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Key Points:

- Fluid-dynamic description of well-characterized abyssal hill
- Comparison of biogeochemical surface-sediment properties of hill and nearby plain
- Hill leads to pervasive spatial fractionation of inorganic and organic sediment components

Supporting Information:

Supporting Information S1

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An abyssal hill fractionates organic and inorganic matter in deep-sea surface sediments

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Abstract Current estimates suggest that more than 60% of the global seafloor are covered by millions of abyssal hills and mountains. These features introduce spatial fluid-dynamic "granularity" whose influence on deep-ocean sediment biogeochemistry is unknown. Here we compare biogeochemical surface-sediment properties from a fluid-dynamically well-characterized abyssal hill and upstream plain: (1) In hill sediments, organic-carbon and -nitrogen contents are only about half as high as on the plain while proteinaceous material displays less degradation; (2) on the hill, more coarse-grained sediments (reducing particle surface area) and very variable calcite contents (influencing particle surface charge) are proposed to reduce the extent, and influence compound-specificity, of sorptive organic-matter preservation. Further studies are needed to estimate the representativeness of the results in a global context. Given millions of abyssal hills and mountains, their integrative influence on formation and composition of deep-sea sediments warrants more attention.

1. Introduction

Deep-sea sediments constitute one of the main biogeochemical compartments of the Earth system [*Berner*, 2004; *Kump et al.*, 2004] and provide essential food supply to most organisms living on/in the seafloor [*Gage and Tyler*, 1991]. A wide range of factors controls sediment biogeochemistry [*Burdige*, 2006] (for organic matter: e.g., extent of oxygenation, biochemical organic-matter composition, mineral composition and surface area, and biological community composition; for calcium carbonate: e.g., extent of carbonate oversaturation/undersaturation). However, so far, the influence of seafloor landscapes has received little attention. This is despite evidence that suggests that on quasi-horizontal scales on the order of 0.1–10 km, large parts of the global seafloor are covered by abyssal hills (relief 300–1000 m), abyssal mountains (relief > 1000 m) and horizontally larger seamounts/ridges/guyots, occupying an estimated 41.3%, 15.9%, and 5.1% of the seafloor, respectively [*Harris et al.*, 2014]. Other estimates suggest that globally, there could be ~ 25 million hill/mountain-scale seafloor features taller than 100 m [*Wessel et al.*, 2010]. Although these numbers are still associated with large uncertainties it seems safe to assume that a very significant part of the global seafloor is covered by hill-sized roughness elements [*Goff et al.*, 2004].

Within a multidimensional fluid-dynamic parameter space [*Nycander*, 2005], hill/mountain-scale features interact with different flow components, most importantly tides and quasi-steady or eddying background flow. These interactions lead to local/regional hydrodynamics that differ greatly from corresponding dynamics that would occur for the same fluid-dynamic parameter-value combination over a flat seafloor.

Resulting flow fields around hills/mountains are complex and can contain areas in which reduced or nondeposition of particles ("winnowing") would be favored and others in which excess deposition ("focusing") is likely to occur [*Webb and Jordan*, 2001a, 2001b; *Turnewitsch et al.*, 2013], with potential implications for biogeochemistry, food supply, and biological community composition [*White et al.*, 2007; *Clark et al.*, 2010; *Durden et al.*, 2015]. Such flow patterns might occur in millions of hill-/mountain-sized areas [*Wessel et al.*, 2010], leading to a "granularity" of depositional patterns that is rarely considered. For the biogeochemical context, we present a case study that aims to be a first step to help fill the knowledge gap.

2. Approach and Methods

The investigated abyssal hill is ~900 m high compared to the surrounding abyssal plain (at ~4800 m depth) and located on the Porcupine Abyssal Plain (PAP) in the temperate, moderately productive Northeast

Atlantic, centered around 49.12°N, 16.62°W (Figure 1). It is estimated that, globally, there are hundreds of thousands of abyssal hills of similar size [*Wessel et al.*, 2010]. In the study area, barotropic tides (current-speed amplitudes: ~1.2–5.6 cm s⁻¹) and quasi-steady background flow toward northerly directions (average current speed: ~2.8 cm s⁻¹ [*Vangriesheim et al.*, 2001]) are typical of many regions of the deep sea. Their interactions with the hill were numerically modeled as described by *Turnewitsch et al.* [2004, 2008, 2013].

