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# The hemisessile lifestyle and feeding strategies of *Iosactis vagabunda* (Actiniaria, Iosactiidae), a dominant megafaunal species of the Porcupine Abyssal Plain

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## ABSTRACT

*Iosactis vagabunda* Riemann-Zürneck, 1997 (Actiniaria, Iosactiidae) is a small endomyarian anemone, recently quantified as the greatest contributor to megafaunal density (48%; 2372 individuals ha<sup>-1</sup>) on the Porcupine Abyssal Plain (PAP). We used time-lapse photography to observe 18 individuals over a period of approximately 20 months at 8-h intervals, and one individual over 2 weeks at 20-minute intervals, and report observations on its burrowing activity, and both deposit and predatory feeding behaviours. We recorded the apparent subsurface movement of an individual from an abandoned burrow to a new location, and burrow creation there. Raptorial deposit feeding on settled phytodetritus particles was observed, as was predation on a polychaete 6-times the estimated biomass of the anemone. Though essentially unnoticed in prior studies of the PAP, *I. vagabunda* may be a key component of the benthic community, and may make a critical contribution to the carbon cycling at the PAP long-term time-series study site.

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## 1. Introduction

*Iosactis vagabunda* Riemann-Zürneck 1997 is a small endomyarian anemone originally described from the Porcupine Abyssal Plain (PAP; 4850 m water depth) in the NE Atlantic (Riemann-Zürneck, 1997b). It was thought to be common (Riemann-Zürneck, 1997b), though infrequently captured in trawl samples (Billett et al., 2010), a problem common to taxa of small size, soft body and burrowing traits (Aldred et al., 1979). Comparisons of data from trawl and photographic surveys at the PAP suggest substantial underrepresentation of smaller megabenthic taxa (such as *I. vagabunda*) in trawl data (Bett et al., 2001; Morris et al., 2014). Recent broad-scale photographic surveys suggest that it may be the most abundant megafaunal species, and a major contributor to megafaunal biomass (Morris et al., 2014). This species may therefore be a key component of the benthic community of the PAP, which has not previously been recognized nor incorporated in prior assessments of the PAP megabenthos and food web (Ruhl et al., 2014; van Oevelen et al., 2012), where holothurians have been assumed to dominate the megafauna. Despite its abundance, previous studies have expressed uncertainty about assigning a feeding type to this species (Iken et al., 2001).

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The life histories and behaviour of most deep-sea taxa are largely unknown. This is the result of very limited in-situ observations. Deep-sea time-lapse photography has proved valuable in recording the feeding behavior and burrow creation of echinoderms (Bett and Rice, 1993; Bett et al., 1995; Ohta, 1984), the foraging behavior of enteropneusts (Jones et al., 2013; Smith et al., 2005) and bathyal shrimp (Lampitt and Burnham, 1983), the activity and bioturbation of echinoderms (Bett et al., 2001; Vardaro et al., 2009), and the behaviour of anthozoans (Ansell and Peck, 2000; Lampitt and Paterson, 1987). Time-lapse imagery has previously been used to observe the movement of *I. vagabunda* between burrows, leading to the suggestion that it had a hemisessile lifestyle (Riemann-Zürneck, 1997b). Here we report new observations on the burrowing and feeding behaviour of *I. vagabunda* from recent time-lapse imagery, and relate these to new photographic evidence of its abundance to re-assess the significance of this species to the PAP megabenthos community.

## 2. Material and methods

The density of *I. vagabunda* was estimated from two large-scale seabed photographic surveys from the long-term time-series station at the PAP (48°50'N 016°30'W) at 4850 m water depth (Hartman et al., 2012); towed-vehicle camera transects conducted

in July 2011 on *RRS James Cook* cruise 062 (Ruhl, 2012), and an Autosub6000 autonomous vehicle survey in July 2012 from *RRS Discovery* cruise 377 (Ruhl, 2013). The benthic environment at this location is characterized by soft sediments and negligible slope angles, with seasonal and interannual variation in the supply of phytodetritus (Billett et al., 1983; Lampitt et al., 2010). In total 726 useful seabed images were acquired in the towed camera survey (seabed area assessed 0.39 ha), and were analysed following the methodology given in Jones et al. (2009). The Autosub6000 mission yielded 28,290 useful images (seabed area assessed 4.79 ha), that were produced and analysed using the methods detailed by Morris et al. (2014). In brief, individuals were enumerated and the seafloor area observed was calculated using the camera altitude and image acceptance angles. Geometric mean densities, conservative in the case of aggregated distributions (Elliott, 1977), were calculated and confidence intervals generated using a bootstrap method in R (Davison and Hinkley, 1997).

