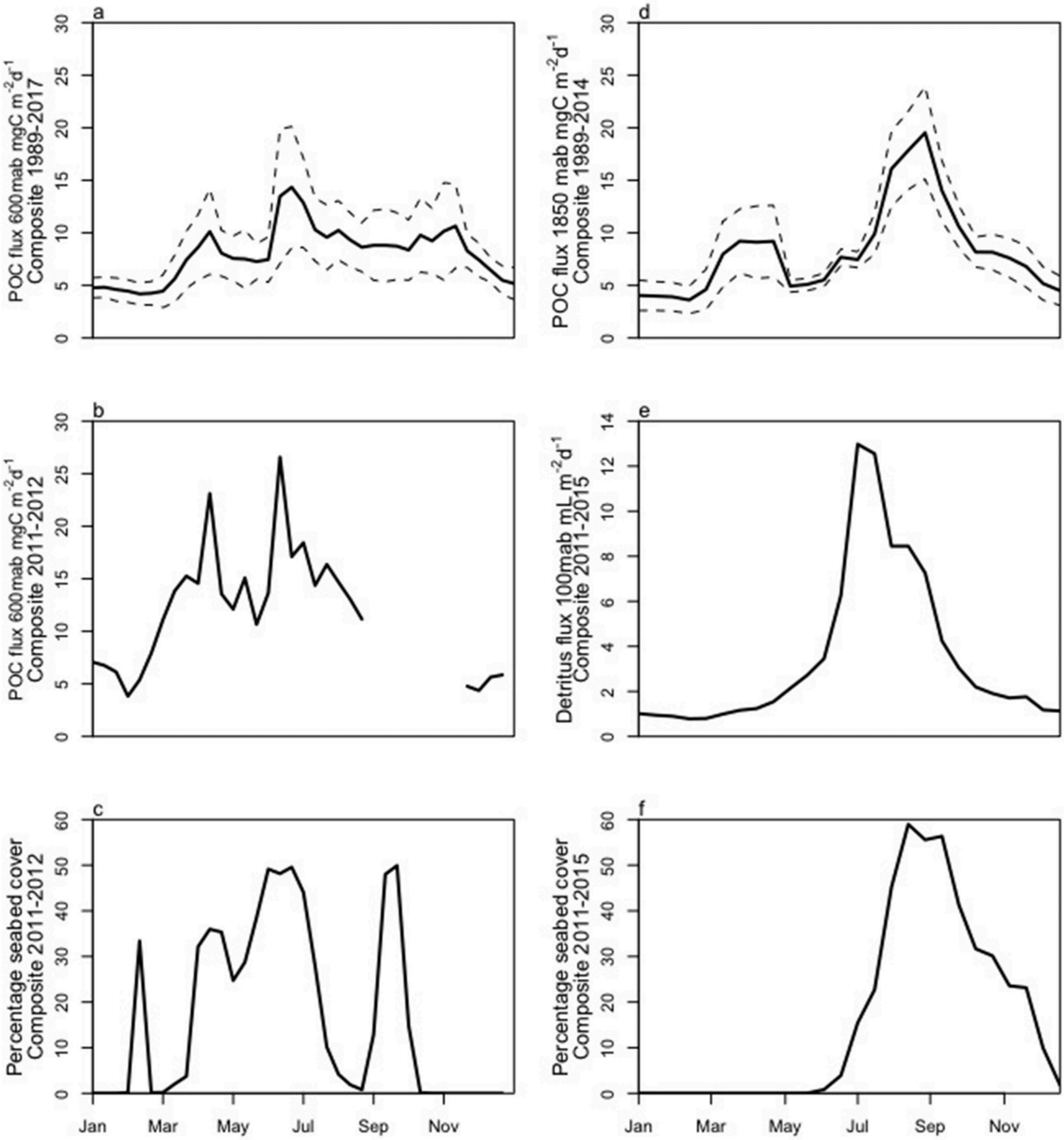

Fig. 2. Seasonality at Station M (a, b, c) and at PAP-SO (d, e, f): Mean POC flux (mg $m^{-2}\ d^{-1}$) measured in the sediment trap (a) at Station M 600 m above bottom (mab) between 1989-2017 at 10-day intervals and (d) at PAP-SO 1850 mab water depth between 1989-2014 at 14-day intervals, with 95% confidence intervals in dashed lines; Mean particle flux (b) at Station M in the 600 mab and (e) at PAP-SO 100 mab sediment trap in the interval corresponding to seabed photographs; Mean percentage seabed cover of detrital aggregates and salps estimated from time-lapse photograph measurements (c) at Station M and (f) at PAP-SO.

were used for tracking rate estimation.

The entire tracked area was calculated in the case of trace-making holothurians that produced continuous tracks. However, asteroids, echiurans, and enteropneusts are contingent (intermittent) trace-makers (Wheatcroft et al., 1989). Asteroids typically transit the seabed rapidly between feeding locations, for these taxa only the feeding trace area was calculated. Similarly, enteropneusts and some echinoids produced visible tracks while transiting the seabed slowly (and feeding), then relocated quickly to another feeding site without leaving a trace (Jones et al., 2013); only the traces were estimated.

2.5. *Statistical treatment*

To investigate the potential relationships between sediment trap estimates of particle flux and seabed cover by detritus, lebensspuren cover, and tracking rates, all data were aggregated as means for time periods matching the sediment trap records. Fractional seabed coverage was arcsine-transformed prior to statistical analysis. The presence/absence of lebensspuren (from Benthic Rover images) and tracking (from oblique time-lapse images) in relation to the particle flux and seabed coverage by detritus was tested using ANOVA, with the former lagged by up to three and four time increments, to similar time periods (i.e. 0–40 days at Station M, 0–42 days at PAP-SO). The change in lebensspuren composition over time at Station M was assessed using nonmetric multidimensional scaling (nMDS) using “Bray-Curtis” dissimilarity between 10-day aggregated seabed cover by lebensspuren in Benthic Rover images. Spearman’s rank correlations were calculated to explore any time lag between observed particle flux (lagged similarly), seabed detrital coverage, and lebensspuren coverage (in Benthic Rover images) and creation rates (from time-lapse images). Statistically significant results are reported at $\alpha = 0.05$, and p-values corrected using the method of Benjamini and Hochberg (1995) to control the false positive rate associated with large numbers of correlations calculated. Only trace types with four or more instances of creation were used for correlation with food supply variables.

