

1 Lebensspuren of the Bathyal Mid-Atlantic Ridge

2 James B. Bell ^{1*}, Daniel O. B. Jones ¹ & Claudia H. S. Alt ¹

3 ¹ *National Oceanography Centre Southampton, Waterfront Campus, European Way, Southampton*

4 *SO14 3ZH, UK*

5 *Corresponding Author: j.bell@soton.ac.uk

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7 Abstract

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

24 Keywords: Bioturbation; megafaunal Lebensspuren; Mid-Atlantic Ridge; Sub-Polar Front; ECOMAR

25 1. Introduction

26 Bioturbation, a process first described by Charles Darwin, is the biological reworking of sediments
27 (Meysman et al., 2006) and is very important in the deep sea (Diaz, 2004; Teal et al., 2008; Barsanti
28 et al., 2011). In the upper layers of deep-sea sediments, bioturbation is the dominant mechanism by
29 which particle transport occurs, except in areas of extreme physical forcing (Middleburg et al., 1997;
30 Lecroart et al., 2010). The action of deposit-feeding fauna creates a three-dimensional mosaic of
31 micro-scale variation in the chemical properties of sediment (Gage & Tyler, 1991; Diaz et al., 1994;
32 Aller et al., 1998; Murray et al., 2002; Meysman et al., 2006). Bioturbation, as an ecological process,
33 is also vitally important to infauna, particularly by increasing the depth of the redox potential
34 discontinuity layer, thus increasing the availability of oxygen to the fauna that live beneath the
35 sediment surface. Depth of the surface mixed layer is thought to be highly variable globally and
36 estimates of the depth of mixing in the temperate North Atlantic vary between < 100 and 497 mm
37 (Thomson et al., 2000; Teal et al., 2008). Bioturbation is responsible for creating substantial fine-
38 scale heterogeneity in the deep-sea (Ewing & Davis, 1967; Young et al., 1985; Gage & Tyler, 1991;
39 Gerino et al., 1999; Murray et al., 2002) and the importance of this spatial influence is illustrated by
40 the marked increase in meiofaunal and bacterial biomass around polychaete burrows (Aller & Aller,
41 1986; Gage & Tyler, 1991). Understanding this three-dimensional mosaic is of key importance in
42 understanding how fauna and physical processes influence the distribution of organic material and
43 other important sedimentary components, such as oxygen or metal ions (Glud et al., 1994; Huettel
44 et al., 1998; Suckow et al., 2001). Under certain environmental conditions biogenic structures,
45 caused through bioturbation, can persist into the geological record (Kitchell & Clark, 1979; Yingst &
46 Aller, 1982; Gage & Tyler, 1991; Uchmann, 2007), though this is thought to be rare given the number
47 of ways that lebensspuren may be destroyed (Mauviel & Sibuet, 1985). Lebensspuren (German:
48 meaning 'life traces') is the collective name for the physical imprints and structures left behind by
49 benthic organisms in sedimentary conditions. The areal coverage of lebensspuren is thought to vary
50 as a function of surface productivity and the flux of organic matter to the deep-sea floor (Stordal et

51 al., 1985; Wheatcroft et al., 1989; Jones et al., 2007; Anderson et al., 2011; Barsanti et al., 2011). The
52 formation of lebensspuren is directly related to biogenic activity and can be diminished by
53 reductions in biological rate processes, such as nutrient limitation (Smith et al., 2008) or low oxygen
54 conditions (Hunter et al., 2011). The feeding mode of benthic organisms controls the nature and
55 abundance of lebensspuren , and lebensspuren formation processes may be related to both optimal
56 foraging theory (Charnov, 1976) and habitat heterogeneity (Anderson et al., 2011). There are many
57 distinct types of faunal lebensspuren in the marine environment which have been classified by
58 Seilacher (1953) into:

- 59 i. Resting lebensspuren – Imprints of stationary animals
- 60 ii. Crawling lebensspuren – Displaced sediment by movement of deposit feeders, sometimes
61 marked by depressions left by the limbs (e.g. Holothurian podia)
- 62 iii. Feeding structures – Faecal casts and pellets
- 63 iv. Grazing lebensspuren – Minor/ fragile disturbances to sediment surface
- 64 v. Dwellings – Mounds and burrows

65 It is difficult to determine the organisms responsible for many of the types of lebensspuren observed
66 (Ewing & Davis, 1967) and some are known to have been produced by several taxa. Crawling
67 lebensspuren of holothurians and echinoids are particularly hard to distinguish, as are movement
68 lebensspuren of asteroids and benthic-pelagic fish. All benthic and benthic-pelagic fauna influence
69 the sediment structure to a varying extent, depending on their size, abundance and activity (Murray
70 et al., 2002). Lebensspuren diversity is usually proportional to faunal diversity (Young et al., 1985;
71 Hughes & Gage, 2004) although Kitchell et al. (1978) suggest that lebensspuren density may be
72 inversely proportional to faunal density, explained by lebensspuren residence time being high in
73 areas of low biomass. Many lebensspuren are created by the echinoderms, which have abundant
74 deposit feeding representatives that feed on or near the sediment surface (Gage & Tyler, 1991;
75 Smith Jr et al., 1993; Lauerman & Kaufmann, 1998; Turnewitsch et al., 2000; Vardaro et al., 2009).

76 Other lebensspuren types of non-echinoderm origin are also readily identifiable, such as those
77 produced by the Enteropneusta (Hemichordata), that are characterised by spiral feeding structures
78 (Holland et al., 2005; Smith Jr et al., 2005), and echiurans, that produce a rosette of proboscis marks
79 around a nodal burrow (Ohta, 1984; de Vaugelas, 1989; Bett & Rice, 1993; Bett et al., 1995).

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

85 2. Methods

86 2.1. Data Collection

87 2.1.1. Study Site

88 The four ECOMAR (Priede & Bagley, 2010) superstations (NE, SE, SW & NW around the Charlie-Gibbs
89 Fracture Zone) were visited in May-July 2010 (Priede & Bagley, 2010) on RRS *James Cook* Cruise
90 JC048. The positions of study sites (Fig. 1) were chosen to test the effects of the Mid-Atlantic Ridge
91 and the Charlie-Gibbs fracture zone on the biology and environment of the area (Bergstad et al.,
92 2008).

93 Data were collected using a down-facing, high-definition fixed video camera (Insite Mini Zeus) and
94 Hydrargyrum medium-arc iodide (HMI) lighting on the NERC ROV *Isis*. For this study, four 500m long
95 straight-line video transects (for positions of flat transects see Table 2 in Gooday et al., this volume)
96 were taken (at constant speed of 0.13 ms^{-1} and altitude of 2 m) at each superstation over flat ($<2^\circ$)
97 sedimentary plains at around 2500 m water depth. Images were scaled by reference to two parallel
98 lasers, mounted 100 mm apart on the ROV video camera and hence visible in all images. The width
99 of field-of-view was accurately maintained at 2 m (± 0.1 m) using the Doppler Velocity Log on the

100 ROV (laser spacing was maintained at 5 % of screen width), so each transect covered 1000 m² of
101 seafloor. The ROV was also equipped with Sonardyne medium frequency ultra-short baseline
102 navigation (USBL). ROV mounted CTD measurements were made simultaneously with the video
103 transects.

104 2.1.2. Video Analysis

105 Still images (JPEGs) were extracted from the video at a rate of one frame per second for
106 quantification of lebensspuren. This was subsequently further sub-sampled to one frame every 3
107 seconds of video, to reduce overlap between frames and minimise the risk of lebensspuren being
108 measured more than once. This still allowed the complete quantification of every discernible
109 lebensspuren on the video transect. A total of 20484 images were measured, covering an area of
110 seabed of 16000 m².

