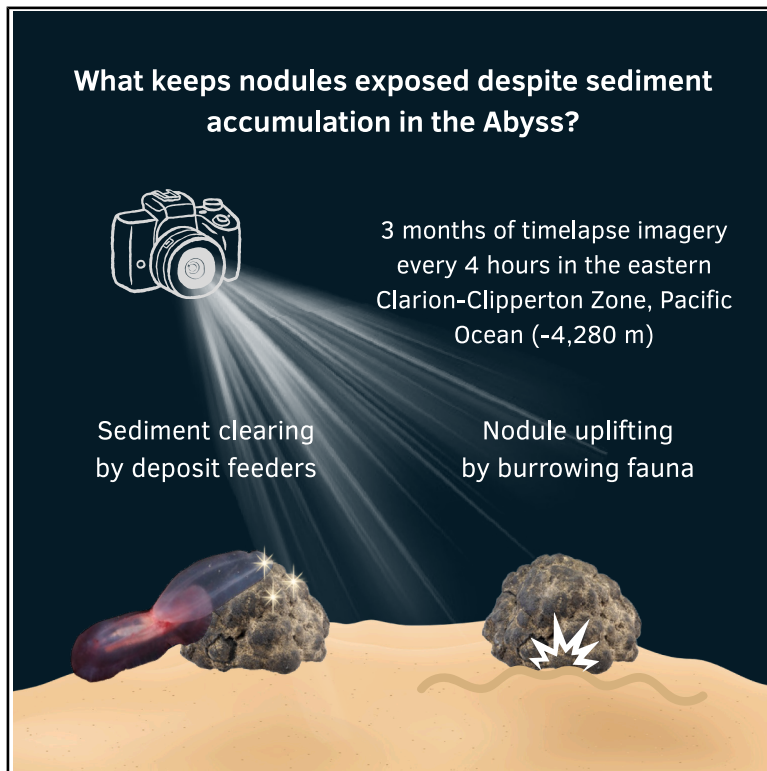


Current Biology

Functional roles of abyssal benthos in sustaining polymetallic nodule fields

Graphical abstract



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In brief

Van Audenhaege et al. identify abyssal benthic species that actively clear sediment and uplift polymetallic nodules, reworking the entire seabed on yearly to decadal timescales. This process maintains hard substrata for colonization, supporting habitat heterogeneity and abyssal biodiversity. Their observations highlight the importance of overlooked processes in designing conservation strategies.

Highlights

- Benthic fauna removes sediments and uplifts nodules
- Benthic activity should rework the entire seabed within decadal timescales
- The abyssal benthos helps keep polymetallic nodules exposed
- This function is essential for maintaining abyssal biodiversity

Report

Functional roles of abyssal benthos in sustaining polymetallic nodule fields

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SUMMARY

Polymetallic nodules form a critical habitat in the abyssal plain ecosystems where they occur, supporting high benthic biodiversity.¹ They form over millions of years in areas of extremely low sediment accumulation rates,^{2,3} but it is unclear how the nodules remain on the surface, and hence are available for benthic biota. Here, we use seabed time-lapse photography to explore the potential role of benthic faunal behavior in the maintenance of polymetallic nodules on the seabed surface. We observed several species directly removing sediment from the nodule surface, mainly holothurians and gastropods, and infauna activity causing nodule uplift. Derived estimates of the area covered by animal movements, as a proxy for benthic activity,^{4,5} indicated that yearly to decadal timescales are needed to remove sediment from and uplift all nodules within the field of view. If these behaviors significantly counteract nodule burial over the long term, then benthic activity may be a key mechanism in nodule maintenance,^{6,7} as hypothesized for over 40 years.⁸ This essential function for the maintenance of abyssal biodiversity in nodule-field seascapes has been largely overlooked, highlighting that substantial gaps in knowledge remain in our understanding of the functioning of nodule-field ecosystems. Improving the assessment of habitat engineers may enhance predictions of ecosystem resilience if commercial mining activities occur. However, this study opens new opportunities for monitoring benthic ecosystem functioning to provide a more holistic understanding of abyssal ecosystem status and dynamics.