3. Results

3.1. *Seasonality of detrital inputs*

3.1.1. *Station M*

Mean POC flux at 600 mab in the composite year (1989–2017) peaked in April and June (Fig. 2a), and seasonality was significant (ANOVA F[36,2] = 5.6, $p < 0.05$). The composite of mean POC flux over the period photographed (Fig. 2b) was correlated to 600 mab composite from 1989-2017 (r_S [28] = 0.74, $p < 0.001$).

In the period covered by time-lapse photography, the POC flux recorded in the sediment trap peaked in June to August 2011, as described by Smith et al. (2014), and the dominant flux in 2012 occurred between March and late May, with a peak in April, and another beginning in mid-August. The detritus observed in the seabed images appeared as a dense, green, flocculent layer, similar to the description of “type 1” provided by Lauerman and Kaufmann (1998); it was visible from late June to July 2011, and late August to October 2012. The latter deposition event was larger than any previously observed deposition event (Smith et al., 2014). Salp carcasses first appeared on the seafloor in February 2012, with peaks in April and July, but were no longer visible by September; in areas where salp carcasses were present, any underlying detritus was not visible. In the 55 10-day intervals over the period of seabed photography, seabed cover (by detritus and salps) was not significantly correlated with sediment trap POC flux (Fig. 4; Table A.2).

3.1.2. *PAP-SO*

Mean POC flux at 1850 mab in the composite year (1989–2014) peaked in mid-July/August with a secondary peak in March/April (Fig. 2d). The composite mean detritus flux (mL m^{-2} d^{-1}) at 100 mab over the photographed period (Fig. 2e) was correlated to the POC flux (mg m^{-2} d^{-1}) in the 1850 mab composite (r_S [25] = 0.97, $p < 0.0001$). In the composite year (Fig. 2e and f), seabed cover by detritus was seasonal (F[25,2] = 22.9, $p < 0.0001$), and best correlated to volume flux at 100 mab at a lag of 42 days (r_S [23] = 0.98, $p < 0.0001$).

The primary detritus flux was observed in seabed images and in the sediment trap record from July to December (Figs. 2 and 5). Detritus appeared as a dense, green, flocculent layer in the seabed images. In the 66 14-day intervals over the period of seabed photography, the volume flux measured by the 100 mab sediment trap was significantly correlated with the fraction of seabed covered by detritus, with the highest correlation occurring at a lag of 28 days (r_S [64] = 0.83, $p < 0.0001$; Table A.4).

3.2. *Spatial coverage and composition of traces at Station M*

The fraction of seabed tracked was measured in 25 10-day periods, including the March–May flux period in 2012 (Fig. 3). Tracking occurred in all periods, to a maximum total tracking of 6% in any one period (Fig. 3b). The diversity (as number of types of traces) in a 10-day period ranged from 2 to 8, and was negatively correlated to seabed cover lagged 40 d (r_S [25] = −0.6, $p < 0.0$). Echinoid tracking (the w-shaped track) appeared in every 10-day period (0.6–3.6% seabed tracked), as did the v-shaped track (0.02–1.4%). Sparse tube feet impressions appeared in the fewest 10-day periods (10). The presence of enteropneust tracking was significantly related to POC flux (F[24,2] = 8.8, $p < 0.05$; Table A.1), and also to seabed cover lagged by 30 (F[24,2] = 10.4, $p < 0.05$) and 40 days (F[24,2] = 8.2, $p < 0.05$); the presence of spoke burrows was significantly related to POC flux lagged 20 days (F[23,2] = 8.6, $p < 0.05$). *Abyssocucumis abyssorum* tracking was not visible in the Rover photos. Variation in trace composition in 10-day periods, summarized as nMDS component 1, was significantly correlated to POC flux (r_S [25] = 0.40, $p < 0.05$; Fig. 3d).

3.3. *Megafaunal activity*

3.3.1. *Station M*

Tracking rates were estimated from 96 observations of eight trace types (Table 2; Fig. 4); 43% of the tracking instances observed was by echinoids and 22% by the holothurian *Abyssocucumis*. A total of 4.99 m^2 of seabed was tracked by megafauna during the period of observation (63 10-day periods), equivalent to 52% seabed tracking annually. Echinoids, producing the w-shaped track, tracked the seabed nearly continuously (Fig. 4h), while other organisms tracked the seabed intermittently. Mean tracking (cm^2 h^{-1}) at Station M was 28% faster than at PAP-SO. The fastest mean tracking (187.1 cm^2 h^{-1}) was the production of the v-shaped track (unknown producer), while the slowest (3.1 cm^2 h^{-1}) was the enteropneust.

Seabed tracking by all quantified megafauna was not correlated to lagged POC flux or lagged detritus and salp cover. The only type of tracking correlated to the POC flux was by *Oneirophanta mutabilis,* which was correlated when POC flux was lagged by 40 days (Table A.2; Fig. 4f); note that it was only observed in 2011.

3.3.2. *PAP-SO*

Tracking rates were estimated from 106 instances of seven types of tracking (Table 2). A total seabed area of 3.33 m^2 was tracked over by megafauna during the period of observation, equivalent to 340% seabed tracking annually. The most numerous instances of tracking were the sparse tube feet impressions (45%), followed by Elpidiidae spp. (22%); only one instance of asteroid feeding was observed. The fastest seabed tracking (59.8 cm^2 h^{-1}) were the sparse tube feet impressions, at ~75% of the rate of the same tracking at Station M. Dense tube feet impressions and the smooth wide depression track were produced at less than half the speed at Station M (40 and 44%, respectively).