111 2.1.3. Lebensspuren classification and quantification

112 Lebensspuren types were pre-categorised, in terms of both morphology and taxonomic origin, with
113 reference to several sources (Bett & Rice, 1993; Bett et al., 1995; de Vaugelas, 1989; Dundas &
114 Przeslawski, 2009; Gage & Tyler, 1991; Heezen & Hollister, 1971; Smith Jr et al., 2005; Smith et al.,
115 2008). A total of 58 distinct types were classified (Fig. 2.). Lebensspuren with unclear origin (i.e. the
116 tracks of echinoids and holothurians and demersal fish and asteroids) were artificially grouped into
117 'Indeterminate origin lebensspuren' (Hughes & Gage, 2004). These lebensspuren may be a result of
118 either taxa whose feeding or locomotion habitats do not permit distinction at a given taxonomic
119 level, or overprinting by a multitude of individuals. Both of these explanations are credible and
120 agreement to either argument depends upon the lebensspuren with the more disturbed
121 lebensspuren seeming more indicative of overprinting. Area coverage was quantified using ImageJ
122 (v1.42q). Areas of lebensspuren (in m²) were calculated by drawing around individual lebensspuren
123 on scaled images (scaled using the 100 mm distance between laser dots on the seabed) with the

124 free-hand tool. The summed area measurements for each individual lebensspuren were reported.
125 Continuous lebensspuren (i.e. tracks) were measured as far as could be seen in the image whereas
126 discrete lebensspuren (e.g. faecal casts) were only measured if they were completely visible.
127 Abundance data were estimated from counts of area measurements of lebensspuren that frequently
128 occurred more than once per frame (17 of the 58 distinct types). The average numbers of each
129 lebensspuren (from 50 frames) were multiplied by the number of area measurements taken for each
130 transect to give an estimate of abundance.

131 2.2. Statistical and Graphical Methods

132 2.2.1. Results Validation

133 A potential source of error in area measurements was that lebensspuren boundaries were
134 subjective. In response to these, measurements of individual lebensspuren were repeated for five
135 randomly selected lebensspuren of varying size and abundance. A pairwise t-test was applied at 5,
136 10, 25 and 50 replicates of each lebensspuren and there was no significant variation in pairs of
137 measurements of individual lebensspuren, suggesting that the results were replicable.

138 2.2.2. Diversity Analysis

139 For all subsequent analysis all individual lebensspuren types were treated as species. Lebensspuren
140 species accumulation curves were constructed (according to Colwell et al., 2004; Gotelli & Colwell,
141 2001; Magurran, 2004) in EstimateS (v8.2.0) using (Mao Tau) expected species richness (with 95%
142 confidence intervals). Diversity indices (Shannon-Wiener H' (\log_e) & Simpson's D) and evenness (J')
143 were calculated from raw abundance data using PRIMER 6 (Clarke & Warwick, 1994; Cox & Cox,
144 2001). The Shannon-Wiener and Simpson's indices were selected for their relative explanatory
145 merits with Shannon-Wiener giving more weight to rarer lebensspuren species in the sample and
146 Simpson's giving more weight to the abundant lebensspuren species in the sample. Diversity indices

147 were compared using ANOVA (with Tukey pairwise multiple comparison procedures) using
148 superstations as factors.

149 2.2.3. Multivariate analysis

150 Multivariate analysis was carried out in PRIMER 6 after a square root transformation, applied to give
151 less weight to the more abundant lebensspuren (according to Clarke & Warwick, 1994; Olsgard et
152 al., 1997; Puente & Juanes, 2008). A resemblance matrix was constructed using Bray-Curtis
153 similarity. Differences in lebensspuren assemblage compositions between superstations were
154 assessed using one-way ANOSIM. Data were subjected to hierarchical cluster analysis and displayed
155 using a multi-dimensional scaling ordination.

156 3. Results

157 3.1. Lebensspuren Assemblages

158 The main lebensspuren responsible for area coverage at each superstation were highly variable (Fig.
159 3) and indeterminate lebensspuren accounted for the major constituent (51.97 - 89.62 %) in all
160 superstations. The NE superstation was occupied mainly by enteropneust lebensspuren, accounting
161 for 25.97 % of the total lebensspuren area (2.30 - 6.47 % elsewhere). Enteropneust lebensspuren
162 were also the dominant identifiable trace, by area (5.33 %), in the SW (Fig. 3). However, at the SW
163 the proportion of indeterminate lebensspuren was very high (89.60 %). Holothurian faecal casts
164 were distinctive and occurred in high abundances across the ECOMAR region, though they
165 accounted for a very small component of the lebensspuren area (2.00 - 6.80 %) owing to their small
166 size. The most significant lebensspuren forms at the NW were attributable to holothurians (16.65 %
167 in terms of area). The variability in the contributions to total bioturbation of lebensspuren forming
168 taxa demonstrated the heterogeneity between superstations and the limited degree of conservation
169 of dominant lebensspuren morphology across the MAR or Charlie-Gibbs Fracture Zone (CGFZ)/ Sub-
170 Polar Front (SPF). Tracks were consistently the most dominant in all but the SW superstation, albeit

171 at varying levels (43.65 - 85.38 % in terms of bioturbated area). At the eastern superstations 43.65 -
172 49.57 % of the lebensspuren area was accounted for by tracks (Fig. 4), though the subsequent
173 lebensspuren had greatly different ranks. For instance, faecal casts were the second most significant
174 lebensspuren group in the NE (36.88 %), whereas in the SE faecal casts were far more limited (8.15
175 %) and it was mounds that accounted for the second most significant coverage after tracks (29.81
176 %). In contrast to the eastern superstations, the western superstations showed considerable
177 disparity in the functional group of the most dominant lebensspuren (Fig. 4). In the NW, 85.38 % of
178 the bioturbated area was comprised of tracks, whereas in the SW the 73.64 % of the bioturbated
179 area was mounds. The western superstations were characterised by an area coverage that was
180 dominated by a single functional group (NW – Tracks and SW – Mounds; Fig. 4). The SW was the only
181 area in which the surface manifestations of infaunal activity (in terms of area) exceeded that of
182 epifaunal activity (Fig. 4). There was a remarkable similarity in terms of total area of bioturbation,
183 (Fig. 5) between the SE and NW (9.69 %).

184 Lebensspuren diversity (H' ; Fig. 6) was significantly different between stations (ANOVA: $F = 47.108$, df
185 $= 15$, $p < 0.001$), pair-wise tests (Tukey) showed that there were significant differences in diversity
186 between the eastern superstations but the western superstations were not significantly different
187 from each other ($p = 0.601$). This pattern was reflected in evenness (J'), which was different between
188 all superstations (ANOVA: $f = 65.523$, $df = 15$, $p < 0.001$) except between the western superstations (p
189 $= 0.974$). Evenness was lowest in the NE ($J' = 0.315-0.401$) and highest in the SE ($J' = 0.674 - 0.750$).
190 High lebensspuren species richness was observed at the eastern superstations (Figs. 7; 8).
191 Contributions of individual lebensspuren to the composition of a superstation were variable and in
192 some cases the area coverage was patchy. As an example, fish tail marks in the NE ranged in
193 abundance between 0 and 420 lebensspuren ha^{-1} and paired burrows in the SE ranged between 1030
194 and 8170 lebensspuren ha^{-1} .

195 There were significant differences in lebensspuren composition between superstations (ANOSIM
196 global $R = 0.984$, $p < 0.02$), when examined further there were significant differences between all
197 pairs of superstations ($p < 0.05$). Cluster analysis indicated similarities between superstations of
198 51.09 - 55.85 % (Fig. 9). Holothurian and enteropneust lebensspuren were usually the most
199 dominant as they accounted for the highest area of the non-indeterminate lebensspuren (Fig. 3). In
200 the southern superstations there was a generally high but spatially variable coverage of pteropod
201 shells on the sediment surface which was not seen in the north.