RESULTS

Abyssal polymetallic nodules occur predominantly at the sediment-water interface, although some are buried within the underlying sediment, in areas characterized by a low sediment accumulation rate ($< 0.5 \text{ cm ka}^{-1}$) and a low maximum surface productivity ($< 300 \text{ mgC m}^{-2} \text{ day}^{-1}$).² Nodules are formed by precipitation of manganese oxides and iron oxyhydroxides⁹ at rates of 1 to 10 mm per million years.^{3,10,11} Their persistence at the sediment surface is intriguing (e.g., “*Why are there any nodules at all?*” Kerr⁸) because: (1) nodule growth rates are 1,000 times lower than sediment accumulation rates (e.g., 3–6 mm per thousand years)^{12,13}; and (2) nodule sinking would be anticipated because nodule density ($\sim 2.4 \text{ g cm}^{-3}$) and size (> 10 up to ~ 200 mm) are higher than those of the bulk sediment ($\sim 1.3 \text{ g cm}^{-3}$).¹⁴ To date, benthic activity is still considered, by default, the most likely process to explain nodule maintenance at basin scales.^{2,7} This study presents observations of benthic activity in time-lapse photographs showing that biological activity could keep nodules at the sediment surface. We characterize and quantify the benthic activity involved in 16 instances of sediment

removal by surface feeding and nodule uplift by subsurface burrowing in an area of 6.25 m^2 over approximately three months. Furthermore, we measured areal benthic activity and associated timescales to assess their relevance in the wider context of abyssal ecosystem functioning and dynamics.

Observations of sediment removal

The light-colored siliceous clay-ooze sediments¹⁵ were covered by nodules < 50 mm that were densely packed, forming a type-1 nodule habitat¹⁶ (Figure 1). Small piles of sediments were observed in the image, possibly caused by resuspension from the landing of the camera system (Figure 1).

Removal of sediments from nodules was repeatedly observed across the field of view (Figure 1) as a change in the nodule color from brown/gray (i.e., sediment covered) to black (i.e., sediment removed; Figures 2A and 2B). This removal was associated with two mobile invertebrate morphotypes, namely one holothurian, likely Psychropotidae gen. indet., and twelve individuals of the Gastropoda order indet (Figures 2C–2E). The holothurian stayed for 2 days within the field of view, leaving a track ranging in width from 50–75 mm (Figure 2C). Owing to its large size, the