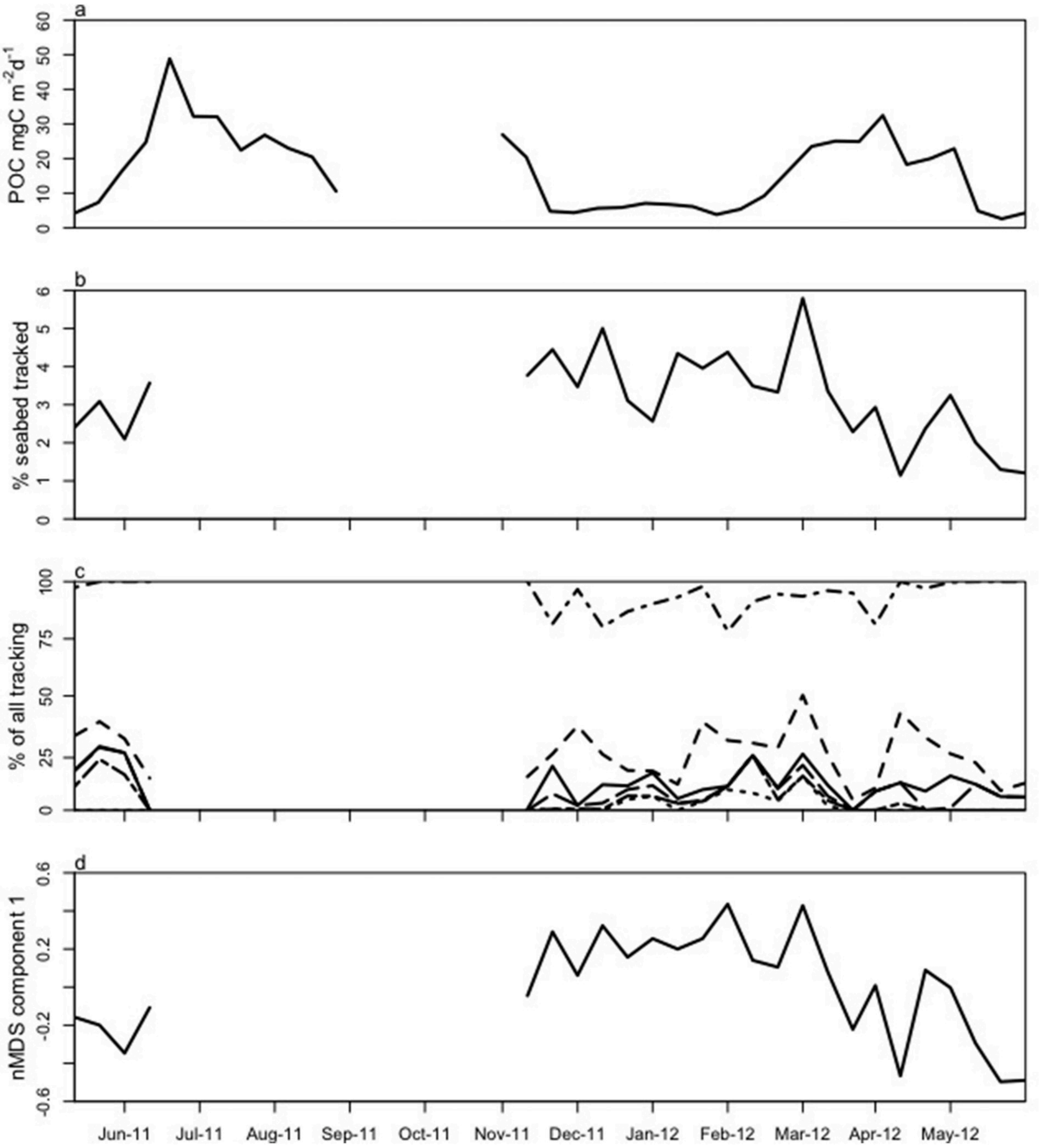

Fig. 3. Composition of traces over 10-day time periods at Station M from Rover data: (a) Mean POC flux at 600 mab; (b) Percent seabed cover by all lebensspuren; (c) Cumulative composition of seabed cover by different types of lebensspuren (from bottom: dotted = sparse tube feet, long dash = spoke burrows, longer dash = smooth wide depression, solid = dense tube feet, spaced dash = v-shaped track, dot-dash = w-shaped track); (iii) nonmetric multidimensional scaling Component 1 of Bray-Curtis dissimilarity between 10-day periods.

The presence of smooth wide depression track was significantly related to the detrital flux (F[65,2] = 7.9, $p < 0.05$; Table A.3), with the strongest relationship when detritus was lagged 42 d (F[62,2] = 18.8, $p < 0.001$). However, the smooth wide depression and dense tube feet tracks were only observed in photographs in 2012-2013. The presence of spoke burrows was best related to detrital flux lagged 42 d (F [62,2] = 7.6, $p < 0.0001$), and to seabed cover in photos, with the strongest relationship when seabed cover lagged 42 days (F [59,2] = 30.4, $p < 0.0001$).

Total seabed tracking was not correlated to lagged detritus flux or lagged detritus cover at 14-day intervals, except for spoke burrow creation by echiurans, which was significantly correlated to detrital flux lagged 14 days and more (Fig. 4, Table A.4), and to seabed cover by detritus at all lag periods tested.

4. Discussion

Our observations of the potential responses of deposit-feeding megafauna to the input of detritus were not consistent across the taxa studied. At Station M, differing responses in terms of timing of feeding and feeding rates both likely contributed to the observed differences in the diversity of traces related to seabed cover. Some deposit feeders did