202 3.2. Intra-superstation variability

203 Intra-superstation similarity in lebensspuren assemblage compositions was generally high (Fig. 9),
204 ranging from 76.24 - 82.46 % lowest common similarity (from cluster analysis), between transects
205 for all superstations except the SE. This consistency was reflected in the top five most dominant
206 lebensspuren (Table 2) with one morphological type that accounted for the largest proportion of the
207 effort (tracks in the northern superstations and mounds in the SW). The SE however had a mixture of
208 tracks and mounds. The lowest within-site similarity between transects was observed at the SE site
209 (66.59 %; Fig 9), which was reflected in the greater lebensspuren diversity at the SE03 and SE04
210 transects.

211 4. Discussion

212 4.1. Lebensspuren

213 Lebensspuren assemblages appear to have been primarily influenced by local-scale controls, both in
214 their abundance and area coverage. Lebensspuren assemblages were largely independent of detrital
215 flux (Abell et al., this volume) particularly in terms of their areal coverage. Lebensspuren area was
216 highest in the SE & NW and detrital flux was notably lower in the NW, compared to the other
217 superstations (Abell et al., this volume). Lebensspuren area and density values reflected the balance
218 between lebensspuren formation by fauna and destruction either by fauna, hydrodynamic forcing or

219 burial. Sediment transport rates influence the burial, and hence degradation rate of lebensspuren
220 (Kaufmann et al., 1989) but also the biomass of the benthic community, and thus its potential for
221 lebensspuren formation and degradation. The NW superstation had a comparatively dense coverage
222 of lebensspuren that may be explained by a low mean flux of organic material compared to the SW
223 and NE, which had higher mean organic fluxes and hence faster potential burial rates (Abell et al.,
224 this volume) and lower faunal activity which reduces lebensspuren destruction rates. Faunal density
225 in the NW was lower than that of the eastern superstations (Alt et al., unpublished) increasing
226 lebensspuren residence time (TRT) and potentially explaining the relatively dense lebensspuren
227 assemblage.

228 In spite of the high proportion of indeterminate lebensspuren, there were several instances in which
229 the abundances of lebensspuren were similar to the abundance of the organisms known to be
230 responsible for their formation (Alt et al., unpublished). While high abundances of holothurian faecal
231 casts at the NE (3.61m² for tightly coiled casts) coincided with the highest holothurian densities at
232 the same site (Alt et al., unpublished), enteropneusts dominated the lebensspuren by area coverage
233 (25.97%). At the SE echinoids accounted for the most area of lebensspuren and were the most
234 abundant (Alt et al., unpublished). Echinoid area coverage and abundance in the SW were very
235 limited (Alt et al., unpublished). In contrast, there was considerable disparity between lebensspuren
236 and faunal data for the enteropneusts. In the NE, enteropneusts were responsible for 25.97% of the
237 lebensspuren area but accounted for only 0.10% of the total number of individuals observed (Alt et
238 al., unpublished). Conversely, in the SE where the enteropneust lebensspuren area coverage was
239 2.72x less than at the NE, their abundance was 7.67x greater. It is possible that the sediments of the
240 SE were more organically-enriched and that this could support a higher abundance of enteropneusts
241 while higher densities of other fauna reduced TRT. A study focussed upon the enteropneusts of the
242 MAR explores these patterns further (Jones et al., this volume). The high dominance of tracks in the
243 NW (an area of lower organic flux [Abell et al., this volume]) indicated an increased significance of
244 moving lebensspuren relative to feeding lebensspuren. When feeding lebensspuren are not found

245 concurrently with moving lebensspuren, fauna may be by-passing an area of lower nutritional
246 quality. Feeding events (and related feeding lebensspuren) may have been reduced in areas of lower
247 flux, such as observed off Australia (Anderson et al., 2011). This could suggest that in areas of low
248 organic matter a greater proportion of faunal activity was dedicated to searching for areas with
249 better resources, as would be predicted by optimal foraging theory (Charnov, 1976).

250 4.2. Comparing the composition of lebensspuren and faunal assemblages

251 Lebensspuren assemblages were distinct between superstations at the MAR, which may have
252 resulted from significant differences in lebensspuren-forming megafaunal assemblages between
253 superstations (Alt et al., unpublished). Intra-superstation similarity was relatively high for
254 lebensspuren assemblages compared with faunal assemblages in all superstations. In the SE intra-
255 superstation similarity was particularly low in both lebensspuren assemblages (66.59 % Bray-Curtis
256 similarity) and megafaunal assemblages (36.18 %), compared to the other superstations (76.24 -
257 82.46 % for lebensspuren; 50.57 - 68.51 % for megafauna; Alt et al., unpublished). The disparity
258 between two pairs of transects from the SE (Fig. 9) was reflected in the faunal data (Bray-Curtis
259 similarities: SE01/ SE02: 72.30 % & SE03/ SE04: 69.93 %; Alt et al., unpublished).

260 The NE superstation, which had the lowest diversity for lebensspuren, also had lowest faunal
261 diversity (Alt et al., unpublished), although variation was high in both indices. The SW had similar
262 lebensspuren diversity to the NW, but the SW had higher faunal diversity. In general, faunal and
263 lebensspuren diversity (D) did not correlate significantly ($R^2 = 0.109$, $p > 0.05$). Improvements in
264 imaging technology allows more refined classification of lebensspuren and species, which may affect
265 the strength of the correlation between faunal and lebensspuren diversity, compared with the more
266 direct proportionality of faunal and lebensspuren diversity demonstrated in older studies (Kitchell et
267 al., 1978; Young et al., 1985). The high standard deviation of faunal diversity in the SE may also have
268 contributed to the poor quality of correlation. The SW was typified by a much higher proportional
269 influence of sub-surface deposit feeders and showed a marked decrease in epifaunal density.

270 Although it is not possible to assess infaunal density from ROV footage, the reduction in epifaunal
271 abundance (Alt et al., unpublished) in the SW supports our observations of higher densities of
272 infaunal lebensspuren compared with those formed by epifauna. At the other ECOMAR sites, where
273 epifaunal densities were higher (Alt et al., unpublished), the contribution to bioturbation was
274 greatest from epifauna. In terms of ecosystem function, it might be reasonable to assume that the
275 SW community, having a greater proportion of infauna, may have higher organic matter
276 sequestration rates, owing to the reduced activity of epifauna (Turnewitsch et al., 2000) and
277 promote bioturbative mixing at depth (Crusius et al., 2004). The bioturbation effect of epifauna is
278 primarily horizontal mixing and may discourage vertical mixing by reducing the organic content of
279 the surface sediment (Turnewitsch et al., 2000). Depth of mixing is beyond the scope of this
280 investigation but is discussed in Teal et al., (2008).

281 4.3. Lebensspuren Density

282 Assuming a TRT of 1-2 weeks (Mauviel & Sibuet, 1985; Smith Jr et al., 2005), the data suggest that
283 surficial bathyal sediments at the MAR were completely reworked over a timeframe of 5-10 months
284 for the NW and SE and 12-25 months for the NE and SW. Megafauna at abyssal regions of the NE
285 Pacific traversed 88% of the observable area over the course of three months (Smith Jr et al., 1993)
286 which seems consistent with the more active ECOMAR superstations.

287 When lebensspuren density was compared to faunal density there was an initially linear rise in
288 lebensspuren density compared to faunal density which reached an asymptote (5400 lebensspuren
289 ha^{-1}) at around 7500 individuals ha^{-1} (Fig. 10). This relationship was presumed to be a result of the
290 limited capacity for faunal degradation of lebensspuren at low faunal density, hence promoting a
291 relatively long TRT. The asymptote (Fig. 10) represents a dynamic equilibrium between lebensspuren
292 formation and destruction and this was apparently the maximum allowable lebensspuren density at
293 any of the ECOMAR superstations. Any increase to faunal density could decrease TRT only without
294 influencing total lebensspuren area. Conversely, a study at the HEBBLE region of the West Atlantic

295 (4800 m) found low lebensspuren densities (1 %) but attributed this to a very active community
296 which reduced lebensspuren area, giving the illusion of a less intensely reworked area (Wheatcroft
297 et al., 1989). Abiotic lebensspuren destruction rates were assumed to be constant over the TRT
298 period so the change in lebensspuren density was attributable to faunal activity only.

