Insights from abyssal lebensspuren

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ABSTRACT

The seasonal input of food to the abyss impacts the benthic community, and changes to that temporal cycle, through changes to the climate and surface ocean conditions impact the benthic assemblage. Most of the benthic fauna are deposit feeders, and many leave traces ('lebensspuren') of their activity in the sediment. These traces provide an avenue for examining the temporal variations in the activity of these animals, with insights into the usage of food inputs to the system. Traces of a variety of functions were identified in photographs captured in 2011 and 2012 from Station M, a soft-sedimented abyssal site in the northeast Pacific. Lebensspuren creation, holothurian tracking, and lebensspuren duration were estimated from hourly time-lapse images, while trace densities, diversity and seabed coverage were assessed from photographs captured with a seabed-transiting vehicle. The creation rates and duration of traces on the seabed appeared to vary over time, and may have been related to food supply, as may tracking rates of holothurians. The density, diversity and seabed coverage by lebensspuren of different types varied with food supply, with different lag times for POC flux and salp coverage. These are interpreted to be due to selectivity of

deposit feeders, and different response times between trace creators. These variations shed light on the usage of food inputs to the abyss.

INTRODUCTION

Deep-sea benthic communities rely on a seasonal food supply of detritus from the surface ocean (Billett *et al.*, 1983, Rice *et al.*, 1986). Previous studies have confirmed the coupling of the detritus found on the seabed to the productivity of the surface ocean (Smith *et al.*, 2008), the fate of that detritus within the epifaunal and infaunal communities (Beaulieu, 2002), and the resulting seasonal alterations to the sediment community structure (Gooday *et al.*, 1990, Thiel *et al.*, 1989). Changes to benthic communities in response to food supply have been studied for macrofauna (Ruhl *et al.*, 2008) (Drazen *et al.*, 1998, Smith Jr *et al.*, 2002), and bacteria and protozoa (Pfannkuche, 1993), and alterations to the megafaunal holothurian community have been ascribed to environmental forcing altering food supply (Billett *et al.*, 2001, Billett *et al.*, 2010). Temporal variation in the quantity and quality of surface production is related to climatic variations such as El Nino/La Nina and anthropogenic climate change (Behrenfeld *et al.*, 2006), and is known to impact the benthic ecosystem structure (Smith *et al.*, 2008), particularly epibenthic megafauna (Ruhl and Smith, 2004).

Many epifaunal and infaunal abyssal megafauna are deposit feeders, including echinoderms, cnidarians, enteropneusts, sipunculids and echiurans (Durden *et al. in prep.*)(Billett *et al.*, 2010, Lauerman *et al.*, 1996). These animals are important to the cycling of carbon in the deep sea, and their feeding behavior varies with food input (Kaufmann and Smith, 1997). Many of these deposit-feeders leave traces of their activity in the sediment ('lebensspuren'), including locomotory tracks, feeding traces, feces, and burrows left by epi-and infaunal mega- and macrofauna. These lebensspuren may thus be used as a proxy for benthic faunal activity. Types, origins and dynamics of these traces have been examined in different sedimentary environments (Wheatcroft *et al.*, 1989, Wheatcroft, 1992,

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Young *et al.*, 1985), shedding light on bioturbation and deposit feeding activity and its role in carbon cycling (Jumars and Wheatcroft, 1989, Smith *et al.*, 1986).

This study aims to investigate the temporal variation in lebensspuren (creation rates, longevity, densities, seabed coverage, and assemblage composition) in relation to the food supply. Rates of lebensspuren creation and longevity of traces are hypothesized to vary with time, in correlation with the influx of detritus. The densities and seabed coverage by lebensspuren, and the composition of the lebensspuren assemblage are hypothesized to vary similarly. Variations in the lebensspuren metrics are derived from photographs, and conclusions are drawn about the temporal variation in the activity of benthic fauna, and the use of lebensspuren as proxies for this activity and/or the faunal community. Finally, comments are made on the use of the rover camera and the tripod camera for capturing lebensspuren and faunal size data.

MATERIALS AND METHODS

LOCATION AND STRATEGY

The study location, Station M in the NE Pacific (at approximately 4000m depth, 34°50'N, 123°06'W) was selected because it is assumed to be spatially homogeneous at the scale of study in terms of habitat and environmental conditions (topography, food input, and sediment nutrient concentrations, particle size distribution, density, water content, etc.), and mega- and macrofaunal communities. It is the site of long-term time-series study of the habitat, benthic assemblage, and food supply, and the impact to these of variations in environmental conditions such as El Nino/La Nina (Ruhl and Smith, 2004) and climate change (Smith *et al.*, 2013).

LEBENSSPUREN CATALOGUE

Lebensspuren visible in the photos were classified into 22 morphotypes, which were grouped by presumed primary function: locomotory tracks (10

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morphotypes), burrows and holes (4 morphotypes), feeding impressions (1 morphotype), fecal matter (5 morphotypes), and unknown traces (2 morphotypes). A catalogue of lebensspuren was created (Appendix 1), including morphology, approximate size and associated trace creators. Morphotypes were named and categorized to match existing names given to similar/identical morphotypes in other locations across the globe (Bell *et al.*, 2013, Bett *et al.*, 1995, Dundas, 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), without conflicting with existing names in VARS. Some lebensspuren types may result from activities of multiple function, for example locomotory traces produced by deposit feeders that feed in transit. These lebensspuren categories and morphotypes were added to MBARI's Video Annotation and Reference System (VARS)(Schlining and Stout, 2006) to facilitate consistent, traceable image annotation.

TRACE CREATION AND DEGRADATION

Trace creation and degradation rates were measured in oblique photographs captured using a timed camera mounted on a tripod (Sherman and Smith Jr, 2009). Images were captured at hourly intervals during three deployments (Pulses) spanning an 18-month period (Table 1). Trace areas were quantified within the centre two-thirds of the image horizontally, and the lower three-quarters of the image vertically, by measuring the width and area of each trace upon completion, and identifying and measuring the width of each trace-maker (radius from center of disk to end of arm in Asteroids). This annotated data was processed to account for the Canadian (perspective) grid using a code developed by Brian Schlining based on Wakefield and Genin (1987); camera acceptance angles were 35° and 50°, and the altitude of camera was 230cm (Kaufmann and Smith, 1997, Sherman and Smith Jr, 2009), resulting in a field of view of 9.5 m^2. Track creation rates were calculated from the start and end date and time, and trace areas were converted to linear distances in the direction of travel using the

measured width. Asteroid creation rates were calculated as trace per time. Trace longevity was calculated from the date of completion of the trace to the last time the trace was visible and identifiable.

