



1 **Approaching the diversity and density dilemma of the lebensspuren-tracemaker**
2 **tandem: a study case from abyssal Northwest Pacific**

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16 **Abstract**

17 In the deep-sea, the interaction between benthic fauna and substrate mainly occurs
18 through bioturbational processes which can be preserved as traces (i.e., lebensspuren).
19 Lebensspuren are common features of deep seafloor landscapes and usually more
20 abundant than the organism that produce them (i.e., tracemakers), rendering them
21 promising proxies to infer biodiversity. The density and diversity relationships between
22 lebensspuren and benthic fauna are to the present day unclear and contradicting
23 hypotheses have been proposed suggesting negative, positive, or even null correlations.
24 To test these hypotheses, in this study lebensspuren, tracemakers (specific epibenthic
25 fauna that produce these traces), degrading fauna (benthic fauna that can erase
26 lebensspuren), and fauna in general were characterized taxonomically at eight deep-sea
27 stations in the Kuril Kamchatka Trench area. No general correlation (over-all study area)
28 could be observed between diversities of lebensspuren, tracemakers, degrading fauna and
29 fauna. However, a diversity correlation was observed between specific stations, showing
30 both negative and positive correlations depending on: 1) the number of unknown



31 tracemakers (especially significant for dwelling lebensspuren); and 2) the lebensspuren
32 with multiple origins; and 3) tracemakers that can produce different lebensspuren.
33 Lebensspuren and faunal density were not correlated. However, lebensspuren density was
34 either positively or negatively correlated with tracemaker densities, depending on the
35 lebensspuren morphotypes. A positive correlation was observed for resting lebensspuren
36 (e.g., ophiuroid impressions, Actinaria circular impressions), while negative correlations
37 were observed for locomotion-feeding lebensspuren (e.g., echinoid trails). In conclusion,
38 lebensspuren diversity may be a good proxy for tracemaker biodiversity when the
39 lebensspuren-tracemaker tandem can be reliably characterized; and lebensspuren-density
40 correlations vary depending the specific lebensspuren residence time, tracemaker density
41 and associated behaviour (rate of movement), but on a global scale abiotic and other biotic
42 factors may also play an important role.

43 **Introduction**

44 Neoichnology studies the interactions between animals and substrates (i.e., bioturbation
45 processes) in modern environments as well as their final products, the so-called
46 lebensspuren (German for “life traces”; e.g., faecal casts, trails, mounds, burrows) (Ewing
47 and Davis, 1967; Gage and Tyler, 1991). Lebensspuren are highly precise portraits of the
48 diverse linkages between environmental conditions and the animal responses to them.
49 Thus, neoichnological analysis provides a useful tool set to infer environmental factors
50 not only in contemporary environments but also deliver evidences to past environments
51 through comparison between lebensspuren and trace fossils (Buatois and Mángano,
52 2011). However, neoichnology as a field is not yet as developed as paleoichnology (i.e.,
53 trace fossil research), and most quantitative studies are restricted to shallow marine
54 environments and tank experiments (e.g., shoreface, foreshore, marginal marine settings)
55 (La Croix et al., 2022 and references therein). Even though the abyssal zone (i.e., 3500-



56 6500 m deep) represents the largest marine ecosystem and covers approx. 75% of the
57 seafloor (Ramirez-Llodra et al., 2010; Watling et al., 2013), neoichnological analyses are
58 scarce and limited, mainly due to the cost of observation and sampling procedures (e.g.,
59 Heezen and Hollister, 1971; Przeslawski et al., 2012; Bell et al., 2013; Miguez-Salas et
60 al., 2022). Thus, neoichnological analyses emerge as a promising tool to enhance our
61 understanding of deep-sea environments and faunal-sediment interactions.

62 Diversity and density analyses are two main components of quantitative marine
63 ecological research (Halpern and Warner, 2002). Deep-sea neoichnological studies have
64 addressed diversity and density characterizations by considering all identified
65 lebensspuren morphotypes as “species” (Przeslawski et al., 2012; Bell et al., 2013).
66 However, tracemaker (i.e., the benthic organisms that produce the observed lebensspuren)
67 diversity and density have been approached from a generalist perspective as megafauna,
68 epifauna, or lebensspuren-forming epifauna (Young et al., 1985; Dundas and Przeslawski,
69 2009; Przeslawski et al., 2012; Bell et al., 2013).

70 Early deep-sea neoichnological studies suggested that lebensspuren diversity is
71 proportional to faunal diversity (Kitchell et al., 1978, Young et al., 1985). However, more
72 recent studies have shown no correlation between epifaunal and lebensspuren richness
73 (Przeslawski et al., 2012) and that lebensspuren diversity was not similar to that of
74 epifaunal lebensspuren-forming diversity (Bell et al., 2013). Bell et al. (2013) stated that
75 “improvements in imaging technology allow more refined classification of lebensspuren
76 and species, which may affect the strength of the correlation between faunal and
77 lebensspuren diversity, compared with the more direct proportionality of faunal and
78 lebensspuren diversity demonstrated in earlier studies”. Thus, in deep-sea research,
79 diversity comparisons based on more precise taxonomic tracemaker identification and



80 differentiation are a pending task, promising a deeper understanding of the dependencies
81 between fauna and lebensspuren variability.

82 In the case of lebensspuren density, early studies revealed an inverse relationship with
83 faunal density (Kitchell et al., 1978, Young et al., 1985; Gerino et al., 1995). These studies
84 suggested that this relationship is related to the fact that lebensspuren formed in low
85 biomass regions have the capacity to persist for a long time (high residence time),
86 ultimately leading to a steady increase of the lebensspuren density through accumulation.
87 Nevertheless, recent data seemed to conflict with this initial assumption. Przeslawski et
88 al. (2012) observed that lebensspuren and epifaunal abundance do not have any
89 relationship; and, contrastingly, Bell et al. (2013) found a strong positive relationship
90 between lebensspuren and faunal densities (see Fig. 10 in Bell et al., 2013). These newer
91 results show that megafaunal activity may not be the only significant factor for
92 lebensspuren destruction or preservation. Small scale biotic factors (e.g., microbial
93 degradation), as well as abiotic factors (e.g., hydrodynamic regimes, sedimentations rates,
94 sediment composition) may limit lebensspuren residence time and density (Wheatcroft et
95 al., 1989; Smith et al., 2005; Miguez-Salas et al., 2020). In summary, strong variability
96 in the few previous studies and conflicting conclusions drawn from these highlight that
97 neoichnology and its fundamental concepts are still in their infancy.