299 The relationship between lebensspuren and faunal density found in this study suggested that, in
300 conditions where the abiotic controls were more influential, perhaps the density of lebensspuren
301 might have been caused by a combination of the bioturbative capacity of the community and the
302 physical controls on lebensspuren residence. The positive relationship between lebensspuren and
303 faunal density found here conflicted with data from several other deep-sea environments that found
304 an inverse relationship (Kitchell et al., 1978; Young et al., 1985; Gerino et al., 1995). The inverse
305 relationship is based on the assumption that lebensspuren, once formed in low biomass regions,
306 have the capacity to persist for a long time, with biotic interactions being the only significant
307 influence upon TRT. However, megafaunal reworking is not the only method by which lebensspuren
308 are destroyed (Wheatcroft et al., 1989; Smith Jr et al., 2005) and that microbial degradation,
309 bioturbation by smaller fauna, hydrodynamic forcing and burial can limit residence time to 1-2
310 weeks.

311 4.4. Comparing the MAR globally

312 The percentage coverage of lebensspuren seen in the SE and NW exceeded the estimated values for
313 the continental slope (~7 % from Laughton, 1963), potentially suggesting a very active community.
314 Surficial bioturbation (fig. 3.3) at the NE (5.24 %) and SW (4.12 %) were similar to expected values
315 (Laughton, 1963) at this depth. It has been suggested that between continental slope and abyssal
316 depths the percentage of visibly reworked area decreased from 7 % at slope depths to 3.5 % at
317 abyssal depths (Laughton, 1963). The disparity in measurements of area coverage between this
318 study and earlier evidence (Laughton, 1963; Heezen & Hollister, 1971) may represent the increased
319 resolution and quality of modern images. The area of bioturbation observed in this study also

320 exceeded values for the Faroe-Shetland channel (Jones et al., 2007) of 0.015 - 2.197 %. In
321 comparison to a study in the abyssal Arctic ocean, where 49 % of the stations had ≥ 70 %
322 lebensspuren coverage and 92 % had > 35 % lebensspuren coverage (Kitchell et al. 1978), the extent
323 of bioturbation (Fig. 5) at the MAR seems very limited. The area coverage of lebensspuren at the
324 MAR was more analogous to data from the deep Bellingshausen Basin (Kitchell et al., 1978) where
325 82 % of stations had a lebensspuren frequency of ≤ 35 %. These studies illustrate the high variability
326 in lebensspuren coverage across a range of depth and geographic regions and the results suggest
327 that local-scale biotic and abiotic factors were more important in controlling lebensspuren
328 assemblages at the MAR than more regional variables.

329 5. Conclusions

330 Lebensspuren assemblages of the Mid-Atlantic Ridge were highly variable, both either side of the
331 ridge axis and the sub-Polar front. We therefore assume that bioturbation intensity was influenced
332 by changes in by environmental factors either side of the MAR or SPF. The lack of continuity
333 between any of the superstations illustrated the potential for local-scale variation in lebensspuren
334 assemblages and areal coverage which appeared to have been largely independent of the variation
335 in measured organic flux. Lebensspuren diversity was generally high and not similar to that of
336 lebensspuren-forming faunal diversity. Lebensspuren and faunal density showed a different
337 relationship to previous studies, which may have resulted from a situation in which megafaunal
338 activity was not the only significant method of lebensspuren destruction.

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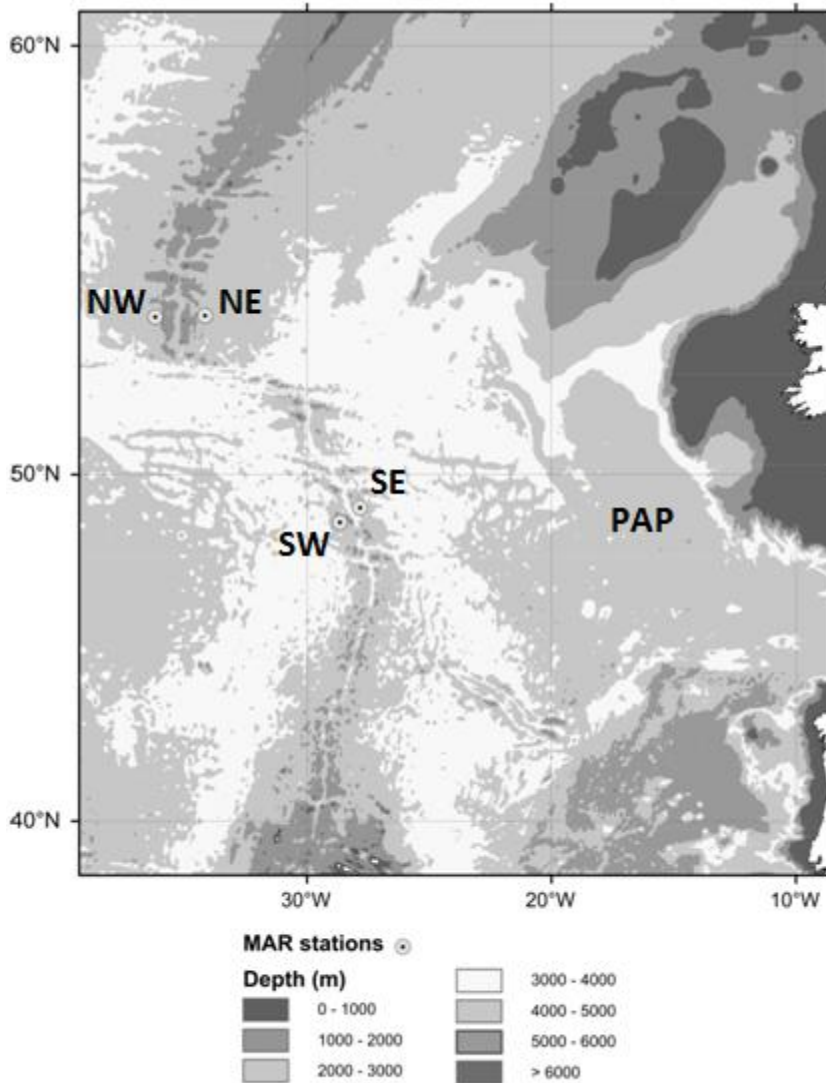
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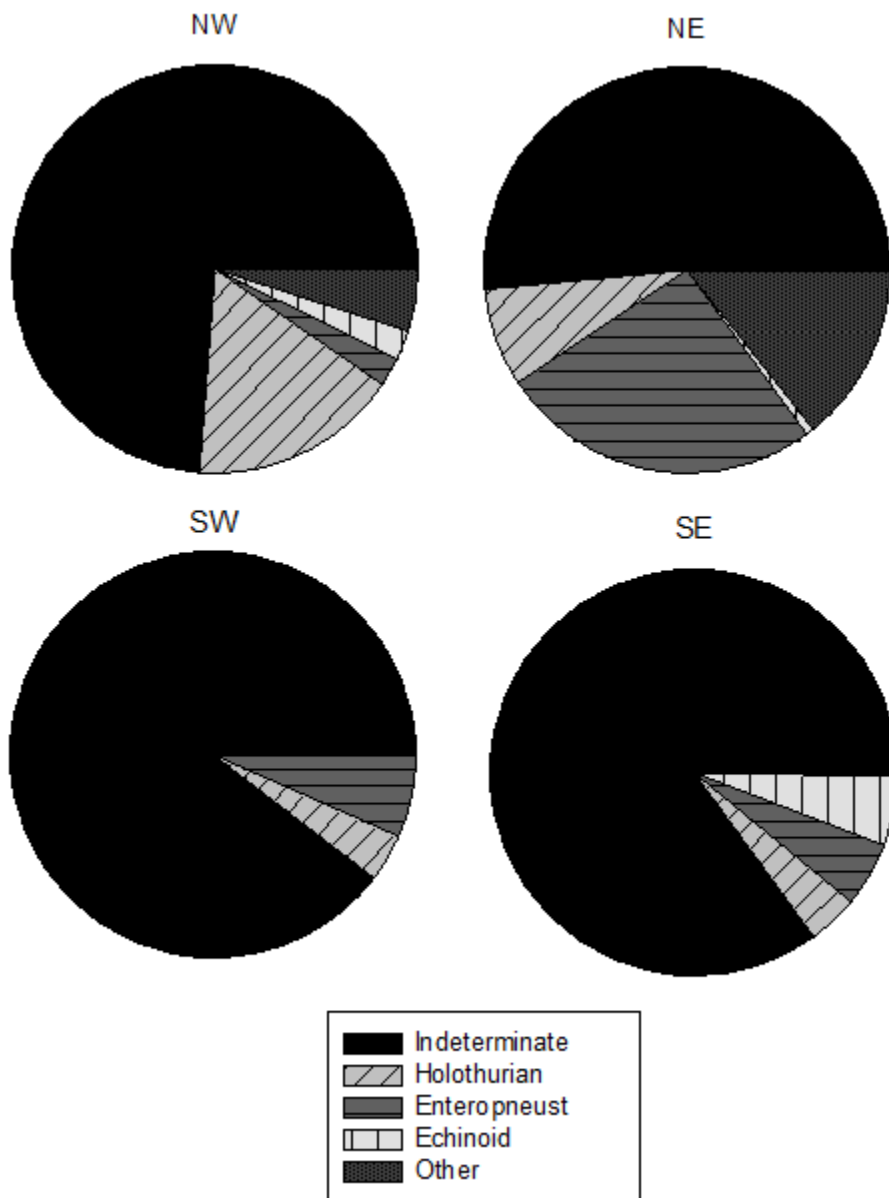
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499 **Fig. 1** – Bathymetric Chart of the Central North Atlantic showing the positions of the four
500 superstations. PAP – Porcupine Abyssal Plain

