Seasonal dynamics of megafauna on the deep West Antarctic Peninsula shelf in response to variable phytodetrital influx

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1. Summary

The deep West Antarctic Peninsula (WAP) shelf is characterized by intense deposition of phytodetritus during spring/summer months, while very little food material reaches the seafloor during winter. The response of the shelf benthic megafauna to this highly variable food supply is still poorly understood. In order to characterize the deposition of phytodetritus and the megabenthic community response, we deployed a seafloor time-lapse camera at approximately 590 m depth on the mid WAP shelf west of Anvers Island for 15 months. Seafloor photographs were taken at intervals of 12 or 24 h nearly continuously from 9 December 1999 (austral winter) to 20 March 2001 (summer) and analysed for phytodetrital deposition and megafaunal dynamics. Seafloor images indicated a marked seasonal arrival of greenish phytodetritus, with large interannual and seasonal variability in the coverage of depositing phytodetrital particles. The surface-deposit-feeding elasipod holothurians Protelpidia murrayi and Peniagone vignoni dominated the epibenthic megafauna throughout the year, frequently constituting more than 80% of the megafaunal abundance, attaining total densities of up to 2.4 individuals m⁻². Elasipod abundances were significantly higher in summer than winter. During summer periods of high phytodetrital flux, Pr. murrayi produced faecal casts at higher rates, indicating intensified population-level feeding activity. In March–June 2000, faecal casts lasted longest, suggesting lower horizontal bioturbation activity during autumn–winter. Our data
indicate that the Pr. murrayi population increases its feeding rates in response to increasing amounts and/or lability of organic matter on the sediment surface. Assuming that this species feeds on the top millimetre of the sediment, we estimate that, during periods of high phytodetrital flux, the Pr. murrayi population reworks one square metre of sediment surface in approximately 287 days. We suggest that Pr. murrayi is an important species for organic-carbon recycling on the deep WAP shelf, controlling the availability of deposited labile phytodetritus to the broader shelf benthic community.

2. Introduction

Oceanic and coastal Polar regions are characterized by extremes in primary productivity during an annual cycle [1–3]. Periods of high phytoplankton production may also be subject to high interannual variation related to longer term climate cycles and climate change [4,5]. Such variations in organic-matter production and phytodetritus flux may affect planktonic and benthic heterotrophic populations through changes in food availability, larval survival, recruitment rates, competition for food, feeding behaviour and other processes [6].

On the West Antarctic Peninsula (WAP) shelf, large phytoplankton blooms can occur in December–March, resulting in intense bouts of particulate organic-carbon (POC) deposition on the seafloor [7–9]. The intense spring–summer phytoplankton blooms sustain the Antarctic food web [7,10] and provide the main food source, in the form of sinking phytodetritus, to seafloor communities on the deep WAP shelf [9,11,12]. These periods of high summer production and phytodetritus flux are separated by seasons of extremely low winter (April–October) productivity, when sea-ice cover and low-light conditions prevail, allowing very little food to reach the benthos [9,13], raising questions on how benthic detritivores survive over winter months [12,14].

In the water column, where seasonal variability in food concentration is especially dramatic, grazers/detritivores exhibit varied life-history strategies. Some animals, e.g. the copepod Paralabidocera antarctica, store lipids to allow fasting over the winter [15,16]. Other animals, such as krill and copepods, can store lipids [6,16,17] but may also feed on ice algae and at the seafloor, or migrate to ice-free oceanic waters [18–20]. On the deep WAP shelf, benthic animals do not appear to store lipids [21,22], and yet can remain active year round [22–24], feeding on a benthic food bank of organic material stored in sediments [9,12,14,25,26].

Surface-deposit-feeding elasipod holothurians are one of the main consumers of labile phytodetritus reaching the deep WAP shelf [23,24] and other Antarctic shelf communities [14,27–29]. Elasipods have also been observed actively foraging and removing phytodetritus material in many deep-sea habitats [8,30–35]. In some abyssal areas, this foraging behaviour may limit the flux of organic material to deeper layers of the sediment column [34,36], in turn restricting the availability of freshly deposited POC to the infaunal biota.

While it has been postulated that deposit-feeding megabenthos play an important role in the flow of organic carbon through Antarctic shelf benthic food webs [28,37,38], little is known about the foraging rates of elasipod holothurians on the WAP shelf, and their response to seasonal deposition of fresh phytodetritus.

In this study, we use a time-lapse camera system deployed on the deep WAP shelf (approx. 590 m depth) to (i) monitor the arrival of phytodetritus and (ii) evaluate variations in megabenthic community structure and surface-deposit faecal production, which is used as a proxy for foraging rates, over a 15-month period at the WAP shelf floor. We find that elasipod holothurians are active throughout the year and increase in population densities through migration, modulating their feeding rates with variations in the export of particulate material from the euphotic zone. Given the high volume of sediment processed, these organisms are likely to be very important in organic-carbon cycling at the WAP shelf seafloor.

3. Material and methods

A film-based time-lapse photographic camera system Photosea 2000 with two 150 J Photosea 1500s strobes and a DeepSea Power & Light 24 V SeaBattery was deployed during the FOODBANCS (FOOD for the Benthos on the ANtarctic Continental Shelf) project at mid-shelf station B (64° 48.00′ S, 65° 21.30′ W; ca 590 m depth) for five contiguous periods of three months (table 1; see Smith & DeMaster [26] for a review on the FOODBANCS programme) on the WAP shelf (figure 1). The system took photographs at 12 or 24 h intervals (table 1) during a 15-month period between 8 November 1999 and 20 March 2001.
Figure 1. Location of the three stations (A–C) sampled on the West Antarctic Peninsula shelf during the FOODBANCS project. The time-lapse camera system was deployed at the mid-shelf station (point B).