Table 1. Time-lapse oblique image details

Pulse	Start Date	End Date	No. images
58	24 May 2011 19:29	18 November 2011 04:26	4249
59	20 November 2011 20:13	11 June 2012 12:25	4897
60	13 June 2012 12:59	15 November 2012 11:00	3720

Some traces were difficult to observe in the time-lapse images due to lighting and the oblique camera angle, so linear tracking rates of some known trace-makers (all holothurians) were calculated as a proxy of trace creation rate. Tracking rates were calculated by measuring the distance between the locations of the animal head in successive images and assuming a direct route of travel. Only animals that appeared in the field of view for a minimum of three successive images were used for tracking rate estimation. Morphotypes for which either tracking rates or creation rates of associated lebensspuren were calculated appear in Figure 1.
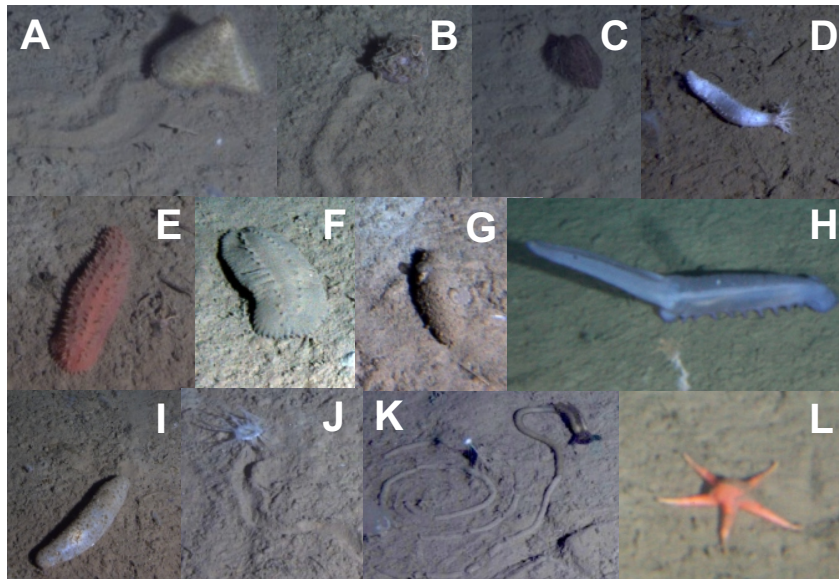
Figure 1. Epibenthic deposit-feeding megafauna found at Station M, for which either tracking rates (*) or creation rates of associated lebensspuren were calculated: Echinoids A *Echinocrepis* sp., B *Cystechinus* sp., C *Cystocrepis* sp.; Holothurians D *Abyssocucumis abyssorum**, E Synallactidae gen. sp. indet., F *Paelopatides* sp., G *Paroriza* sp., H *Psychropotes longicauda*, I *Pseudostichopus mollis*; J Unidentified Cnidarian; Enteropneust K *Tergivelum* sp.; Asteroid L *Pseudarchaster* sp.

Mean trace creation rates, trace duration and tracking rates were computed over 10-day increments for comparison with food supply data, using the trace creation start date, the trace creation end date and the tracking start date, respectively.

LEBENSSPUREN DENSITY AND SEABED COVERAGE, LEBENSSPUREN AND ANIMAL SIZING

The density and seabed coverage of lebensspuren was assessed using images from the benthic rover (Sherman and Smith Jr, 2009) with a time frame that coincided with a portion of the images from the tripod (Table 2). No rover images were captured between June and November 2011. A camera mounted on the rover captured oblique photographs of the seabed as the rover advanced along transects of the seabed, at an approximate rate of one photograph per hour during a set, and one set of 9 photographs every third day. The camera is mounted 112 cm above

the seabed, with a vertical acceptance angle of 33.6^o, a horizontal angle of 42°, and a camera tilt of 39° from the horizontal. Thus, each photo represented 2.71 m^2 of the seabed. Images obscured by suspended sediment were removed from the analysis. The field of view was selected to ensure no overlap between successive images, and large areas obscured by shadows were subtracted.

Table 2. Rover oblique image details

Pulse	Dates	Images	Total area (m^2)	Mean photo area (m^2)
58	23 May–17 Jun 2011	84	108.0	1.29 ± 0.35
59	22 Nov–10 Jun 2011	816	1006.6	1.23 ± 0.28

Images were randomized prior to annotation to reduce annotator bias (due to fatigue, increase in skill over time, etc.). Lebensspuren in the images were identified, and a size dimension and the area of seabed covered by the trace were measured for each. The areas were converted to a percentage of the viewed area (% seabed coverage). Data from individual images were aggregated over 10-day intervals to represent a sufficient seabed area: the mean 10-day field of view was 46.4 ± 12.5 m^2. Ranked seabed coverage by lebensspur type was computed at time intervals representing high phytodetrital input, low phytodetrital input, and during the peak of salp detritus on the seabed.

DATA ON FOOD SUPPLY

Lebensspuren and faunal data were compared to existing temporal data on food supply to Station M: 10-day mean organic carbon flux to the seabed (mg.m^{-2}) measured using sediment traps located 600m above the seabed (Smith Jr *et al.*, 2014), and seabed coverage (%) by phytodetritus and salps measured in the rover images (Smith Jr *et al.*, 2014). Detritus and salp coverage was supplied on a daily basis, but converted to 10-day means to give similar seabed area representation to the lebensspuren data. POC flux and salp coverage were lagged by 0, 10, 20, 30 and 40 days for comparison with lebensspuren data to assess response to food

input by the benthic community using Spearman rank correlations, with significance at 5% reported.

COMPARISON BETWEEN ROVER AND TRIPOD IMAGE DATA

Sizes of echinoids measured in rover and tripod images were selected for comparison using ANOVA due to the plethora of data points across the full rover time scale.

RESULTS

FOOD SUPPLY TO STATION M

As described by Smith et al. (2014), the main POC flux in 2011 occurred between June and August. The main POC flux in 2012 occurred between March and late May, with a peak in April 2012. Salp aggregates began to collect on the seafloor in March 2012, with peaks in April and July 2012, but had disappeared by September. Detrital aggregates were visible on the seabed in September, but were gone by October 2012.

OBSERVATIONS FROM PHOTOGRAPHS

Behaviour of deposit-feeding epifauna megabenthos were noted during image analysis, particularly in the tripod images. Many, particularly holothurians, created a constant trace as they transited the seabed. Others, such as the asteroid *Pseudarchaster* sp., moved rapidly between feeding locations without making a trace, then paused and created a trace whilst feeding. The echinoid *Echinocrepis* sp. created the deep w-shaped track while moving slowly (presumeably feeding), then moved quickly to another location while leaving only a slight trace on the seabed, before commencing the w-shaped track again. The enteropneusts also exhibited similar behavior, making traces in one area, followed by rapid movement without trace-making, possibly by swimming (Smith Jr *et al.*, 2005).

This rapid movement without trace-making suggests that Echinoids and Enteropneusts are facultative trace-makers, similar to Asteroids and Ophiuroids, rather than obligate trace-makers as asserted by Wheatcroft (Wheatcroft *et al.*, 1989).

Some surface deposit feeding holothurians were observed in transit without trace creation. *Abyssocucumis abyssorum* was not observed to create traces in the sediment, and was also observed on worm tubes and sponge spicules above the seabed. The ubiquitous *Peniagone* sp. did not appear to make traces either, although it may have contributed to sparse tube feet impressions, as it has previously been noted to leave some sparse footprints of a similar trace morphology (Heezen and Hollister, 1971).

Two enteropneusts were observed foraging in the time-lapse images, behavior in line with that described by Smith *et al.* (2005). In one instance the animal appeared and began tracking a small spiral before transforming to a hairpin track, but in the second the enteropneust began tracking the seabed out of the image. Both animals tracked in the 'hairpin' configuration, followed by a small clockwise spiral over a portion of the hairpin-tracked area before disappearing.