*I. vagabunda* individuals were observed in time-lapse imagery collected at the PAP using Bathysnap time-lapse camera systems (Bett, 2003). Bathysnap deployments and recoveries occurred on research cruises *RRS James Cook* 062, 071 and 085 (Lampitt, 2013, 2014; Ruhl, 2012). The camera was stationed 0.8 m above the seabed, tilted 30° below the horizontal, with a vertical acceptance angle of 26.6°, and a horizontal acceptance angle of 35.0°. Oblique seafloor images were captured at 20-min intervals from 4 August 2011 (16:37) to 18 August 2011 (13:19), and at 8-h intervals from 21 August 2011 (13:05) to 3 May 2012 (05:41) and 6 May 2012 (14:49) to 19 April 2013 (13:30). A single unusable image (where an apparently flash failure occurred) was removed, resulting in the assessment of 999 images over 13.9 days (20-min interval), and 768 images over 255.6 days and 1044 images over 348 days (8-h interval). Observations of the feeding and burrowing activity were made in the 8-h interval images, restricted to the centre 80% of the image horizontally, and the upper 80% of the image vertically to discount areas of the image that were distorted, resulting in an assessed field of view of 1.8 m<sup>2</sup>. Detailed observations of the burrowing activity of a single individual were made in the 20-min interval images.

Individuals were identified as *I. vagabunda* by their general size, translucent body, 24 tentacles, position in a burrow, and oral disk flush to sediment surface, characteristics consistent with the description provided by Riemann-Zürneck (1997b). A substantial reference collection of trawl-caught megabenthos from the PAP is maintained in the 'Discovery Collections' at the National Oceanography Centre, Southampton, UK, including 28 specimens identified as *I. vagabunda* collected from trawls undertaken during cruise *RRS James Cook* 062. For each instance (where an individual remained in the same burrow in a series of consecutive images), the date and time of apparent arrival to and departure from the field of view, and burrowing or feeding activity were noted. Thus, the same animal may have been observed in multiple instances. The sizes of individuals and a single associated polychaete were measured in the Monterey Bay Aquarium Research Institute Video Annotation and Reference System (Schlining and Stout, 2006). The resulting measurements were converted to real-world dimensions using a perspective grid method based on Wakefield and Genin (1987). Wet weight data was collated from 140 trawl-caught *I. vagabunda* specimens collected from the PAP (August 1996–October 2002), and was estimated for the polychaete using a length-to-wet weight conversion derived from 167 trawl-caught specimens (polychaete wet weight in grams = 0.0002 \* L<sup>2.31</sup>, where L is body length in mm).

### 3. Results and discussion

The geometric mean density of *I. vagabunda* in the towed camera images was 1623 individuals ha<sup>-1</sup> (95% confidence interval: 1446 to

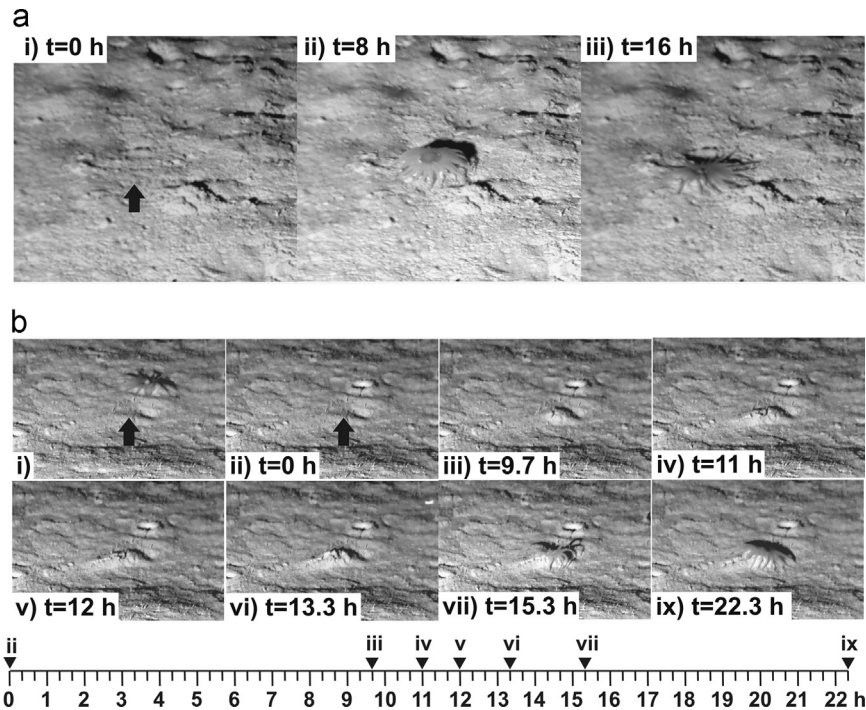
1801 ind ha<sup>-1</sup>), and from the Autosub 6000 images was 2434 ind ha<sup>-1</sup> (95% CI: 2386 to 2483 ind ha<sup>-1</sup>). An area weighted mean of the two surveys gave a mean value of 2372 ind ha<sup>-1</sup> and an overall total megabenthos density of 4963 ind ha<sup>-1</sup>, thus a relative abundance of 48% for *I. vagabunda*. The wet weights of trawl-caught preserved specimens ranged from 0.2 g to 1.4 g, with a median of 0.6 g.