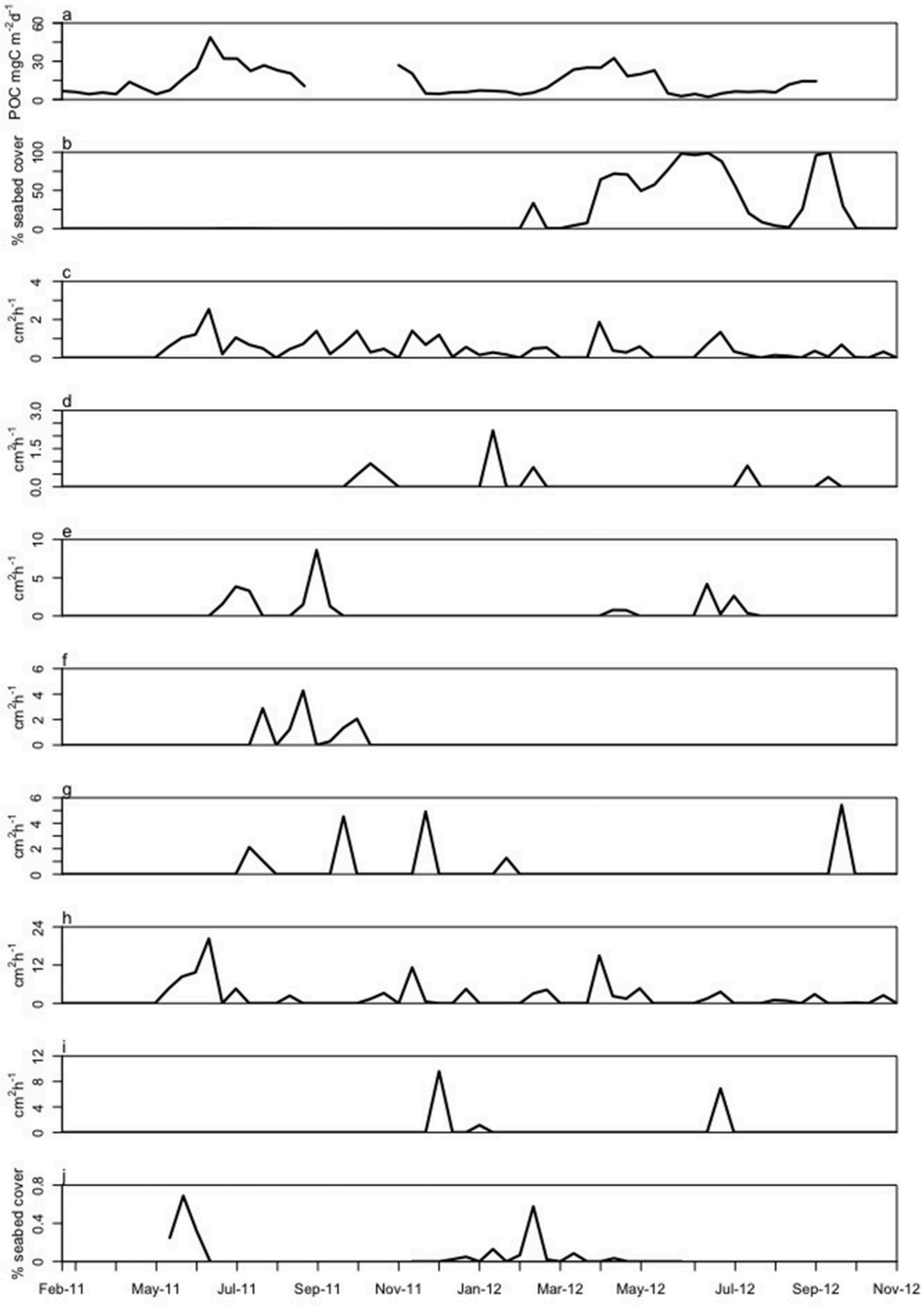

Fig. 4. Temporal variation in food supply and megafaunal tracking rates at Station M. Ten-day mean values of observations in seabed photographs between May 2011 and November 2012: detrital inputs, measured as (a) POC in sediment traps and (b) seabed coverage (%) by detritus and salps, and tracking rates (cm^2 h^{-1}) by (c) all fauna and track types, (d) asteroid feeding impressions (e) *Abyssocucumis abyssorum*, (f) *Oneirophanta mutabilis*, (g) smooth wide depression, (h) w-shaped track, (i) v-shaped track, and (j) spoke burrows (cm^2).