It was only possible to sample sediments on the hill and in an upstream region (Far Field) where direct topographic effects could be ruled out (Figure 1). Off-hill sites to the left and right of the hill (looking downstream) and downstream of the hill that can still be influenced by the hill could not be sampled. Future studies will need to capture a hill's whole "sphere of influence."

In detecting hill effects, variability at different spatial scales (intrasite, between hill sites, and between hill and off-hill sites) needs to be considered. Hill sites were chosen to capture different sectors of the flow-field asymmetry that results from the interactions of the background flow with the hill (Figure 1c). Sediment cores were collected with multiple corers from the Summit and North, East and West Slopes (Figures 1b and 1c). Further sediment cores were retrieved from the abyssal plain on the upstream side (south) of the hill (Far Field), using multiple corers and benthic lander chambers. One abyssal-plain site, Far Field SW, was located within the area influenced by the hill's flow-field asymmetry (Figure 1c). Moreover, Far Field SW is located within a few hundreds of meters of a short, steep seafloor elevation that is associated with increased tidal flow dynamics (Figure 1b). Therefore, Far Field SW is also viewed as topographically influenced. Seafloor photographs from the north-northeastern summit-rim area showed that even a more exposed part of the hill is covered by sediments. See the online supporting information (SI) for sample photographs and more information on sampling and environmental setting.

Sediment samples were analyzed for bulk biogeochemical composition and specific organic compounds elucidating selective deposition or preservation of organic material: particulate inorganic carbon (PIC: here, the calcium-carbonate form calcite), biogenic silica, organic carbon (OC), nitrogen (N), total and individual hydrolysable amino acids (AA), the hexosamines (HA) glucosamine (Gluam) and galactosamine (Galam), and lithogenic (nonbiogenic inorganic) material (LM). See Text S1 in the supporting information for details on analytical methods. Grain-size distributions and inventories of the particle tracer excess-²¹⁰Pb (²¹⁰Pb_{xs}) were also determined [*Turnewitsch et al.*, 2004, 2013], the latter allowing to determine recent (decadal) sediment focusing/winnowing. Predominant particle types were identified through scanning electron microscopy.

Sediment sampling was carried out during the arrival of a settling plankton bloom. However, in the supporting information we show that the reported sediment-biogeochemical hill-versus-Far-Field differences are in fact a spatial (hill-induced) rather than a temporal (bloom-related) phenomenon. The following discussion focuses on the bioturbated surface sediments (in this study, the topmost \leq 10 cm of the sediment columns) that reflect most closely the modern-day fluid dynamics.

For organic-geochemical properties, the robustness of hill-versus-Far-Field differences was tested through the "probability of error," α , with the one-sided *U* test. Because of a sediment-depth dependence of some of the parameters, data for each parameter were grouped according to the layers 0–2, 2–5, and 5–10 cm of the sediment columns. The α values for layers 0-2, 2-5, and 5-10 cm are identified as α_{0-2} , α_{2-5} , and α_{5-10} . Differences with an $\alpha > 0.1$ are viewed as statistically insignificant (s.i.).

3. Results and Discussion

3.1. Sedimentary Imprint of Hill-Controlled Fluid Dynamics

Interactions of the quasi-steady background flow and barotropic tide with the hill lead to a flow-field asymmetry around the hill and numerous areas of increased maximum tidal current speeds (Figures 1b and 1c). Many areas on the hill (including all sampling sites on the hill) are characterized by maximum current speeds that are higher than in the Far Field (maxima typically ~10 cm s⁻¹) and also higher than critical near-seafloor current speeds (~7 cm s⁻¹ at ~1 mab; Figure 2a) for resuspension of phytodetrital particle aggregates [*Beaulieu*, 2002] that typically represent the bulk of the most recently introduced particulate matter.

Higher-frequency (tidal) directional flow variability is thought to also influence sediment formation. To quantify the combined effects of current speed and higher-frequency directional flow variability, the parameter I_F was



Figure 1. (a) Bathymetric map of the wider study region in the Northeast Atlantic (based on *Smith and Sandwell* [1997]). White rectangle: area covered by Figure 1b. (b) Modeled maximum near-seafloor current speeds of the total tidal flow component, u_{tmax} [*Turnewitsch et al.*, 2013]. Isobaths at 50 m intervals; surrounding abyssal plain at typically 4800–4850 m depth. (c) Example of a modeled near-seafloor flow field for a background-component inflow from the south ([*Turnewitsch et al.*, 2004, 2013]; inflows from the southeast and southwest were also modeled). Sampling sites and equipment are indicated in Figures 1b and 1c.