A total of 18 instances of *I. vagabunda* individuals were observed in the 8-h interval images; at least one individual appeared in 366 photos (20% of images). In each instance the individual appeared buried with the oral disk flush with the surface, and the tentacles extended. The mean oral disc diameter (excluding tentacles) was 32 mm (±SD 8.3 mm, n=18). The estimated size of individuals was broadly consistent with that reported by Riemann-Zürneck (1997b): the diameter of the oral disk (mean of 32 mm) and the length of the column (an observed maximum of 109 mm) were larger than those reported for the ~400 trawl-caught specimens examined in the initial description of the species (specimens were 4–10 mm in diameter and 10–25 mm in height). The difference between oral disk size in the photos and preserved body diameter is not surprising, since the disk is extended over the edge of the burrow in the images, and is thus greater than the width of the retracted trawl-caught specimens. Column lengths estimated from images were measured when the animal was extended above the burrow into the water column, which may involve stretching of the musculature, such that these dimensions would not correspond to those of preserved trawl-caught specimens.

#### 3.1. Burrowing activity

Burrows are visible on the sediment surface as single holes with a diameter of the resident anemone, and a raised rim with imprints from the 24 tentacles, which is often visible once the individual has vacated the burrow (Fig. 1a and b). Observations from the 8-h interval images indicated that the time spent in a particular burrow ranged from 32 to 1136 h (1.3 to 47.3 days, n=17), and the mean was 458 h (±SD 384 h, or 19 days ± 16 days, n=17). Individuals in these images were observed moving into or between burrows on two occasions. The first individual lowers its aboral end until the oral disk is flush with the surface 8 h later (Fig. 1). The second individual is noted burrowing under the sediment from its old burrow to a new location, creating a broken raised patch of sediment at the new burrow site 8 h later, before the animal is observed with its oral disk flush to the surface 16 h later.

The 20-min interval images provided a more detailed view of the burrowing behaviour of a single individual (Fig. 1b, Supplementary material). A single individual was observed either in its burrow or burrowing over a period of 9.8 days. In each burrow move, the animal disappears from view by retreating into its burrow, then a small mound appears a short distance from the original burrow. This mound grows and is broken along the crest before the animal emerges from the apex of the mound, tentacles first, and establishes itself in the new burrow with its disk flush with the sediment surface and tentacles extended. The first movement to a new burrow lasted a total of 22.3 h: the time following disappearance from the original burrow to the first indication of mound building was 9.7 h, the small mound grew in size over 4.7 h before the animal began to emerge, finally the emergence from the mound and establishment in the new burrow took a further 8 h. The animal spent 151.3 h in this burrow, before moving again. The second move occurred over 19 h, with a period of 13.3 h between disappearance and mound-building, 3.3 h of mound-building, and 2.3 h from emergence to establishment. The burrowing behaviour of *I. vagabunda* observed here suggests that



**Fig. 1.** Oblique photographic sequences showing burrowing activities of *Losactis vagabunda*. (a) Consecutive images showing superficial burrowing activity. Not present (i), location of future burrow is indicated by a black arrow; (ii) individual appears and begins to burrow, aboral end first; (iii) individual established in burrow, oral disk and tentacles flush with the sediment. Times indicated are elapsed from (i). (b) Selected images and timeline showing subsurface burrowing activity. Highlights of the image sequence show the (i) individual in its original burrow, with the location of the future burrow indicated by a black arrow; (ii) disappearance; (iii) initiation of mound at new burrow location; (iv) and (v) mound grows and is furrowed; (vi) and (vii) individual emerges, tentacles first; and (viii) established in new burrow. Times indicated are elapsed from (ii). The timeline shows all images in the sequence as tick-marks, with the events pictured above noted.

the subsurface motion of the animal between burrows is similar to the consecutive 'U-shaped' burrowing behaviour described for echiurans (Bett, 2003; Bromley, 1996), as they produce a 'volcano-series' burrow system (Bett et al., 1995). Subsurface transit between burrow locations may reduce the risk of predation; alternative interpretations for episodic subsurface behaviour by deep-sea megabenthos (e.g. caching, Jumars et al., 1990) have been suggested but seem unlikely in this case.