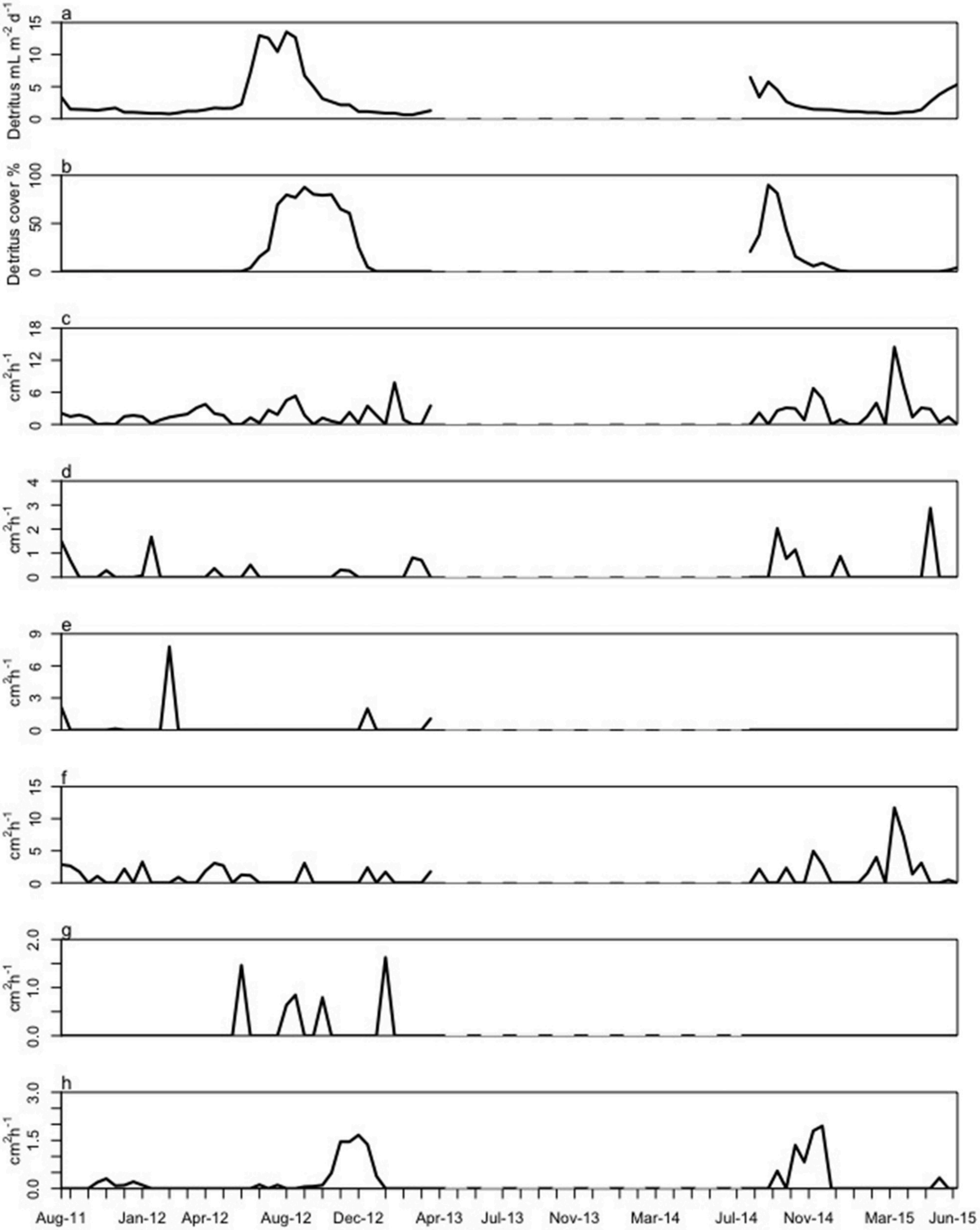

Fig. 5. Temporal variation in food supply and megafaunal tracking rates at PAP-SO. Fourteen-day mean values of observations in seabed photographs between August 2011 and June 2015 at PAP-SO: detrital inputs, measured as (a) detrital flux in sediment traps (mL m^{-2} d^{-1}) and (b) seabed coverage (%) by detritus, and tracking rates (cm^2 h^{-1}) by (c) all types, (d) Elpidiidae spp., (e) dense tube feet impressions, (f) sparse tube feet impressions, (g) smooth wide depression, (h) spoke burrows. Dashed x-axis interval represents period not sampled.

Table 2

Observations of seafloor tracking rates ($cm^2\ h^{-1}$) of deposit-feeding megabenthos (mean and 95% confidence limits) in time-lapse photographs at Station M and PAP-SO.

Indication of megafaunal activity	Station M			PAP-SO		
	No.	Mean [95% CI]	Range	No.	Mean [95% CI]	Range
Asteroid feeding depression	11	71.6 [20.4, 122.8]	0.5–211.5	1	1.5	-
Abyssocucumis track	21	39.8 [22.5, 57.1]	8.9–160.8	-	-	-
Elpidiidae spp.	-	-	-	24	13.2 [6.7, 19.5]	1.5–49.6
Benthothuria/ Benthodytes track	-	-	-	4	47.0 [1.4, 92.6]	14.6–115.0
Dense tube feet impressions	2	110.24	47.3–173.2	8	44.2 [16.8, 71.6]	5.2–136.2
Sparse tube feet impressions	9	80.8 [47.4, 114.3]	23.7–162.7	48	59.8 [48.3, 71.3]	14.3–167.7
Smooth wide depression track	6	40.0 [15.1, 64.8]	7.4–86.8	4	17.5 [5.2, 29.9]	6.7–34.1
W-shaped track	41	26.4 [15.4, 37.4]	1.9–217.0	-	-	-
V-shaped track	4	187.1 [78.0, 296.2]	68.6–331.0	-	-	-
Enteropneust track	2	3.1	2.8–3.4	-	-	-
Spoke burrow	-	-	-	17	11.0 [0.9, 21.2]	0.1–75.5
Total	96	48.4 [36.2, 60.7]	0.5–331.0	106	37.6 [30.1, 45.1]	0.1–167.7

appear to exhibit seasonal variation in their feeding, either by feeding seasonally, or with increased rates associated with the arrival of detritus to the seabed. Fauna exhibiting this behavior were, generally, relatively uncommon deposit feeders, such as enteropneusts at Station M and echiurans at PAP-SO, and may be specialist feeders on fresh organic matter, as feeding behavior of enteropneusts and echiurans has been related to the deposition and renewal of organic matter at the sediment surface (Carey and Mayer, 1990; Smith et al., 1993a). The seasonality in their feeding, as either tracking ($cm^2\ h^{-1}$) or simple presence of traces, was not mirrored in the whole-community feeding rates ($cm^2\ h^{-1}$), because community rates were dominated by the relatively constant feeding of the numerically-dominant deposit feeders. These dominant deposit feeders included echinoids and *Abyssocucumis abyssorum* at Station M, and the holothurians *Psychropotes longicauda* and *Oneirophanta mutabilis* at PAP-SO.

Our results suggest that seasonality in deep-sea invertebrate deposit feeding may be related to life history traits, specifically feeding and foraging modes. For example, echiurans are thought to cache food (Hughes et al., 1994; Jumars et al., 1990), a behavior that enables them to actively gather food primarily when suitable fresh detritus is available (Shields and Hughes, 2009). Alternation of feeding modes to include detritivory may be common in the deep-sea benthos (e.g. Jeffreys et al., 2011), including the hemisessile predator *Iosactis vagabunda* (Durden et al., 2015b), the most common megafaunal taxon at PAP-SO. In the case of deposit-ingesting asteroids, such as *Dytaster* sp., they may also predate on macro-infauna (Howell et al., 2003). This diversification of diet, while difficult to quantify, reduces their direct dependence on detrital input, thus decoupling their feeding from its seasonal input.

Mobile epibenthic megafauna, such as holothurians, forage large surface areas (Billett, 1991; Lauerman and Kaufmann, 1998; Roberts et al., 2000). This strategy may assist these deposit feeders to exploit the resource available at the time most effectively. Both the total particle flux and the composition of that organic matter, such as the fatty acid and low molecular weight alcohol content, are known to vary seasonally (Kiriakoulakis et al., 2001). This resource can be partitioned through selective feeding based on particle quality, which may allow continuous feeding by the deposit-feeding holothurians (Wigham et al., 2003). Seasonal changes in the gut contents of *Oneirophanta mutabilis* revealed that it fed selectively on fresh material, but that it continued to feed when fresh detritus was scarce (FitzGeorge-Balfour et al., 2010), operating as a 'conveyor belt feeder' (Moore and Roberts, 1994). This selectivity may account for the seasonality observed in the apparent feeding rate of *Oneirophanta mutabilis* at Station M; however, Witbaard et al. (2001) suggested that *O. mutabilis* does not appear to actively search for fresh detritus. The seasonality observed in feeding by *O. mutabilis* may instead be related to its consumption of bacteria in the sediment (as evidenced by fatty acids in gut contents; Drazen et al., 2008), the population of which may respond rapidly to the introduction of fresh detritus (see below). The larger holothurians that are assumed to feed on a thicker/deeper layer of surficial sediment, such as *Molpadiodemas* sp. (Roberts et al., 1996), appear to be less selective feeders (FitzGeorge-Balfour et al., 2010), with their gut contents suggesting decoupling from seasonality in food supply as assessed by stable isotope analysis (Iken et al., 2001). Prokaryotes/bacteria in the sediment are important to the diet of bulk sediment feeders (Amaro et al., 2012), so selectivity in these organisms may not be in preference of fresh detritus. Selectivity (or lack thereof) for fresh detritus may be related to the contrasting foraging modes in mobile megafauna. Foraging motions facilitating a high degree of such selectivity by exploiting food patches, such as the 'run and mill' or 'loop' patterns of motion observed in *A. abyssorum* (Kaufmann and Smith, 1997), versus continuous movement likely related to non-selective bulk ingestion, such as the 'run' observed in *Echinocrepis* sp. and *O. mutabilis* (Kaufmann and Smith, 1997; Vardaro et al., 2009), and *Molpadiodemas* sp. (Billett, 1991). Although the deposit feeding rate may not vary with time for the latter type of foragers, the carbon consumed over time may vary as the carbon content of the deposited detritus and surface sediment changes seasonally (Kiriakoulakis et al., 2001). This variation in the quality of organic matter consumed could be quantified via seasonal sampling of surficial sediments and detrital aggregates, with any biogeochemical signal in the response of the megafauna (Jeffreys et al., 2009; Wigham et al., 2003) discerned through specimen collection at similar timescales.