98 Despite the presence of many lebensspuren on the deep seafloor (Heezen and Hollister,
99 1971), very few organisms are recognized in the process of forming these features. Thus,
100 understanding the density-diversity relationship between lebensspuren and benthic
101 megafauna may help decipher variability of the former indirectly (i.e., without having
102 seen the organisms). The research presented here aims to compare diversities indices and
103 densities of lebensspuren, specific tracemakers, and megabenthic fauna from the
104 Northwest Pacific Abyssal Plain in the direct vicinity of the Kuril Kamchatka Trench



105 (KKT) (Fig. 1). By conducting a detailed classification of both lebensspuren and
106 tracemakers, this research wants to go one step further with the main objective to test
107 previous diversity and density hypotheses about the relationship between the variability
108 of lebensspuren and fauna. The geographic region is well-studied as it has a long research
109 history that began with eleven expeditions onboard of R/V *Vityaz* (Russian expeditions;
110 1949, 1953 and 1966) and was further extended during recent campaigns with R/V *Sonne*
111 (German-Russian expeditions; KuramBio I (2012) and KuramBio II (2016)). All of these
112 expeditions resulted in one of the best taxonomic baseline of the fauna (e.g., Zenkevitch
113 et al., 1955, Zenkevitch, 1963; Belyaev, 1983; Brandt and Malyutina, 2015; Brandt et al.,
114 2020; Saeedi and Brandt, 2020 among others).

115 **Material and methods**

116 *Study sites, data acquisition, and video analysis*

117 The joint German–Russian expedition KuramBio 1 (Kurile Kamchatka Biodiversity
118 Studies) on board of the RV *Sonne* (cruise SO223) to the Kuril–Kamchatka Trench and
119 adjacent abyssal plain took place between July 21st and September 07th 2012 (Brandt
120 and Malyutina, 2012). During the expedition, 13 Ocean Floor Observation System
121 (OFOS) deployments were conducted (Table 1) to study eleven deep-sea stations between
122 34°–48°N and 147°–157°E (Fig. 1) with video cameras. Stations 3 and 4 were located at
123 the upper slope of the KKT, and stations 1, 2, and 5–11 in the adjacent abyssal plains
124 (Fig. 1). The depths of the stations ranged from 4,868 m to 5,768 m.

125 The OFOS was lowered into the water at the CTD position. The first 300 meters lowering
126 was conducted with 0.5 m/s, and then the speed was increased to 0.8 m/s while the ship
127 was kept in position. At 500 meters above ground, the speed was reduced to 0.5 m/s, and
128 further reduced to 0.3 m/s at 200 meters above ground. As soon as visual contact with the
129 bottom was established, the winch was stopped. The ship started moving with 0.5 knots



130 above ground in the appropriate direction, which was chosen depending on the current
131 and wind situation. Then, the winch operator manually kept the OFOS at an appropriate
132 distance from the seafloor to observe the seafloor benthos. Two laser pointers having a
133 distance of 10 cm between each other were used as a scale. The first four deployments
134 were aborted due to technical problems, affecting stations 1–3 (Table 1). Thus, limited
135 video footage was obtained. Moreover, station 7 has no HD video (i.e., this station is not
136 considered for the current analysis). All technical work, including preparation before and
137 caretaking after (including video download) the deployment was conducted by the
138 scientific-technical service (“WTD”, Wissenschaftlich-Technischer Dienst, Jörg Leptien,
139 Reederei).

140 At each station, still images were extracted from the OFOS videos at a rate of one frame
141 per five seconds. These still images were subsequently further sub-sampled to delete
142 frames that were out of focus — as the rolling of the ship in the ocean swell resulted in
143 an up and down movement of the OFOS — and to reduce overlap between frames. Then,
144 50 randomly selected frames per station were studied (400 still images in total), covering
145 a seafloor area of 878 m² (109 m² per station approx.). These still images were uploaded
146 to the BIIGLE 2.0 software for later annotation and measurements (Langenkämper et al.,
147 2017). Specific frames were treated with Fiji software (Schindelin et al., 2012) to enhance
148 the visibility (CLAHE tool) of certain lebensspuren features (Miguez-Salas et al., 2019).

149 *Lebensspuren classification and tracemaker identification*

150 Lebensspuren morphotypes were categorized in terms of inferred tracemaker behaviour
151 during the construction, morphology, and tracemaker taxonomic origin. The behavioural
152 classification was adapted from Seilacher’s (1954) categories for marine lebensspuren: i.
153 Resting (imprints of stationary animals); ii. Locomotion-feeding (sediment displaced by
154 the movement of deposit feeders and surface sediment disturbances formed as organisms



155 are foraging); iii. Wasting (e.g., faecal casts, pellets); and iv. Dwelling (e.g., mounds and
156 burrows). Morphological features measured included in the classification were length,
157 width, and diameter. Lebensspuren with unclear morphology and origin (e.g., degraded
158 faecal casts, trails with diffuse outlines) were not considered in this study. Also, as the
159 resolution of the still images is below high-definition (<1280x720 pixels) lebensspuren
160 and fauna smaller than 1 cm (macrofauna and smaller) have not been considered in this
161 study. Hence, this study focusses on megafauna (i.e., fauna > 1 cm) which is implied
162 throughout this study when fauna is mentioned from hereon.

163 Open nomenclature has been used for megafauna taxonomic identification following the
164 recommendations for image-based identifications proposed by Horton et al. (2021). All
165 differentiated morphotypes are henceforward referred to as “species” for simplicity.
166 Then, fauna has been grouped into different categories for comparisons with the diversity
167 and density of lebensspuren: 1) tracemakers (fauna that has been clearly recognized as
168 maker of a trace); 2) degrading fauna (fauna that can affect lebensspuren density
169 negatively by eroding the seafloor); and 3) benthic fauna (all fauna identified in the still
170 images).