Lebensspuren penetrated the sediment to different depths, corresponding to the feeding mode of the trace-creator. In general, surface-feeding Holothurians left shallow or depressed tracks, such as the dense tube feet impression left by *Psychropotes longicauda*, which is known to feed on the top 5 mm of sediment (Roberts *et al.*, 2000), and a suspected sparse tube foot impression creator, *Oneirophanta* sp., which feeds on top ~1 mm of sediment (Roberts *et al.*, 2000). Subsurface-feeding Asteroids and Echinoids created deep traces exposing underlying sediment. Although trace depths were not measured, those of echinoid tracks (0-2 cm) described by Vardaro (2009) seem applicable. Deep traces that penetrate the subsurface sediment assist in vertical bioturbation, as do deeper lebensspuren, such as burrows created by infauna.

Phytodetritus observed in the tripod images appeared as a green dense flocculated layer, similar to the description of type 1 by Lauerman and Kaufman (1998) when

aggregated. It was first noted to be present on the seabed on 20 July 2011 and 24 August 2012. W-shaped track creation by echinoids penetrated the detrital layer, but other tracks did not.

TRACE CREATION

Trace creation was observed by 64 individuals of 7 different morphotypes (Table 3): Echinoids *Echinocrepis* sp. and *Cystechinus* sp., Enteropneusta, Holothuroids *Paelopatides* sp., *Psychropotes longicauda*, *Pseudostichopus mollis*, and the Asteroid *Pseudarchaster* sp. (A, B, F, H, I, K, L in Figure 1). Mean linear creation rates were highest for the v-shaped track, where the greatest variation was also found, and lowest for the enteropneust fecal trace. Asteroid feeding depression creation ranged over two orders of magnitude. Creation rates of deep traces, including the w-shaped and v-shaped tracks, were significantly lower than those of shallow traces, including the shallow wide depression and the dense tube feet impressions (ANOVA $F[47,1] = 5.2$, $p < 0.05$).

Table 3. Lebensspuren creation rates and duration by trace type estimated from time-lapse images from May 2011 to November 2012. Note that the creation of asteroid feeding depressions was estimated as h^{-1} (noted by *), since a continuous track was not created.

Lebensspuren	No.	Trace Creation (cm.h^{-1})		Duration (h)	
		Mean±SD	Range	Mean ±SD	Range
Overall	64	18.3±23.6	1.2-104.0	384.4±320	0-1252
W-shaped	41	11.3±15.8	1.2-96.3	371.6±310.4	2-1252
V-shaped	4	58.1±33.5	26.3-104.0	714.3±102.2	648-832
Shallow wide depression	3	41.2±5.0	36.6-46.5	55.3±16.2	45-74
Enteropneust mixed	2	2.6±0.04	2.6-2.7	252.5±21.9	237-268
Asteroid feeding depression	11	26.7±42.6*	1-140*	533.2±351.3	7-1152

Trace creations by echinoids (Figure 2b) occurred throughout the year, but appeared to increase during periods of high food input. The linear w-shaped track creation rate was not significantly related to which Echinoid made the trace (*Echinocrepis* sp. or *Cystechinus* sp.). Asteroid feeding depression creation was

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more sporadic, and increased two orders of magnitude in times of low food input over times of high food input, if the traces were created then at all (Figure 2e). Instances of creation of the v-shaped track (Figure 2d) and the shallow wide depression track (Figure 2c) were even more intermittent, the former occurring during low food input times, and the latter in higher food input periods. Despite these observations, creation of the w-shaped track and asteroid feeding depressions were not significantly correlated to the POC flux.
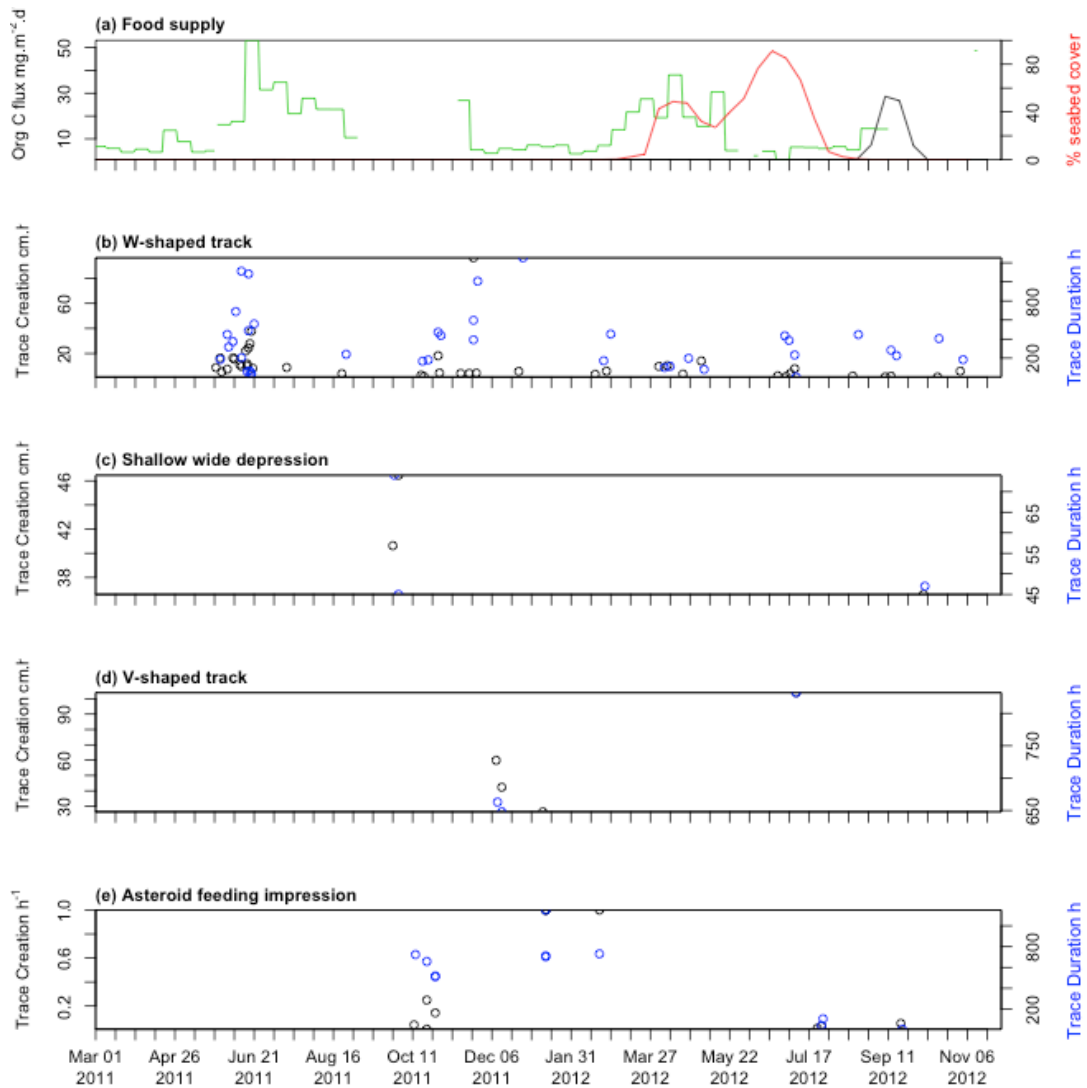

Figure 2. Time-series measurements of lebensspuren creation rates and duration from March 2011 to November 2012 at Station M. Food supply (a) is shown as particulate organic carbon flux from sediment traps (green), and salp (red) and phytodetritus (black) coverage of the seabed from rover

images. Lebensspuren creation rates and duration measured from tripod images for major traces are shown (b-e).