Variations in community-wide consumption of detritus are also likely to be linked to the densities of deposit feeders. Multi-annual variations in megafaunal community structure have been observed at Station M (Kuhnz et al., 2014). Similarly, intra-annual variations in detritus flux (Bett et al., 2001; Lampitt et al., 2001) and megabenthic community structure (Billett et al., 2010) have been documented at the PAP-SO, with an increase in the tracking of the seabed by the mobile megafauna related to increases in their densities (Bett et al., 2001). Major variations recorded related to substantial variations in the density, biomass, body size structure and proportions of the fauna in different feeding groups, with direct implications for community ingestion rates. For example, at PAP-SO Bett et al. (2001) reported that the time taken to track 100% of the seabed varied from 6 weeks to 2.5 years during the course of a 10-year period, primarily driven by a change in the density of the *Amperima rosea* (a component of Elpidiidae spp.) population. During the period of our observations, the density of Elpidiidae spp. at PAP-SO appeared to be in an intermediate state between its 'boom-bust' density extremes (see Billett et al., 2010). The increase in the density of the holothurian *Peniagone* sp. A at Station M observed 14 weeks after the salp deposition (Smith et al., 2014) occurred near the end of our study period. Unfortunately, tracking by *Peniagone* sp. A could not be quantified reliably in this study because of its high density and lack of trace-making.

The combination of inter- and intra-annual factors that impact carbon cycling at the two study sites are discussed by Smith et al. (2009) in the context of climate variations and surface ocean processes. In terms of inputs to the abyssal benthos, a larger and later peak in the annual detrital input occurs at PAP-SO than at Station M, as evidenced by the composite particle fluxes at 3000 m and 3400 m water depth (1850 mab and 600 mab), respectively (Fig. 2a, d; 19.5 mg m^{-2} d^{-1} in August versus 14.3 mg m^{-2} d^{-1} in June). These differences were also apparent at the seafloor in terms of seabed cover during the period photographed, despite the exceptional input at Station M in 2012. The apparent lag between the appearance of detritus in the near-seabed sediment trap at PAP-SO and its appearance in seabed photos (42 days), may be complicated by the resuspension after its initial deposition on the seafloor. Similar factors likely influence the lag time between the sediment trap signal and the appearance of detritus on the seabed at Station M, and may be further confounded by the salp deposition clogging the sediment trap (Smith et al., 2014).

While the two study sites were similar in mean flux (8.0 mgC $m^{-2}d^{-1}$ at Station M and 8.3 mgC m^{-2} d^{-1} at PAP-SO in the composite year), the seasonality in the flux was greater at PAP-SO. At PAP-SO, detritus appeared at depth more rapidly, as evidenced by the shorter Flux Stability Index (minimum time for 50% of the annual flux to be achieved; 140 days at Station M and 112 days at PAP-SO; Lampitt and Antia, 1997). The contrast between sites in the uptake of deposited detrital material was substantial: mean tracking per period at PAP-SO was five times that of Station M (1.9 cm^2 $h^{-1}$and 0.4 cm^2 h^{-1}, respectively). This slow uptake at Station M, and the offset between sites, may be largely because the typically high numerical density deposit-feeding holothurians *Peniagone* sp. A, *Peniagone vitrea*, *Peniagone* sp. 1, *Scotoplanes globosa* and *Elpidia minutissima* at Station M (totalling 33–48% of megafaunal individuals in 2011-2012; Kuhnz et al., 2014; Kuhnz et al., this issue) were not included because they are non-tracemakers. The time for these holothurians to track the seabed, assuming a tracking rate equivalent to that of Elpidiidae spp. at PAP-SO, may have reached 4.6 weeks during periods of low density (1.0 ind m^{-2} in November 2011) to 1.4 weeks in periods of high density (3.2 ind m^{-2} in November 2012). These estimates suggest that the true time to track the seabed was less at Station M than at PAP-SO, in accord with the order of magnitude higher density of holothurian deposit feeders at Station M above that of PAP-SO in 2011/2012 (Durden et al., 2015a; Kuhnz et al., 2014). The higher rates of deposit-feeding at Station M, particularly between organisms that exist at both sites (e.g. *Oneirophanta mutabilis*), are likely a result of the larger body sizes of those organisms at Station M (Durden et al., 2019). The high numerical density population of *Iosactis vagabunda* at PAP-SO was excluded because its detritivory could not be quantified.

Differences in deposit feeding between the two sites may also be related to the varying quality of the detritus deposited at each site, and differing community composition altering the partitioning of this resource. Occurrences of feeding by taxa with similar feeding modes were similar between the sites, such as the superficial deposit feeders *Abyssocucumis abyssorum* and Elpidiidae spp., and the subsurface bulk ingestion makers of the smooth wide depression. However, a greater abundance of deep subsurface sediment feeders (e.g. echinoids, asteroids) were observed at Station M. The notable paucity of observations of *Oneirophanta mutabilis* (sparse tube feet impressions) at Station M in comparison to PAP-SO may be related to the increase in densities of *Peniagone* spp., *Scotoplanes globosa* and *Elpidia minutissim*a that occurred in 2011-2012, but whose deposit feeding was not quantified here. These holothurians may feed similarly, based on mouth/tentacle morphology, and may compete for a similar portion of the detrital resource.