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Figure 2

defined (see *Turnewitsch et al.* [2013] and Text S1 for details). Increased I_F values indicate increased current speeds and/or increased directional current variability.

We find that there is evidence for the average extent of focusing and winnowing to be related to I_F (Figures 2a and 2b). In the Far Field, sediments are neither winnowed nor focused (the ratio of average sediment-derived and water-column-derived ²¹⁰Pb fluxes into the sediment is ~1). By contrast, on the hill, sediments are winnowed in some areas (²¹⁰Pb flux ratio <1: Summit, West Slope) and focused in others (²¹⁰Pb flux ratio >1: North Slope), thus indicating that sediments are partly redistributed on the hill. These trends need to be viewed with caution as the intrasite uncertainties of the ²¹⁰Pb flux ratios are large. However, the intriguingly consistent negative relation of the average flux ratios with I_F ($r^2 = 0.99$) gives confidence that the described trends of sediment redistribution are real.

Overall, surface sediments at the sampling sites on the hill are coarser-grained than in the Far Field, with the grain-size distribution among sites being related to maximum current speeds ($r^2 = 0.60$) which are consistently higher at the sampling sites on the hill than in the Far Field (Figures 2a and 2c).

3.2. Complex Calcite Distribution on the Hill

The quantitatively most important sediment components are LM and foraminiferal and coccolithophorid PIC. The hill introduces considerable kilometer-scale (and possibly even smaller-scale) variability (up to a factor of 1.4) in PIC contents (Figure 2d). The PIC distribution on the hill is not a simple function of water depth: the three Slope stations are at very similar water depths but differ considerably in their PIC contents. LM can be viewed as chemically inert on the time scales on the order of 1000 years that are captured by the sampled sediments [*Rabouille et al.*, 2001]. Moreover, given the proximity of the sampling sites to each other, horizontal variability in the chemical composition of the input flux of particulate material from the surface and interior ocean is very unlikely. Hence, the differences in sedimentary PIC contents must be due to differential deposition and/or redistribution of PIC and/or LM; topographically controlled, vertical deflection of more/less calcite-corrosive near-seafloor waters (the lower parts of the hill are probably within the calcite lysocline but still above the carbonate compensation depth [*Rabouille et al.*, 2001; *Dunne et al.*, 2012]); and/or a diagenetic influence on metabolic PIC dissolution [*Archer and Maier-Reimer*, 1994; *Morse et al.*, 2007].

Background flow toward northerly directions is the driving flow component for any "up-/downwelling" (rather than tidal flow components whose horizontal excursion length scales are too short to sustain up-/downwelling over sufficiently large vertical distances). Horizontal near-seafloor current vectors cross isobaths in many places on the hill (Figure 1c), implying that there are hill areas in which upwelling (especially on the southern hill side) or downwelling (especially on the northern hill side) occurs.

PIC contents on the East and West Slopes are even lower than in the (deeper) Far Field. This suggests that dilution by other sediment components should have played a role. However, given upwelling waters at East and West Slope, an added influence of more calcite-corrosive waters may in fact also have occurred at these sites. Sediment focusing on the North Slope then suggests that the high PIC contents at this locality are due to downslope transport (focusing) of PIC-enriched particles in combination with downwelling of less calcite-corrosive waters that were entrained from shallower depths. This interpretation is consistent but