TRACE LONGEVITY

Deep traces that extended below the surface sediment, including the w-shaped track and v-shaped tracks, and asteroid feeding depressions, lasted longer than the shallow wide track and the dense tube feet impressions (Table 3; ANOVA F[54,1] = 5.2, p < 0.05). However, ranges in duration were less in the shallow wide track and Enteropneust cast than the deep traces, where the range was nearly two months (w-shaped track). These vast differences in duration of deep traces appear to be related to food supply; traces created during times of low food input lasted longer than those created during high food input. However, the duration of the deep w-shaped track and asteroid feeding depressions were not significantly correlated to POC flux.

HOLOTHURIAN TRACKING

Tracking rates were estimated in 35 individuals where trace creation rates could not be measured (Table 4). Generally, tracking rates were faster in smaller holothurians (e.g. *Abyssocucumis* abyssorum and *Oneirophanta* sp.) than larger ones, but the slowest tracking was by an Enteropneust. However, the range of tracking rates in these smaller holothurians was large, and similar ranges might occur for the large holothurians if more individuals were sampled.

Table 4. Tracking rates estimated from time-lapse images from March 2011 to November 2012.

Morphotype	No.	Mean Time Observed (h)	Tracking Rate (cm.h^{-1}) Mean±SD	Range
Abyssocucumis abyssorum	21	16.7±25.3	14.1±9.5	3.9-36.4
Benthothuria sp.	1	10	--	2.0
Oneirophanta sp.	9	4.9±2.4	19.2±12.0	7.4-42.0
Paelopatides sp.	2	30.5	--	2.6-3.6
Pseudostichopus mollis	1	103	--	1.0
Enteropneust	1	26	--	0.04

The creation rate of the shallow wide depression (Table 3) was more than an order of magnitude greater than the tracking rates of holothurians that produce this track (*Benthothuria* sp., *Paelopatides* sp. and *Pseudostichopus mollis*).   The Enteropneust tracking rate was two orders of magnitude lower than the trace creation rate reported above.
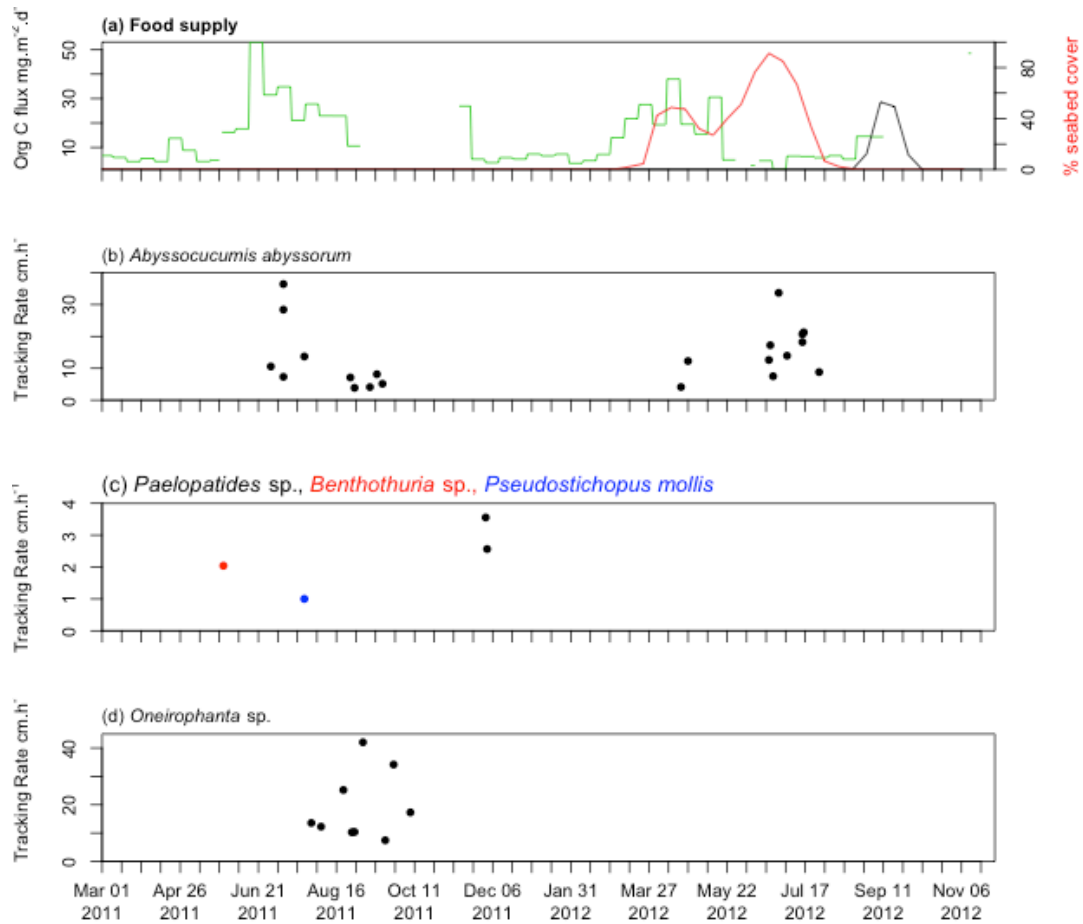
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Figure 3. Time series measurements of holothurian tracking rates from March 2011 to November 2012 at Station M. Food supply (a) is represented as in Figure 2. Tracking rates of selected holothurians measured from tripod images are grouped by presumed trace made: no trace (b), shallow wide depression (c), sparse tube feet impressions (d).

Seabed tracking by holothurians also appeared to be correlated to the food supply (Figure 3). Tracking by both *Abyssocucumis abyssorum* and *Oneirophanta* sp. appeared to occur during periods of high food input to the benthic environment, although *Oneirophanta* sp. appeared slightly after *Abyssocucumis abyssorum*. However, mean aggregated 10-day tracking rates of *Abyssocucumis abyssorum* and *Oneirophanta* sp. were not correlated to POC flux or salp coverage (lagged 0-40 days).

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TRACE DENSITY, COVERAGE AND DIVERSITY

Densities of lebensspuren (Table 5) were generally less than 1 m^{-2}, except for fecal matter. Only two types of tracks occurred at mean densities greater than 0.1 m^{-2}, the w- and v-shaped tracks. The w-shaped track occurred at the highest densities and seabed coverage.

Table 5. Densities and seabed coverage by lebensspuren for selected lebensspur types estimated from Rover images from May 2011 to June 2012 (n = 24).