The similar lag times between detrital flux measured in the sediment traps and its appearance on the seabed, and the deposit feeding by those taxa exhibiting some seasonality suggests an immediate response by those deposit feeding megafauna, in agreement with findings from uptake experiments on holothurians (Lauerman et al., 1997). This immediate response may be important in terms of competition with other size classes of the benthos for the same resource. The rapid ingestion of sedimented detritus, suggesting a near-immediate response, by macrofauna has been observed, as has a near-immediate change in the sediment community oxygen consumption (Jeffreys et al., 2013; Laguionie Marchais et al., this issue; Smith et al., 2014). A size-based model of ingestion succession, where larger fauna rework fresh detritus before small classes (e.g. meiofauna and microbes) has been suggested (Witte et al., 2003). Size-related implications for taxon-specific seasonality have not been explored here; however, individual megafaunal deposit feeding rates at these sites is consistent with a mass- and temperature-specific constant feeding rate that is broadly constant (Durden et al., 2019). The deposit feeding (ingestion) rates estimated in this study may be useful in refining the concepts of resource partitioning between feeding types and size classes in abyssal plain environments (e.g. Dunlop et al., 2016; Durden et al., 2017; Kelly-Gerreyn et al., 2014), in combination with refinements to estimates of suspension feeding based on recent behavioral observations (Kahn et al., this issue). Further, they may be valuable in assessing the potential impacts of variation in the flux of carbon to the seafloor, such as may occur through episodic deposition events (Billett et al., 2006; Smith et al., 2018) and more generally via climate change (Jones et al., 2014; Yool et al., 2017).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

Table A.1

ANOVAs of presence of megafaunal activity in Rover images with POC flux (mg m^{-2} d^{-1}) in sediment traps at 600 m above bottom and seabed cover (%) by detritus and salps in time-lapse images in 10-day intervals at Station M, F values given, significant relationships noted in bold, corrected p values are denoted as follows: $^{*}p < 0.05$.

	ANOVAs with POC flux					ANOVAs with seabed cover in photos (%)				
	No lag (n = 23)	10d (n = 23)	20d (n = 22)	30d (n = 21)	40d (n = 20)	No lag (n = 23)	10d (n = 23)	20d (n = 22)	30d (n = 21)	40d (n = 20)
Asteroid feeding depression	0.8	0.6	0.3	1.1	1.2	1.6	1.4	0.8	2.1	3.9
Abyssocucumis track (tripod)	1.2	6.1	4.4	4.6	1.6	3.2	5.7	5.1	2.6	1.1
Dense tube feet impressions	0.5	0.2	1.1	1.1	0.1	4.2	0.7	0.2	0.7	4.5
Sparse tube feet impressions	4.1	5.8	3.7	5.5	4.7	5.1	4.6	3.4	2.5	4.6
Smooth wide depression track	0.5	1.4	0.5	1.1	1.2	0.1	0.5	0.6	1.8	0.2
W-shaped track	1.0	0.2	0.0	1.0	0.6	0.5	0.5	0.4	0.3	0.3
V-shaped track	1.0	0.2	0.0	1.0	0.6	0.5	0.5	0.4	0.3	0.3
Enteropneust track	**8.8***	3.5	1.9	2.2	1.6	3.2	3.8	2.7	**10.4***	**8.2***
Spoke burrows	0.9	6.7	**8.6***	3.0	1.4	2.4	2.0	6.9	2.6	5.2

Table A.2

Spearman's rank correlations of megafaunal activity (cm^2 h^{-1}; except as noted) from time-lapse images with POC flux (mg m^{-2} d^{-1}) in sediment traps at 600 m above bottom and seabed cover (%) by detritus and salps in 10-day intervals at Station M, r_S values given, significant relationships noted in bold, corrected p values are denoted as follows: $^{*}p < 0.05$.

	Correlations with POC flux					Correlations with seabed cover in photos (%)				
	No lag (n = 51)	10d (n = 52)	20d (n = 53)	30d (n = 54)	40d (n = 55)	No lag (n = 30)	10d (n = 30)	20d (n = 30)	30d (n = 30)	40d (n = 30)
Detritus and salp cover	−0.03	0.01	0.06	0.06	0.05					
Asteroid feeding depression	−0.14	−0.13	−0.15	−0.17	−0.20	0.002	−0.04	−0.11	−0.11	−0.10
Abyssocucumis track	0.13	0.20	0.16	0.18	0.21	0.24	0.22	0.17	0.12	0.16
Sparse tube feet impressions	0.19	0.23	0.30	0.32	**0.37***	−0.23	−0.22	−0.17	−0.10	−0.15
Smooth wide depression track	0.04	0.22	0.31	0.21	0.21	−0.07	−0.01	−0.02	−0.12	−0.20
W-shaped track	0.27	0.15	0.08	−0.02	0.07	0.08	0.07	0.02	−0.03	−0.02
V-shaped track	−0.21	−0.29	−0.10	−0.11	−0.20	−0.02	0	−0.01	−0.004	−0.02
Spoke burrows (seabed cover) (n = 25 for all tests)	−0.04	−0.44	−0.51	−0.36	−0.23	−0.27	−0.33	−0.45	−0.40	−0.41
All tracking	0.25	0.21	0.26	0.21	0.24	−0.06	−0.06	−0.12	−0.19	−0.19

Table A.3

ANOVAs of presence of megafaunal activity in time-lapse images with detrital volume flux (mL m^{-2} d^{-1}) in sediment traps 100 m above the bottom and seabed cover (%) in 14-day intervals at PAP-SO, F values given, significant relationships noted in bold, corrected p values are denoted as follows: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; ****$p < 0.0001$

	ANOVAs with detritus (mL m^{-2} d^{-1})				ANOVAs with seabed cover in photos (%)			
	No lag (n = 64)	14d (n = 63)	28d (n = 62)	42d (n = 61)	No lag (n = 64)	14d (n = 63)	28d (n = 62)	42d (n = 61)
Asteroid feeding impressions	0.7	1.0	0.8	0.0	0.0	0.9	1.5	0.3
Dense tube feet impressions (*Psychropotes longicauda*)	0.8	1.3	0.6	0.3	1.7	0.5	0.1	0.1
Sparse tube feet impressions (*Oneirophanta mutabilis*)	3.1	1.7	1.9	3.2	4.8	4.2	2.5	2.1
Smooth wide depression track (*Molpadiodemas* sp.)	**7.9***	**7.2***	**7.9***	**18.8*****	5.4	4.7	3.0	1.4
Benthothuria/Benthodytes track	0.0	0.0	0.0	0.0	0.2	0.0	0.2	0.3
Spoke burrows	0.2	1.8	3.9	**7.6****	**10.8****	**15.4****	**21.7******	**30.4******
Elpiididae spp. tracking	0.7	1.0	0.8	0.0	0.0	0.9	1.5	0.3