171 *Statistical analysis*

172 For statistical analysis, all identified lebensspuren and fauna morphotype were treated as
173 “species”. Diversity indices (Shannon–Wiener H' (\log_e) and Simpson’s D) and evenness
174 (J') were calculated for the four groups: lebensspuren, tracemaker fauna, degrading fauna,
175 and fauna. As the data from all groups show non-parametric distribution throughout all
176 stations, diversity variability among stations was tested using Wilcoxon signed-rank test
177 (considering all groups and all indices). Then, the Spearman rank correlation was used to
178 test the relationships between the diversity indices of all groups.



179 For density correlations (Spearman rank correlation), since the number of frames was the
180 same (i.e., same observation area), the analyses were conducted considering the total
181 density per station of all groups individually. Additionally, lebensspuren and tracemakers
182 densities were subdivided into wasting, resting and locomotion-feeding (dwelling was not
183 considered because the tracemakers of most dwelling lebensspuren are unknown).

184 To investigate potential differences within the four groups (lebensspuren, tracemakers,
185 degrading fauna, and total benthic fauna) between stations, multivariate analysis was
186 conducted. First, a square root transformation was carried out to give less weight to the
187 more abundant species and lebensspuren. Then, differences in the composition of the four
188 groups between stations were assessed using hierarchical cluster analysis and displayed
189 as non-metric multidimensional scaling plots (n-MDS). Both plots were constructed using
190 the Bray–Curtis similarity index. All statistical procedures were conducted using PAST
191 v. 4.12 (Hammer, 2001).

192 **Results**

193 A total of 9,426 lebensspuren were identified and classified from 400 still images,
194 corresponding to 23 morphotypes associated with dwelling, wasting, resting, and
195 locomotion-feeding behaviours (Fig. 2; Table 2). The fauna comprised a total of 4,009
196 individual animals that were classified into 93 different species, of which 66 were
197 classified as degrading fauna and 43 as tracemakers (with 790 and 676 individuals
198 respectively) (Table 3; Supplementary file 1). Linking dwelling lebensspuren with
199 tracemakers was mostly impossible except for rare and ambiguous cases where
200 vermiform organisms, most likely polychaetes, partially emerged from paired burrows
201 (Fig. 2P). Tracemaker identification was possible in the majority of the cases for wasting
202 lebensspuren, however, it is common that different tracemakers produce the same
203 lebensspuren morphotypes and that several morphotypes of lebensspuren are produced



204 by one tracemaker species (see Table 2). However, in the case of cf. *Elpidia* — the most
205 abundant tracemaker of station 4 (see Supplementary file 1) — the complete
206 characterization of its associated rounded faecal cast (smaller than 1 cm) was impossible
207 due to image resolution limitations. Tracemaker identification of locomotion-feeding
208 lebensspuren was mostly possible except for mounded trails which have been produced
209 by endobenthic organisms. However, as for wasting lebensspuren, also in this case
210 different tracemakers can be responsible for similar trails (see Table 2). Tracemaker
211 identification of resting lebensspuren has been possible in most cases.

212 The Wilcoxon signed-rank test revealed that for all groups the median diversity was
213 significantly different between stations, being lower at stations 9 and 11 (Fig. 3).
214 Moreover, faunal diversity showed a standard deviation three orders smaller than the
215 values reported for lebensspuren, tracemakers, and degrading fauna. Lebensspuren
216 diversity indices (Shannon–Wiener, Simpson’s and Evenness) of the over-all KKT area
217 (considering all the eight stations together) showed no correlation with the other three
218 groups (tracemakers, degrading fauna, and benthic fauna). The only strong diversity
219 correlation resulting from the Spearman rank analysis was between tracemakers and
220 degrading fauna ($R^2 > 0.88$, $p < 0.01$).

221 The density correlation matrix revealed no significant correlation between the fauna and
222 the other groups (see Fig. 4). The degrading fauna showed a positive correlation with
223 tracemaker and wasting tracemakers densities. Also, tracemakers and wasting
224 tracemakers densities are positively correlated (Fig. 4). In case of the lebensspuren data,
225 a positive density correlation was obtained between lebensspuren and wasting
226 lebensspuren as well as resting lebensspuren and resting tracemakers while a negative
227 correlation was observed for locomotion-feeding lebensspuren and their tracemakers
228 (Fig. 4).



229 Inter-station similarity of lebensspuren assemblage composition was generally high (Fig.
230 5 A), ranging from 75–82% similarity in the cluster analysis. The n-MDS showed that
231 lebensspuren assemblages from stations 5, 6, 8, and 10 are different from the trench
232 (stations 3 and 4) and the southern stations (stations 9 and 11) (Fig. 6 A). The southern
233 stations were less diverse, similar (82% similarity; Fig. 5A) and dominated by rounded
234 faecal casts produced by *Scotoplanes* spp. The trench stations were characterised by
235 diverse and slightly less similar assemblages (75% of similarity) dominated by dwelling
236 lebensspuren (e.g., paired, lined or cluster burrows), knotted faecal casts (*Peniagone*
237 spp.), ophiuroid impressions (Ophiuroidea), circular impressions (Actinaria) and thick M-
238 trails (Asteoridae and *Echinocrepis* spp.). Stations 5, 6, 8, and 10 showed diverse
239 lebensspuren assemblages dominated by smooth (cf. *Benthodytes*, *Psychropotidae*) and
240 coiled faecal casts (*Psychropotidae*), rosette-shaped traces and thick flat trails
241 (Asteoridae, cf. *Benthodytes*, *Psychropotidae*) (Fig. 6 A).

242 The hierarchical cluster diagram for tracemakers, degrading fauna and fauna showed less
243 similarity between stations than it was the case for lebensspuren, especially for
244 tracemakers and degrading fauna (values ranging from 20–55% similarity in the cluster
245 analysis) (Fig. 5 B–D). However, the trench stations (Stations 3 and 4) and the southern
246 stations (Stations 9 and 11) seemed to have similar compositions respectively. The low
247 inter-station similarity of tracemakers, degrading fauna and fauna assemblages was also
248 reflected in the n-MDS plots where the spacing between stations was considerably higher
249 than in the lebensspuren plot (Fig. 6 B–D).