The burrowing behaviour observed here is consistent with the hemisessile lifestyle reported for the species by Riemann-Zürneck (1997b), though the maximum time spent by an individual in a burrow was 13 days, much shorter than observed here (mean 19.1 days, maximum 47.3 days). We conclude that the animal facultatively moves between burrow locations both over the sediment surface (described by Riemann-Zürneck, 1997b), and also beneath the surface. Anemones are commonly perceived to be sessile, and this hemisessile behavior appears to be unique among the known Actiniaria of the PAP, including *Amphianthus bathybius* (Riemann-Zürneck, 1987), *Sicyonis biotrans* (Riemann-Zürneck, 1991), *Daontesia porcupina* (Riemann-Zürneck, 1997a), and *Actinauge abyssorum* (Riemann-Zürneck, 1986). *Kadosactis commensalis* (Bronsdon et al., 1993) is not mobile itself, but gains mobility by attaching to the holothurian *Paroriza* sp. *Segonzactis platypus* (Riemann-Zürneck, 1979) is a free-living (non-attaching) non-burrowing form that also exists at the PAP, but detailed observations of its life history have not been made. Free-living forms have been observed elsewhere (Foell and Pawson, 1986; Riemann-Zürneck, 1998), such as the deep-sea hemisessile species *Liponema brevicornis* (Fautin Dunn and Bakus, 1977), and *Bolocera tuediae* (Riemann-Zürneck, 1986; Rowe and Menzies, 1969). The cogener *Losactis antarctica* (Rodríguez, 2012) has a similar morphology to *L. vagabunda*, and is known from soft sediment habitats, so may also be a free-living form. Other burrowing actinarians, such as *Halcampoides* sp., have also been found to flourish in other soft-

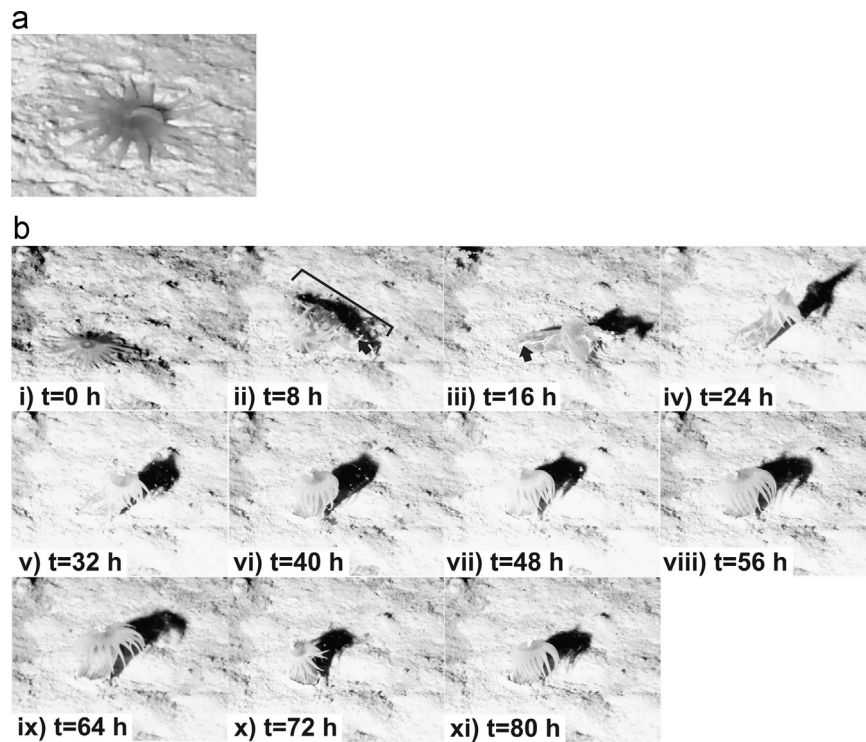
sediment habitats (Ansell and Peck, 2000). This hemisessile lifestyle, with frequent burrow relocation, may be to allow more effective exploitation of resources and thus be linked to feeding behaviour.

### 3.2. Feeding behaviour

The main feeding behaviour observed involved moving particles of surface detritus into the mouth opening using individual tentacles (see Fig. 2a); this was observed in the images as tentacles holding detrital particles with the tentacle partly or fully extended. This behaviour was observed in all individuals, and was assumed to occur continuously.