Table A.4

Spearman's rank correlations of megafaunal activity (cm^2 h^{-1}; except as noted) from time-lapse images with detrital volume flux (mL m^{-2} d^{-1}) in sediment traps 100 m above the bottom and seabed cover (%) in 14-day intervals at PAP-SO, r_S values given, significant relationships noted in bold, corrected p values are denoted as follows: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; **** $p < 0.0001$

	Correlations with detritus (mL m^{-2} d^{-1})				Correlations with seabed cover in photos (%)			
	No lag (n = 66)	14d (n = 65)	28d (n = 64)	42d (n = 63)	No lag (n = 66)	14d (n = 64)	28d (n = 62)	42d (n = 60)
Detritus cover	**0.75******	**0.82******	**0.83******	**0.81******				
Dense tube feet impressions (*Psychropotes longicauda*)	−0.07	−0.15	−0.10	−0.08	−0.19	−0.06	−0.03	−0.05
Sparse tube feet impressions (*Oneirophanta mutabilis*)	−0.12	−0.12	−0.12	−0.15	−0.24	−0.23	−0.23	−0.20
Smooth wide depression track (*Molpadiodemas* sp.)	0.19	0.20	0.22	0.25	0.20	0.27	0.27	0.18
Benthothuria/Benthodytes track	0.003	0.02	0.06	−0.02	0.02	−0.02	−0.03	−0.02
Spoke burrows	0.18	**0.33***	**0.41****	**0.51******	**0.47*****	**0.51******	**0.55******	**0.59******
Elpidiidae spp. tracking	0.06	0.01	0.01	0.11	−0.03	0.07	0.10	0.02
All tracking	0.05	0.02	0.02	−0.002	−0.02	−0.02	0.00	0.06

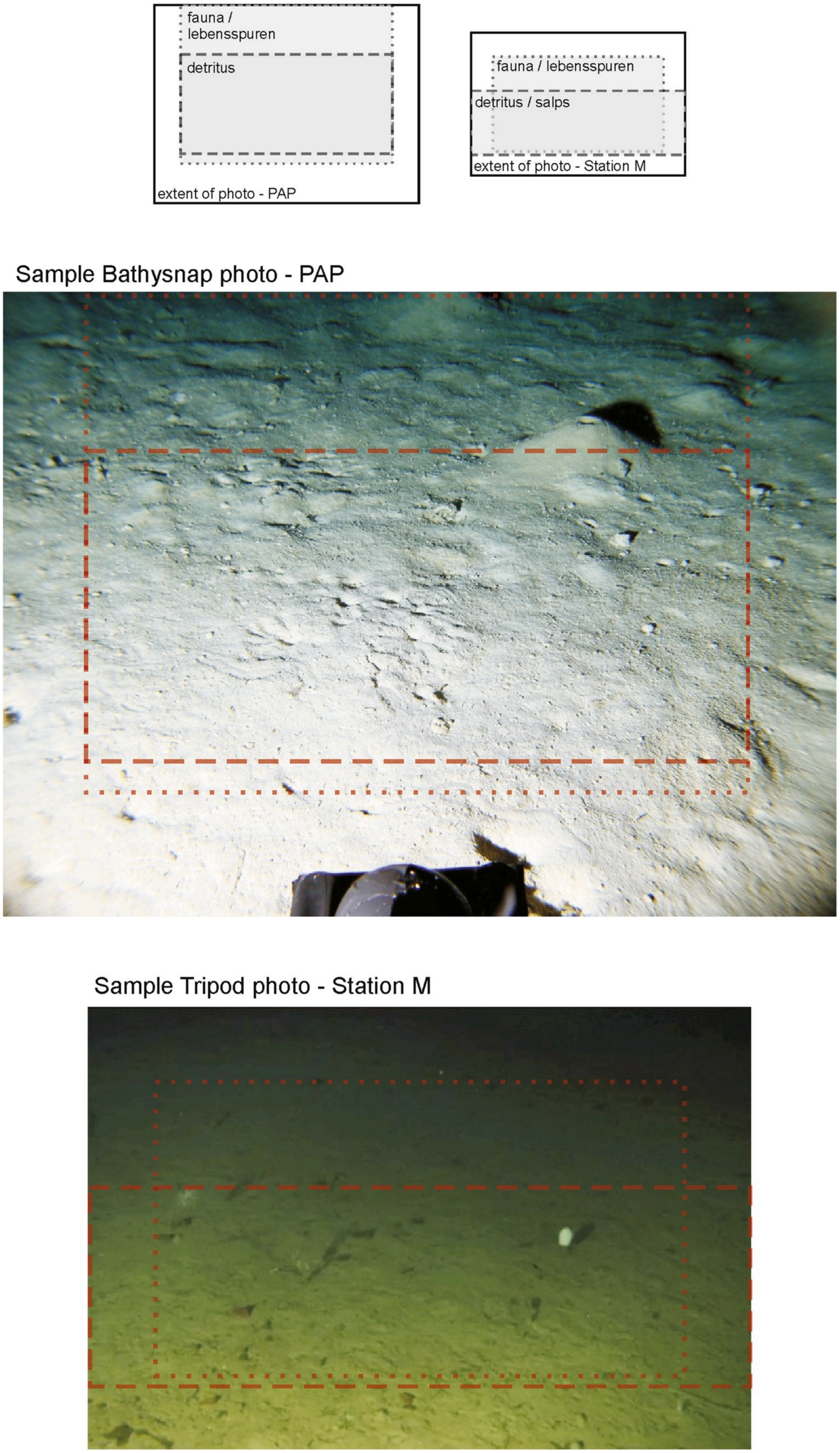

Fig. A.1. Fields of view used for quantification of detritus / salps and fauna / lebensspuren in time lapse photographs captured with Bathysnap at PAP-SO and with the camera tripod at Station M (diagram to scale).

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