501 **Fig. 2** – Types of lebensspuren observed and quantified in this study. White bars represent 10cm, as
502 dictated by the parallel lasers on *Isis*. Four additional lebensspuren types excluded from this figure
503 because of categorical duplications of certain types between indeterminate and determinate
504 lebensspuren (e.g. track lebensspuren found in indeterminate, holothurian and echinoid groupings)
505 depending upon confidence in identification.

506 Lebensspuren 1-30: Indeterminate Origin, 31-32: Xenophyophore (32 discounted from further
507 analysis), 33: Osteichthyes, 34-35: Enteropneust, 36-44: Holothurian, 45-46: Asteroid, 47: Ophiuroid,
508 48-50: Echinoid, 51-54: Echiuran. The lebensspuren numbers correspond with the names in table 1.

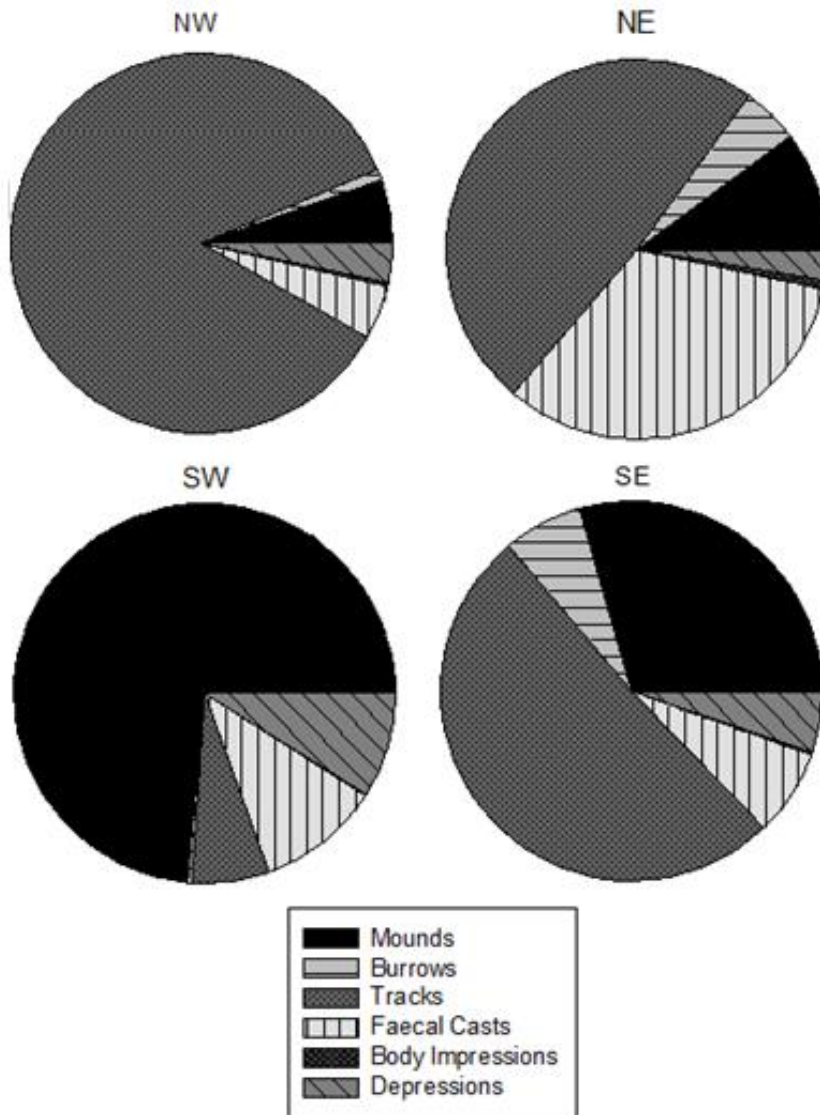




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511 **Fig. 3** (above) – Pie chart array explaining the relative contribution of major taxonomic groups to the
 512 total area coverage of lebensspuren measured at each superstation. The ‘Other’ category accounts
 513 for lebensspuren of echiuran, asteroid, ophiuroid, and vertebrate origin. In view of their
 514 comparatively minor individual contributions, these lebensspuren assemblages have been grouped
 515 for simplicity of representation.

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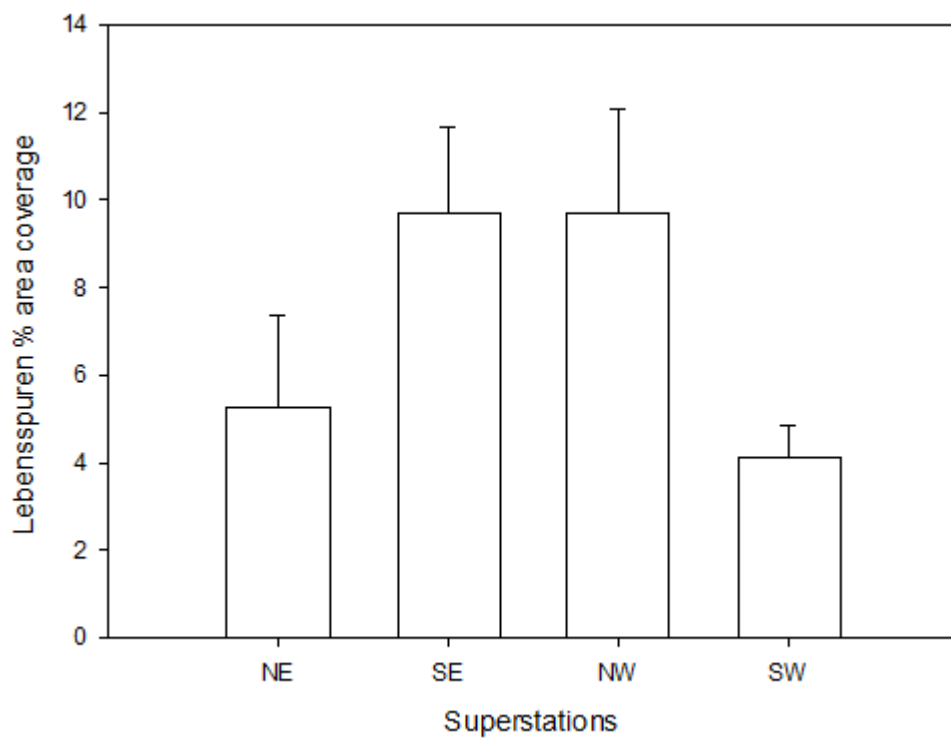