Predatory feeding was also observed. The most obvious instance occurred 80 h after the arrival of an anemone (Fig. 2b), when the individual (22 mm in diameter) appeared to have captured a polychaete with visible chaetae (possibly genus *Buskiella* McIntosh, 1885, L. Kuhn and S. Van Thun, pers. comm.), 105 mm in length on 1 September 2012 (21:22). The mouth of the anemone was expanded to allow the polychaete to be ingested whole; 8 h after capture, the polychaete had been largely consumed, save for one protruding end, and was completely engulfed 16 h after capture. The chaetae of the polychaete were visible through the body wall of the anemone. The estimated wet mass of the polychaete was 9.2 g, approximately 15 times the median wet mass of trawl-caught *L. vagabunda* specimens. Following the consumption of the polychaete, the anemone spent a further 56 h with its body erect and extended to a maximum column height of 109 mm (approximately the polychaete body length) above the burrow into the water column. Other individuals were also observed to spend time with their columns extended above the sediment (Table 1), potentially reflecting similar feeding behaviour, although prey capture was not observed in those cases. Neither feeding behaviour appeared to be modified by the





**Fig. 2.** Oblique photographs showing feeding activities of *Losactis vagabunda*. (a) Single image showing raptorial feeding. A single tentacle appears to be placing particle in mouth opening. (b) A sequence of consecutive photographs showing predation. (i) individual in resting state; (ii) polychaete prey captured (polychaete indicated with bracket, individual cheta with arrow); ingestion of prey and extension of anemone into water column follow in (iii–xi). Times indicated are elapsed from (i).

presence of a layer of phytodetritus on the seabed, which was observed in the images between 17 June and 17 December 2012.

Many deep-sea anemones are thought to be suspension feeders, and have been observed to modify their feeding behaviour to capture particles efficiently (Lampitt and Paterson, 1987; Van Praët, 1985). Burrowing actinarians have been thought to exploit dissolved organic content in the sediment (Ammons and Daly, 2008). Our observations suggest that *I. vagabunda* is a surface deposit feeder (exploiting phytodetritus, as suggested by Riemann-Zürneck, 1997b) and a predator, rather than a suspension feeder. Iken et al. (2001) initially classed this species as a suspension feeder, but acknowledged that benthic cnidarians are often opportunistic omnivores, with gut contents that include both sediment and prey organisms. Our observations of predatory behaviour suggest that predation may be a significant component of this anemone's feeding strategy. By consuming a large pelagic polychaete, the anemone demonstrated a potentially very broad trophic niche and possible body-size independence in trophic relations among the deep-sea benthos (Kelly-Gerreyn et al., 2014). In food limited deep-sea environments, other suspension-feeders are known to use mixed feeding habits (e.g. tunicates; Monniot and Monniot, 1975). Similarly, the deep-sea sediment-dwelling anemone *Actinoscyphia aurelia* has been found to prey on polychaetes from gut content analyses, but was previously thought to be an obligate detritivore (Lampitt and Paterson, 1987).

*I. vagabunda* occupies an intermediate trophic position at the PAP. Iken et al. (2001) assessed trophic relations among PAP benthos and demersal fish via  $\delta^{15}\text{N}$  values: the presumed primary food source (particulate organic matter) having a value of 8.15‰, primary consumers among the invertebrate megabenthos (*Ophiocten hastatum*, *Amperima rosea*) having values of 10.70–10.75‰, and *I. vagabunda* at 14.92‰, enriched some 7‰ above source material and 4‰ above the primary consumers. Assuming a 3–4‰ enrichment between trophic levels (see e.g. Gutierrez-Rodriguez et al. 2014), *I. vagabunda* might reasonably be placed in trophic level 2,

**Table 1**

Observations of individual specimens of *I. vagabunda* with column extended above the sediment surface, interpreted as evidence of a recent predatory event. Prey capture was observed in the first case only.

First observation of column extension (potential predatory behaviour)	Duration of behaviour (h)	Maximum height above seabed (mm)
1 September 2012 21:22	72	109
22 October 2012 21:11	8	31
18 March 2013 12:38	8	38
7 April 2013 04:33	16	66
8 April 2013 20:33	8	62

as Iken et al. (2001) indicated. Similarly, *S. platypus* yielded a  $\delta^{15}\text{N}$  value of 16.23‰, equally suggestive of the significance of predation in its feeding strategy. These mobile species had the highest  $\delta^{15}\text{N}$  values amongst the actinarians. A hemisessile predator poses interesting questions of optimal foraging theory (MacArthur and Pianka, 1966); 'sit-and-wait' predators may favour larger prey items (e.g. Griffiths, 1980), as we have potentially observed with *I. vagabunda*, but routine relocation suggests local (patch) resource depletion consistent with 'marginal value theorem' (Charnov, 1976). It was not obvious from the images whether individuals relocated once detritus resources were depleted, or whether the new location was selected based on detritus availability or adopted mechanistically, as appeared to be the case in U-tube looping echinurans (Bett, 2003).