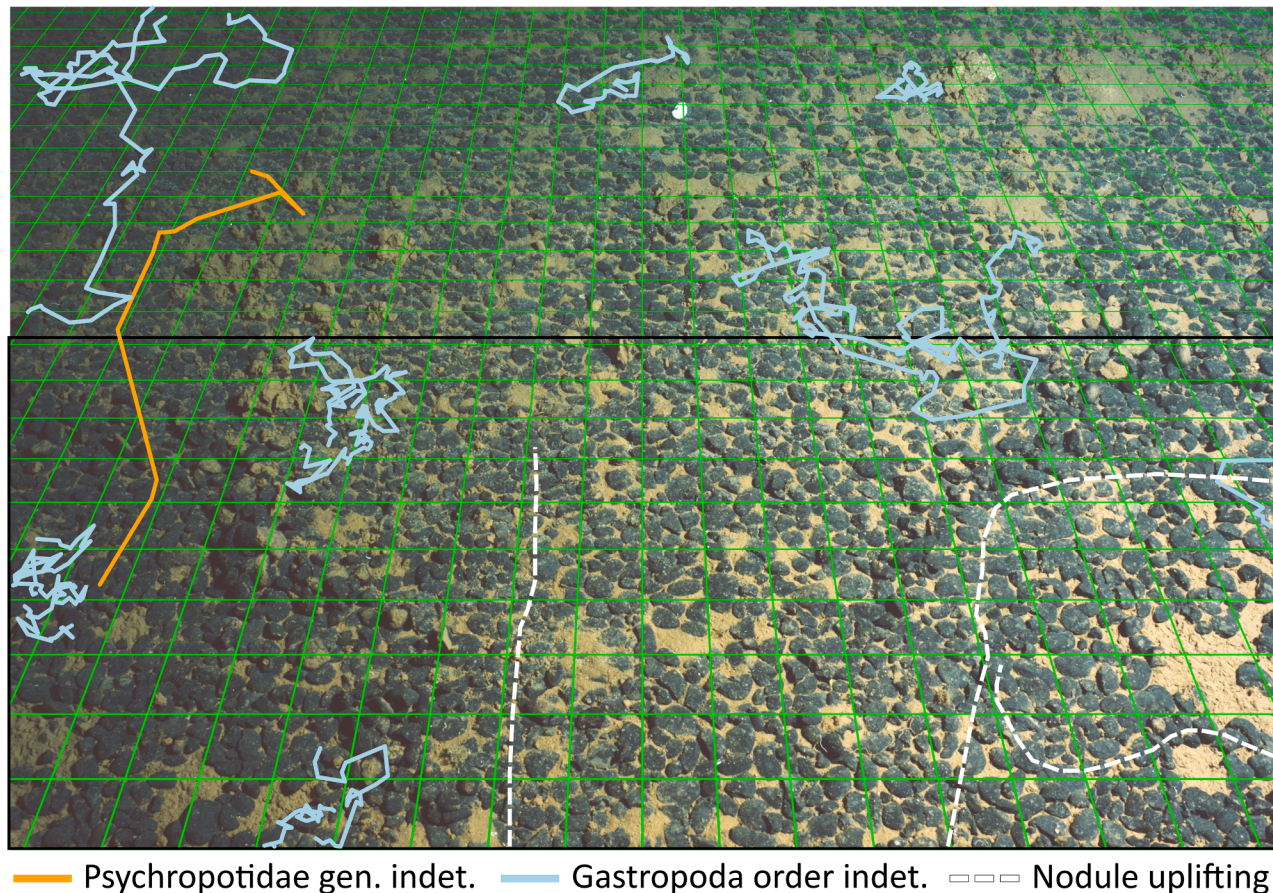


Figure 1. Mapping of specimen tracks over the time-lapse field of view

Location of the 16 observations of benthic activity by mobile organisms, including Gastropoda order indet. ($n = 12$) and Psychropotidae gen. indet. ($n = 1$) clearing the nodules, and nodule uplift caused by unidentified infaunal organisms ($n = 3$). Nodule clearance was annotated across the whole photographed area (6.25 m^2), and nodule uplift annotated only in the center foreground delimited by a black rectangle (2.07 m^2), over the 90.5-day observation period, with a perspective grid ($100 \text{ mm} \times 100 \text{ mm}$) overlaid in green.

See also [Data S1](#).

holothurian simultaneously crawled over both nodules and seabed sediment. Gastropods exhibited longer residency times, varying from a few days to 3 weeks. They crawled exclusively on nodules leaving clearance tracks ranging in width from 5–15 mm (Figures 1, 2D, and 2E). Observations of nodule clearance were frequent for mobile organisms $<10 \text{ mm}$ (Figure 2F).

The holothurian removed sediment at a mean speed of 36 mm h^{-1} , with a maximum rate of 109 mm h^{-1} , clearing $0.07\text{--}0.12 \text{ m}^2$ in total (Figure 2C; Table 1). The arithmetic mean of the gastropod clearance rate was 7 mm h^{-1} , with a maximum of 62 mm h^{-1} (Figures 2D and 2E), clearing $0.09\text{--}0.26 \text{ m}^2$. Over the 90.5 days of recording, the area of sediment removed from nodules by the holothurian and 12 gastropods combined represented 2.6%–6.1% of the field of view. If these rates were consistent for a year, then the fractional areal coverage rate cleared by the holothurian combined with the gastropods could be 10%–25% of seabed area year^{-1} (Table 1).

