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1   Lebensspuren of the Bathyal Mid-Atlantic Ridge

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6

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.

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 (Diaz, 2004; Teal et al., 2008; Barsanti et al., 2011). 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 (Middleburg et al., 1997; Lecroart et al., 2010). The action of deposit-feeding fauna creates a three-dimensional mosaic of micro-scale variation in the chemical properties of sediment (Gage & Tyler, 1991; Diaz et al., 1994; Aller et al., 1998; Murray et al., 2002; Meysman et al., 2006). 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 & Davis, 1967; Young et al., 1985; Gage & Tyler, 1991; Gerino et al., 1999; Murray et al., 2002) and the importance of this spatial influence is illustrated by the marked increase in meiofaunal and bacterial biomass around polychaete burrows (Aller & Aller, 1986; Gage & 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 (Kitchell & Clark, 1979; Yingst & Aller, 1982; Gage & Tyler, 1991; Uchmann, 2007), though this is thought to be rare given the number of ways that lebensspuren may be destroyed (Mauviel & 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 (Stordal et

al., 1985; Wheatcroft et al., 1989; Jones et al., 2007; Anderson et al., 2011; Barsanti et al., 2011). 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 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:

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 of the types of lebensspuren observed (Ewing & 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 (Young et al., 1985; Hughes & Gage, 2004) 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 & Tyler, 1991; 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°)

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 m^2 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 m^2.

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 m^2) 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 (3.61m^2 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 (Turnewtisch et al., 2000) and

277 promote bioduffisive 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.

339 Acknowledgements

344   References

345   Abell. R et al., this volume

346   Aller, J. Y., Aller, R. C., 1986. Evidence for localized enhancement of biological activity associated

347   with tube and burrow structures in deep-sea sediments at the HEBBLE site, western North Atlantic.

348   Deep-Sea Research.33A, 755-90

349   Aller, C. R., Hall, P. O. J., Rude, P. D., Aller, J. Y., 1998. Biogeochemical heterogeneity and suboxic

350   diagenesis in hemipelagic sediments of the Panama Basin. Deep-Sea Research I. 45, 133-165

351   Anderson, T. J., Nichol, S. L., Syms, C., Przeslawski, R., Harris, P. T. 2011., Deep-sea bio-physical

352   variables as surrogates for biological assemblages, an example from the Lord Howe Rise. Deep-Sea

353   Research II. 58, 979-91

354   Barsanti, M., Delbono, I., Schirone, A., Langone, L., Miserocchi, S., Salvi, S., Delfanti, R., 2011.

355   Sediment reworking rates in deep sediments of the Mediterranean Sea. Science of the Total

356   Environment. 409, 2959-2970

357   Bergstad, O. A., Falkenhaug, T., Astthorsson, O. S., Byrkjedal, I., Gebruk, A. V., Piatowski, U., Priede, I.

358   G., Santos, R. S., Vecchione, M., Lorance, P., Gordon, J. D. M., 2008. Towards improved

359   understanding of the diversity and abundance patterns of the mid-ocean ridge macro- and

360   megafauna. Deep-Sea Research II. 55, 1-5

361   Bett, B. J., Rice, A. L., 1993. The feeding behaviour of an abyssal echiuran revealed in situ time-lapse

362   photography. Deep-Sea Research I. 40, 1767-1779

363   Bett, B. J., Rice, A. L., Thurston, M. H., 1995. A Quantitative Photographic Survey of 'Spoke-Burrow'

364   Type Lebensspuren on the Cape Verde Abyssal Plain. Internationale Revue gesamten Hydrobiologie.

365   80. 153-70

366   Charnov, E. L., 1976. Optimal foraging: the marginal value theorem. Theoretical Population Biology.

367   9, 129-136

368   Clarke, K. R., Warwick, R. M. 1994. Change in Marine Communities: An Approach to Statistical

369   Analysis and Interpretation. Plymouth: Plymouth Marine Laboratory

370   Colwell, R. K., Mao, C. X., Chang, J., 2004. Interpolating, Extrapolating, and Comparing Incidence-

371   Based Species Accumulation Curves. Ecology. 85, 2717-2727

372   Cox, T. F., Cox, M. A. A., 2001. Multidimensional Scaling. (2nd ed.) Chapman and Hall/ CRC Press, Boca

373   Raton

374   Crusius, J., Bothner, M. H., Sommerfield, C. K., 2004. Bioturbation depths, rates and processes in

375   Massachusetts Bay sediments inferred from modelling of ^{210}Pb and $^{239+240}$Pu profiles. Estuarine,

376   Coastal and Shelf Science. 61, 643-655

377   de Vaugelas, J., 1989. Deep-sea Lebensspuren: remarks on some echiuran Lebensspuren in the

378   Porcupine Seabight, northeast Atlantic. Deep-Sea Research. 36, 975-982

379   Diaz, R. J., Cutter, G. R., Rhoads, D. C., 1994. The importance of bioturbation to continental slope

380   sediment structure and benthic processes off Cape Hatteras, North Carolina. Deep-Sea Research II.