#### 4. Perspectives

The importance of *I. vagabunda* to the megabenthos of the PAP has only been quantified recently, but even those estimates from images may not fully represent the true density and biomass of this species as a result of its burrowing habit. If all individuals



**Video S1.** Complete oblique photographic sequence of subsurface burrowing activity by *Losactis vagabunda* shown in Fig. 1b. Images were captured at 20-min intervals, and are shown at 1 second intervals in the video. A video clip is available online. Supplementary material related to this article can be found online at doi:10.1016/j.dsr.2015.04.010.

spend similar proportions of time invisible to seabed photography as the individual observed in the 20-min interval images (9% of the two-week period observed), then the density of this species is likely closer to 2585 ind ha<sup>-1</sup>, or 52% of the total observed megafaunal density. At this density, the corresponding biomass of 0.16 g m<sup>-2</sup> would be equivalent to 52–111% of the total trawl-caught invertebrate biomass at the PAP in 14 surveys from 1995 to 2005 (Billett et al., 2010).

This major contribution to megabenthic abundance and biomass, in combination with our new observations of feeding behaviour and burrowing have implications for the current understanding of community dynamics and the use of resources at the PAP. Given its small body size among the megabenthos and correspondingly higher mass-specific metabolic rate, and its predatory capability, *I. vagabunda* may play a key role in the carbon stocks and flows of the PAP. The most comprehensive study of carbon cycling at the PAP (van Oevelen et al., 2012) used estimates of Actiniarian density and biomass obtained from trawl data that are two orders of magnitude and twenty times smaller, respectively, than those reported for *I. vagabunda* here. In addition, this mobile anemone may create a dynamic mosaic of patches on the seabed, which may have implications for diversity.

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## Appendix A. Supplementary material

The following are the supplementary data to this article:

**Video S1** indicates that the time-lapse microscopy shows intramoebic oocysts with conserved morphology and organelle motility.