Table 1. Sampling period and photographic coverage of FOODBANCS programme. FB I–V are the FOODBANCS cruises. Time-series photographs were collected between cruises.

| period       | station ID | deployed     | recovered    | frame interval (h) | days of good coverage |
|--------------|------------|--------------|--------------|--------------------|-----------------------|
| FB I–II      | CRS 481    | 7 Dec 1999   | 9 Mar 2000   | 12                 | 28                    |
| FB II–III    | CRS 562    | 18 Mar 2000  | 15 Jun 2000  | 12                 | 88                    |
| FB III–IV    | CRS 635    | 19 Jun 2000  | 27 Oct 2000  | 24                 | 97                    |
| FB IV–V      | CRS 716    | 3 Nov 2000   | 2 Mar 2001   | 12                 | 121                   |

*Number of continuous days with appropriate light conditions, i.e. proper functioning of the flash, that allowed analysis of epifauna.

The camera was mounted on an aluminium tripod at an elevation of 152 cm above the seafloor and took pictures at a 45° angle of ca 4 m² of seafloor. All deployments used Kodak 5279 Vision 500 T motion picture film (ASA 500). The camera malfunctioned between 19 January 2000 and its recovery on 9 March 2000, and between 25 September 2000 and 25 October 2000, so there were no photographs during these intervals. In addition, no photographs were collected during the ca 10-day periods between recovery and redeployment during mid-project cruises. At each deployment/recovery, at least one otter trawl sample was taken to capture local megafauna for identification and reproductive studies.

In the laboratory, images were digitalized using a Nikon Super Coolscan 5000ED 35 mm/APS (IX240) film scanner into tagged image file format (TIFF) for later analysis. The automatic colour compensation provided by the scanner was reversed to recover the original slide colours. The reversal process used the black frame as a reference. Each of the original 1008 × 672 pixel TIFF images was converted to four (RGBI) matrices, centred through a pattern-recognition Matlab program that identified the position of the central crosshatch in the Photosea 2000 image. An area of 800 × 620 pixels centred on the crosshatch was kept and outside areas cropped from all images. A Canadian perspective grid (50 × 50 cm squares) was then constructed based on the camera elevation and angle relative to the seafloor and superimposed on each oblique image using Matlab. As the oblique grid cells represented squares in the seafloor, the edges of a larger square (1 × 1 m) formed by the four bottom centre cells were used for a perspective transformation. This transformation places the image viewpoint at a right angle from the seafloor (assumed to be planar) allowing distances and areas to be calculated. The quantitative part of the study focused on the epibenthic megafauna living on soft sediments. During the course of the study the camera never faced hard bottoms. Owing to different lighting conditions and to minimize perspective correction...
errors, only the well-illuminated bottom area of the images (1.6 m\(^2\) or 491 × 491 pixels) was used in the analysis, thus reducing errors in the counting and identification of species [40]. We could resolve and identify animals exceeding approximately 2 cm in minimum dimension.

Epifaunal organisms were counted in each image (\(N = 452\)) and numerical density presented as individuals per square metre. The number of times a single individual appeared in consecutive images was recorded in order to evaluate the activity of benthic organisms (mostly holothurians). Individuals were visually identified by their size, position in the frame and bioturbation track in consecutive frames. Holothurian movement rates were calculated as the average linear distance of single individuals between consecutive frames (12 h). As these animals move irregularly, distances represent minimal movement rates and are likely to be underestimated, as we could not estimate the distance travelled (or direction of movement) from individuals that only appeared once in photographs.

Faecal-cast numerical densities and persistence times were calculated for the entire period for the holothurian *Protelpidia murrayi*, which produced the most conspicuous faecal casts (figure 2). Faecal casts appearing in images were marked and tracked in each successive photograph until they could no longer be resolved. For each cast, length (i.e. the uncoiled faecal cast) and width (i.e. the diameter of a faecal-cast section) were measured and the volume of sediment processed was calculated assuming the faecal casts to be cylindrical. Individual faecal-cast production was estimated for individuals that could be tracked in pictures. Population-level faecal production was calculated using the total volume of faeces produced per day in a given area. Faecal-cast parameters were compared using either one-way ANOVA or Kruskal–Wallis test after testing for the homogeneity of variances. Differences were considered significant at \(p < 0.05\). When significant differences were found, we applied the post hoc tests of Tukey or Dunn depending on the assumptions of normality of data (Bartlett’s test).

Sediment reworking time for individual *Pr. murrayi* was calculated assuming that animals feed on the top millimetre of the sediment surface based on observations of animals kept in the laboratory. Therefore, total reworking of the top millimetre of 1 m\(^2\) of sediment implies 1000 cm\(^3\) of sediment ingestion. The total reworking time of *Pr. murrayi* population at a given season was then calculated dividing 1000 cm\(^3\) m\(^{-2}\) by the production of faecal casts per day. Therefore, this measurement represents the time of foraging required to rework a square metre of sediment. Seasonal ingestion rates were also tested by ANOVA or Kruskal–Wallis tests at a significance level of 0.05 and the same post hoc tests applied as explained above. Data on faecal casts and reworking times were compared with POC fluxes obtained by Smith *et al.* [9] during the same period.