	Density (ind.m^{-2})		Coverage (%)	
Lebensspur type	Mean±SD	Range	Mean ±SD	Range
All lebensspuren	NA	NA	3.3±1.3	1.3-6.3
W-shaped	0.73±0.22	0.33-1.03	2.1±0.7	0.9-3.5
V-shaped	0.12±0.09	0-0.4	0.4±0.4	0-1.3
Shallow wide depression	0.038±0.045	0-0.2	0.1±0.2	0-0.8
Sparse tube feet impression	0.025±0.034	0-0.11	0.1±0.2	0-0.5
Spoke burrow cluster long	NA	NA	0.06±0.1	0-0.3
Spoke burrow cluster short	NA	NA	0.02±0.06	0-0.2
All Enteropneust traces	0.044±0.059	0-0.2	0.2±0.3	0-1.1
Asteroid feeding depression	0.04±0.05	0-0.18	0.03±0.05	0-0.2
Irregular-shaped scar	0.012±0.015	0-0.043	0.02±0.05	0-0.2
All fecal matter	1.99±1.46	0.4-5.28	NA	NA

Densities of lebensspuren varied with time (Figure 4), as did the seabed coverage by lebensspuren. Significant correlations between lebensspuren coverage and both lagged POC flux and lagged salp coverage are listed in Tables 4 and 5.
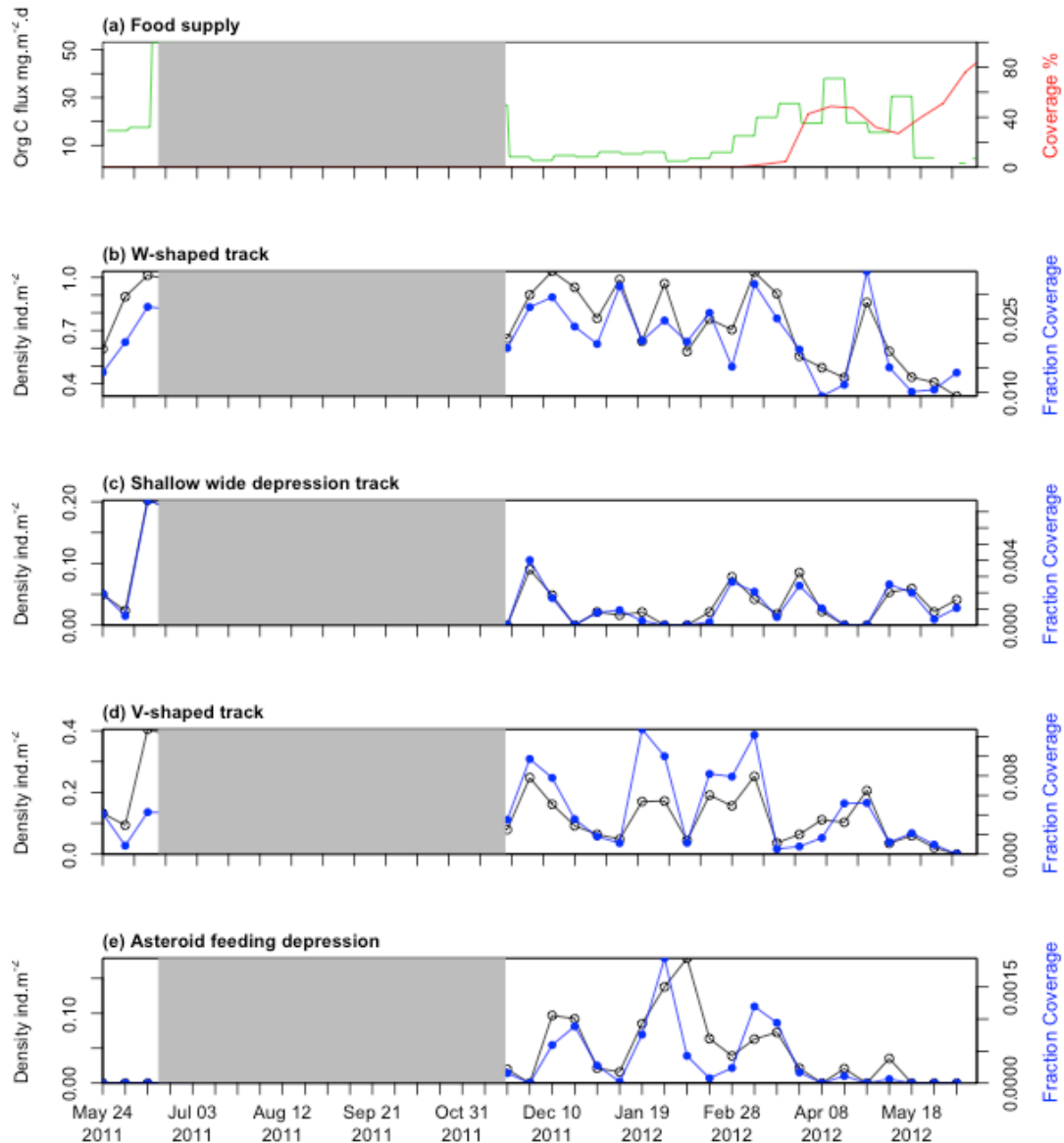
Figure 4. Time series measurements of the lebensspuren assemblage from May to June 2011, and November 2011 to June 2012. The time period without data (June to November 2011) is shown in grey. Food supply (a) is as described in Figure 2. Lebensspuren densities and seabed coverage determined from rover images are shown for major traces (b-e).

Correlations between food supply and lebensspuren coverage generally involved a lag in the food supply data, with at least a 10 day lag in the POC flux data. Significant correlations with lebensspuren coverage with food supply were short-lived for some lebensspur types (e.g. 10 days only for spoke burrows, and 20-30

days for the w-shaped track with POC flux), while others were significantly correlated with food supply over longer lag periods (e.g. sparse tube feet impressions with both POC flux and salp coverage for 10-40 days). Lags between food supply and seabed coverage by traces were different with different types, with some lebensspuren correlated to food supply with lags of 40 days (e.g. asteroid feeding depressions). Similar to the decrease in asteroid feeding trace production rates, the seabed coverage by asteroid feeding depressions was negatively correlated with both POC flux and salp coverage, with lags of 30-40 and 40 days, respectively. Seabed coverage by the w-shaped track was negatively correlated with POC flux (lagged 20-30 days) and salp coverage (lagged 0 and 20-40 days).

Table 6. Spearman rank correlations between POC flux (lagged 0 to 40 days) and lebensspuren coverage for lebensspur types with significant correlations at 5% (n.s. = not significant).

| Lebensspuren coverage | POC flux | | | | |
	0d	10d	20d	30d	40d
Total lebensspuren	n.s.	n.s.	r = -0.04, p < 0.05	r = -0.54, p < 0.05	n.s.
W-shaped track	n.s.	n.s.	n.s.	r = -0.61, p < 0.01	n.s.
Sparse tube feet impression	n.s.	r = -0.50, p < 0.05	r = -0.60, p < 0.01	r = -0.54, p < 0.05	r = -0.47, p < 0.05
Spoke burrow cluster long	n.s.	r = -0.59, p < 0.01	n.s.	n.s.	n.s.
Spoke burrow cluster short	n.s.	r = -0.42, p < 0.05	n.s.	n.s.	n.s.
Asteroid feeding depression	n.s.	n.s.	n.s.	r = -0.50, p < 0.05	r = -0.46, p < 0.05
Irregular-shaped scar	n.s.	r = -0.36, p < 0.1	r = -0.49, p < 0.05	n.s.	n.s.
	n = 24	n = 23	n = 22	n = 21	n = 20

Table 7. Spearman rank correlations between seabed salp coverage (lagged 0 to 40 days) and lebensspuren coverage for lebensspur types with significant correlations at 5% (n.s. = not significant).