Figure 2. (a) Values of two numerically modeled fluid-dynamical parameters (maximum current speed and flow indicator I_F) for the main sediment sampling sites on and off the hill. Squares and light grey area: maximum current speeds of combined total tidal and background flow components (horizontal grey area: range of critical current speeds for resuspension of phytodetrital particle aggregates [*Beaulieu*, 2002]); triangles and dark grey area: maximum values of the flow indicator I_F (see the Text S1 and *Turnewitsch et al.* [2013] for more details). White, grey and black symbols: far-field back-ground inflow from the southwest, southeast, and south, respectively. For both current speeds and I_F , bold lines connect the maximum values that were found for each sampling site. These maxima are viewed as the sediment-dynamically relevant parameters [*Turnewitsch et al.*, 2013]. (b) Indicator of sediment focusing and winnowing (i.e., more and less sediment deposition (sediment-derived ²¹⁰Pb flux) than expected from the primary flux in the interior ocean (water-column-derived ²¹⁰Pb flux)) [*Turnewitsch et al.*, 2004]. Grey symbol: Far Field SW. (c) Dry-weight percent contents of grain sizes in whole sediment cores (core length: 11 cm). (d) Dry-weight percent contents of PIC in the bioturbated layers of surface sediments. Grey diamond symbol: Far Field SW. Values in plots Figures 2b–2d: numbers of sediment cores analyzed per sampling site. "r": error bars indicate range; "s": error bars indicate one standard deviation. More details on Figures 2a–2d, including uncertainties, can be found in Text S1 and in *Turnewitsch et al.* [2004, 2013].

needs to be viewed with caution as there is no direct information on the extent of calcite corrosiveness of near-seafloor waters and also not on the potential added effect of metabolic calcite dissolution.

It is crucial to note that the sampling sites on the hill are only on the order of 1 km apart and show PIC differences typically thought to occur over much larger distances of hundreds to thousands of kilometers [*Dunne et al.*, 2012]. PIC dynamics play a key role in the marine and global carbon cycle [*Archer and Maier-Reimer*, 1994; *Kump et al.*, 2004], and our PIC results therefore raise an important question as to the effect of hill-scale seafloor topography on integrative PIC deposition in deep-sea sediments.

3.3. Reduced Sedimentary Organic-Matter Contents on the Hill

Several organic sediment properties show overall differences between the hill and the Far Field, with Far Field SW often displaying intermediate properties. OC contents were consistently lower (by an average factor of ~2) on the hill than in the Far Field (Figure 3a; $\alpha_{0-2} = 0.001$, $\alpha_{2-5} = 0.005$, α_{5-10} : not applicable (na) as too few data) as were N contents (Figure 3b; $\alpha_{0-2} = 0.005$, $\alpha_{2-5} = 0.025$, α_{5-10} : na) and AA and HA concentrations (see Text S1). The finding implies that topographically induced flow dynamics reduce net organic-matter deposition on the hill. Two scenarios could explain this observation.

First, organic matter that is "missing" on the hill was simply "blown" off the topographic feature and into the downstream water column. The material's residence time before any deposition in the downstream far field would then increase. For phytodetritus (often the main primary-flux vehicle for recently introduced particulate matter), this leaves more time for particulate-organic-matter decomposition in the water column (rather than in sediments).

Second, reduced organic-matter contents could be due to reduced preservation of material that was deposited into the surface sediments, a phenomenon potentially related to the coarser sediment particles on the hill which imply reduced particle-surface area and, hence, reduced potential for sorptive organic-matter preservation [see *Müller and Suess*, 1977; *Carter and Mitterer*, 1978; *Wang and Lee*, 1993; *Keil et al.*, 1998; *Aufdenkampe et al.*, 2001; *Ding and Henrichs*, 2002].

In this second context, hill effects also need to be considered with regards to spatial granularity of the composition of biological seafloor communities: the primary fluid-dynamic hill effects might lead to biological communities on the hill that differ from communities on the adjacent plain and potentially even between hill sites [*Clark et al.*, 2010; *Durden et al.*, 2015]. It can therefore not be ruled out that there are causal feedback loops that operate through links between community composition, biogenic particle and solute mixing in sediments, sediment ventilation, and aerobic organic-matter decomposition [*Aller et al.*, 2001], with implications for the amount and composition of preserved organic matter. Unfortunately, no benthic community sampling could be carried out to scrutinize this aspect.