**Figure 2.** Seafloor photographs taken at four different periods in the West Antarctic Peninsula (WAP) shelf Station B. (a) Picture taken in the November 1999–March 2000 period. Note the presence of a thin layer of phytodetritus at the seafloor. (b) March 2000–June 2000. During this period, no phytodetritus was found. (c) In June 2000–October 2000, no phytodetritus layer was observed. (d) November 2000–March 2001. Dense carpets of phytodetritus (approx. 2 cm thick) were found over the seafloor. Inset: faecal casts of the two main elasipod holothurians on the WAP shelf: (e) *Pr. murrayi* and (f) *Pe. vignoni*. The scale bar of the larger picture represents 20 cm. In the inset, the scale bar is 2 cm.
Echinoderms constituted the vast majority of the epibenthic megafauna at the WAP shelf station throughout the study period. The elasipod holothurians *Pr. murrayi* and *Peniagone vignoni* were the most abundant throughout the year, with lower densities during winter months (June 2000 to October 2000; table 2). *Protelpidia murrayi* represented over 52% of the epibenthic megafauna during spring/summer of 2000–2001 (table 2). Other echinoderms included the sea stars *Psilaster charcoti*, *Henricia* spp., and an unidentified species, as well as the sea urchins *Amphipneustes* spp. and *Ctenocidaris perrieri*. Crinoids and ophiuroids were observed occasionally, as were molluscs, including the octopus *Pareledone charcoti* and the gastropod *Harparvoluta charcoti*. Giant nereitans (*Parborlasia corrugatus*) and fish were also present in small numbers. A number of species present in pictures, including small penatulaceans and shrimps, were not counted because they were difficult to identify and the densities were very low.

The full time series showed that there was a marked increase in the number of epibenthic megafauna towards the end of the study period (figure 3). Total megafaunal densities were highest during the

| Table 2. Benthic megafauna density (individuals m\(^{-2}\)) from time-lapse photographs during the FOODBANCS project. |
|----------------------------------------------------------|
| **mean density (s.d.)** | **minimum and maximum** | **per cent** |
| (individuals m\(^{-2}\)) | density (individuals m\(^{-2}\)) | of total |
|-------------------------|--------------------------|-----------|
| FB I–II (Nov 99–Mar 00) | | |
| *Pr. murrayi* | 0.34 (0.36) | 0/1.08 | 72.1 |
| *Pe. vignoni* | 0.04 (0.12) | 0/0.43 | 8.3 |
| *Amphipneustes* spp. | 0.03 (0.10) | 0/0.43 | 6.5 |
| *Asteroidea* | 0.06 (0.11) | 0/0.43 | 13.1 |
| total megafauna | 0.48 (0.42) | 0/1.52 |
| FB II–III (Mar 00–Jun 00) | | |
| *Pr. murrayi* | 0.22 (0.34) | 0/1.08 | 45.7 |
| *Pe. vignoni* | 0.22 (0.31) | 0/1.52 | 46.1 |
| *Echinoidea* | 0.02 (0.11) | 0/0.43 | 4.5 |
| *Asteroidea* | 0.02 (0.07) | 0/0.43 | 3.7 |
| total megafauna | 0.48 (0.43) | 0/1.52 |
| FB III–IV (Jun 00–Oct 00) | | |
| *Pr. murrayi* | 0.06 (0.15) | 0/0.43 | 26.3 |
| *Pe. vignoni* | 0.08 (0.18) | 0/0.87 | 36.5 |
| *Amphipneustes* spp. | 0.03 (0.08) | 0/0.52 | 11.4 |
| *C. perrieri* | 0.02 (0.05) | 0/0.52 | 6.8 |
| *Asteroidea* | 0.04 (0.14) | 0/0.58 | 19.0 |
| total megafauna | 0.23 (0.29) | 0/0.87 |
| FB IV–V (Nov 00–Mar 01) | | |
| *Pr. murrayi* | 0.38 (0.33) | 0/1.73 | 52.7 |
| *Pe. vignoni* | 0.26 (0.36) | 0/1.96 | 36.1 |
| *Amphipneustes* spp. | 0.02 (0.08) | 0/0.43 | 2.6 |
| *Asteroidea* | 0.06 (0.13) | 0/0.65 | 7.9 |
| *Mollusca* | 0.004 (0.05) | 0/0.52 | 0.7 |
| total megafauna | 0.71 (0.54) | 0/2.39 |

4. Results

4.1. Epibenthic megafauna composition, numerical density and size

Echinoderms constituted the vast majority of the epibenthic megafauna at the WAP shelf station throughout the study period. The elasipod holothurians *Pr. murrayi* and *Peniagone vignoni* were the most abundant throughout the year, with lower densities during winter months (June 2000 to October 2000; table 2). *Protelpidia murrayi* represented over 52% of the epibenthic megafauna during spring/summer months, whereas *Pe. vignoni* had two peaks of abundance during the austral autumn/winter and summer of 2000–2001 (table 2). Other echinoderms included the sea stars *Psilaster charcoti*, *Henricia* spp., and an unidentified species, as well as the sea urchins *Amphipneustes* spp. and *Ctenocidaris perrieri*. Crinoids and ophiuroids were observed occasionally, as were molluscs, including the octopus *Pareledone charcoti* and the gastropod *Harparvoluta charcoti*. Giant nereitans (*Parborlasia corrugatus*) and fish were also present in small numbers. A number of species present in pictures, including small penatulaceans and shrimps, were not counted because they were difficult to identify and the densities were very low.