381   41, 719-34

382   Diaz, R. J., 2004. Biological and physical processes structuring deep-sea surface sediments in the

383   Scotia and Weddell Seas, Antarctica. Deep-Sea Research II. 51. 1515-32

384   Dundas, K., Przeslawski, R., 2009. Deep-Sea Lebensspuren - Biological Features on the Seafloor of the

385   Eastern and Western Australian Margin. GA Record 2009/26. Geoscience Australia: Canberra

386   Ewing, M., Davis, R. A., 1967. Lebensspuren photographed on the ocean floor. In: Brackett Hersey, J.,

387   (Ed.) 1967. Deep-Sea Photography. John Hopkins Press, Baltimore

388 Gage, J. D., Tyler, P. A., 1991. Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea

389 Floor. Cambridge University Press, Cambridge.

390 Gerino, M., Stora, G., Poydenot, F., Bourcier, M., 1995. Benthic fauna and bioturbation on the

391 Mediterranean continental slope: Toulon Canyon. Continental Shelf Research. 15, 1483-96

392 Gerino, M., Stora, G., Weber, O., 1999. Evidence of bioturbation in the Cap-Ferret Canyon in the

393 deep northeastern Atlantic. Deep-Sea Research II. 46, 2289-2307

394 Glud, R. N., Gundersen, J. K., Jørgensen, B. B., Revsbech, N. P., Schulz, H. D., 1994. Diffusive and total

395 oxygen uptake of deep-sea sediments in the eastern South Atlantic Ocean: *In situ* and laboratory

396 measurements. Deep Sea Research I. 41, 1767-1788

397 Gooday, A. J. et al., this volume

398 Gotelli, N. J., Colwell, R. K., 2001. Quantifying biodiversity: procedures and pitfalls in the

399 measurement and comparison of species richness. Ecology Letters. 4, 379-91

400 Heezen, B. C., Hollister, C. D., 1971. The Face of the Deep. Oxford University Press

401 Holland, N. D., Clague, D. A., Gordon, D. P., Gebruk, A., Pawson D. L., Vecchione, M., 2005.

402 'Lophenteropneust' hypothesis refuted by collection and photos of new deep-sea hemichordates.

403 Nature. 434, 374-76

404 Huettel, M., Ziebis, W., Forster, S., Luther III, G. W., 1998. Advective Transport Affecting Metal and

405 Nutrient Distributions and Interfacial Fluxes in Permeable Sediments. Geochimica et Cosmochimica

406 Acta. 62, 613-631

407 Hughes, D. J., Gage, J. D., 2004. Benthic metazoan biomass, community structure and bioturbation at

408 three contrasting deep-water sites on the northwest European continental margin. Progress in

409 Oceanography. 63, 29-55

410 Hunter, W. R., Oguri, K., Kitazato, H., Ansari, Z. A., Witte, U., 2011. Epi-benthic Megafaunal zonation

411 across an oxygen minimum zone at the Indian continental margin. Deep-Sea Research I. 58, 699-710

412 Jones, D. O. B. et al., this volume

413 Jones, D. O. B., Bett, B. J. & Tyler, P. A., 2007. Megabenthic ecology of the deep Faroe-Shetland

414 channel: a photographic study. Deep-Sea Research I. 54, 1111-1128

415 Kaufmann, R. S., Wakefield, W. W., Genin, A., 1989. Distribution of epibenthic Megafauna

416 Lebensspuren on two central North Pacific seamounts. Deep-Sea Research. 36, 1863-96

417 Kitchell, J. A., Kitchell, J. F., Johnson, G. L., Hunkins, K. L., 1978. Abyssal Lebensspuren and

418 Megafauna: comparison of productivity, diversity and density in the Arctic and Antarctic.

419 Paleobiology. 4, 171-80

420 Kitchell, J. A., Clark, D. L., 1979. A Multivariate approach to biofacies analysis of deep-sea

421 Lebensspuren from the central Arctic. Journal of Paleontology. 53, 1045-67

422 Lauerman, L. M. L., Kaufmann, R. S., 1998. Deep-sea epibenthic echinoderms and a temporally

423 varying food supply: results from a one year time series in the NE Pacific. Deep-Sea Research II. 45,

424 817-842

425 Laughton, A. S. 1963. Microtopography. In: The Sea, vol. 3, ed. Hill, M. N., pp. 437-472. New York:

426 Wiley-Interscience

427 Lecroart, P., Maire, O., Schmidt, S., Grémare, A., Anschutz, P., Meysman, F. J. R., 2010. Bioturbation,

428 short-lived radioisotopes, and the Lebensspurenr-dependence of biodiffusion coefficients.

429 Geochimica et Cosmochimica Acta. 74, 6049-63

430 Magurran, A. E., 2004. Measuring Biological Diversity. Blackwell Science Ltd., Oxford

431   Mauviel, A., Sibuet M., 1985. Repartition des Lebensspuren animales et importance de la

432   bioturbation. In: Laubier, L., Monniot, C. L., editors. Peuplements Profonds du Golfe de Gascogne.