3.4. Increased Amino-Acid Preservation on the Hill

Overall, weight percent fractions of AA-bound carbon in OC (AA_C/OC: Figure 3c) and AA-bound nitrogen in N (AA_N/N: see Text S1) did not differ between the hill and the Far Field. By contrast, weight percent fractions of HA-bound carbon in OC (HA_C/OC: Figure 3d; $\alpha_{0-2} = 0.005$, $\alpha_{2-5} = 0.025$, $\alpha_{5-10} = 0.05$) and HA-bound nitrogen in N (HA_N/N: see Text S1) were notably lower (by an average factor of ~2) on the hill than in the Far Field. This is then reflected in the molar AA/HA ratio being higher on the hill than in the Far Field (Figure 3e; $\alpha_{0-2} = 0.005$, $\alpha_{2-5} = 0.025$, $\alpha_{5-10} = 0.05$). Thus, on the hill, HAs are less likely to be deposited/formed and/or more likely to be decomposed than in the Far Field. AAs are not affected by the hill in this way. In the following, we will show that the evidence for the divergent behavior of AAs and HAs is also supported by Gluam/Galam ratios and aspects of the AA composition.

In all sediments of this study, molar Gluam/Galam ratios are <3 and in most cases \leq 1.3 (Figure 3f), indicating predominantly prokaryotic and/or phytoplanktonic (rather than chitinaceous) organic matter [*Benner and Kaiser*, 2003]. The majority of Gluam occurs as a precursor metabolite in the biochemical synthesis of glycosylated proteins and lipids (rather than in prokaryote cell walls [*Benner and Kaiser*, 2003]). Very low Gluam/Galam values in surface sediments therefore not only indicate almost complete absence of chitinaceous material but also suggest a drop of active prokaryote biomass. Because of the slightly lower Gluam/Galam ratios on the hill (α_{0-2} = 0.01, α_{2-5} = 0.025, α_{5-10} = s.i.), these trends are more pronounced on the hill than in the Far Field. That is, the amount of active prokaryote biomass in surface sediments of the hill



Figure 3. Influence of the abyssal hill on measures of sedimentary organic matter quantity and composition. (a) Organic-carbon (OC) and (b) nitrogen (N) contents as weight percentages of dry sediment. (c) Amino-acid- (AA-) and (d) hexosamine- (HA-)associated carbon as a weight percentage of OC. (e) Molar ratio of total AAs and total HAs. (f) Molar ratio of the HAs glucosamine (Gluam) and galactosamine (Galam). A version of this figure that identifies all sampling stations and profiles can be found in Text S1.

is suggested to be lower than in the Far Field, which could result in decreased microbial decomposition and an increased "freshness" of organic matter.

The notion of increased organic-matter freshness on the hill is supported by aspects of the sedimentary AA composition. The nonprotein AAs β -alanine (β -Ala) and γ -aminobutyric acid (γ -Aba) are viewed as decompositional products of the protein AAs aspartic acid (Asp) and glutamic acid (Glu), respectively. Consequently, lower Asp/ β -Ala and Glu/ γ -Aba ratios have been used as indicators of more advanced decomposition of proteinaceous



Figure 4. Influence of the abyssal hill on amino-acid-(AA-)related measures of organic-matter fractionation. (a) Molar ratios of the protein-AA aspartic acid (Asp) and the nonprotein-AA β -alanine (β -Ala). (b) AA degradation index (DI) as defined by *Dauwe and Middelburg* [1998] and *Dauwe et al.* [1999]. Crosses: North Slope. (c) Molar AA fraction of the sulphur-containing AA methionine (Met). (d) Molar ratio B/(B + A) of basic AAs (positively charged side chains; B = histidine + arginine + lysine) and the sum (B + A) of basic and acidic AAs (negatively charged side chains; A = Asp + Glu). A version of this figure that identifies all sampling stations and profiles can be found in Text S1.

material [*Ittekkot et al.*, 1984; *Cowie and Hedges*, 1994]. On the hill, Asp/ β -Ala (Figure 4a; $\alpha_{0-2} = 0.025$, $\alpha_{2-5} = 0.025$, $\alpha_{5-10} = 0.01$) and, to a lesser degree, Glu/ γ -Aba (see Text S1) were increased relative to the Far Field, indicating less advanced decomposition of proteinaceous material as compared to the Far Field.

This trend is also supported by a slight (statistically largely insignificant) tendency toward increased values on the hill of the AA degradation index (DI) as defined by *Dauwe and Middelburg* [1998] and *Dauwe et al.* [1999] (with the exception of the North Slope) (Figure 4b; α_{0-2} : s.i., α_{2-5} : s.i., $\alpha_{5-10} = 0.05$). Lower DI values indicate more advanced degradation.