## References

- Aldred, R.G., Riemann-Zürneck, K., Thiel, H., Rice, A.L., 1979. Ecological observations on the deep-sea anemone *Actinoscyphia aurelia*. *Oceanolog. Acta* 2 (4), 389–395.
- Ammons, A.W., Daly, M., 2008. Distribution, habitat use and ecology of deepwater Anemones (Actiniaria) in the Gulf of Mexico. *Deep Sea Res. Part II: Topical Stud. Oceanogr.* 55 (24), 2657–2666.
- Ansell, A.D., Peck, L.S., 2000. Burrowing in the Antarctic anemone, *Halcampoides* sp., from Signy Island, Antarctica. *J. Exp. Mar. Biol. Ecol.* 252 (1), 45–55.
- Bett, B.J., 2003. Time-lapse photography in the deep sea. *Underwater Technol.* 25 (3), 121–127.
- Bett, B.J., Malzone, M.G., Narayanaswamy, B.E., Wigham, B.D., 2001. Temporal variability in phytodetritus and megabenthic activity at the seabed in the deep Northeast Atlantic. *Prog. Oceanogr.* 50 (1–4), 349–368.
- Bett, B.J., Rice, A.L., 1993. The feeding-behavior of an abyssal echiuran revealed by in-situ time-lapse photography. *Deep Sea Res. Part I: Oceanogr. Res. Papers* 40 (9), 1767–1779.
- Bett, B.J., Rice, A.L., Thurston, M.H., 1995. A quantitative photographic survey of spoke-burrow type lebensspuren on the cape-verde abyssal-plain. *Int. Rev. Gesamten Hydrobiol.* 80 (2), 153–170.
- Billett, D.S.M., Bett, B.J., Reid, W.D.K., Boorman, B., Priede, I.G., 2010. Long-term change in the abyssal NE Atlantic: the ‘Amperima Event’ revisited. *Deep Sea Res. Part II: Topical Stud. Oceanogr.* 57 (15), 1406–1417.
- Billett, D.S.M., Lampitt, R.S., Rice, A.L., Mantoura, R.F.C., 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature* 302 (5908), 520–522.
- Bromley, R.G., 1996. *Trace Fossils: Biology, Taphonomy and Applications*. Chapman & Hall, London.
- Bronsdon, S.K., Tyler, P.A., Rice, A.L., Gage, J.D., 1993. Reproductive biology of two epizoic anemones from the deep North-Eastern Atlantic Ocean. *J. Mar. Biol. Assoc. U.K.* 73, 531–542.
- Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* 9 (2), 129–136.
- Davison, A.C., Hinkley, D.V., 1997. *Bootstrap Methods and Their Application*. Cambridge University Press.
- Elliott, J.M., 1977. *Some Methods for Statistical Analysis of samples of Benthic Invertebrates*. Freshwater Biological Association, Ambleside.
- Fautin Dunn, D., Bakus, G.J., 1977. Redescription and Ecology of *Liponema brevicornis* (McMurrich, 1893), with Definition of the Family Liponematidae (Coelenterata, Actiniaria). *Astarte*.
- Foell, E.J., Pawson, D.L., 1986. Photographs of invertebrate megafauna from abyssal depths of the North-Eastern Equatorial Pacific Ocean. *Ohio J. Sci.* 86 (3), 61–68.
- Griffiths, D., 1980. Foraging Costs and Relative Prey Size. *The American Naturalist* 116, 743–752.
- Gutierrez-Rodriguez, A., Decima, M., Popp, B.N., Landry, M.R., 2014. Isotopic invisibility of protozoan trophic steps in marine food webs. *Limnol. Oceanogr.* 59 (5), 1590–1598.
- Hartman, S.E., Lampitt, R.S., Larkin, K.E., Pagnani, M., Campbell, J., Gkrizalis, T., Jiang, Z.-P., Pebody, C.A., Ruhl, H.A., Gooday, A.J., Bett, B.J., Billett, D.S.M., Provost, P., McLachlan, R., Turton, J.D., Lankester, S., 2012. The Porcupine Abyssal Plain fixed-point sustained observatory (PAP-SO): variations and trends from the Northeast Atlantic fixed-point time-series. *ICES J. Mar. Sci.: J. Cons.*
- Iken, K., Brey, T., Wand, U., Voigt, J., Junghans, P., 2001. Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. *Prog. Oceanogr.* 50 (1–4), 383–405.
- Jones, D.O.B., Alt, C.H.S., Priede, I.G., Reid, W.D.K., Wigham, B.D., Billett, D.S.M., Gebruk, A.V., Rogacheva, A., Gooday, A.J., 2013. Deep-sea surface-dwelling enteropneusts from the Mid-Atlantic Ridge: their ecology, distribution and mode of life. *Deep Sea Res. Part II: Topical Stud. Oceanogr.* 98, 374–387, Part B (0).
- Jones, D.O.B., Bett, B.J., Wynn, R.B., Masson, D.G., 2009. The use of towed camera platforms in deep-water science. *Int. J. Soc. Underwater Technol.* 28 (2), 41–50.
- Jumars, P.A., Mayer, L.M., Deming, J.W., Baross, J.A., Wheatcroft, R.A., 1990. Deep-sea deposit-feeding strategies suggested by environmental and feeding constraints. *Philos. Trans. R. Soc. London, Ser. A: Math. Phys. Sci.* 331 (1616), 85–101.
- Kelly-Gerrey, B.A., Martin, A.P., Bett, B.J., Anderson, T.R., Kaariainen, J.I., Main, C.E., Marcinko, C.J., Yool, A., 2014. Benthic biomass size spectra in shelf and deep-sea sediments. *Biogeosci. Discuss. Biogeosci. Discuss.* 11 (1), 901–942.
- Lampitt, R.S., 2013. RRS *James Cook* Cruise 71, 29 Apr–12 May 2012. In: *Porcupine Abyssal Plain: Sustained Ocean Observation*. National Oceanography Centre, Southampton, Southampton, 111 pp.
- Lampitt, R.S., 2014. RRS *James Cook* Cruise 85, 14–29 Apr 2013. *Porcupine Abyssal Plain: sustained ocean observation*. National Oceanography Centre, Southampton, Southampton, 92 pp.
- Lampitt, R.S., Billett, D.S.M., Martin, A.P., 2010. The sustained observatory over the Porcupine Abyssal Plain (PAP): insights from time series observations and process studies Preface. *Deep Sea Res. Part II: Topical Stud. Oceanogr.* 57 (15), 1267–1271.
- Lampitt, R.S., Burnham, M.P., 1983. A free fall time lapse camera and current meter system ‘Bathysnap’ with notes on the foraging behaviour of a bathyal decapod shrimp. *Deep Sea Res. Part A: Oceanogr. Res. Rep.* 30 (9), 1009–1017.
- Lampitt, R.S., Paterson, G.L.J., 1987. The feeding behaviour of an abyssal sea anemone from in situ time lapse photographs and trawl samples. *Oceanolog. Acta* 10 (4), 455–461.