433   IFREMER, Brest; 157–73.

434   Meysman, F. J. R., Middleburg, J. J., Heip, C. H. R., 2006. Bioturbation: a fresh look at Darwin's last

435   idea. Trends in Ecology and Evolution. 21, 688-695

436   Middleburg, J. J., Soetaert, K., Herman, P. M. J., 1997. Empirical relationships for use in global

437   diagenetic models. Deep-Sea Research I. 44, 327-44

438   Murray, J. M. H., Meadows, A., Meadows P. S., 2002. Biogeomorphological implications of

439   microscale interactions between sediment geotechnics and marine benthos: a review.

440   Geomorphology. 47, 15-30

441   Ohta, S., 1984. Star-shaped feeding Lebensspuren produced by echiuran worms on the deep-sea

442   floor of the Bay of Bengal. Deep-Sea Research. 31, 1415-1432

443   Olsgard, F., Somerfield, P. J., Carr, M. R., 1997. Relationships between taxonomic resolution and data

444   transformations in analyses of a macrobenthic community along an established pollution gradient.

445   Marine Ecology Progress Series. 149, 173-181

446   Paul, A. Z., Thorndike, E. M., Sullivan, L. G., Heezen, B. C., Gerard, R. D., 1978. Observations of the

447   deep-sea floor from 202 days of time-lapse photography. Nature. 272, 812-14

448   Priede, I. G., Bagley, P. M., 2010. RRS James Cook Cruise 048: ECOMAR Ecosytem of the Mid-Atlantic

449   Ridge at the Sub-Polar Front and Charlie-Gibbs Fracture Zone, 26 May – 3 July. OCEANLAB, University

450   of Aberdeen, Cruise Report.

451   Puente, A., Juanes, J. A., 2008. Testing taxonomic resolution, data transformation and selection of

452   species for monitoring macroalgae communities. Estuarine, Coastal and Shelf Science. 78, 327-40

453   Seilacher, A., 1953. Studien zur palichnologie. 1. Uber die Methoden der Palichnologie. Neues

454   Jahrbruch der Geologie und Palaontologie. 96, 421-52

455   Smith, C. R., De Leo, F. C., Bernardino, A. F., Sweetman, A. K., Arbizu, P. M., 2008. Abyssal food

456   limitation, ecosystem structure and climate change. Trends in Ecology & Evolution. 23, 518-528

457   Smith Jr, K. L., Kaufmann, R. S., Wakefield, W. W., 1993. Mobile megafaunal activity monitored with

458   a time-lapse camera in the abyssal North Pacific. Deep-Sea Research I. 40, 2307-2324

459   Smith Jr, K. L., Holland, N. D., Ruhl, H. A., 2005. Enteropneust production of spiral fecal trails on the

460   deep-sea floor observed with time-lapse photography. Deep-Sea Research I. 52, 1228-1240

461   Stordal, M. C., Johnson, J. W., Guinasso Jr, N. L., Schink, D. R., 1985. Quantitative evaluation of

462   Bioturbation rates in deep ocean sediments. II. Comparison of rates determined by ^{210}Pb and ^{239,}

463   ^{240}Pu. Marine Chemistry. 17, 99-114

464   Suckow, A., Treppke, U., Wiedicke, M. H., Weber, M. E., 2001. Bioturbation coefficients of deep-sea

465   sediments from the Peru Basin determined by gamma spectrometry of ^{210}Pb$_{exc}$. Deep-Sea Research

466   II. 48, 3569-3592

467   Teal, L. R., Bulling, M. T., Parker, E. R., Solan, M., 2008. Global Patterns of bioturbation intensity and

468   mixed depth of marine soft sediments. Aquatic Biology. 2, 207-218

469   Thomson, J., Brown, L., Nixon, S., Cook, G. T., MacKenzie, A. B., 2000. Bioturbation and Holocene

470   sediment accumulation fluxes in the north-east Atlantic Ocean (Benthic Boundary Layer experiment