Lebensspuren coverage	Salp coverage				
	0d	10d	20d	30d	40d
Total lebensspuren	$r = -0.55$,	$r = -0.51$,	$r = -0.57$,	$r = -0.60$,	$r = -0.68$,
	$p < 0.001$	$p < 0.05$	$p < 0.01$	$p < 0.01$	$p < 0.001$
W-shaped track	$r = -0.45$,	n.s.	$r = -0.46$,	$r = -0.48$,	$r = -0.55$,
	$p < 0.05$		$p < 0.05$	$p < 0.05$	$p < 0.01$
Sparse tube feet impression	n.s.	$r = -0.42$,	$r = -0.46$,	$r = -0.53$,	$r = -0.61$,
		$p < 0.05$	$p < 0.05$	$p < 0.01$	$p < 0.01$
Spoke burrow cluster long	n.s.	$r = -0.41$,	$r = -0.49$,	$r = -0.49$,	$r = -0.54$,
		$p < 0.05$	$p < 0.05$	$p < 0.05$	$p < 0.01$
V-shaped track	n.s.	n.s.	n.s.	n.s.	$r = -0.48$,
					$p < 0.05$
Asteroid feeding depression	n.s.	n.s.	n.s.	n.s.	$r = -0.43$,
					$p < 0.05$
Irregular-shaped scar	$r = -0.43$	$r = -0.41$	n.s.	$r = -0.42$	n.s.
	$p < 0.05$	$p < 0.05$		$p < 0.05$	
	$n = 26$	$n = 26$	$n = 26$	$n = 26$	$n = 26$

The lebensspuren assemblage also varied with time, as illustrated in Figure 5. The w-shaped track dominated the lebensspuren coverage of the seabed at all times, but had greater dominance over other lebensspur types when seabed salp coverage was high. When food input to the seabed was lower, seabed coverage by lebensspuren was more even between different types. During this time, enteropneusts contributed greatly to seabed coverage by lebensspuren, and other locomotory tracks and asteroid feeding impressions were present. Spoke burrows contributed greatly to seabed coverage immediately prior to the time of high POC flux.
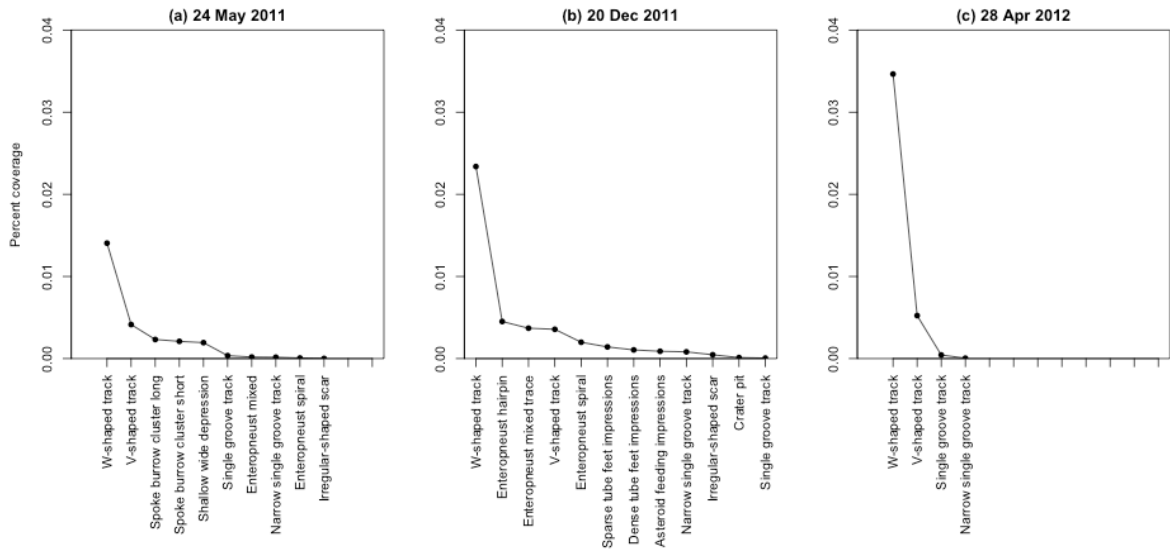
Figure 5. Ranked lebensspuren coverage for 10-day periods beginning with dates listed, immediately preceding a period of high POC flux/detrital input (a), low detrital input (b), and during high POC input and high coverage of the seabed by salps (c).

FECAL MATTER

Densities of fecal matter visible on the seabed also varied with time (Figure 6). More fecal matter was visible during periods of low food input to the seabed, and less during high POC flux or salp coverage times: both knotted ($r_S[27] = -0.79$, $p < 0.001$) and coiled casts were negatively correlated with salp coverage ($r_S[27] = -0.43$, $p < 0.05$).
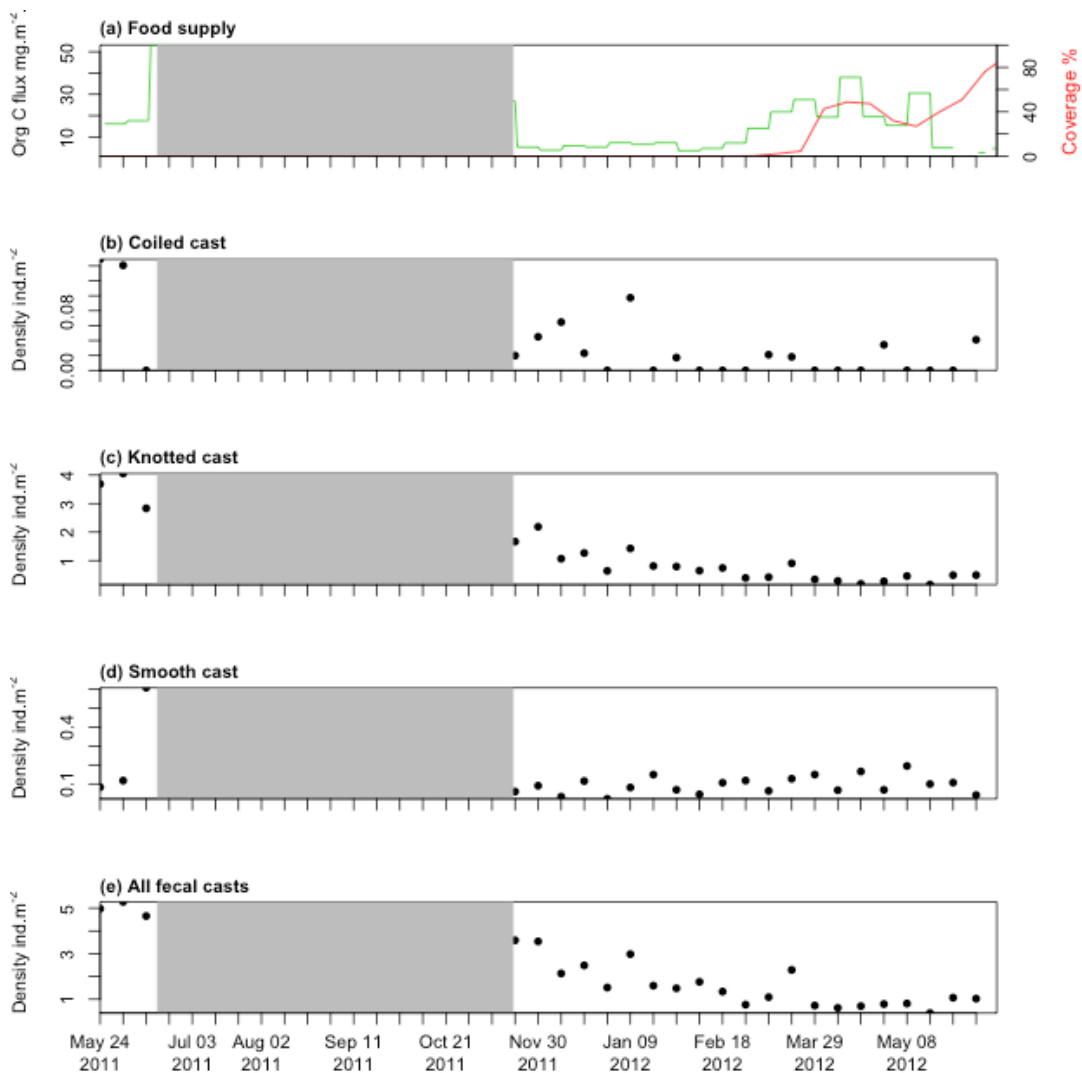
Figure 6. Time series measurements of fecal matter from May to June 2011, and November 2011 to June 2012. The time period without data (June to November 2011) is shown in grey. Food supply (a) is as described in Figure 2. Densities of selected fecal casts observed in rover images are shown (b-e).