250 Discussion

251 The obtained results from the KKT area reveal that the relationship between lebensspuren,
252 tracemakers, and fauna may be more complicated than previously hypothesized. On the
253 one hand, a general null diversity correlation has been observed between lebensspuren,



254 tracemakers and fauna. On the other hand, density correlations seem to be morphospecific
255 (e.g., depending on the lebensspuren-associated behaviour). But to what extent do the
256 obtained results contradict or corroborate previous results and what are the limitations
257 when addressing the diversity and density of lebensspuren?

258 *Fauna, tracemakers and lebensspuren diversity: a complex relationship*

259 Previous comparisons between lebensspuren and faunal diversity have given rise to
260 different contrasting hypotheses. Pioneering research showed positive correlations (e.g.,
261 Kitchell et al., 1978, Young et al., 1985). Later on, several studies showed no correlation
262 at all (e.g., Tilot, 1995; Turnewitsch et al., 2000; Przeslawski et al., 2012). All these
263 studies have in common that the diversity comparison was addressed from a general
264 perspective, especially for tracemaker organisms. Comparisons were done either
265 considering megafaunal species (Young et al., 1985), epifaunal species (Przeslawski et
266 al., 2012) or certain taxonomic groups of organisms (e.g., fish, holothurians, crinoids;
267 Kitchell et al., 1978). Only Bell et al. (2013) approached the comparison between
268 lebensspuren and fauna in greater detail considering groups of lebensspuren-forming
269 epifauna and using indices to quantify lebensspuren diversity (e.g., Simpson, Shannon-
270 Wiener), discovering that “Lebensspuren diversity was generally high and not similar to
271 that of lebensspuren-forming faunal diversity”. However, the links between specific
272 tracemakers and their lebensspuren and the subsequent tracemaker diversity indexes are
273 missing in Bell et al.’s (2013) study. In this study we have tried to close this knowledge
274 gap by comparing the lebensspuren diversity with not only the faunal diversity but also
275 the tracemaker and degrading fauna (i.e., fauna that may alter the lebensspuren
276 assemblage by erosion/degradation). Our results show that lebensspuren diversity
277 (Simpson, Shannon-Wiener, and Evenness) is not related to fauna, tracemaker or
278 degrading fauna diversity. This finding seems to corroborate the latest results of a non-



279 existent correlation (Przeslawski et al., 2012; Bell et al., 2013), but can this lack of
280 correlation be expected in all deep-sea settings?

281 Before answering this question, the limitations of quantifying deep-sea lebensspuren
282 diversity should be considered. There are several problems when it comes to quantifying
283 lebensspuren diversity (e.g., image resolution, camera systems, unknown tracemakers,
284 observation scale, trace degradation), but the most important is linked to their genesis. In
285 other words, the same lebensspuren morphotypes (or indistinguishable lebensspuren) can
286 be produced by different tracemakers and one tracemaker can produce different
287 lebensspuren (see Table 2). For example, in case of this study, smooth faecal casts could
288 have been produced by different holothurians (e.g., cf. *Pseudostichopus*, *Psychropotes*,
289 *Synallactidae*, *Benthodytes*) and *Psychropotes* can be linked to the production of coiled
290 and smooth faecal casts as well as thick flat trails (Fig. 2G). Thus, when comparing their
291 diversity, the basis that each lebensspuren morphotypes may not be related to one specific
292 species and *vice versa*, should be considered. However, the fact that in our study general
293 lebensspuren diversity did not correlate with tracemaker diversity does not mean that this
294 will be the case in all deep-sea settings if the tracemaker-lebensspuren tandem can be
295 characterised more precisely or tracemakers produce just one specific lebensspuren
296 morphotypes.

297 In our study area, different correlations between tracemakers and lebensspuren could be
298 observed when comparing the diversity among specific stations. For example, when
299 restricting the comparison to the southern stations (stations 9 and 11), a correlation was
300 observed between Simpson and Shannon-Wiener indexes of tracemakers and
301 lebensspuren (Fig. 3). This was due to the fact that the assemblage is dominated by traces
302 for which we have been able to identify the tracemakers (e.g., rounded faecal casts of
303 *Scotoplanes*). On the contrary, when focussing on the trench stations (stations 3 and 4), a



304 negative correlation could be observed between Simpson and Shannon-Wiener indexes
305 of tracemaker and lebensspuren diversities (Fig. 3). This could be attributed to the
306 relatively large gap in our data regarding the origin of most traces of the lebensspuren
307 assemblage (stations 3 and 4 have a high abundance of dwelling lebensspuren (see Table
308 3); single burrows, mounds, cluster burrows for which tracemakers are unknown) and
309 dominant tracemakers (*Elpidia*) whose traces cannot be correctly quantified due to image
310 resolution limitations (small rounded faecal casts).

311 The enhancement of image resolution and the increase of deep-seafloor area covered by
312 still image surveys may allow to improve lebensspuren classification and their tracemaker
313 identification. There is a lot of room for improvement, especially with regard to
314 locomotion and feeding lebensspuren. High definition still images will allow to
315 characterize, for example, small morphological features of trails (e.g., podia marks from
316 asteroids, echinoid spine impressions), allowing for a much more detailed classification
317 than what could be achieved for this study. In the case of dwelling lebensspuren diversity
318 comparison is significantly more complicated because trace morphology is largely hidden
319 below the seafloor surface, reducing the possibility to differentiate between different
320 burrow morphologies while tracemakers are mostly unknown due to a predominantly
321 endobenthic lifestyle (e.g., Brandt et al., 2023). Furthermore, burrows and other dwelling
322 lebensspuren also could potentially have multiple origins (e.g., a paired burrow can be
323 produced by multiple species of polychaetes or bivalves).