Observations of nodule uplift

In addition to sediment removal, we captured three instances in which nodules were sequentially uplifted by $<10 \text{ mm}$ along

meter-scale tracks, hereafter referred to as “nodule uplift” (Figures 3A–3D). Within these tracks, we observed that nodules were uplifted along tracks with a width range of $\sim 50\text{--}100 \text{ mm}$. These tracks progressed unidirectionally over 10.5–27.5 days (Video S1). Occasionally, depressions were made within the sediment along the track of the uplifted nodules (Video S1), which suggested that burrowing was taking place under nodules. Nodule uplift was not necessarily associated with an organism visible at the seabed surface, although an unidentified morphotype extended its biological appendages from the sediment twice in one instance (Video S1). Nodule uplift was observed over a similar seabed area as nodule clearance, reaching $0.12\text{--}0.24 \text{ m}^2$ (Table 1). By extrapolation of the nodule uplift rates observed in the image fraction (2.07 m^2), we estimated a fractional areal coverage rate of 25%–50% year^{-1} (Table 1).

DISCUSSION

Significance of the findings

This paper quantifies the functional contributions of abyssal benthos to ecosystem processes that sustain nodule-field

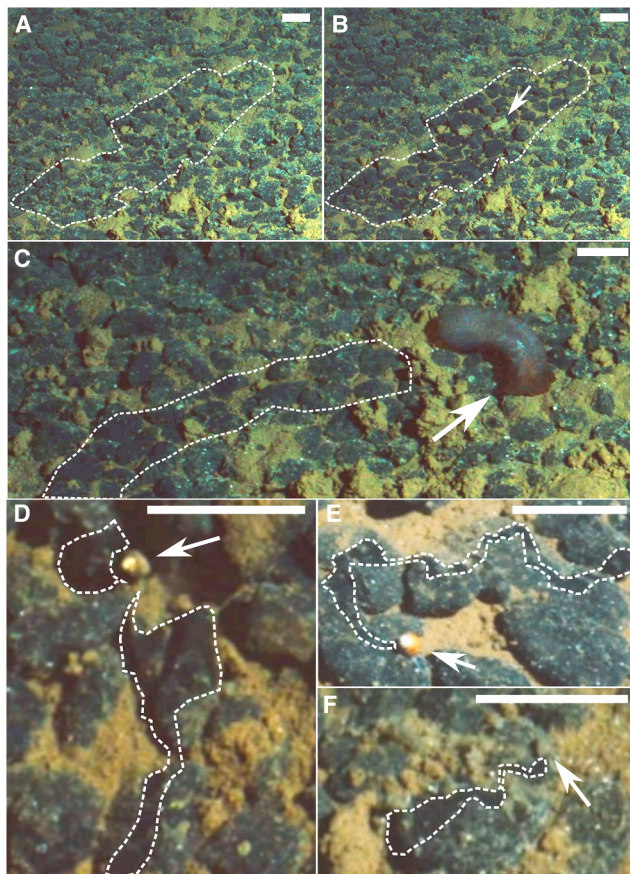


Figure 2. Examples of benthic organisms removing sediment of nodules

(A and B) Examples of nodule clearance indicated by dashed polygons: (A) before and (B) after clearance of an unobserved specimen; the fecal cast (white arrow) indicates that nodule clearance was done by a holothurian (area cleared $\sim 0.1 \text{ m}^2$).

(C) Psychropotidae gen. indet. (white arrow; area cleared $\sim 0.03 \text{ m}^2$).

(D and E) Two specimens of Gastropoda order indet. $\geq 10 \text{ mm}$ (white arrows; area cleared $\sim 10^{-3} \text{ m}^2$).