471   sites). Marine Geology. 169, 21-39

472   Turnewitsch, R., Witte, U., Graf, G., 2000. Bioturbation in the abyssal Arabian sea: influence of fauna

473   and food supply. Deep-Sea Research II. 47, 2877-2911

474   Uchman, A., 2007. Deep-Sea Ichnology: Development of Major Concepts. In, Miller III, W., (ed.) 2007.

475   Lebensspuren Fossils: Concepts, Problems, Prospects.

476   Vardaro, M. F., Ruhl, H. A., Smith Jr, K. L., 2009. Climate variation, carbon flux, and bioturbation in

477   the abyssal North Pacific. Limnology & Oceanography. 54, 2081-2088

478   Wheatcroft, R. A., Smith, C. R., Jumars, P. A., 1989. Dynamics of surficial Lebensspuren assemblages

479   in the deep sea. Deep-Sea Research. 36, 71-91

480   Yingst, J. Y., Aller, R. C., 1982. Biological Activity and Associated Sedimentary Structures in Hebble-

481   Area deposits, Western North Atlantic. Marine Geology. 48, 7-15

482   Young, D. K., Jahn, W. H., Richardson, M. D., Lohanick, A. W., 1985. Photographs of Deep-Sea

483   Lebensspuren: A comparison of sedimentary provinces in the Venezuela Basin, Caribbean Sea.

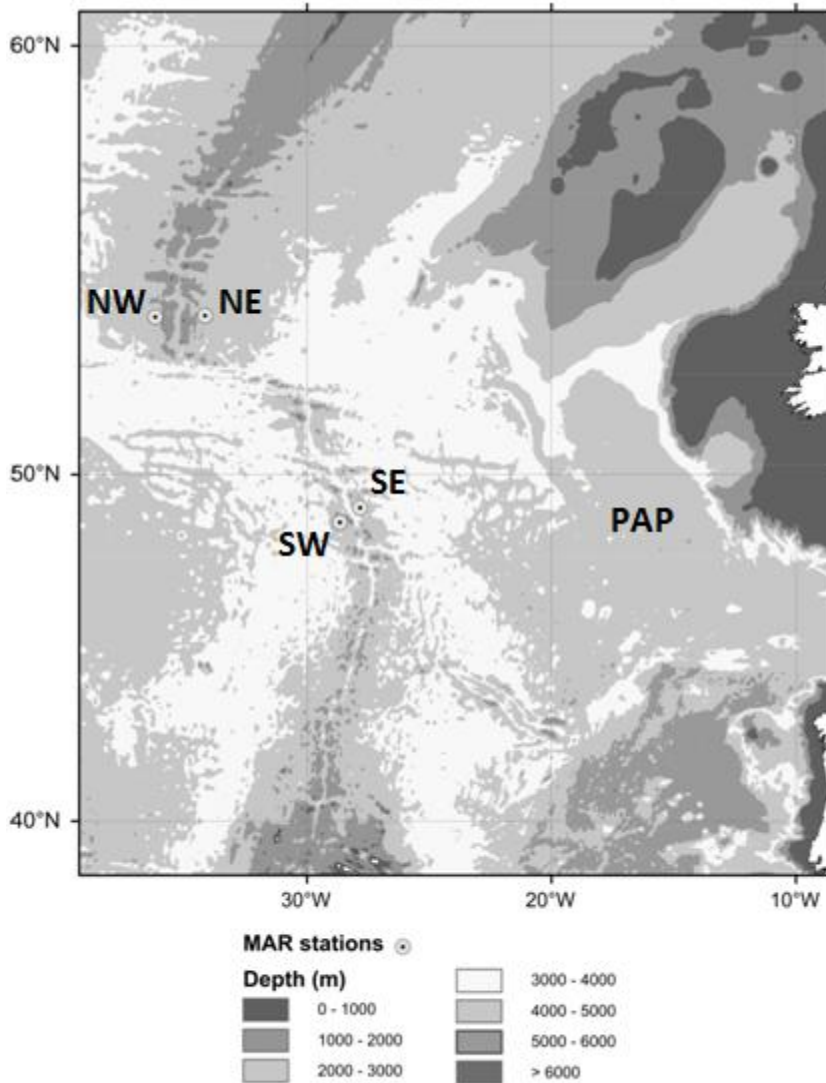484   Marine Geology. 68, 269-301

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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.

NW   NE

SW   SE

Legend:
- ■ Indeterminate
- ▨ Holothurian
- ▥ Enteropneust
- ▯ Echinoid
- ▦ Other
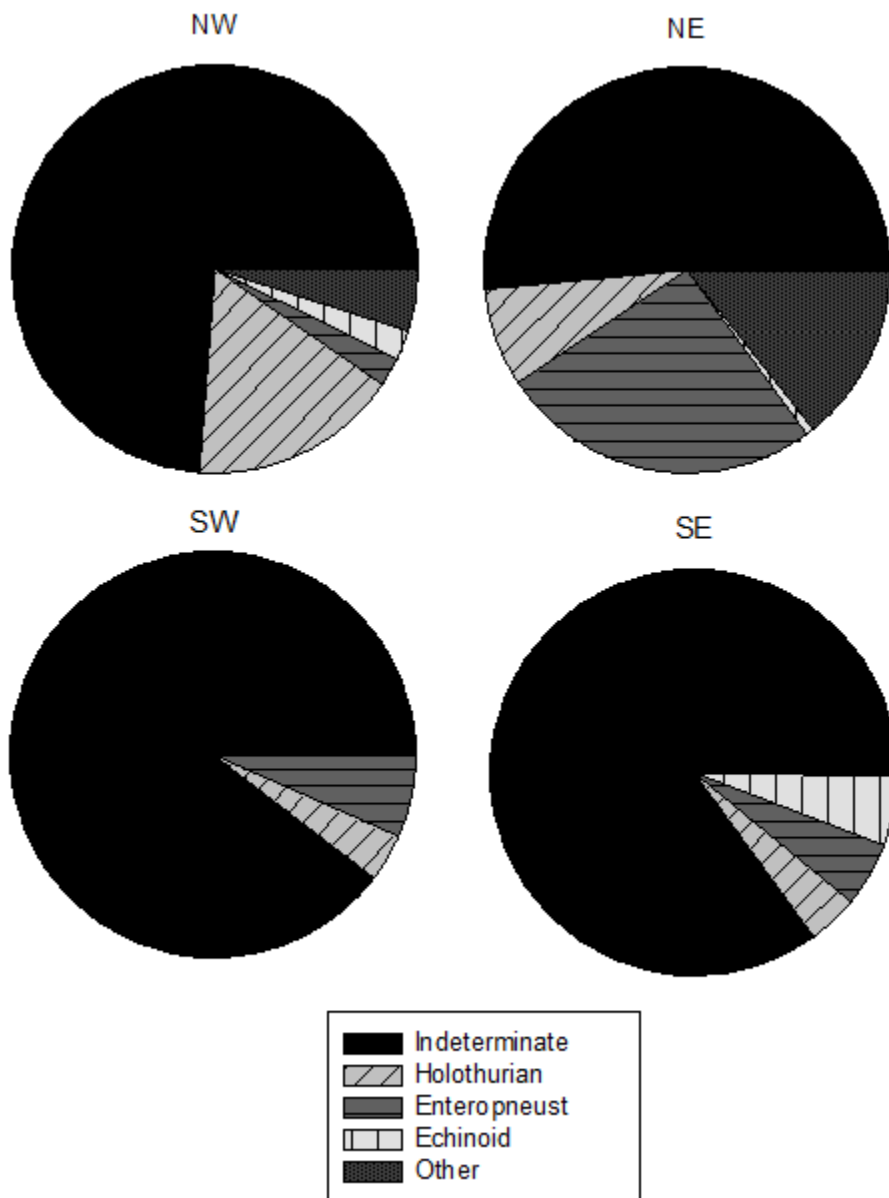
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511   **Fig. 3** (above) – Pie chart array explaining the relative contribution of major taxonomic groups to the