The full time series showed that there was a marked increase in the number of epibenthic megafauna towards the end of the study period (figure 3). Total megafaunal densities were highest during the
summer months, especially in November 2000–March 2001 (table 2), when numbers were significantly higher than in all other intervals (Tukey test, *p* < 0.05). During this period, megaфаunal numbers reached peaks of 2.4 individuals m$^{-2}$. The lowest mean densities (less than 50% of spring/summer) were observed during winter months (June 2000–October 2000; table 2; Tukey test, *p* < 0.05).

The two most numerous megaфаunal species, *Pr. murrayi* and *Pe. vignoni*, exhibited significant temporal variations in abundance. The density of *Pr. murrayi* was significantly lower during June 2000–October 2000 (0.07 ± s.d. 0.02 individuals m$^{-2}$) than in the remaining sampling periods (maximum in November 2000–March 2001 of 0.45 ± s.d. 0.03 individuals m$^{-2}$; Tukey test, *p* < 0.01). *Proteolidia murrayi* individuals were larger during June 2000–October 2000 (mean length 5.9 cm) than in November 1999–March 2000 (3.6 cm; Tukey test, *p* < 0.01; figure 4). The density of *Pe. vignoni* ranged from 0.05 to 0.26 individuals m$^{-2}$ (figure 4), with densities in November 1999–March 2000 significantly lower than in November 2000–March 2001 (Tukey test, *p* < 0.01). The mean size of *Pe. vignoni* individuals was significantly smaller in November 2000–March 2001 (5.4 ± s.d. 2.2 cm) than in the first two periods (10.1 ± s.d. 2.8 cm and 7.0 ± s.d. 0.4 cm, respectively; Tukey test, *p* < 0.01; figure 4).

### 4.2. Movement rates and feeding dynamics

Individual holothurian movement, based on the average linear distance travelled by single individuals between consecutive 12 h interval frames (*N* = 2 to 14 individuals), showed that *Pr. murrayi* individuals had similar seasonal movement rates (1.1–2.0 cm h$^{-1}$), whereas *Pe. vignoni* individuals moved almost twice as fast during winter months compared with November 2000–March 2001 (Tukey test, *p* < 0.01; table 3). Movement rates of *Pe. vignoni* were higher than *Pr. murrayi* during winter (Tukey test, *p* < 0.01; table 3) but did not differ during the summer bloom period of November 2000–March 2001 [9]. We observed no influence from animal size on movement rates, but note that our sample size was small.

The average faecal-cast volume for both holothurians varied from 1.8 to 6.5 cm$^3$ and was only significantly different between November 1999–March 2000 and March 2000–June 2000 (Dunn test, *p* < 0.05). Faecal-cast volume was positively correlated with animal length for *Pr. murrayi* (*N* = 190; Pearson *r* = 0.5468, *p* < 0.001). We observed no marked trend in the number of faecal casts with time until the end of January 2001, when larger quantities of faecal casts were found (figure 5). This followed closely the amount of phytodetritus found on the surface of sediments (figure 5) [9]. The mean number of faecal casts of *Pr. murrayi* averaged over each sampling period was significantly different, with the highest mean during the November 2000–March 2001 period (Dunn test, *p* < 0.05). The average density of faecal casts during this period (1.3 ± 1.9 s.d. faecal cast m$^{-2}$) was twice as high as that measured in the previous summer (0.6 ± 1.0 s.d. faecal cast m$^{-2}$), when no phytodetritus carpet was evident. During the winter period, the mean number of faecal casts was approximately three to five times lower (0.4 ± s.d.
Production of faecal casts by *Pr. murrayi* at both individual and population levels was significantly higher from June 2000 to March 2001, especially during the phytodetritus bloom (Dunn test, *p* < 0.05; figure 6a,b). Average faecal-cast production rates per individual varied seasonally (figure 6a) with an increase in faecal production in June 2000–November 2000, when phytodetritus flux was low. Although *Pr. murrayi* were on average largest during the March 2000–October 2000 interval (figure 4), per individual faecal-cast production was highest during the November 2000–March 2001 bloom months, which had smaller *Pr. murrayi* (figure 6). The average persistence time of faecal casts on the seafloor was lowest in the summer of 1999–2000 (mean of 135 h) and highest (317 h) in the subsequent winter (March 2000–June 2000; Dunn test, *p* < 0.05). During the high phytodetritus flux period (November 2000–March 2001, especially during the phytodetritus bloom (Dunn test, *p* < 0.05; figure 6a,b). Average faecal-cast production rates per individual varied seasonally (figure 6a) with an increase in faecal production in June 2000–November 2000, when phytodetritus flux was low. Although *Pr. murrayi* were on average largest during the March 2000–October 2000 interval (figure 4), per individual faecal-cast production was highest during the November 2000–March 2001 bloom months, which had smaller *Pr. murrayi* (figure 6). The average persistence time of faecal casts on the seafloor was lowest in the summer of 1999–2000 (mean of 135 h) and highest (317 h) in the subsequent winter (March 2000–June 2000; Dunn test, *p* < 0.05). During the high phytodetritus flux period (November 2000–March 2001, especially during the phytodetritus bloom (Dunn test, *p* < 0.05; figure 6a,b). Average faecal-cast production rates per individual varied seasonally (figure 6a) with an increase in faecal production in June 2000–November 2000, when phytodetritus flux was low. Although *Pr. murrayi* were on average largest during the March 2000–October 2000 interval (figure 4), per individual faecal-cast production was highest during the November 2000–March 2001 bloom months, which had smaller *Pr. murrayi* (figure 6). The average persistence time of faecal casts on the seafloor was lowest in the summer of 1999–2000 (mean of 135 h) and highest (317 h) in the subsequent winter (March 2000–June 2000; Dunn test, *p* < 0.05). During the high phytodetritus flux period.