(F) Example of a specimen too small ($< 10 \text{ mm}$) for inclusion in analyses despite observable clearance track ($\sim 10^{-4} \text{ m}^2$); possibly a gastropod (white arrow). White bars are approximately 50 mm in the upper-right corner of the image.

seascapes found in abyssal sedimentary plains (3,000–6,000 m water depth). Occurring in the Pacific, Atlantic, and Indian Oceans, these habitats harbor vast quantities of critical mineral resources³ and high benthic species richness.^{17–19} Many studies have documented aspects of the biodiversity and taxonomic structuring of biological communities,^{17,20,21} including showing that the nodules provide a critical habitat for many species.^{1,22,23} However, much less is known about the processes governing the stability and resilience of these ecosystems, faunal interactions with the nodules, and the functional roles of benthic communities. Seabed photographs have repeatedly suggested that the meter-scale unevenness of sediment covering adjacent nodules results from the asynchronous feeding activity of some abyssal deposit feeders.^{6,24} Monthly changes in sediment microtopography were attributed to frequent local modification by biological activity observed in hourly photographs.^{25,26}

Our results add to the increasing number of observations of faunal interactions with sediment from seabed photographs in nodule areas of the Clarion-Clipperton Zone (CCZ) in the Pacific Ocean. These include the activities of a wide array of megafauna through burrowing (Amphipoda, Annelida, Decapoda, and Nemertea) and deposit feeding (Echinoidea, Ophiuroidea, and Asteroidea).²⁷ As in other areas of the abyssal Pacific, this study highlights the importance of the activity of large epibenthic organisms, such as holothurians, in contributing to overall areal coverage rates, used as a proxy for benthic activity.^{4,5} These organisms are widespread in the CCZ,²⁰ but despite the bioturbation potential of these communities, the significance of specific behaviors for nodule maintenance has not been established. Here, our results confirm the influence of fauna on the nodule habitat, thus demonstrating that their activity is a central process to consider when assessing the dynamics of these ecosystems.

Processes maintaining nodules at sediment surface

We regularly observed the removal of sediment from nodules by invertebrate deposit feeders including a holothurian, gastropods, and smaller ($< 10 \text{ mm}$) organisms. Assuming that the areal coverage rates of mobile organisms are sustained over the long term and ignoring the spatial overlap of their tracks,^{4,28} total nodule clearance could occur within yearly to decadal timescales, indicating “frequent” clearing. Thus, the rate of removal of the thin layer of surface sediment by deposit feeders should be sufficient to counter the natural levels of sediment blanketing, typically occurring at a rate of around 1 cm per millennium.¹² Deposit feeders are widespread in the CCZ,²⁰ suggesting sustained clearance may prevent long-term sediment burial at regional scales, without ruling out local processes driving nodule habitat variability at finer scales (e.g., nodule exhumation/burial or migration along topography, and the effect of local stratigraphy).^{29–31}

Surface clearance alone cannot fully explain the maintenance of nodules, since net sediment removal around nodules and/or nodule uplift is required to prevent nodules from sinking.¹⁴ It has long been hypothesized that biological excavation could produce a downward sediment flux through eventual replacement by more compacted material,¹⁴ as with feces produced by buried annelids.²⁶ These excavations would be consolidated over time by sediment infill,³² which is consistent with observations of infilled burrows in sediment cores.³³ Similar to observations at other abyssal plains of the Pacific Ocean,^{34,35} our study revealed the ability of the infauna to perform visible sediment/nodule displacement over periods shorter than a day. Although the infauna responsible could not be robustly identified, these tracks indicate that active wedging of burrowing organisms regularly uplifts nodules without changing their orientation.¹⁴ Sediment displacement and potentially compaction support the role of the infauna in nodule maintenance by producing a downward flux of sediment.³² Furthermore, sediment displacement by infauna may trigger size segregation within sediments (i.e., the Brazil nut effect), whereby sediment mixing causes the largest particles, such as nodules and potential nuclei, tend to concentrate at the sediment surface.⁷ A regime of infradecadal nodule uplift and burrowing by fauna is consistent with the short intervals between nodule internal layers,³⁶ which are possibly created by a sudden shift from diagenetic to hydrogenetic

