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Lebensspuren of the Bathyal Mid-Atlantic Ridge

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ABSTRACT

The extent of megafaunal bioturbation was characterised at flat sedimented sites on the Mid-Atlantic Ridge (MAR) at 2500 m depth. This study investigated the properties of and spatial variation in surficial bioturbation at the MAR. Lebensspuren assemblages were assessed at four superstations either side of the MAR and in two different surface productivity regimes, north and south of the sub-polar front. High-definition ROV videos from these superstations were used to quantify area and abundance of 58 lebensspuren types. Lebensspuren area was lowest at the SW with 4.12% lebensspuren coverage and the SE & NW had the greatest area coverage of lebensspuren (9.69% for both). All stations except the SW were dominated by epifaunal, particularly track-style, lebensspuren. Infaunal mounds were more significant in the southern superstations, particularly in the SW. In terms of lebensspuren assemblage composition, all superstations were significantly different from one another, which directly corresponded with the composition of lebensspuren-forming epifauna. Lebensspuren assemblages appeared to have been primarily influenced by local-scale environmental variation and were independent of detrital flux. This investigation presented a novel relationship between lebensspuren and faunal density that conflicted with the traditionally held view of inverse proportionality and suggests that, at the MAR, megafaunal reworking was not the only significant control on lebensspuren assemblages.

1. Introduction

Bioturbation, a process first described by Charles Darwin, is the biological reworking of sediments (Meysman et al., 2006) and is very important in the deep sea (Barsanti et al., 2011; Diaz, 2004; Teal et al., 2008). In the upper layers of deep-sea sediments, bioturbation is the dominant mechanism by which particle transport occurs, except in areas of extreme physical forcing (Lecroart et al., 2010; Middleburg et al., 1997). The action of deposit-feeding fauna creates a three-dimensional mosaic of micro-scale variation in the chemical properties of sediment (Aller et al., 1998; Diaz et al., 1994; Gage and Tyler, 1991; Meysman et al., 2006; Murray et al., 2002). Bioturbation, as an ecological process, is also vitally important to infauna, particularly by increasing the depth of the redox potential discontinuity layer, thus increasing the availability of oxygen to the fauna that live beneath the sediment surface. Depth of the surface mixed layer is thought to be highly variable globally and estimates of the depth of mixing in the temperate North Atlantic vary between <100 and 497 mm (Thomson et al., 2000; Teal et al., 2008). Bioturbation is responsible for creating substantial fine-scale heterogeneity in the deep-sea (Ewing and Davis, 1967; Gage and Tyler, 1991; Gerino et al., 1999; Murray et al., 2002; Young et al., 1985) and the importance of this spatial influence is illustrated by the marked increase in meiofaunal and bacterial biomass around polychaete burrows (Aller and Aller, 1986; Gage and Tyler, 1991). Understanding this three-dimensional mosaic is of key importance in understanding how fauna and physical processes influence the distribution of organic material and other important sedimentary components, such as oxygen or metal ions (Glud et al., 1994; Huettel et al., 1998; Suckow et al., 2001). Under certain environmental conditions biogenic structures, caused through bioturbation, can persist into the geological record (Gage and Tyler, 1991; Kitchell and Clark, 1979; Uchman, 2007; Yingst and Aller, 1982), though this is thought to be rare given the number of ways that lebensspuren may be destroyed (Mauviel and Sibuet, 1985). Lebensspuren (German: meaning 'life traces') is the collective name for the physical imprints and structures left behind by benthic organisms in sedimentary conditions. The areal coverage of lebensspuren is thought to vary as a function of surface productivity and the flux of organic matter to the deep-sea floor (Anderson et al., 2011; Barsanti et al., 2011; Jones et al., 2007; Stordal et al., 1985; Wheatcroft et al., 1989). The formation of lebensspuren is directly related to biogenic activity and can be diminished by reductions in biological rate processes, such as nutrient limitation (Smith et al., 2008) or low oxygen conditions (Hunter et al., 2011). The feeding mode of benthic organisms controls the nature and abundance of lebensspuren, and lebensspuren

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formation processes may be related to both optimal foraging theory (Charnov, 1976) and habitat heterogeneity (Anderson et al., 2011). There are many distinct types of faunal lebensspuren in the marine environment which have been classified by Seilacher (1953) into the following:

i. Resting lebensspuren—imprints of stationary animals.
ii. Crawling lebensspuren—displaced sediment by movement of deposit feeders, sometimes marked by depressions left by the limbs (e.g. *Holothurian podia*).
iii. Feeding structures—faecal casts and pellets.
iv. Grazing lebensspuren—minor/fragile disturbances to sediment surface.
v. Dwellings—mounds and burrows.