### Table 3. Seasonal average movement rates for *Protelpidia murrayi* and *Peniagone vignoni* based on individuals identified on consecutive time-lapse photographs.

| Period       | *Protelpidia* | *Peniagone* | *Protelpidia* | *Peniagone* |
|--------------|---------------|-------------|---------------|-------------|
| Nov 99–Mar 00| 8             | n.a.        | 1.1 (0.3)     | 2.0 (1.4)   |
| Mar 00–Jun 00| 17            | 15          | 4.5 (1.2)     | 7.2 (4.1)   |
| Jun 00–Oct 00| 7             | 2           | 4.1 (2.4)     | 6.3 (3)     |
| Nov 00–Mar 01| 43            | 26          | 5.5 (3.3)     | 5.1 (1.4)   |

0.8 faecal cast m⁻² for March 2000–June 2000 and 0.3 ± s.d. 0.8 faecal cast m⁻² for June 2000–October 2000). Also, during the first three sampling periods November 1999–October 2000, many frames had no freshly deposited faecal casts (figure 5). On the other hand, *Pr. murrayi* individuals deposited new faecal casts almost continuously from November 2000 to March 2001 (figure 5).
Figure 5. Mean number of faecal casts deposited on the seafloor by the holothurian Pr. murrayi pooled per sampling period. The right Y-axis represents scores for phytodetritus coverage of the seafloor as follows: no greenish, flocculent phytodetritus visible at the seafloor (score = 0); diffuse, greenish, flocculent material visible in some areas but bioturbation traces readily visible (score 1); much of the seafloor (50–90%) covered with greenish phytodetritus, with bioturbation traces partially filled (score = 2); more than 90% phytodetritus cover (score = 3) [9]. Score 4 represents dense, up to 2 cm thick phytodetritus carpets. Vertical lines are ±1 s.e.

Figure 6. Mean faecal-cast volumetric production rate per individual (a) and population-level faecal-cast production rate (b) for the holothurian Pr. murrayi. Data were pooled for each sampling period. Also shown in (b) is the POC flux in the study area collected during the same period by Smith et al. [9]. Vertical lines are ±1 s.e.

2001), mean faecal persistence time was approximately 189 h. In general, higher individual faecal-cast volume was positively correlated with faecal-cast persistence time (N = 292; Pearson r = 0.3816, p < 0.001).

Population-level faecal-cast production rates (surface-sediment reworking rates) for Pr. murrayi varied across seasons, being highest during the period of high POC flux and phytodetritus concentration (figures 6 and 7). During November 2000–March 2001, population-level faecal production rates exceeded faecal production rates in all previous periods by a factor of 3.5 (Dunn test, p < 0.05; figure 6b). In addition, surface-sediment reworking times in November 2000–March 2001 were 1/7 of those in winter/spring 2000, with the equivalent of the top 1 mm of sediment being reworked during the period of high phytodetrital availability with approximately 287 days (figure 7).
5. Discussion

Our time-lapse photographic record shows evidence of strong interannual and seasonal variability in deposition of phytodetritus over the WAP shelf, associated with significant changes in megafaunal abundance. This high variability is consistent with previous studies documenting substantial seasonal and interannual variability in the flux of particulate organic matter (POM) and chlorophyll a to the WAP shelf sediments [7,9,10,12,41,42]. The time-lapse images revealed no phytodetrital coverage of sediments from the summer of 1999–2000 until the winter of 2000, which was followed by a rapid (i.e. days) increase in detritus accumulation in November 2000 [9]. The high interannual variability of phytodetrital accumulation may result from complex pelagic nutrient dynamics and variable ice retreat controlling phytoplankton blooms, variable grazing by zooplankton and lateral transport of surface phytoplankton-rich waters over the WAP shelf [43–45]. During summer periods of high primary productivity, POM fluxes are enhanced by the formation of larger, heavier marine snow aggregates and zooplankton faecal pellets [46,47]. During the spring–summer of 2001, thick carpets (approx. 2 cm) of phytodetritus were observed on the seafloor and appear to have provided an important food supply to the deposit-feeding megafauna [9,12,45].

Previous studies have indicated that temporal variability in the abundance and/or activity of macro- and megabenthos over a 15-month period on the deep WAP shelf was largely decoupled from phytodetritus accumulation and POC flux at the seafloor [24]. The weak coupling between seasonal POC flux and megafaunal and macrofaunal communities in the WAP shelf has been postulated to result from the presence of a sediment ‘food bank’ for deposit feeders [12,24,26,45]. The time-lapse images give further support for the food bank hypothesis, revealing that holothurians forage across the seafloor (i.e. inferred from movements), and consume and egest sediments, even during winter periods of very low food flux to the WAP shelf floor.