COMPARING LEBENSSPUREN AND FAUNA IN ROVER AND TRIPOD IMAGES

Fewer types of fauna were noted in the rover images than the tripod images. Eight trace types were visible in the tripod images: w-shaped track, enteropneust hairpin, shallow wide depression track, dense tube feet impression, single groove track, v-shaped track, asteroid feeding depression and the irregular-shaped scar.

Twenty-six lebensspuren types were noted in the rover images, including all trace types visible in the tripod images: w-shaped track, v-shaped track, shallow wide depression track, wide shallow grooved track, repeating v-shaped track, dense tube feet impressions, sparse tube feet impressions, single groove track, narrow raised track, narrow single groove track, enteropneust hairpin, enteropneust spiral, enteropneust mixed, spoke burrow cluster long, spoke burrow cluster short, asteroid feeding depression, hole pair burrow, rayed mound, irregular shaped scar, and crater pit.   Note that fecal casts are not considered as they were omitted from the analysis of tripod images.

Sizes of common animals (though not common individuals) were also different between rover and tripod images. Echinoid (*Cystechinus* and *Echinocrepis* sp.) widths were significantly greater in the rover images than in the tripod images (ANOVA $F(1,198) = 78.9$, $p < 0.0001$). When measured in the rover images, *Cystechinus* sp. were smaller than *Echinocrepis* sp. (ANOVA $F(1,179) = 164$, $p < 0.0001$), but larger when measured in the tripod images (ANOVA $F(1,17) = 14$, $p < 0.01$).

DISCUSSION

FAUNAL TRACKING AND TRACE CREATION RATES

The tracking rates estimated here for holothurians do not appear to be good proxies for lebensspuren creation by those animals, and as such may not be good proxies for sediment ingestion/feeding by deposit-feeding trace makers. Order of magnitude differences were found between trace creation of the shallow wide depression (~40 cm.h^{-1}) and the tracking of creators *Paelopatides* sp. (~3 cm.h^{-1}) and *Pseudostichopus mollis* (1 cm.h^{-1}), and between Enteropneust trace creation (2.6 cm.h^{-1}) and tracking (0.04 cm.h^{-1}). This is likely due to the small sample sizes involved (n<4 in each case). However, the assumption of straight-line movement of the animals between hourly positions in photos is also likely too simplistic, possibly removing very rapid changes in position or swimming. Previous studies have shown that both abyssal benthic holothurians and echinoids

transit in meandering or random patterns (Smith *et al.*, 1997, Smith *et al.*, 1993). In addition, the individuals considered in the tracking rate estimation may not have been producing a trace, so tracking rates may overestimate trace creation rates since trace creation reduces movement rate (e.g. in *Echinocrepis* sp.). In the case of the Enteropneust trace creation rates, the area tracked may be incorrectly estimated by using the width of the head, particularly as this width is reported to vary almost two-fold (Smith Jr *et al.*, 2005), since width of the fecal trail left does not represent the area of seabed cleared.

The tracking rates computed here do, however, provide a means of comparing the results with those from previous studies. Wheatcroft *et al.* (1989) estimated the crawling rates of deep-sea megafauna to be 6-42 cm.h^{-1}, a narrower range than the range of trace creation and tracking rates estimated here. Previous estimates for seabed tracking by *Echinocrepis* sp. in the abyssal NE Pacific have varied from 6.2±7.0 cm.h^{-1} (Smith *et al.*, 1993), to 2.1-16.7 cm.h^{-1} (Vardaro *et al.*, 2009), encompassing the w-shaped track creation rate estimated here. Tracking rates of *Oneirophanta* sp. have been estimated to be highly variable, though generally higher than those found here (84.8±80.9 cm.h^{-1} (Smith *et al.*, 1993); 128.9±68.3 cm.h^{-1} in the NE Atlantic by (Smith *et al.*, 1997)), while tracking by *Abyssocucmis abyssorum* was found to be similar (17.8±13.4 cm.h^{-1} (Smith *et al.*, 1993)). Enteropneust trace creation was previously estimated to be 3.5-15.5 cm.h^{-1} (Smith Jr *et al.*, 2005), higher than estimated here, although both estimates were created using small sample sizes (n=2 or less). Thus, the estimates of tracking and trace creation made herein are reasonable in comparison to previously reported rates.

VARIATION IN FAUNAL ACTIVITY WITH FOOD SUPPLY

The variations in trace creation and tracking rates, and in the trace assemblages in relation to food supply suggest that both the quantity and quality of food are important to the activity of trace makers. Although the creation of w-shaped tracks occurred year-round, the negative correlation of the seabed coverage of

these tracks with POC flux (lagged 20-30 days) corroborates previously-found seasonal fluctuations in tracking rates by *Echinocrepis* sp. linked to sea surface temperature (Vardaro *et al.*, 2009). The lag indicates a combination of time for the POC to reach the seafloor and the animal's response time, while the negative correlation suggests that the animals prefer an environment without fresh POC (i.e. they prefer 'old' or remineralised detritus). The negative correlation or seabed coverage by the w-shaped track with un-lagged salp coverage could be due to the Echinoids' dislike for salps, or due to the high density of salp detritus obscuring the tracks. Food supply was also linked to the asteroid feeding depressions: the creation rate increased during low food input, and seabed coverage was correlated to both POC and salp detritus. Seabed coverage was best (negatively) correlated with POC flux lagged 30-40 days, and with salp coverage lagged 40 days, indicating that a longer response time to the food input by Asteroids than Echinoids.