It is difficult to determine the organisms responsible for many types of lebensspuren that are observed (Ewing and Davis, 1967) and some are known to have been produced by several taxa. Crawling lebensspuren of holothurians and echinoids are particularly hard to distinguish, as are movement lebensspuren of asteroids and bentho-pelagic fish. All benthic and bentho-pelagic fauna influence the sediment structure to a varying extent, depending on their size, abundance and activity (Murray et al., 2002). Lebensspuren diversity is usually proportional to faunal diversity (Hughes and Gage, 2004; Young et al., 1985) although Kitchell et al. (1978) suggest that lebensspuren density may be inversely proportional to faunal density, explained by lebensspuren residence time being high in areas of low biomass. Many lebensspuren are created by the echinoderms, which have abundant deposit feeding representatives that feed on or near the sediment surface (Gage and Tyler, 1991; Lauerman and Kaufmann, 1998; Smith et al., 1993; Turnewitsch et al., 2000; Vardaro et al., 2009). Other lebensspuren types of non-echinoderm origin are also readily identifiable, such as those produced by the Enteropneusta (Hemichordata), that are characterised by spiral feeding structures (Holland et al., 2005; Smith et al., 2005), and echiurans, that produce a rosette of proboscis marks around a nodal burrow (Bett and Rice, 1993; Bett et al., 1995; de Vaugelas, 1989; Ohta, 1984).

This study aims to describe the nature of lebensspuren assemblages, quantify surficial bioturbative activity at the Mid-Atlantic Ridge and determine how lebensspuren composition varies spatially. Specifically, we aim to test the null hypothesis that bioturbation intensity (lebensspuren number and area) and the diversity and structure of lebensspuren assemblages are not altered by environmental variability either side of the Mid-Atlantic Ridge and the Sub-Polar Front.

2. Methods

2.1. Data collection

2.1.1. Study site

The four ECOMAR (Priede and Bagley, 2010) superstations (NE, SE, SW and NW around the Charlie-Gibbs Fracture Zone) were visited in May–July 2010 (Priede and Bagley, 2010) on RRS James Cook Cruise JC048. The positions of study sites (Fig. 1) were chosen to test the effects of the Mid-Atlantic Ridge and the Charlie-Gibbs fracture zone on the biology and environment of the area (Bergstad et al., 2008) Table 1.

Data were collected using a down-facing, high-definition fixed video camera (Insite Mini Zeus) and Hydrargyrum medium-arc iodide (HMI) lighting on the NERC ROV *Isis*. For this study, four 500 m long straight-line video transects (for positions of flat transects see Table 2 in Gooday et al. (2013)) were taken (at constant speed of 0.13 ms^{-1} and altitude of 2 m) at each

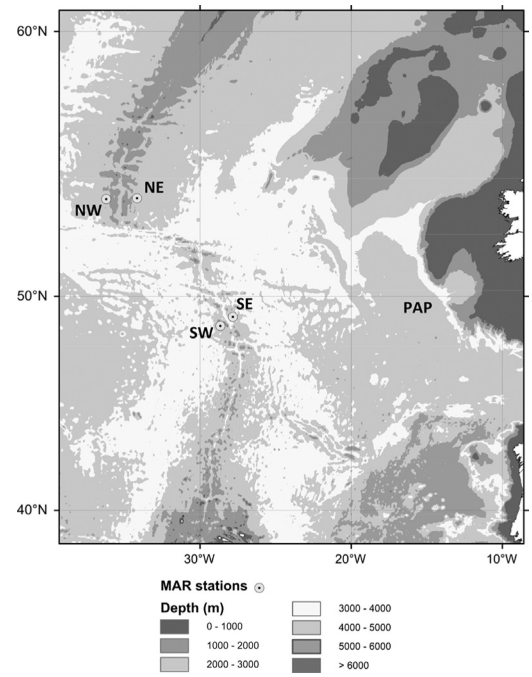

Fig. 1. Bathymetric chart of the Central North Atlantic showing the positions of the four superstations. PAP—Porcupine Abyssal Plain.

superstation over flat ($<2^{\circ}$) sedimentary plains at around 2500 m water depth. Images were scaled by reference to two parallel lasers, mounted 100 mm apart on the ROV video camera and hence visible in all images. The width of field-of-view was accurately maintained at 2 m ($\pm$0.1 m) using the Doppler Velocity Log on the ROV (laser spacing was maintained at 5% of screen width), so each transect covered 1000 m^2 of seafloor. The ROV was also equipped with Sonardyne medium frequency ultra-short baseline navigation (USBL). ROV mounted CTD measurements were made simultaneously with the video transects.

2.1.2. Video analysis

Still images (JPEGs) were extracted from the video at a rate of one frame per second for quantification of lebensspuren. This was subsequently further sub-sampled to one frame every 3 s of video, to reduce overlap between frames and minimise the risk of lebensspuren being measured more than once. This still allowed the complete quantification of every discernible lebensspuren on the video transect. A total of 20,484 images were measured, covering an area of seabed of 16,000 m^2.

2.1.3. Lebensspuren classification and quantification

Lebensspuren types were pre-categorised, in terms of both morphology and taxonomic origin, with reference to several sources (Bett and Rice, 1993; Bett et al., 1995; de Vaugelas, 1989; Dundas and Przeslawski, 2009; Gage and Tyler, 1991; Heezen and Hollister, 1971; Smith et al., 2005; Smith et al., 2008). A total of 58 distinct types were classified (Fig. 2). Lebensspuren with unclear origin (i.e. the tracks of echinoids and holothurians and demersal fish and asteroids) were artificially grouped into ‘Indeterminate origin lebensspuren’ (Hughes and Gage, 2004). These lebensspuren may be a result of either taxa whose feeding or locomotion habitats do not permit distinction at a given taxonomic level, or overprinting by a multitude of individuals. Both of these explanations are credible and agreement to either argument depends upon the lebensspuren with the more disturbed lebensspuren seeming more indicative of overprinting. Area coverage was quantified using ImageJ (v1.42q).