Table 1. Compilation of benthic activity measurements

Morphotype	Psychropotidae gen. indet.	Gastropoda order indet.	Unidentified infauna
Effect on nodules	clearance	clearance	uplift
Number of individuals observed	1	12	3
Mean $\pm$ SD distance traversed per individual (length of track, mm)	1,594	1,457 $\pm$ 1,349	784 $\pm$ 303
Range of track widths (mm)	50–75	5–15	50–100
Range of total areal coverage (m ²)	0.07–0.12	0.09–0.26	0.12–0.24
Range of fractional areal coverage rate (% seabed area year ⁻¹)	4.6–7.7	5.6–16.9	22.9–45.8

Measurements in images of benthic activity resulting in nodule clearance or uplift over the observational period of 90.5 days. Ranges of fractional areal clearance and uplift are based on the total distance traversed multiplied by the minimum and maximum track widths extrapolated to a year of observation. The total area used to calculate the range of fractional areal coverage rate differed between clearance (6.25 m²) and uplift observations (2.07 m²).

mineralization conditions as the nodule is uplifted³⁷; thus, our results are consistent with the claim that nodule maintenance may result from a combination of biological and physical processes.

Implications of spatial and temporal variability

Our estimates of both clearance and uplift are limited because the observations did not capture habitat variability. Nodule coverage is patchy at fine scales (e.g., < 1 km),^{30,31} while sediment accumulation rates can vary by around 1 cm ka⁻¹ across the eastern CCZ region.³⁸ In turn, epi- and infauna densities and composition can vary substantially at multiple scales,³⁹ locally in relation to nodule coverage,^{1,16} and at basin scales in relation to particulate organic carbon (POC) fluxes or to the depth of the seabed.^{20,40} The abyssal seafloor is also subject to episodic, seasonal, and interannual variations in fluxes to the seabed, which influence faunal populations^{41,42} and benthic activity.^{28,43,44} Faunal composition and density are particularly important in determining specific behavior affecting cumulative areal coverage.^{4,5} Although not observed in our study, the influence of erasers, organisms whose traces override those of others, cannot be ruled out,⁴⁵ which could repeatedly cancel out the effect of clearance and/or uplift. Thus, biogenic processes likely vary across space and time; systematic time-lapse studies could quantify this variability. Nevertheless, our study provides a first estimate of these rates, highlighting the potential ecological significance and functional implications for nodule-field ecosystems.

Ecological implications

Our observations support abyssal benthos activity as a driver of nodule habitat maintenance in the CCZ, as previously theorized.^{2,14} The organisms frequently interacting with the nodule habitat (here identified as holothurians and gastropods and unidentified infaunal organisms) may be ecosystem engineers because of their possible role in modifying and sustaining the physical habitat.⁴⁶ By maintaining the nodule hard substratum available for biological colonization, these organisms inherently maintain the heterogeneity of the habitat, thus providing a wider range of niches allowing species coexistence, which supports the high biodiversity characteristic of abyssal nodule-field communities.^{1,47}

Our study sheds light on knowledge gaps in the functional ecology of abyssal nodule ecosystems providing important

information for the environmental management of deep-sea nodule mining.⁴⁸ Modern nodule collectors blanket the seafloor with sediment, and trials of this equipment provide unique conditions to monitor activity rates of trace-making fauna using photogrammetric surveys.⁴⁹ However, removal of nodules and sediment blanketing are also likely to alter community density and functional/taxonomic structure.^{50–52} If the community interacting with nodule dynamics were to be reduced and/or if the blanketing occurred at a large scale (e.g., commercial-scale mining), then this could potentially reduce the frequency and diversity of faunal activity over longer timescales. Such alteration of the regime of biological activity could compromise nodule retention at the sediment surface in areas adjacent to mining activities, ultimately affecting the post-impact recovery of nodule-obligatory fauna.⁵⁰ This scenario illustrates how persistent knowledge gaps in our understanding of nodule ecosystem functioning may limit our ability to predict ecosystem resilience and to develop effective conservation practices.