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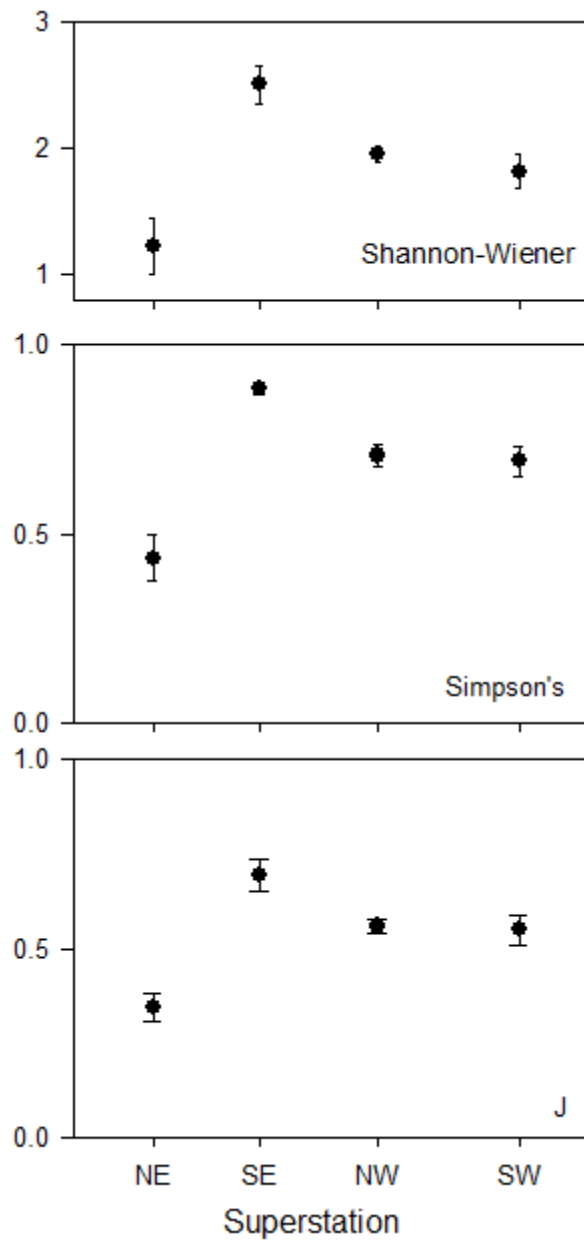
518 **Fig. 4** (above) – Pie chart array explaining the contribution of lebensspuren types (by area) grouped
 519 into functional morphology (i.e. lebensspuren is categorised by its method of formation).

520

521 **Fig. 5** (below) – Lebensspuren percentage area coverage measured for each superstation (measured
522 as the % of transect area bioturbated) Error bars represent ± 1 s.d. of superstation mean.



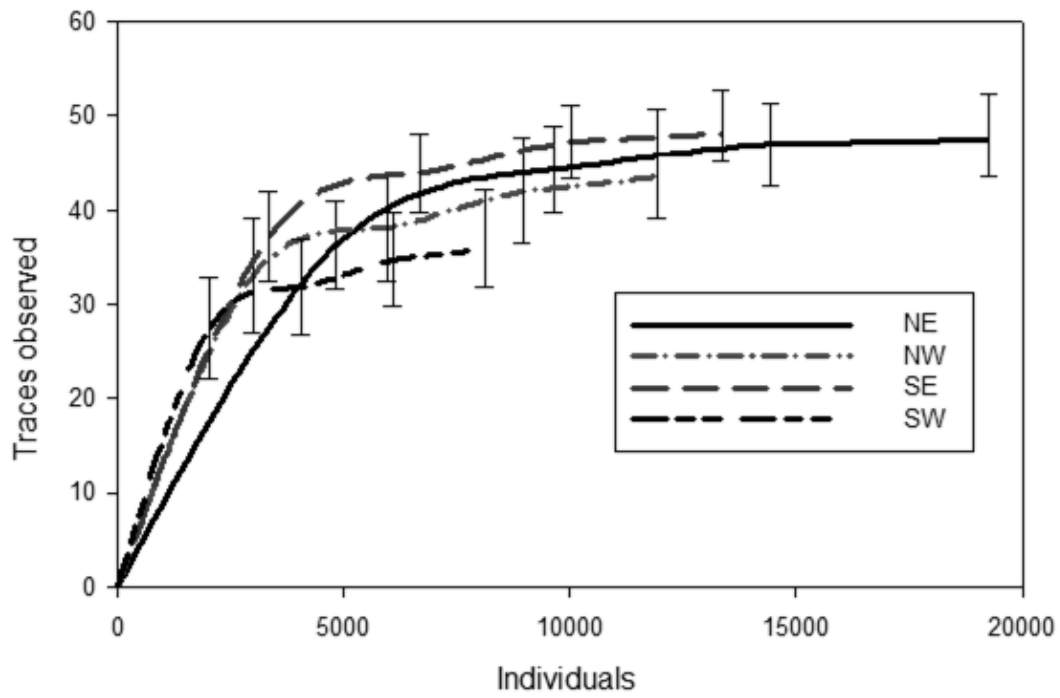
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525 **Fig 6** – Comparison of mean diversity indices (Shannon-wiener, Simpson's & J') grouped by
 526 superstation, where each lebensspuren type is regarded as a different species. Error bars represent
 527 1s.d. of the four transect mean.

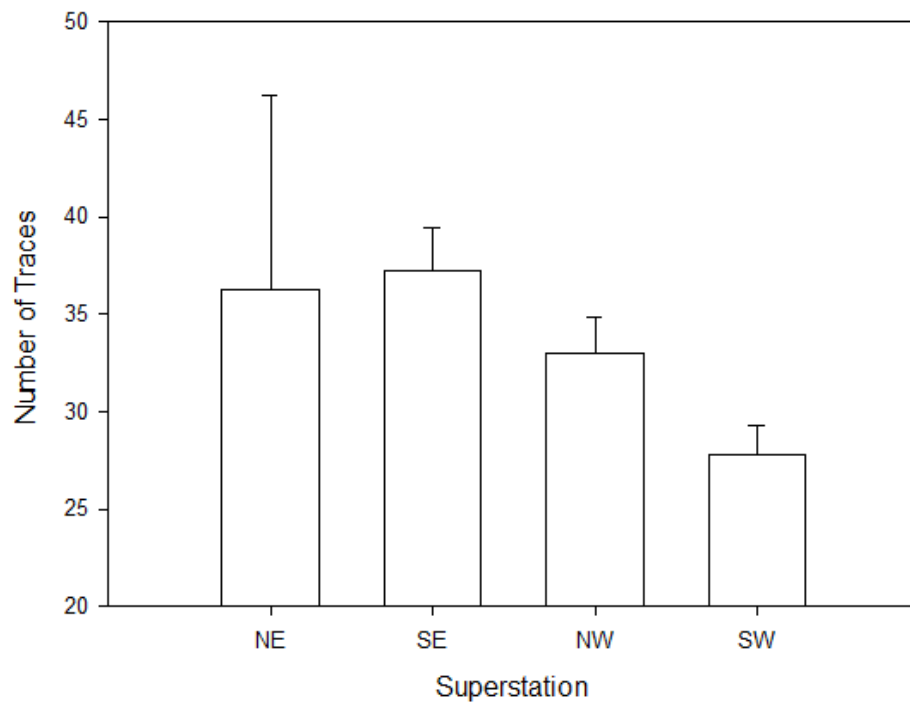
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530 **Fig. 7** – Species-accumulation curves (treating each lebensspuren type as a species), grouped by
 531 superstation. Standard number of permutations (50) were used to construct these curves. Error bars
 532 represent 95% confidence intervals.