Further supportive evidence for a reduced extent of AA decomposition in hill sediments comes in the form of much higher molar fractions of total AAs of the sulphur-containing AA methionine (Met) on the hill (Figure 4c; $\alpha_{0-2} = 0.005$, $\alpha_{2-5} = 0.025$, α_{5-10} : s.i.). Met is an important metabolite and protein AA. In proteins, most Met units tend to be located inside the more hydrophobic cores of the protein macromolecules [*Brosnan and Brosnan*, 2006]. Increased molar fractions of Met on the hill can therefore be interpreted as a larger fraction of intact proteinaceous macromolecules or, in other words, a reduced extent of degradation of proteinacous compounds.

Overall, the combination of lower HA contents and lower Gluam/Galam ratios on the hill is indicative of a drop in active prokaryote biomass which results in a reduced extent of decomposition of other organic compounds on the hill, a notion that is supported by the indicators of the extent of degradation of AAs and proteinaceous material. On the hill, this leads to the counterintuitive situation of reduced sedimentary contents of organic matter that, however, is characterized by an enhanced freshness.

3.5. Selective Amino-Acid Preservation on the Hill

The topographically controlled flow field around the hill leads to the aforementioned complex distribution of calcite particles (Figure 2d). In marine settings, calcite surfaces have a positive surface charge whereas other particles have negative surface charges [*Stumm*, 1992]. The spatially variable surface charge may therefore influence the compound specificity of sorptive preservation of sedimentary organic matter [*Müller and Suess*, 1977; *Carter and Mitterer*, 1978; *Wang and Lee*, 1993; *Keil et al.*, 1998; *Aufdenkampe et al.*, 2001; *Ding and Henrichs*, 2002]. Here the net effect of the hill may have been reflected in the reduced molar B/(B + A) ratios, where A represents acidic AAs with a net negative side-chain charge and B basic AAs with a net positive side-chain charge (Figure 4d; $\alpha_{0-2} = 0.005$, $\alpha_{2-5} = 0.025$, $\alpha_{5-10} = 0.025$).

4. Conclusions

The observed sediment-biogeochemical hill imprint is interpreted to be a result primarily of the impact of hillcontrolled near-seafloor fluid dynamics, influencing the amount (focusing versus winnowing) and types (POC; PIC versus LM; grain size) of depositing material. Secondary hill-related effects of particle surface area (through increased grain sizes) and surface charge (through variable PIC contents) are then proposed to control the amounts and types of organic compounds that can escape or delay degradation within sediments through sorption onto particle surfaces.

Our results indicate that the sampled hill leads to pervasive compound-specific spatial fractionation of organic and inorganic sediment components between hill and not hill-affected off-hill areas: (1) The flow/hill interactions probably result in an overall reduction of organic-matter deposition and/or preservation, and in different compound-specificity of preservation of the organic matter that is deposited. (2) The hill sediments contain less organic matter, but, at the same time, there is also evidence for this organic matter to be less decomposed. (3) Because of the considerable hill-scale variability of calcite contents and limited sample coverage, the overall hill impact on calcite deposition remains unclear but could be substantial.

Many different factors can play a role in controlling how sediments are deposited on and near submarine hills, most importantly the magnitude and variability of far-field flow components, size and shape of hills, and magnitude and composition of the primary particle flux from the surface and interior ocean. As the hill of our study occupies only one point in this multidimensional parameter space, it remains an open question how transferable our results are to other hills. However, four other hills that are near this study's hill on the PAP and only ~80 m to ~470 m high also show a fluid-dynamic imprint in the form of coarser grain-size distributions in their summit sediments [*Durden et al.*, 2015]. Hence, even hills as short as ~100 m might be associated with fractionation of inorganic and organic sediment components. Given the large estimated global numbers and areal coverage of abyssal hills and mountains, the impact of hill- and mountain-controlled fluid dynamics on biogeochemistry, biology, and ecology of deep-sea sediments warrants more attention.

Acknowledgments

Data may be obtained from the authors via the corresponding author RT (e-mail: robert.turnewitsch@sams.ac.uk). This study was supported by grant 03F0177A of the "Bundesministerium für Bildung, Wissenschaft, Forschung und Technologie" (BMBF), Germany, and grant NE/C006415/1 of the NERC, United Kingdom.

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