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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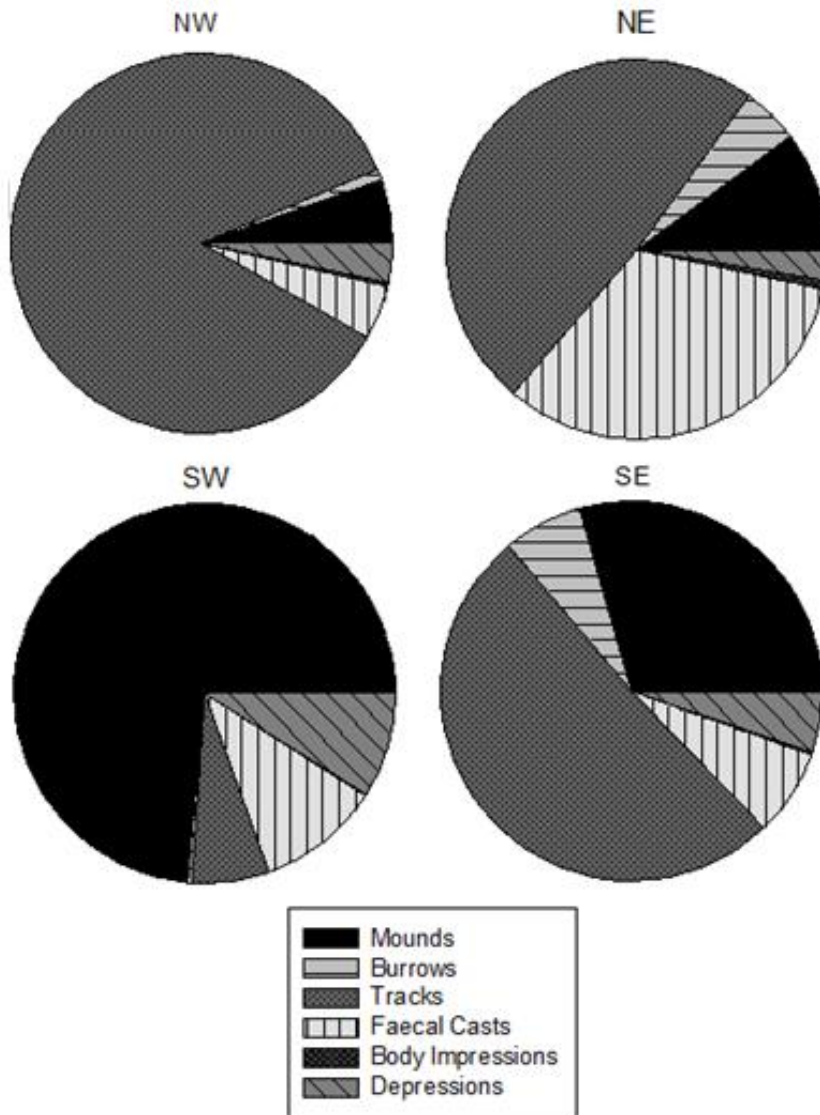
Fig. 4 (above) – Pie chart array explaining the contribution of lebensspuren types (by area) grouped

into functional morphology (i.e. lebensspuren is categorised by its method of formation).