The community dominant Pr. murrayi fed continuously on surface sediments throughout the year, as indicated by the production of faecal casts during all our study intervals (figure 5). Similar continuous feeding on the labile organic matter available in surface sediments and on fresh phytodetritus deposited on the seafloor during the spring/summer season has been documented for infaunal echiurans and holothurians on the WAP shelf [12,23,26]. These finding indicate the presence of a sediment food bank on the WAP shelf fuelled by summer blooms, which may persist due to low bacterial organic-matter degradation rates in the extremely cold Antarctic shelf temperatures [9,12].

Although Pr. murrayi does feed year round, this abundant surface-deposit feeder does appear to modulate its sediment ingestions rates in response to increased food availability at the seafloor, as suggested by Sumida et al. [24]. This response is indicated by a nearly fourfold increase in the production of faecal casts per individual during the summer of 2000–2001 in comparison with the previous summer,
leading to diminished gut residence times presumably owing to the higher food quality [9,45,48,49]. *Protelpidia murrayi*, which is relatively unselective during particle ingestion [25], relies on selective digestion of organic matter; the presence of higher concentrations of labile phytodetrital material may allow it to pass sediment through the gut at higher rates, while maintaining adequate digestive yield [50,51].

At the *Pr. murrayi* population level, the production of faecal casts is seven times higher during summer of 2000–2001 than the previous summer, as a consequence of higher population densities probably resulting from immigration, larger body sizes and higher individual-level feeding rates. These variations in *Pr. murrayi* population densities and faecal-cast production rates yield substantial temporal variation in reworking times for the top millimetre of the sediment, with a turnover time approximately 287 days during the period of intense phytodetrital accumulation and approximately 2114 days when fluxes were lowest in winter months (figure 7).

Faecal-cast duration suggests that the benthic community as a whole passes through cycles of low and high bioturbation rates, with faecal casts persisting approximately twice as long (approx. 317 h) during winter months than during summer periods. Megafaunal movement rates and foraging activities are likely to be the main cause of the disappearance of faecal coils in this low-flow environment [52]. We found no evidence of sediment resuspension in our images, which suggests that currents are not important in erasing megafaunal traces and faecal casts from the sediment surface. These cycles of bioturbation activity may also be important in the vertical mixing of POM across the sediment–water interface [53]. Such vertical transport will make food available to subsurface feeders and can ultimately lead to carbon burial. For example, the Antarctic sea urchin *Abatus ingens* reworks the top 2 cm of shallow-water sediments 2 to 17 times per year, influencing a variety of sediment processes including nutrient mixing and oxygen penetration to lower layers [54]. In our study area, faecal-cast duration seems likely to be controlled by a combination of ‘retracking’ by epifauna and diffusive sediment mixing by infauna (cf. Wheatcroft et al. [52]). The higher population-level sediment reworking rates for *Pr. murrayi* during the period of high phytodetritus availability suggests that ‘retracking’ by epibenthos contributed to the reduction in faecal-cast duration during November 2000–March 2001.

Because of high population densities and high feeding and faecal-cast production rates, *Pr. murrayi* may be geochemically important [55], modulating the distribution of labile organic matter at the sediment–water interface, and within the sediment column, on the deep WAP shelf. During periods of high phytodetrital flux, the *Pr. murrayi* population appears capable of processing the top 1 mm of sediment, and the recently deposited phytodetritus, on 200–300 day time scales, i.e. over time scales roughly similar to the spring–summer bloom period and the occurrence of phytodetritus at the seafloor [9]. As a consequence, much of the labile phytodetritus depositing on the WAP floor during the summer bloom may pass through a holothurian ‘filter’, becoming assimilated or redistributed as faecal casts by surface-deposit-feeding holothurians before becoming available to the broader deposit-feeding community. Thus, the dynamics of deposit-feeding megafauna, in particular *Pr. murrayi*, should be included in models of biogeochemical cycling and climate change on the WAP shelf. Because surface-deposit-feeding elasipod holothurians similar to *Pr. murrayi* are abundant globally at bathyal depths and have been shown to actively consume labile phytodetritus [56], these holothurians are likely to modulate the distribution of labile organic matter on many continental margins.

Data accessibility. Data available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.k5s15.

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References

1. Smith Jr WQ, Marra Jr H, Hiscock MR, Barber RT, 2000 The seasonal cycle of phytoplankton biomass and primary productivity in the Ross Sea, Antarctica. Deep Sea Res. II 47, 3199–3211. (doi:10.1016/S0967-0645(00)00604-7)

2. Arrigo KR, van Dijken GL, 2011 Secular trends in Arctic Ocean net primary production. J. Geophys. Res. 116, C09011. (doi:10.1029/2011JC007151)

3. Brown ZW, Arrigo KR, 2012 Contracting trends in sea ice and primary production in the Bering Sea and Arctic Ocean.ICES J. Mar. Sci. 69, 1180–1193. (doi:10.1093/icesjms/fsr171)

4. Clarke A, 2001 Benthic organisms and environmental variability in Antarctica: responses to seasonal, decadal and long-term change. Ocean Polar Res. 23, 433–440.

5. Clarke A, Murphy EJ, Meredith MP, King JC, Peck LS, Barnes SJA, Smith RC, 2007 Climate change and the marine ecosystem of the western Antarctic Peninsula. Phil. Trans. R. Soc. B 362, 149–166. (doi:10.1098/rstb.2006.1958)

6. Clarke A, 1988 Seasonality in the Antarctic marine environment. Comp. Biochem. Physiol. 90B, 461–473. (doi:10.1016/0305-0491(88)90285-4)
7. Karl DM, Christian JR, Dore JE, Letelier RM. 1996 Microbiological oceanography in the region west of the Antarctic Peninsula: microbial dynamics, nitrogen cycle and carbon flux. In Foundations for ecosystem research west of the Antarctic Peninsula (eds R Ross, E Hoffmann, L Quetin), pp. 303–332. Washington, DC: American Geophysical Union.