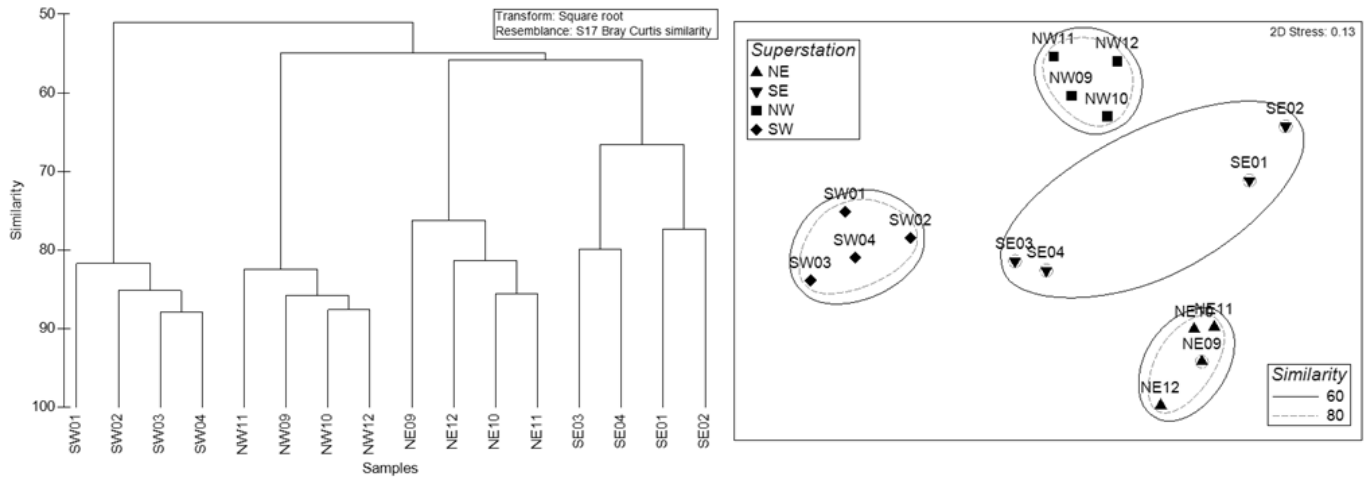
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535 **Fig. 8** – Number of lebensspuren types measured at each superstation. Error bars represent ± 1 s.d.
536 of superstation mean. Total numbers of lebensspuren observed at each superstation were: NE – 48;
537 SE – 49; NW – 44; SW – 37.

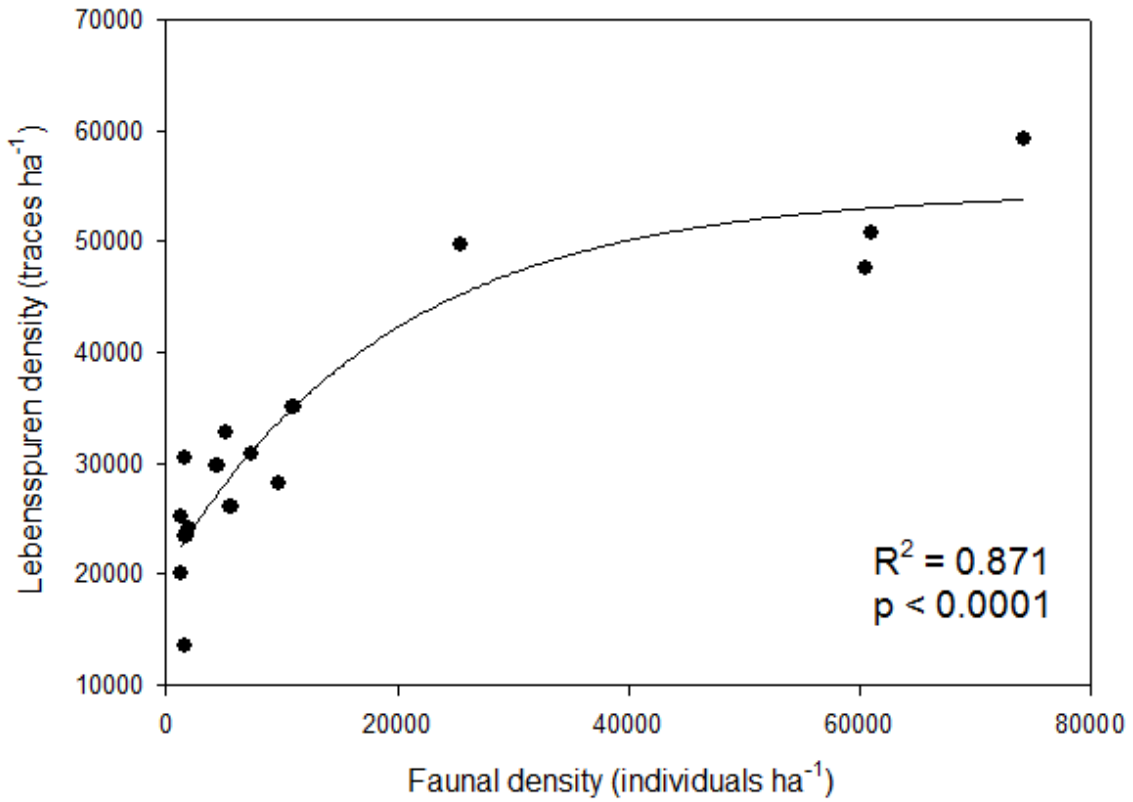
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540 **Fig. 9** – Multivariate similarity of the abundances of lebensspuren types at each of the 16 transects
 541 (4 per superstation). Presented as hierarchical cluster diagram (left) and multi-dimensional scaling
 542 ordination (right).

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545 **Fig. 10** (above) – Lebensspuren density vs. lebensspuren-forming epifaunal density. Grey lines
 546 represent 95% CI of curve. Fitted line R^2 and significance value (ANOVA df = 15) are displayed.

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Taxa/ lebensspuren type		NE		SE	
		Area (m ²)	Abundance	Area (m ²)	Abundance
Indeterminate Origin	Pincushion Rosette (2)	0.643	18.000	0.096	9.000
	Elongate depression (3)	1.082	40.000	1.240	25.000
	Circular depression (4)	1.104	174.000	0.548	44.000
	Pockmarks (5)	1.827	108.000	1.630	144.000
	Fracturing (6)	1.615	54.000	0.493	17.000
	Nodules (7)	0.000	0.000	0.080	4.000
	Star Impression (8)	0.631	22.000	0.310	24.000
	Fish/ Star Trail (9)	4.056	36.000	0.060	2.000
	Large Trough (10)	0.579	2.000	8.355	29.000
	Single Burrow (11)	0.349	574.000	0.901	2104.000
	Paired Burrows (12)	0.193	114.000	2.493	1372.000
	Burrow Clusters (13)	0.858	116.000	4.038	751.000
	Trapdoor Burrow (14)	0.144	68.000	0.247	126.000
	Mounded Burrow (15)	0.000	0.000	0.041	12.000
	Small mound (16)	2.480	391.000	7.334	833.000
	Large mound (17)	2.310	22.000	22.394	124.000
	Elongate mound (18)	0.486	18.000	16.691	348.000
	Irregular/ Disrupted mounds (19)	0.000	0.000	0.000	0.000
	Spotted mound (20)	0.000	0.000	0.059	7.000
	Mounded cast (21)	0.155	77.000	0.417	121.000
	Rounded Crater Ring (22)	3.307	15.000	7.987	84.000
	Pogo Stick Trail (23)	0.000	0.000	0.061	3.000
	Thin trail (24)	8.426	744.000	28.594	1869.000
	Alternating Trail (25)	0.308	7.000	0.095	5.000
	Thick Trail (26)	6.734	200.000	5.857	169.000
	Hoof Trail (27)	1.081	20.000	0.000	0.000
	Indeterminate Track Trail	0.000	0.000	11.413	203.000
	Indeterminate Perforated Trail	0.000	0.000	0.000	0.000
	Fern Feature (28)	0.337	5.000	0.000	0.000
	Elongate/ Drag Tracks (29)	3.442	79.000	3.676	32.000
Disturbed/ Irregular Trail (30)	11.316	190.000	35.754	1324.000	
Xenophyophora	Rayed Mound (31)	0.075	3.000	0.577	2.000
Actinopterygii	Tail Marks (33)	10.698	82.000	0.047	2.000