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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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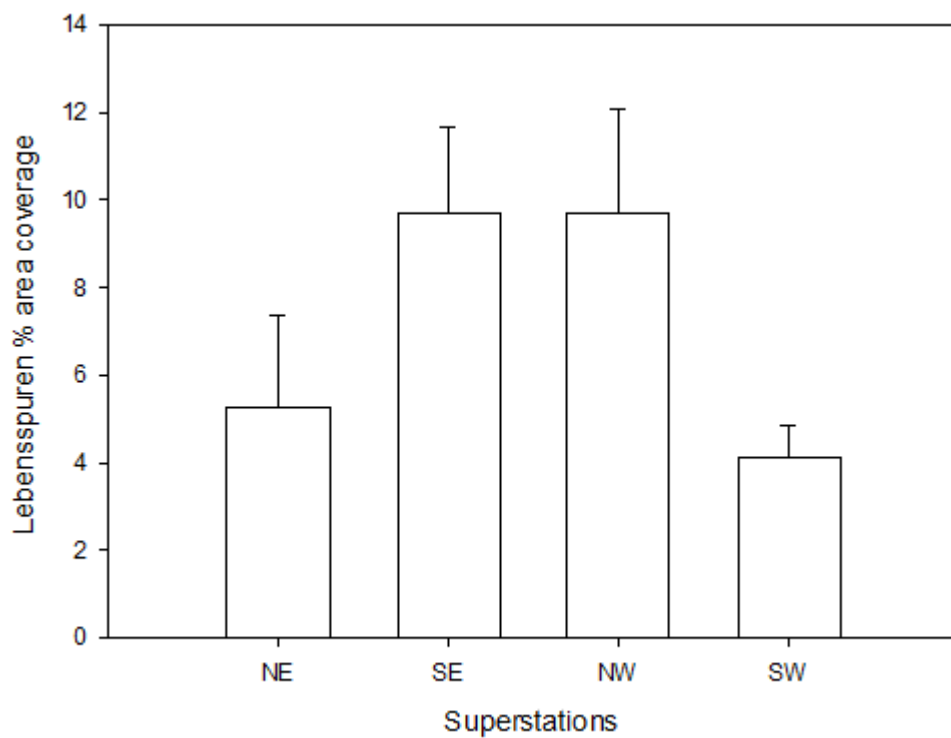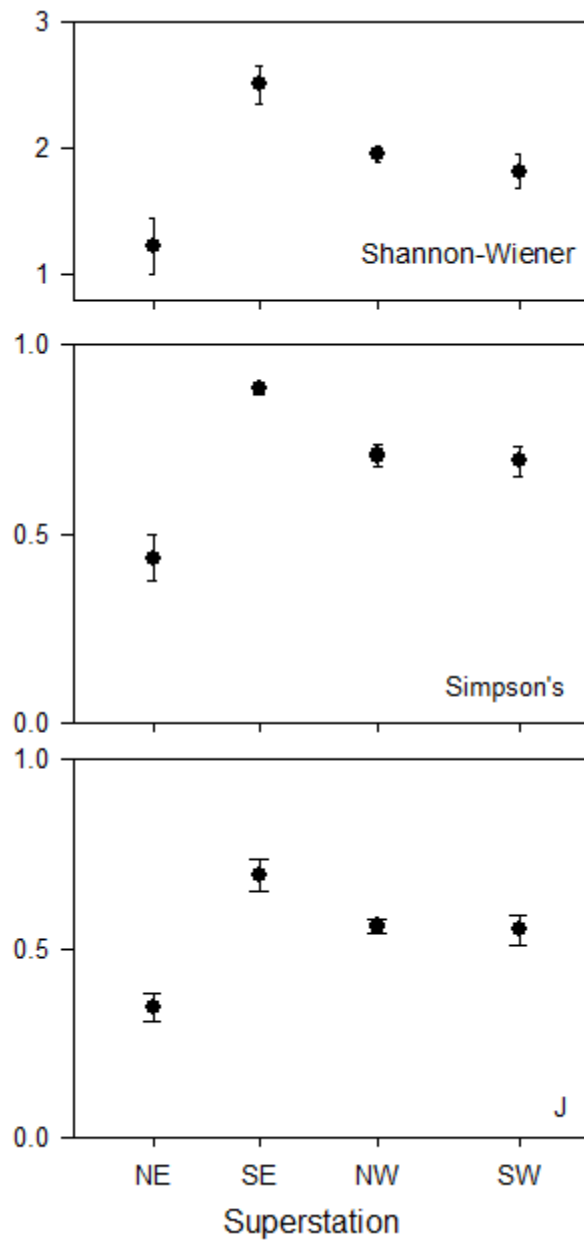
Fig 6 – Comparison of mean diversity indices (Shannon-wiener, Simpson's & J') grouped by

superstation, where each lebensspuren type is regarded as a different species. Error bars represent

1s.d. of the four transect mean.