Variations in the response of holothurians to different food inputs, as observed in the best correlation of sparse tube feet impression coverage with POC at 20 days and with salp coverage at 30-40 days, suggests a preference for food quality. The selectivity in deposit-feeding by holothurians has been studied extensively in relation to particle size and particle quality (Ginger *et al.*, 2001) (Roberts *et al.*, 2000), and the quality of food input has been suggested to alter the composition of the holothurian assemblage in the abyss (Wigham *et al.*, 2003), while the presence of detrital aggregates (quantity/quality) altered their tracking rates at Station M (*Peniagone vitrea*, *Abyssocucumis abyssorum*, *Elpidia minutissima*, *Amperima* sp.) (Smith *et al.*, 1994). Populations of one possible creator of the sparse tube feet impressions, *Peniagone* sp., was previously observed to lag 7 weeks behind this salp coverage (Smith Jr *et al.*, 2014), slightly longer than the longest lag tested here. Oneirophanta sp., another possible creator of the sparse tube feet impression, is known to select for fresh detritus (Lauerman *et al.*, 1997) similar to the 20 day lag POC flux with the trace seabed coverage, but does not search for hotspots of phytodetritus (Witbaard *et al.*, 2001), instead adapting to the changing availability of food resources (Neto *et al.*, 2006), which here would cause its

eventual switch to a salp diet, and the correlation of seabed coverage of the trace to salp coverage, with a longer lag time. Despite leaving no trace, the apparent tracking of the seabed by Abyssocucumis abyssorum during times of high POC flux, before the tracking by *Oneirophanta* sp., corroborates the finding by Lauerman et al. (1997) that it consumes fresh detritus. It appears that these differences in selectivity by deposit feeders alter the activity of trace-making fauna and the absolute and relative seabed coverage of different lebensspuren.

It is difficult to draw conclusions regarding food supply usage from the fecal matter data without knowing the originators of the different fecal casts. The reduction in fecal casts during the high food input period may be due to the absence or reduced activity of the cast producers during this period (e.g. holothurians that select for 'old' detritus), or may be due to the salp coverage obscuring fecal casts in the images.

Lastly, variations in the longevity of traces with food supply may indicate variations in infaunal (or macro and microfaunal) activity, if environmental conditions remain constant. The evidence presented here suggests greater infaunal and non-trace making epifaunal activity during periods of high food input, causing the erasure of traces. The presence/activity of enteropneusts (infauna) was connected to increased food availability by Smith et al. (2005).

LEBENSSPUREN IN PHOTOS AS A PROXY FOR ACTIVITY

Lebensspuren in images provide insight into temporal variation in deposit feeding, but some problems exist in using trace data from images captured at only one period in time as a proxy for immediate faunal activity. Variation in the longevity of traces between trace types (or with trace penetration depths) and with time may skew trace density, diversity and coverage results, since the 'freshness' of the tracks is not quantifiable in this situation. Factors influencing the longevity of traces include sediment type, hydrodynamic regime, and both trace erasure and alteration of sedimentary conditions through epifaunal and infaunal bioturbation, including activity by bacteria and protozoa (Gray, 1974, Rhoads, 1974, Snelgrove

and Butman, 1994), each of which is subject to spatial and temporal variation. Wheatcroft *et al.* (1989) modeled these dynamics in two deep-sea habitats with different sedimentary conditions and trace assemblages than those at Station M. In the empirical data from Station M presented here, the longevity of the w-shaped track was high, and this trace was also visible in images throughout the year. Therefore, a portion of the traces visible in any image may not have been recent, and may have been created a long time before the image was captured. As such, these long-lived traces may not represent the current activity of their creator fauna. Short-lived traces (e.g. shallow tracks), or traces made during periods of high seabed coverage by detritus or salps may be a better indication of the current activity of their creators. If snapshots of lebensspuren are used as a proxy for activity, then consideration for the variations presented must be made.

DETECTION AND SIZING OF FAUNA AND LEBENSSPUREN IN PHOTOS FROM DIFFERENT CAMERAS

Differences in the traces seen in the rover and tripod images were likely due to both technical/design aspects and environmental factors. Although both the rover and tripod produce oblique images, their orientation to the seafloor and lighting differed slightly, offering different shadows of seafloor features, and their altitude above the seafloor also differed, making some traces easier to discern from the surrounding sediment. The difference in orientation of camera to the seabed also alters the portion of each animal or trace that is visible, so measured dimensions that are intended to be identical may be biased if viewed at a camera angle that does not show the full dimension (similar to the idea of the 'false summit'). The Canadian 'perspective' grid could exacerbate this error, since the angle at which each individual is viewed is also dependent on where it appears in the field of view.

Although the same morphotypes have been used for comparison, the images were captured of many (likely different) individuals. As the rover progressed along the seabed, local-scale variation in the benthic environment (such as sediment particle

size or quality) was captured in the images, whereas the stationary tripod camera would not capture this environmental variation and the resulting variation in faunal assemblage and activity. If the tripod were stationed in a location with local benthic conditions unsuitable for particular fauna (due to near bed flow, lack of food, or unsuitable sediment for tracking/burrowing, for example), then those fauna would be reduced or excluded from the images captured, biasing the presumed assemblage. This may also have contributed to the size difference in echinoids detected between the rover and tripod images, since the sample size from the tripod images was much smaller than that from the rover images.

CONCLUSIONS

The creation rates and duration of traces on the seabed vary over time, and may have been related to food supply, as may tracking rates of holothurians. The density, diversity and seabed coverage by lebensspuren of different types varied with food supply, with different lag times for POC flux and salp coverage. These are interpreted to be due to selectivity of deposit feeders, and different response times between trace creators. These variations shed light on the usage of food inputs to the abyss.

FUTURE WORK

A comparison of the data presented herein with that from another long time-series abyssal site at the Porcupine Abyssal Plain in the northeast Atlantic would provide insight into the response of similar fauna to food supply under similar conditions. Data on the megafaunal community composition, lebensspuren densities, diversity and coverage, and detrital cover have been collected from downward-looking images captured with a towed-camera in June 2011 (Durden, *in prep.*). Concurrent images from a time-lapse platform are also available for analysis, as is data on the POC flux to the site.

It may also be useful to express the tracking rates and lebensspuren creation rates reported here in terms of the body size of the individual – either body length/width, or an estimated biomas based on these measurements. Vardaro (Vardaro *et al.*, 2009) determined that speed of tracking by Echinocrepis sp. Was related to body size. These data were collected, and could be incorporated to give better insight into the size implications of food consumption.

Finally, since some lebensspuren are created by infauna, a correlation of lebensspuren coverage at Station M with sediment community oxygen consumption measurements could provide further insight into the role of bioturbation in carbon cycling in the deep sea.

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