8. Smith CR, Hooper DJ, Doan SE, Pope RH, DeMaster DJ, Dobbs FC, Altabet MA. 1996 Phyto- and zoopelagic carbon in the abyssal seafloor across 10° of latitude in the central equatorial Pacific. Deep Sea Res. II, 43, 1309–1338.

9. Smith CR, Mincks SL, DeMaster DJ. 2008 The FOODOBCNS project: introduction and sinking fluxes of organic carbon, chlorophyll-a and phaeopigments on the western Antarctic continental shelf. Deep Sea Res. II, 55, 2404–2414.

10. Ducklow HW, Fraser W, Karl DM, Christian JR, Dore JE, Letelier RM. 1996 Lipid metabolism of the Antarctic krill: implications for stock assessment, Curr. Biol. 10, 203–213. (doi:10.1016/0022-0981(96)01005-X)

11. Galley EA, Tyler PA, Clarke A, Smith CR. 2005 Reproductive biology and biochemical composition of the brooding echnoid Amphipneustes forlor on the Antarctic continental shelf. Mar. Biol. 148, 59–71. (doi:10.1007/s00227-006-0069-3)

12. Galley EA, Tyler PA, Smith CR, Clarke A. 2008 Reproductive biology of two species of holothurian from the deep-sea oligo Elasipoda, on the Antarctic continental shelf. Deep Sea Res. II, 55, 2525–2526. (doi:10.1016/j.dsr2.2008.07.002)

13. Sumida PTG, Bernardino AF, Smith CR, Stedall VP. 2008 Temporal changes in benthic megafauna across the West Antarctic Peninsula. Deep Sea Res. II, 55, 2465–2470. (doi:10.1016/j.dsr2.2008.06.006)

14. Pierrot B, DeMaster DJ, Thomas CJ, Smith CR. 2008 ¹³C as a tracer of labile organic matter in Antarctic benthic foods. Deep Sea Res. II, 55, 2438–2450. (doi:10.1016/j.dsr2.2008.06.004)

15. Smith CR, DeMaster DJ. 2008 Preface and brief synthesis for the FOODOBCNS volume, Deep Sea Res. II, 55, 2399–2403. (doi:10.1016/j.dsr2.2008.08.001)

16. Gutt J. 1991 On the distribution and ecology of holothurians in the Weddel Sea (Antarctica). Polar Biol. 11, 145–155. (doi:10.1007/BF02420201)

17. Gutt J, Starrams A, Dieckmann G. 1998 Phaeopigments deposited on the Antarctic shelf and upper slope: its relevance for the benthic system. J. Mar. Syst. 17, 435–444. (doi:10.1016/S0924-7963(98)00054-2)

18. Gutt J et al. 2011 Biodiversity change after climate-induced ice-shelf collapse in the Antarctic. Deep Sea Res. I, 58, 74–83. (doi:10.1016/j.dsr2.2010.05.024)

19. Billett DSM, Leathem C, Watson J. 1988 Are deep-sea holothurians selective feeders? In Echinoderm biology (eds R Burke, P Maldeon, P Lambert, R Pasley), pp. 421–429. Rotterdam, The Netherlands: Balkema.

20. Tyler PA, Billett DSM, Geje JD. 1990 Seasonal reproduction in the seastar Dasyaster grandis from 4000 m in the north-east Atlantic Ocean. J. Mar. Biol. Assoc. UK 70, 173–180. (doi:10.1017/S0025315400034299)

21. Billett DSM. 1991 Deep-sea holothurians. Oceanogr. Mar. Biol. Ann. Rev. 29, 259–317.

22. Tyler PA, Young CM, Billett DSM, Giles LA. 1992 Painting behaviour, reproduction and diet in the deep-sea holothurian genus Paramia (Holothuroidea: Synallactidae). J. Mar. Biol. Assoc. UK 72, 447–462. (doi:10.1017/S0025315400037814)

23. Smith JR, Kaufmann RS, Wakefield WW. 1993 Mobile megafaunal activity monitored with a time-lapse camera in the abyssal North Pacific. Deep Sea Res. I, 40, 2307–2324. (doi:10.1016/0967-0637(93)90106-D)

24. Kaufmann RS, Smith JR KL. 1997 Activity patterns of mobile epibenthic megafauna at an abyssal site in the eastern North Pacific: results from a 17-month time-lapse photographic study. Deep Sea Res. II, 44, 559–579. (doi:10.1016/S0967-0637(97)00005-8)

25. Smith JR, Gläs R, Baldwin RJ, Beaulieu SE, Uhlnma AH, Horn RC, Reimers CE. 1997 An autonomous, bottom-transecting vehicle for making long-time-series measurements of sediment community oxygen consumption to abyssal depths. Limnol. Oceanogr. 42, 1601–1612. (doi:10.4319/lo.1997.42.7.1601)

26. Mincks SL, Smith CR, Jeffreys RM, Sumida PG. 2008 Trophic structure on the West Antarctic Peninsula shelf: detritivory and benthic inertia revealed by δ¹³C and δ¹⁵N analysis. Deep Sea Res. II, 55, 2502–2514. (doi:10.1016/j.dsr2.2008.06.009)