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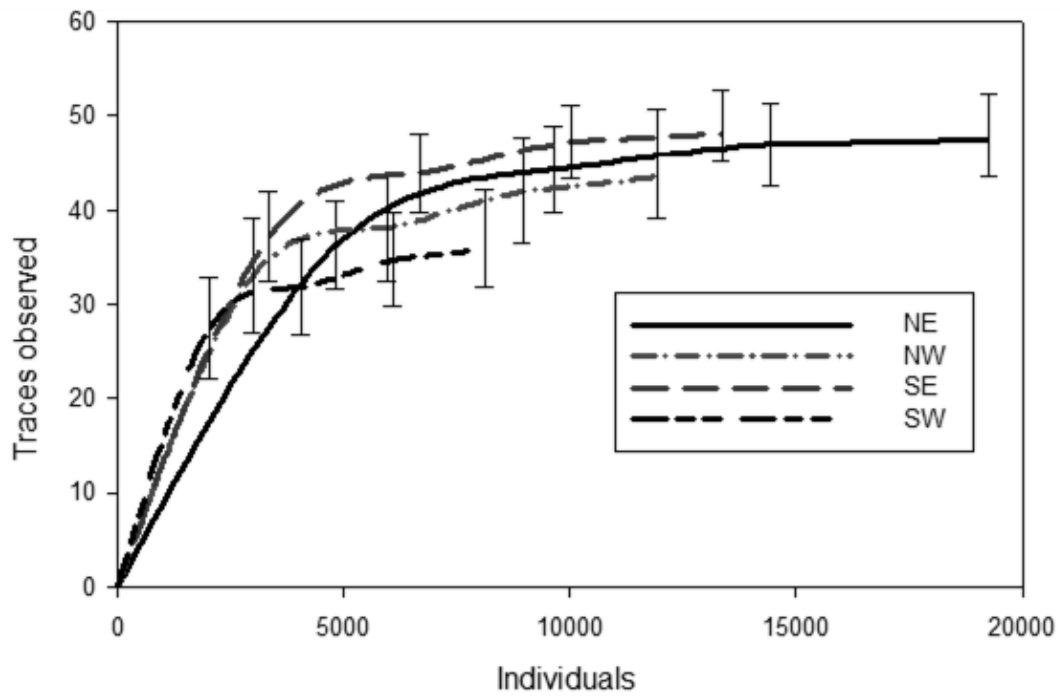
Fig. 7 – Species-accumulation curves (treating each lebensspuren type as a species), grouped by superstation. Standard number of permutations (50) were used to construct these curves. Error bars represent 95% confidence intervals.

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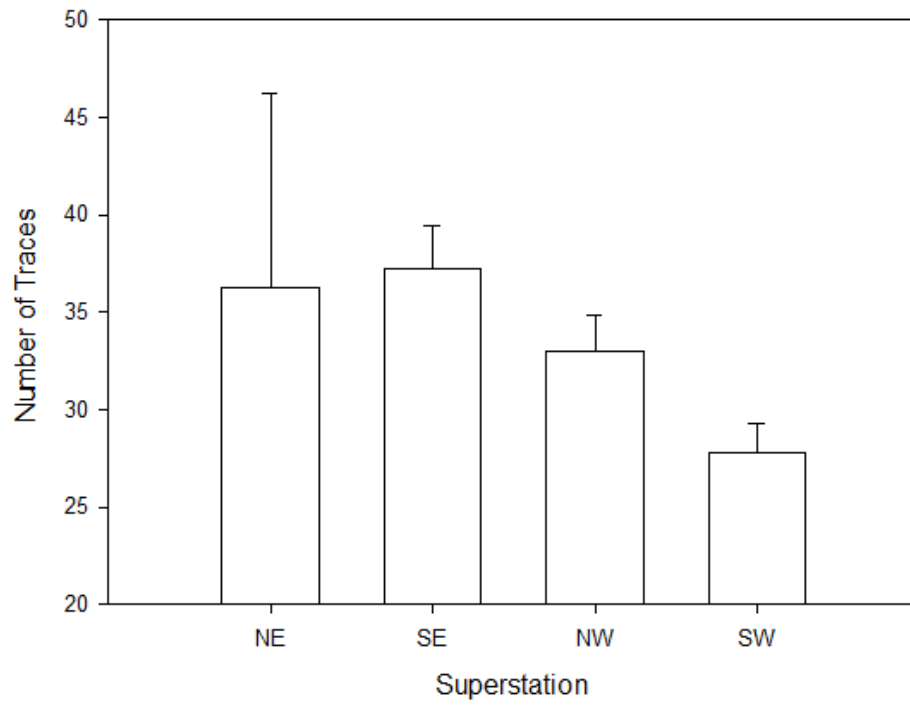
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535   **Fig. 8** – Number of lebensspuren types measured at each superstation. Error bars represent ±1 s.d.