Enteropneusta	Switchback casts (34)	1.786	49.000	4.205	307.000
	Spiral Casts (35)	25.296	680.000	5.780	246.000
	Switchback casts (in progress)	0.122	181.000	0.013	3.000
Holothurian	Track Trail (37)	0.059	1.000	0.422	11.000
	Noduled Trail (36)	0.000	0.000	0.420	9.000
	Tightly coiled casts (38)	6.513	14437.000	1.716	1563.000
	Wavy/ uncoiled casts (39)	0.634	584.000	0.232	122.000
	Round casts (40)	0.003	2.000	0.074	39.000
	Curly/ Segmented casts (41)	0.014	5.000	1.851	306.000
	Mounded casts	0.000	0.000	0.000	0.000
	Abandoned Molpadiid burrow (42)	0.149	2.000	0.000	0.000
	Occupied Molpadiid burrow (43)	0.190	2.000	1.214	9.000
	Multi-hole paths (44)	0.731	9.000	1.828	57.000
Asteroid	Star impression (45)	0.047	4.000	0.000	0.000
	Perforated trail (46)	3.170	23.000	0.021	1.000
Ophiuroid	Star impression (47)	0.006	2.000	0.000	0.000
Echinoid	Thin Trail	0.020	1.000	0.000	0.000
	Urchin Trail (48)	0.617	75.000	10.662	816.000
	Urchin Track (49)	0.000	0.000	0.022	4.000
	Urchin lebensspuren (50)	0.047	7.000	0.059	15.000
Echiuran	Small/ messy rosette (51)	0.179	5.000	0.400	19.000
	Fractured mound (52)	0.057	5.000	0.099	5.000
	Large Rosette (53)	0.071	1.000	1.231	4.000
	Large Rosette Segment (54)	0.676	8.000	2.007	25.000
	Petal Rosette (1)	0.164	6.000	0.011	1.000

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	Taxa/ lebensspuren type	NW		SW	
		Area (m ²)	Abundance	Area (m ²)	Abundance
Indeterminate Origin	Pincushion Rosette (2)	0.007	2.000	0.000	0.000
	Elongate depression (3)	3.291	104.000	1.015	62.000
	Circular depression (4)	3.172	224.000	0.524	71.000
	Pockmarks (5)	1.387	43.000	0.000	0.000
	Fracturing (6)	0.031	3.000	0.000	0.000
	Nodules (7)	0.003	1.000	0.610	45.000
	Star Impression (8)	0.531	36.000	0.083	9.000

	Fish/ Star Trail (9)	11.017	95.000	0.000	0.000
	Large Trough (10)	0.000	0.000	5.787	25.000
	Single Burrow (11)	0.097	107.000	0.055	116.000
	Paired Burrows (12)	0.045	21.000	0.038	24.000
	Burrow Clusters (13)	0.016	2.000	0.012	4.000
	Trapdoor Burrow (14)	0.054	24.000	0.093	43.000
	Mounded Burrow (15)	0.010	3.000	0.406	73.000
	Small mound (16)	2.814	554.000	26.762	4262.000
	Large mound (17)	3.814	22.000	14.604	104.000
	Elongate mound (18)	3.586	377.000	16.846	457.000
	Irregular/ Disrupted mounds (19)	0.000	0.000	0.596	10.000
	Spotted mound (20)	0.000	0.000	0.000	0.000
	Mounded cast (21)	0.135	49.000	0.565	278.000
	Rounded Crater Ring (22)	0.000	0.000	0.505	2.000
	Pogo Stick Trail (23)	0.000	0.000	0.000	0.000
	Thin trail (24)	74.934	6177.000	3.642	306.000
	Alternating Trail (25)	0.688	6.000	0.000	0.000
	Thick Trail (26)	16.235	205.000	0.893	15.000
	Hoof Trail (27)	0.000	0.000	0.000	0.000
	Indeterminate Track Trail	0.066	2.000	0.000	0.000
	Indeterminate Perforated Trail	4.330	33.000	0.000	0.000
	Fern Feature (28)	0.529	3.000	0.000	0.000
	Elongate/ Drag Tracks (29)	1.905	26.000	0.000	0.000
	Disturbed/ Irregular Trail (30)	14.228	171.000	0.665	21.000
Xenophyophora	Rayed Mound (31)	0.000	0.000	0.024	1.000
Actinopterygii	Tail Marks (33)	6.659	39.000	0.000	0.000
Enteropneusta	Switchback casts (34)	0.005	1.000	2.657	389.000
	Spiral Casts (35)	4.444	245.220	2.673	97.000
	Switchback casts (in progress)	0.000	0.000	0.002	1.000
Holothurian	Track trails (37)	1.755	32.000	0.143	6.000
	Noduled Trail (36)	8.690	167.000	0.000	0.000
	Tightly coiled casts (38)	2.186	990.000	1.187	1176.000
	Wavy/ uncoiled casts (39)	1.004	826.000	0.353	272.000

	Round casts (40)	0.014	8.000	0.016	10.000
	Curly/ Segmented casts (41)	1.141	140.000	1.142	210.000
	Mounded casts	0.026	1.000	0.003	1.000
	Abandoned Molpadiid burrow (42)	0.000	0.000	0.035	1.000
	Occupied Molpadiid burrow (43)	0.227	2.000	0.239	2.000
	Multi-hole paths (44)	17.215	506.000	0.029	1.000
Asteroid	Star impression (45)	0.000	0.000	0.000	0.000
	Perforated trail (46)	2.661	16.000	0.000	0.000
Ophiuroid	Star impression (47)	0.000	0.000	0.000	0.000
Echinoid	Thin Trail	0.000	0.000	0.000	0.000
	Urchin Trail (48)	4.453	634.000	0.000	0.000
	Urchin Track (49)	0.024	2.000	0.010	1.000
	Urchin lebensspuren (50)	0.075	16.000	0.022	7.000
Echiuran	Small/ messy rosette (51)	0.205	6.000	0.018	1.000
	Fractured mound (52)	0.005	1.000	0.039	4.000
	Large Rosette (53)	0.000	0.000	0.000	0.000
	Large Rosette Segment (54)	0.000	0.000	0.081	1.000
	Petal Rosette (1)	0.003	1.000	0.000	0.000

557 **Table 1** – Summed data for abundance (individual Lebensspuren per superstation) & area (m²),
558 presented for each superstation. Numbers in parentheses correspond to their number in fig. 2

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Rank	NE	SE	NW	SW
1	Spiral casts ^[35]	Disturbed/ Irregular trail ^[30]	Thin trail ^[24]	Small mound ^[16]
2	Disturbed/ Irregular trail ^[30]	Thin trail ^[24]	Multi-hole paths ^[44]	Elongate mound ^[18]
3	Tail marks ^[33]	Large mound ^[17]	Thick trail ^[26]	Large mound ^[17]
4	Thin trail ^[24]	Elongate mound ^[18]	Disturbed/ Irregular trail ^[30]	Large trough ^[10]
5	Thick trail ^[26]	Track trail ^[37]	Fish/Star trail ^[9]	Thin trail ^[24]

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566 **Table 2** (above) – Top five most dominant lebensspuren for each superstation (by area coverage).

567 Numbers in superscript parentheses correspond to their number in fig. 2 and Table 1.

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