- MacArthur, R.H., Pianka, E.R., 1966. On optimal use of a patchy environment. *Am. Nat.* 100 (916), 603–609.
- Monniot, C., Monniot, F., 1975. Abyssal tunicates: an ecological paradox. *Annales de l'Institut Océanographique (Paris)* 51, 99–129.
- Morris, K.J., Bett, B.J., Durden, J.M., Huveene, V.A.I., Milligan, R., Jones, D.O.B., McPhail, S., Robert, K., Bailey, D., Ruhl, H.A., 2014. A new method for ecological surveying of the abyss using autonomous underwater vehicle photography. *Limnol. Oceanogr.: Methods* 12 (11), 795–809.
- Ohta, S., 1984. Star-shaped feeding traces produced by echiuran worms on the deep-sea floor of the Bay of Bengal. *Deep Sea Res. Part A: Oceanogr. Res. Pep.* 31 (12), 1415–1432.
- Riemann-Zürneck, K., 1979. Two disc-shaped deep sea Anthozoa from the Gulf of Biscay, with a survey of adaptation types in the Actiniaria. *Zoomorphologie* 93 (3), 227–243.
- Riemann-Zürneck, K., 1986. On some abyssal sea anemones of the North Atlantic (Actiniaria: Hormathiidae). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 83, 7–29.
- Riemann-Zürneck, K., 1987. *Amphianthus bathybius* Hertwig, 1882 aus der Iberischen Tiefsee. Redeskription der Typusart (Actiniaria: Hormathiidae). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 84, 7–15.
- Riemann-Zürneck, K., 1991. A new species of *Sicyonis* (Actiniaria: Actinostolidae) from the abyssal NE Atlantic. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 88, 7–15.
- Riemann-Zürneck, K., 1997a. The deep-sea anemones *Bathypheilia margaritacea* and *Daontesia porcupina* sp. nov. with comments on the family Bathypheiliidae. *J. Mar. Biol. Assoc. U.K.* 77 (02), 361–374.
- Riemann-Zürneck, K., 1997b. A Hemisessile Sea Anemone from the Porcupine Abyssal Plain, North Atlantic Ocean: *Iosactis vagabunda* gen. nov., sp. nov. *J. Mar. Biol. Assoc. U.K.* 77 (04), 1025.
- Riemann-Zürneck, K., 1998. How Sessile are Sea Anemones? A review of free-living forms in the Actiniaria Cnidaria: Anthozoa. *Mar. Ecol.* 19 (4), 247–261.
- Rodriguez, E., 2012. Another bipolar deep-sea anemone: new species of *Iosactis* (Actiniaria, Endomyaria) from Antarctica. *Helgol. Mar. Res.* 66 (2), 211–218.
- Rowe, G.T., Menzies, R.J., 1969. Zonation of large benthic invertebrates in the deep-sea off the Carolinas. *Deep Sea Res. Oceanogr. Abstr.* 16 (5), 531–537.
- Ruhl, H., 2012. RRS *James Cook* Cruise 62, 24 Jul–29 Aug 2011. Porcupine Abyssal Plain—sustained observatory research. National Oceanography Centre, Southampton, Southampton, 119 pp.
- Ruhl, H., 2013. RRS *Discovery* Cruise 377 & 378, 05–27 July 2012. Autonomous ecological surveying of the abyss: understanding mesoscale spatial heterogeneity at the Porcupine Abyssal Plain. National Oceanography Centre, Southampton, Southampton, 73 pp.
- Ruhl, H., Bett, B.J., Hughes, S.J.M., Alt, C.H.S., Ross, E.J., Lampitt, R.S., Pebody, C.A., Smith Jr, K.L., Billett, D.S.M., 2014. Links between deep-sea respiration and community dynamics. *Ecology* 95 (6), 1651–1662.
- Schlining, B.M., Stout, N.J., 2006. MBARI's Video Annotation and reference system. *OCEANS* 2006, 1–5.
- Smith Jr, K.L., Holland, N.D., Ruhl, H.A., 2005. Enteropneust production of spiral fecal trails on the deep-sea floor observed with time-lapse photography. *Deep Sea Res. Part I: Oceanogr. Res. Pep.* 52 (7), 1228–1240.
- van Oevelen, D., Soetaert, K., Heip, C., 2012. Carbon flows in the benthic food web of the Porcupine Abyssal Plain: the (un)importance of labile detritus in supporting microbial and faunal carbon demands. *Limnol. Oceanogr.* 57 (2), 645–664.
- Van Praët, M., 1985. Nutrition of sea anemones. In: Blaxter, J.H.S., Russell, F.S., Yonge, M. (Eds.), *Advances in Marine Biology*. Academic Press, London, pp. 65–99.
- Vardaro, M.F., Ruhl, H.A., Smith Jr, K.L., 2009. Climate variation, carbon flux, and bioturbation in the abyssal North Pacific. *Limnol. Oceanogr.* 54 (6), 2081–2088.
- Wakefield, W.W., Genin, A., 1987. The use of a Canadian (perspective) grid in deep-sea photography. *Deep Sea Res. Part A: Oceanogr. Res. Pep.* 34 (3), 469–478.