27. Whigham BD, Galley EA, Smith CR, Tyler PA. 2008 Inter-anual variability and potential for selectivity in the diets of deep-water Antarctic echinoderms. Deep Sea Res. II, 55, 2478–2490. (doi:10.1016/j.dsr2.2008.06.007)

28. Wakefield WW, Genin A. 1987 The use of a Canadian (perspective) grid in deep-sea photography. Deep Sea Res. A, 34, 469–478. (doi:10.1016/0967-0637(87)90148-8)

29. Nino R, Delean S, Osborne K, Sweatman H. 2003 Estimating cover of benthic organisms from underwater video images: variability associated with multiple observers. Mar. Ecol. Prog. Ser. 265, 107–116. (doi:10.3354/meps265107)

30. Ducklow HW, Baker K, Martinson DG, Quetin LB, Ross RM, Smith CR, Stammepers S, Vernet M, Fraser W. 2007 Marine pelagic ecosystems: the West Antarctic Peninsula. Phil. Trans. R. Soc. B, 362, 67–94. (doi:10.1098/rstb.2006.1955)

31. Ducklow HW, Erickson M, Kelly J, Montes-Hugo M, Ribic CA, Smith CR, Stammepers S, Kari DM. 2008 Particle export from the upper ocean over the continental shelf of the West Antarctic Peninsula: a long-term record, 1992–2007. Deep Sea Res. II, 55, 2118–2131. (doi:10.1016/j.dsr2.2008.04.028)

32. Garibotti IA, Vernet M, Ferrario ME, Smith CR, Ross RM, Quentin LB. 2003 Phytoplankton spatial distribution patterns along the western Antarctic Peninsula (Southern Ocean). Mar. Ecol. Prog. Ser. 261, 21–39. (doi:10.3354/meps261021)

33. Garibotti IA, Vernet M, Ferrario ME. 2005 Annually recurrent phytoplanktonic assemblies during summer in the seasonal ice zone west of the Antarctic Peninsula (Southern Ocean). Deep Sea Res. 52, 1823–1841. (doi:10.1016/j.dsr.2005.05.003)

34. Smith CR, Mincks SL, DeMaster DJ. 2006 A synthesis of benthic-pelagic coupling on the Antarctic shelf: food banks, ecosystem inertia and global climate change. Deep Sea Res. II, 53, 875–894. (doi:10.1016/j.dsr2.2006.02.001)

35. Asper VL, Smith Jr WD. 2003 Abundance, distribution and sinking rates of aggregates in the Ross Sea, Antarctica. Deep Sea Res. I, 50, 131–150. (doi:10.1016/S0967-0637(02)00462-1)

36. Glebe MR, Steinberg DK, Ducklow HW. 2012 Time series of vertical flux of zooplankton falcpellets on the continental shelf of the western Antarctic Peninsula. Mar. Ecol. Prog. Ser. 471, 23–36. (doi:10.3354/meps09021)

37. Jumars PA, Wheatcroft RA. 1989 Responses of benthos to changing food quantity and quality, with a focus on deposit feeding and bioturbation. In Productivity of the ocean: present and past (eds WH Berger, VS Smetske, G Wener), pp. 235–253. New York, NY: Wiley Interscience.

38. Hollertz K. 2002 Feeding biology and carbon budget of the sediment-burrowing heart urchin Bryssopsis lirifera (Echinoidae: Spathangidae). Mar. Biol. 140, 959–969. (doi:10.1007/s00227-001-0764-7)
50. Taghon GL. 1988 The benefits and costs of deposit feeding in the polychaete Abarenicola pacifica. Limnol. Oceanogr. 33, 1166–1175. (doi:10.4399/lo.1988.33.5.1166)

51. Dade WB, Jumars P, Penny DL. 1990 Supply-side optimization: maximizing absorptive rates. In Behavioural mechanisms of food selection (ed. RH Hughes). NATO ASI Series, vol. G20, pp. 531–556. Berlin, Germany: Springer. (doi:10.1007/978-3-642-75118-9_26)

52. Wheatcroft RA, Smith CR, Jumars PA. 1989 Dynamics of surficial trace assemblages in the deep sea. Deep Sea Res. A 36, 71–91. (doi:10.1016/0967-0645(89)90019-8)

53. Nedwell DB, Walker TR. 1995 Sediment-water fluxes of nutrients in an Antarctic coastal environment: influence of bioturbation. Polar Biol. 15, 57–64. (doi:10.1007/BF00236125)

54. Thompson BAW, Riddle MJ. 2005 Bioturbation behaviour of the spatangoid urchin Abatus ingens in Antarctic marine sediments. Mar. Ecol. Prog. Ser. 290, 135–143. (doi:10.3354/meps290135)

55. Austen MC, Lamberts JD, Hutchings PA, Boucher G, Snedgroe PV, Heip C, King G, Koike I, Smith CR. 2002 Do biodiversity links above and below the marine sediment–water interface affect stability of benthic and pelagic communities? Biodivers. Conserv. 11, 113–136. (doi:10.1023/A:1014098997535)

56. Smith CR, Demopoulos AWJ. 2003 Ecology of the deep Pacific Ocean floor. In Ecosystems of the world volume 28: ecosystems of the deep ocean (ed. PA Tyler), pp. 179–218. Amsterdam, The Netherlands: Elsevier.