324 The fact that the same lebensspuren morphotypes can be produced by different
325 tracemakers and one tracemakers can produce different lebensspuren will affect the
326 establishment of a positive or negative diversity correlation. Also, the existence of
327 unknown tracemakers will contribute to the correlation variability. However, as the
328 obtained results show in specific stations, when the assemblage is dominated by traces



329 with identifiable tracemakers, lebensspuren analysis emerges as a promising tool to
330 predict tracemaker diversity. Despite of these optimistic results, it is fair to say that much
331 more research is needed — with high definition surveys (e.g., videos, images) — to close
332 existent knowledge gaps in the lebensspuren-tracemaker tandem. Moreover, we
333 emphasize that when using lebensspuren as a proxy for biodiversity, the diversity
334 correlation should be made between lebensspuren and tracemakers, rather than with
335 overall benthic fauna as no correlation has been observed in case of comparison with the
336 latter.

337 *Tracemaker and lebensspuren density: morphospecific relationship*

338 The density comparisons between lebensspuren, degrading fauna and total fauna revealed
339 no correlation, similar to previous research (Przeslawski et al., 2012). However, when
340 comparing lebensspuren and tracemakers a positive and negative correlation can be
341 observed (Fig. 4). The density of locomotion-feeding lebensspuren is inversely correlated
342 with their tracemaker density while resting lebensspuren are positively correlated with
343 their tracemakers densities. These group-specific correlations conflict with previous
344 research that showed generally positive (e.g., Bell et al., 2013) or generally negative
345 density correlations (e.g., Kitchell et al., 1978; Young et al., 1985). The difference with
346 these previous studies may be due to the fact that their density comparisons considered
347 the total fauna instead of separate functional groups (see Fig. 10 in Bell et al., 2013), not
348 considering their specific impact on the sediment.

349 Trace residence time is the period during which a trace is recognizable on the sea floor
350 before it is destroyed (Wheatcroft et al., 1989). It is commonly accepted that lebensspuren
351 density values reflect the balance between lebensspuren formation and lebensspuren
352 destruction/degradation either by biotic (e.g., microbial degradation, degrading fauna,
353 epifaunal rate of movement) or abiotic factors (e.g., hydrodynamics, burial) (Wheatcroft



354 et al., 1989). However, not all lebensspuren have the same residence time. Thus, traces
355 not actively maintained by animals are usually ephemeral features with lifespans of days
356 to weeks (e.g., faecal casts can be degraded within 1-2 weeks; Smith et al., 2005) while
357 locomotion-feeding and resting lebensspuren have higher residence time as they are
358 impressions on the seafloor (see Fig. 8 in Wheatcroft et al., 1989 or Fig. 5 in Miguez-
359 Salas et al., 2020). Very little is known about the residence time of dwelling lebensspuren,
360 some tracemakers live inside them for their whole life while others change several times
361 and their burrows get passively filled. Thus a wide range of residence times may be
362 expected. However, in any of the cases since the sedimentation rate is usually low in the
363 deep-sea, dwelling lebensspuren should have higher residence time than wasting
364 lebensspuren and similar or higher than locomotion-feeding and resting lebensspuren.

365 In case of this study the density of locomotion-feeding lebensspuren (e.g., thick M-trails),
366 on the one hand, was inversely correlated with tracemaker density. This could be for two
367 reasons: 1) a high residence time of these lebensspuren while the respective tracemakers
368 may no longer be in the study area; and 2) these lebensspuren represent a foraging
369 behaviour in which the tracemakers tend to continuously search the seabed for food, often
370 over a wide area (i.e., high rate of movement). Thus, a large quantity of lebensspuren may
371 be produced by a single individual tracemaker in continuous movement. The density of
372 resting lebensspuren (e.g., circular impressions, asteroid impressions), on the other hand,
373 was in this study directly correlated with tracemaker density. This is not surprising
374 because even though these lebensspuren have a high residence time, their tracemakers
375 (e.g., asteroids, actinarians) have low rates of movement (Durden et al., 2015; 2019). In
376 such cases, a high density of resting lebensspuren should always be linked to a high
377 density of their tracemakers.



378 The density correlation between wasting lebensspuren and their tracemakers showed a
379 slightly positive but not significant correlation (Fig. 4). Maybe this is due to the fact that
380 in some cases we were not able to quantify the exact number of faecal casts. For example,
381 in station 4, the lebensspuren of the dominant tracemakers (*Elpidia*; more than 150
382 specimens were identified) were not correctly quantified due to image resolution
383 limitations (small rounded faecal casts). Thus, presumably a positive density correlation
384 between wasting lebensspuren and their tracemakers should be expected. However, this
385 assumption may be disturbed by their tracemakers behaviours since their feeding activity
386 can be expected to depend on grain size, availability and quality of the nutrients among
387 other environmental factors (e.g., Jumars and Wheatcroft 1989; Ginger et al., 2001).

388 The observed variability in the lebensspuren density correlations show a complex
389 scenario even without considering biotic and abiotic factors that cannot be characterized
390 through still images. For example, it has been demonstrated that meiofauna and
391 microfauna have the ability to smoothen and eventually fully erase surficial biogenic
392 structures through small scale, grain-by-grain jostling of particles (e.g., Cullen, 1973).
393 These “small” biotic processes are impossible to quantify through images, however, it has
394 to be kept in mind that these will have affected also the lebensspuren density that we
395 quantified for this study. Moreover, previous studies assumed that abiotic lebensspuren
396 degradation rates are constant over the lebensspuren residence time period, but recent
397 studies show that this may not be always true (Miguez-Salas et al., 2020). The effects of
398 abiotic factors on the density of the studied assemblages as well as those of some biotic
399 factors (e.g., microbial degradation which cannot be characterized in a still image) are out
400 of the scope of this research but should be considered in future studies and need to be
401 kept in mind when interpreting seafloor images.

402



403 **Conclusions**

404 The neoichnological analysis of the KKT area reveals a general null diversity correlation
405 between lebensspuren, tracemakers and fauna while density correlations vary depending
406 on the lebensspuren morphotypes. The further conclusions of this study are:

407 The fact that the same lebensspuren morphotypes can be produced by different
408 tracemakers and one tracemakers can produce different lebensspuren will affect the
409 establishment of a positive or negative diversity correlation.

410 The existence of unknown tracemakers will contribute to the diversity correlation
411 variability. However, lebensspuren diversity may be a good proxy for tracemaker
412 biodiversity when the lebensspuren-tracemaker tandem can be reliable characterized.