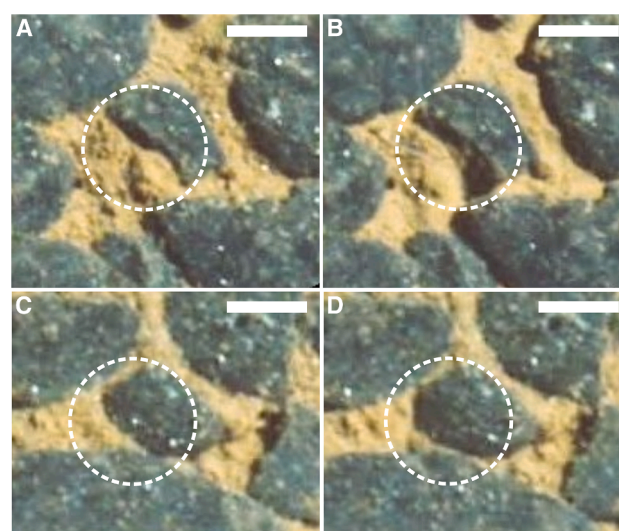


Figure 3. Examples of nodule uplifted by unidentified infauna

(A–D) Examples of individual nodule uplifted along a larger track, with pairs of images (A–D) showing before (A and C) and after (B and D) a portion of the nodule becoming visibly exposed (white dashed circles). White bars are approximately 10 mm in the upper-right corner of the image.

See also [Video S1](#).

RESOURCE AVAILABILITY

Lead contact

Requests for further information should be directed to the lead contact, Loïc Van Audenhaege (loic.van.audenhaege@noc.ac.uk).

Materials availability

This study did not generate any new, unique materials.

Data and code availability

The image set is available in the ISA Deep Seabed and Ocean Database. The Python script correcting perspective in images and annotations is available online.⁵³ Processed data and R code are provided in [supplemental information](#).

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AUTHOR CONTRIBUTIONS

Funding acquisition, D.O.B.J., A.K.S., and E.S.-L.; investigation, B.F.M.F., A.K.S., and E.S.-L.; conceptualization, L.V.A., D.O.B.J., B.F.M.F., and A.M.-S.; methodology, L.V.A., D.O.B.J., and E.S.-L.; validation, L.V.A. and J.M.D.; data curation, software, formal analysis, writing—original draft, L.V.A.; writing—review and editing, L.V.A., D.O.B.J., J.M.D., B.F.M.F., A.M.-S., A.K.S., and E.S.-L.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- [KEY RESOURCES TABLE](#)
- [EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS](#)
 - Timelapse camera deployment
- [METHOD DETAILS](#)
 - Tracking of benthic activity
 - Perspective correction
- [QUANTIFICATION AND STATISTICAL ANALYSIS](#)
 - Areal activity rates

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2026.09.080>.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Timelapse image set	ISA Deep Seabed and Ocean Database	https://isa.org.jm/deepdata-database/
Annotated data of specimen tracking	This study	Data S1
Video observations of nodule uplifting and nodule clearance	This study	Video S1
Homography matrix encoding perspective correction	This study	Table S1
Software and algorithms		
R script to compute areal activity rates from specimen tracking data	This study	Table S2
Python script correcting perspective in images and annotated data	Zenodo linking to GitHub repository	https://doi.org/10.5281/zenodo.21380584
ImageJ (v.1.54)	GitHub	https://imagej.net/ij/download.html
Manual Tracking plug-in (v.1.0)	Imagej.net	https://imagej.net/ij/plugins/track/track.html
OpenCV (v.4.9.0.80)	GitHub	https://github.com/opencv
Python (v.3.7)	python.org	https://www.python.org/downloads/release/python-370/
R (v.4.3.2)	CRAN	https://cran.r-project.org/bin/windows/base/old/
Other		
Benthic camera lander platform	This study	Figure S1