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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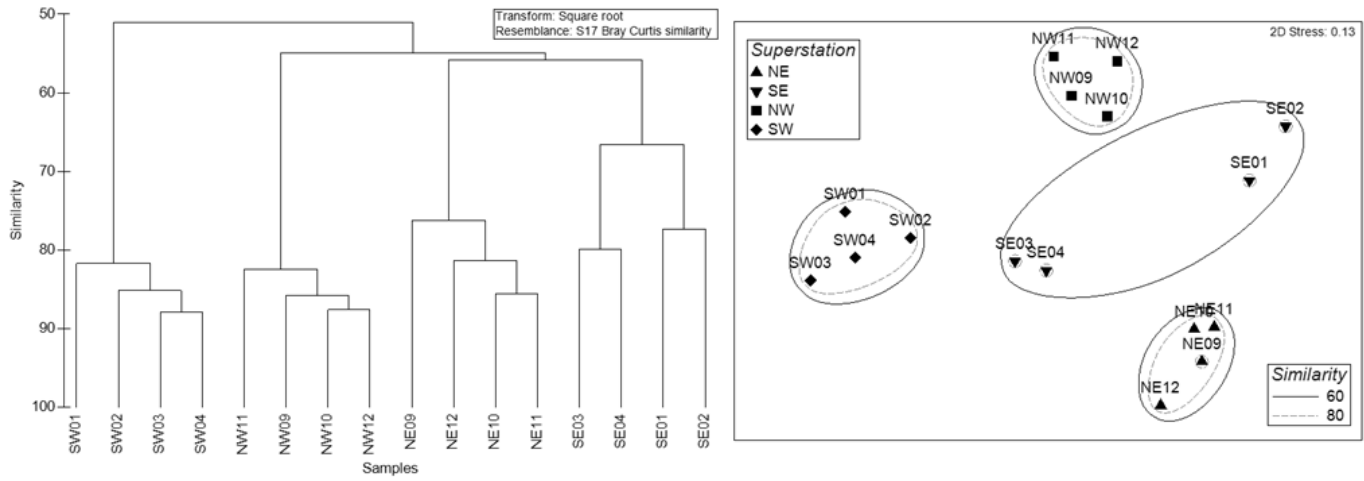
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540 **Fig. 9** – Multivariate similarity of the abundances of lebensspuren types at each of the 16 transects

541 (4 per superstation). Presented as hierarchical cluster diagram (left) and multi-dimensional scaling

542 ordination (right).

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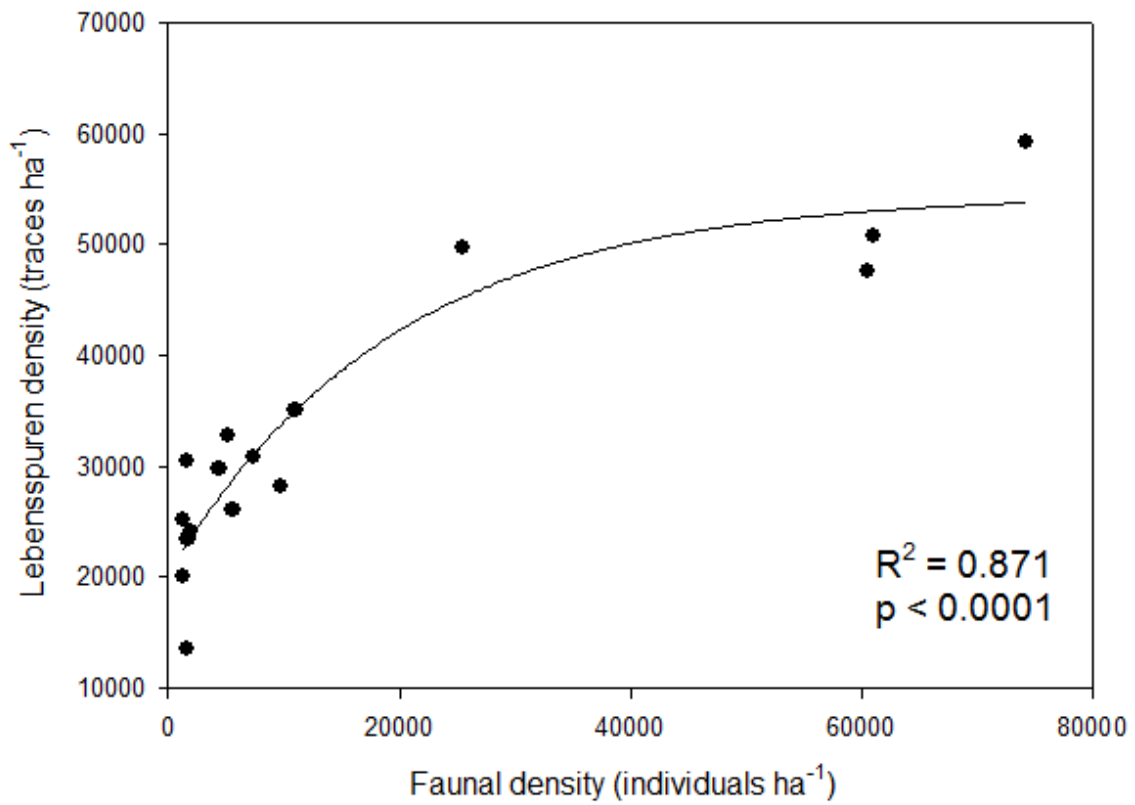
Fig. 10 (above) – Lebensspuren density vs. lebensspuren-forming epifaunal density. Grey lines
represent 95% CI of curve. Fitted line R^2 and significance value (ANOVA df = 15) are displayed.

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	Taxa/ lebensspuren type	NE		SE	
		Area (m²)	Abundance	Area (m²)	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

	Taxa/ lebensspuren type	NW Area (m²)	NW Abundance	SW Area (m²)	SW Abundance
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 (m²)	Abundance	Area (m²)	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 (m^2),

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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