413 Lebensspuren density can be positively or negatively correlated with tracemaker
414 densities depending on the specific lebensspuren residence time and tracemaker
415 behaviour (e.g., locomotion, resting).

416 Lebensspuren-density correlations may be control on a global scale by abiotic
417 (e.g., hydrodynamics, grain size, organic matter) and biotic factors (e.g., microbial
418 degradation).

419 **Acknowledgments**

420 Special thanks to the German Federal Ministry of Education and Research (BMBF) for
421 funding this project (PTJ, Grant 03G0223A to A. Brandt). We also thank the crew of *R. V.*
422 *Sonne*. We thank the Russian coordinator of the expedition M. Malyutina. The research
423 of O. Miguez-Salas was funded by a Humboldt Postdoctoral Fellowship from the
424 Humboldt Foundation. This is contribution #7 of the Senckenberg Ocean Species
425 Alliance (SOSA).

426

427 **Author's contributions**



428 O.M.S., T.R., performed the data acquisition and treatment. O.M.S., T.R., and A.B., wrote
429 and designed the main manuscript text. O.M.S., H.K., prepared all figures, tables, and
430 supplementary material. All authors reviewed and edited the manuscript at multiple stages
431 and approved it for submission.

432

433 **Availability of materials and data**

434 All data generated or analysed during this study are included in this published article. The
435 raw data used for this study is in the Supplementary Information file.

436

437 **Competing interests**

438 The authors declare no competing interests

439

440 **References**

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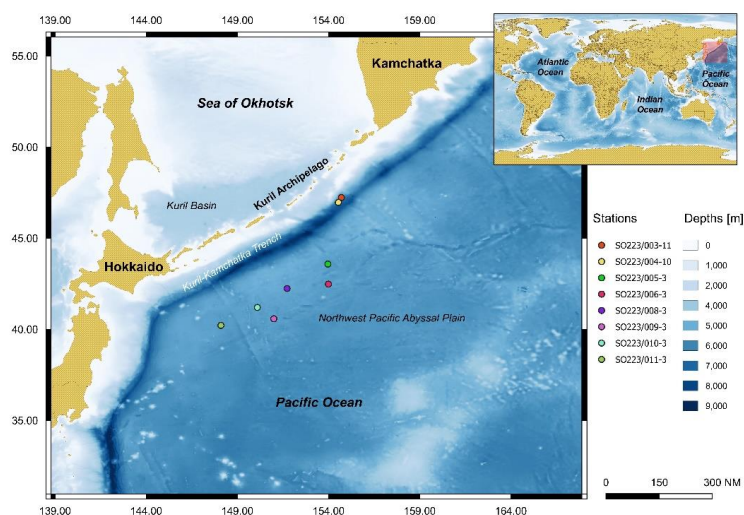


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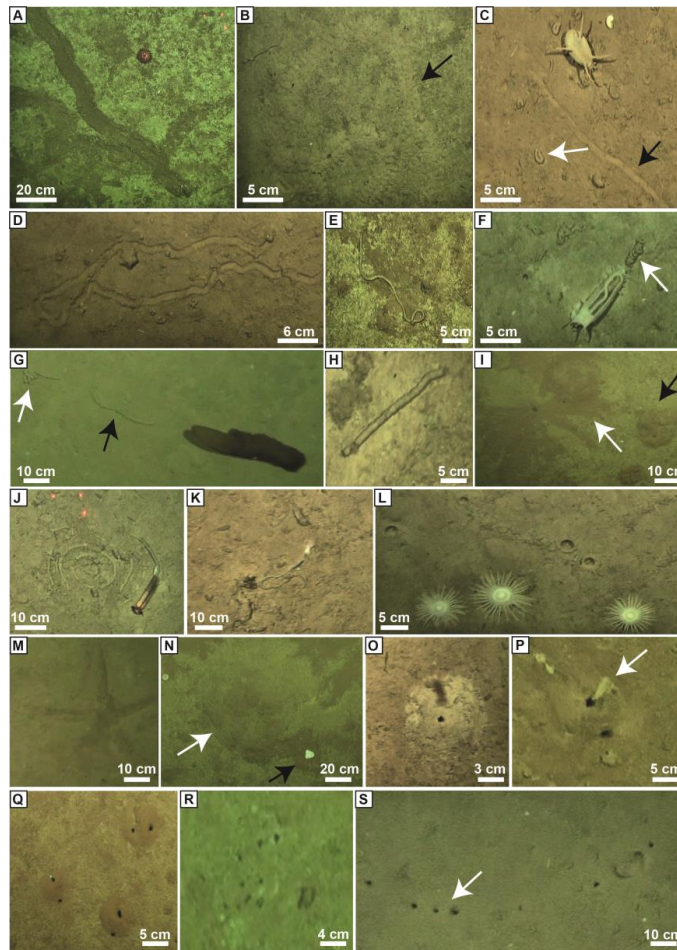
565 **Figure captions**

566 **Fig. 1** Map of the study area (Kuril-Kamchatka Trench area) and the location of the
567 analyzed deep-sea stations.