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Timelapse camera deployment

A timelapse camera mounted on a large free-fall lander system (Figure S1) was deployed in a flat seabed area of high nodule density from the M.V. *Maersk Launcher* during the Campaign 5D at the Nauru Ocean Resources Incorporated exploration area in the eastern CCZ (NORI-D; 10°20.103' N, 117°10.445' W, water depth 4,280 m). It was recovered during the Campaign 5E. The camera (Ocean Imaging Systems DSC24000 deep-sea camera⁵⁴) recorded a total of 543 seabed photographs at a 4-hour interval for 90.5 days (the duration of the battery), starting on 31 May 2021 (22:10 UTC) and ending on 30 August 2021 (06:01 UTC). It was mounted in an oblique orientation (height above seafloor 1450 mm, camera inclination below horizontal 45°), with a wide-angle view (horizontal and vertical acceptance angles of 57° and 40°, respectively) and pixel dimensions of 6000 × 4000.

METHOD DETAILS

Tracking of benthic activity

We screened the entire image set at a consistent zoom level (1) to detect a change in nodule position or sediment cover indicative of nodule maintenance, and (2) to identify organisms responsible for the observed change using ImageJ v.1.54.⁵⁵ All annotations were performed on original images. Surface nodule clearance was observable across the entire image. Megafaunal organisms (≥ 10 mm in body size) were tracked over the whole image by recording the XY position of each specimen in consecutive images, from first appearance until the organism was no longer visible or exited the field of view. These positions were recorded using the 'Manual Tracking' plugin of ImageJ.⁵⁶ The position of an individual was noted using a feature that could be repeatedly observed over time, such as the anterior of a holothurian or the centre of a gastropod shell. Nodule uplift was only noted in areas where image resolution was ≤ 0.25 mm² per pixel, hereafter referred to as the 'centre foreground', accounting for 2.07 m² of seabed where the image resolution was sufficient to detect centimetre-scale nodule uplift. Subsurface activity was presumed from the progression of a bio-turbation track, along which nodules visibly underwent a positional change. A range of track widths for clearance/uplift tracks was

assigned to each type of observation and/or morphospecies, based on the minimum and maximum of three measurements of track width per bioturbation type and morphospecies, randomly selected from the list of image coordinates tracking each specimen over time.

Perspective correction

These annotations in pixels were converted to real-world units by accounting for the perspective in the oblique images⁵⁷ after correction according to Durden et al.,⁵⁸ using a numerical procedure written with the OpenCV (v.4.9.0.80) library in Python (v.3.7) available on GitHub.⁵³ Using the height above seabed, tilt and acceptance angles of the camera, the procedure finds the trigonometric correspondence between the image corners in pixels and meters, to generate a 3×3 homography matrix that codes the pixel-to-real-world transformation (Table S1). This approach enabled the generation of a Canadian perspective grid. Resolution (mm^2 per pixel) was mapped at the pixel scale throughout the image, by iteratively computing the real-world area covered by each pixel (i.e., homography applied to pixel corner coordinates). A single image represented 6.25 m^2 of seabed, with a resolution ranging from 0.08 to 0.76 mm^2 per pixel.

QUANTIFICATION AND STATISTICAL ANALYSIS

Areal activity rates

Areal activity rates were calculated for each tracked specimen by multiplying the cumulative distance travelled by the mean track width and dividing by the total tracking duration. The cumulative distance travelled represents the integrated path length over the entire observation period, calculated as the sum of Euclidean distances between consecutive perspective-corrected positions, from which the arithmetic mean of morphospecies-specific speed was also derived.⁵⁹ Minimum and maximum areal coverage rates were estimated by multiplying the real-world total distance traversed by the range of track widths.^{5,60} Tracking duration was defined as the elapsed time between the initial and final observations for each specimen and was used to express movement as a time-standardised estimate of potential seabed area affected. The fraction of seabed reworked per year (hereafter, fractional areal coverage rate) and the time needed for full seabed reworking were estimated by temporal extrapolation.⁴³ Data analyses were conducted in the R environment (v.4.3.2; see also Table S2).