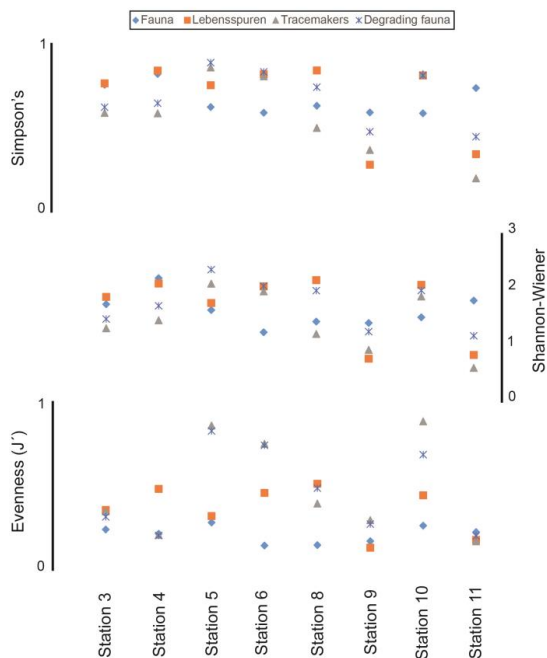
568

569 **Fig. 2** Examples of lebensspuren morphotypes observed and quantified in this study. A)
570 Thick M-trail produced by Asteroidea. fam. gen. sp. 1; B) Mounded trail (unknown
571 tracemaker); C) Thin flat trail (black arrow; unknown tracemaker) and rounded faecal
572 casts (white arrow) produced by *Scotoplanes* sp. 1; D) Thick M-trail produced by
573 Echinoidea. fam. gen. sp. 5; E) Wavy faecal cast produced by *Peniagone* sp.1 to
574 *Peniagone* sp. 3; F) Knotted faecal cast produced by *Peniagone* sp.1 to *Peniagone* sp. 3;
575 G) Coiled (white arrow) and smooth (black arrow) faecal cast produced by *Psychropotes*
576 morphospecies 2; H) Smooth (black arrow) faecal cast produced by various tracemakers
577 (see Table 2); I) Rosette-shape trace (white arrow) produced by an echiuran worm and
578 mound shape nearby (black arrow); J) Spirals faecal cast produced by Enteropneusta gen.
579 sp. 1; K) Switchbacks faecal cast produce by Torquaratoridae. gen. sp. 1; L) Circular
580 impression produce by Actiniaria. fam. gen. sp. 1; M) Asteroid impression produced by
581 an Asteroidea (Asteroidea. fam. gen. sp. 3, 4, 7, 8, 9); N) Mound (white arrow) with a
582 semi-buried asteroidean nearby (black arrow); O) Single burrow located in the apex of a
583 cone-shaped mound; P) Paired burrow with an unidentified organism coming out; Q)
584 Three paired burrows; R) Cluster burrows; S) Lined burrows (black arrow).



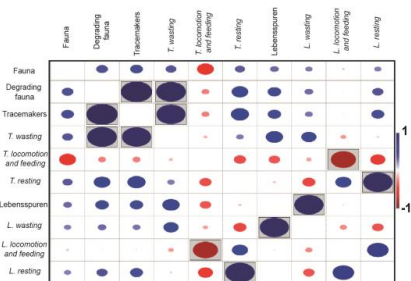
585

586 **Fig. 3** Comparison of median diversity indices (Simpson's, Shannon–Wiener and
587 Evenness) of lebensspuren, tracemakers, degrading fauna and fauna at each station. Each
588 lebensspuren morphotypes was considered a different species for calculations.



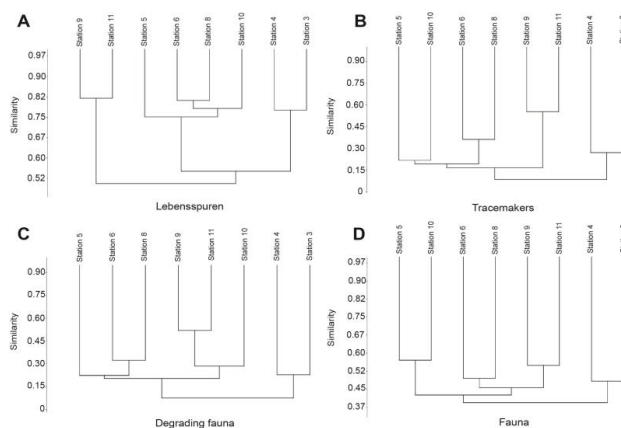
589

590 **Fig. 4** Density correlation matrix for lebensspuren, tracemakers, degrading fauna and
 591 fauna. Lebensspuren and tracemakers densities were subdivide into wasting, resting and
 592 locomotion-feeding (dwelling was not considered since the tracemakers of most dwelling
 593 lebensspuren are unknown). Boxed dots indicate correlations where $p < 0.05$.



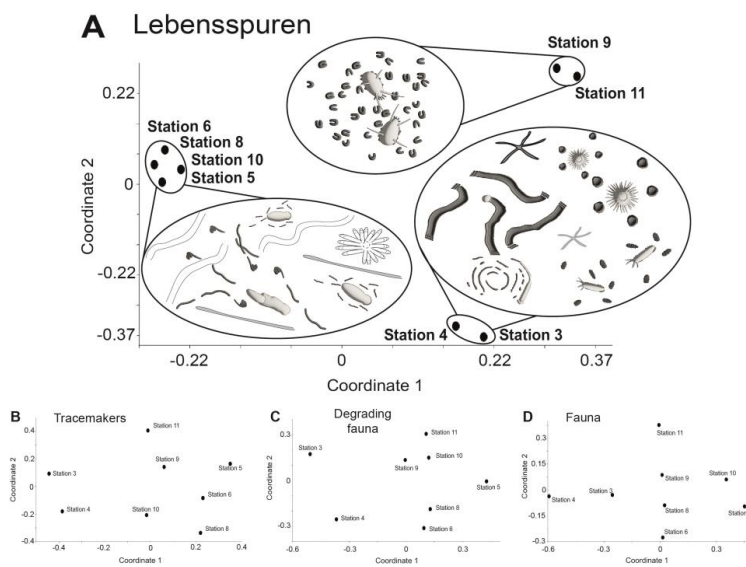
594

595 **Fig. 5** Hierarchical cluster diagram (constructed with Bray-Curtis similarity matrix) of
 596 the abundances of lebensspuren (A), tracemakers (B), degrading fauna (C) and fauna (D)
 597 at each station.



598

599 **Fig. 6** Multivariate similarity represented with a non-metric multidimensional scaling (n-
600 MDS) plots of lebensspuren (A), tracemakers (B), degrading fauna (C) and fauna (D)
601 at each station. Note that the only plot that stations are together is for lebensspuren
602 abundance.



603

604



605 **Table captions**

606 **Table 1.** Station data of the OFOS deployments during KuramBio (2012). “Start” and
 607 “End” coordinates refer to the time between bottom view and beginning of heaving
 608 (survey duration). Notes: The first four deployments were aborted due to technical
 609 problems.

Station	Start Date	Start	End	Depth (m)	Survey duration /min	Notes
01-03	28.07.2012	44°0.03' N 157°18.52' E	44°0.01' N 157°18.50' E	5315-5312	7	Not enough good frames
01-09	30.07.2012	-	-	-	-	No video
02-03	01.08.2012	46°14.04' N 155°33.05' E	46°14.04' N 155°33.05' E	4868-4868	4	Not enough good frames
03-03	04.08.2012	-	-	-	-	No video
03-11	06.08.2012	47°14.31' N 154°42.35' E	47°13.80' N 154°43.16' E	4990-5073	75	
04-10	08.08.2012	46°58.00' N 154°32.48' E	46°58.48' N 154°31.44' E	5768-5591	152	
05-3	09.08.2012	43°35.03' N 153°57.95' E	43°34.64' N 153°58.60' E	5377-5374	125	
06-3	13.08.2012	42°28.97' N 153°59.91' E	42°28.18' N 153°59.90' E	5298-5308	81	
07-3	16.08.2012	43°2.23' N 152°59.16' E	43°1.81' N 152°59.70' E	5222-5221	71	Video with not enough definition
08-3	19.08.2012	42°14.61' N 151°43.50' E	42°14.42' N 151°42.91' E	5125-5125	61	
09-3	22.08.2012	40°34.99' N 151°0.03' E	40°34.47' N 151°0.38' E	5404-5398	62	
10-3	25.08.2012	41°12.01' N 150°5.70' E	41°12.19' N 150°6.40' E	5249-5248	62	
11-3	28.08.2012	40°12.93' N 148°6.04' E	40°12.92' N 148°5.41' E	5348-5344	61	

610

611 **Table 2.** Lebensspuren and associated tracemakers identified in the present study. Note
 612 that several lebensspuren can be produced by different tracemakers.

Behaviour	Morphology	Description	Tracemaker taxonomy	Notes
Dwelling	Mounds	Large, smooth-sided cone structures. The diameter of the mounds ranged between 5 to 20 cm.	Unknown	Probably crustaceans
	Single burrows	Single entry holes within the flat sediment surface. Occasionally, a smooth, cone-shaped mound with a burrow entry hole at the apex. The diameters were varied, as large as 2 cm, but usually between 0.5 to 1 cm.	Unknown	
	Paired burrows	Two burrow entry holes that are closely spaced. The spacing between burrows was between 2 and 4 cm.	Bivalves and polychaetes	
	Cluster burrows	Three or more burrow entry holes that are closely and randomly spaced. The spacing between burrows was between 2 and 10 cm.	Unknown	Probably crustaceans
	Lined burrows	Three or more burrow entry holes that are aligned following a rectilinear or slightly sinuous pattern.	Unknown	Probably crustaceans



	Crater cones	Large central mounds surrounded by distinctive clusters of round, shallow impressions.	Unknown	
Wasting	Crater	Depression holes related to the collapse of horizontal burrows	Actiniaria fam. gen. sp. 3	Probably also other actinarians
	Rounded faecal cast	Neat, short spirals of thick faecal matter	cf. <i>Elpidia</i> sp. 1, <i>Scotoplanes</i> sp. 1, <i>Scotoplanes</i> sp. 2	Due to image resolution, <i>Elpidia</i> rounded faecal casts (which are commonly <1cm in size) have only been recognized on a few occasions (when it was in focus)
	Smooth faecal cast	Smooth thick faecal matter with a straight or slightly sinuous shape.	cf. <i>Pseudostichopus</i> sp. <i>Psychropotes</i> morphospecies 1, <i>Psychropotes</i> morphospecies 2, <i>Synallactidae</i> morphospecies 1 (Amon et al. 2017), <i>Benthodytes</i> sp. 1 Unknown	Smooth faecal cast from <i>Benthodytes</i> sp. 1 may present compressed appearance.
	Mounded faecal cast Coiled faecal cast	Discrete piles of faecal matter which are not associated with burrow entry holes. Thick faecal strings appearing compressed and curled with one straight coil at the end. May be present along thick trail lines.	<i>Psychropotes</i> morphospecies 1, <i>Psychropotes</i> morphospecies 2, <i>Benthodytes</i> sp. 1	
Locomotion and Feeding	Knotted faecal cast	Tightly loop faecal trails, often with a characteristic loop-hook at the end.	<i>Peniagone</i> sp.1 <i>Peniagone</i> sp. 3	The bigger morphotypes of this faecal cast belong to <i>Benthodytes</i> sp. 1
	Wavy faecal cast	Tiny (less than 0.5 cm in thickness) meandering faecal remains with variable length and often in fragmented form.	<i>Peniagone</i> sp.1 <i>Peniagone</i> sp. 3	Possibly formed by uncoiling of knotted faecal cast
	Switchbacks faecal cast	Switchback or meandering feature often beginning or ending in a spiral. The acorn worm is often observed making the feature.	<i>Torquaratoridae</i> . gen. sp. 1	
	Spirals faecal cast	Faecal spirals with both clockwise and anti-clockwise paths. The acorn is often observed making the feature.	Enteropneusta gen. sp. 1, Enteropneusta gen. sp. 2	
	Rosette-shape	Small burrow entry hole with thick, radial spokes from the central burrow. Partially completed rosettes are commonly observed. Spokes vary in thickness and length. Mounds are often found in close proximity to the rosette.	Unknown	This trace is usually related with echiuran worms but none has been observed in this study
	Thick trails	M-Complex concave crawling structures, ranging in width from 3 to 15 cm. Both sides of the trail have small sediment ridges (forming a M-shape trail) due to the movement of the tracemaker through the seafloor. The trails are straight and most commonly sinuous; occasionally observed with the echinoids forming the track.	Asteroidea. fam. gen. sp. 1, Asteroidea. fam. gen. sp. 4, Echinochrepis. sp. 1; Echinoidea. fam. gen. sp. 5	
	Thick trails	flat Smooth concave trails of varying length with occasional small sediment puncture marks. Thickness ranges from 2 to 10 cm. Trails may form linear, meandering, or discontinuous paths.	cf. <i>Benthodytes</i> sp. 1, <i>Psychropotidae</i> , Asteroidea. fam. gen. sp. 3; Echinoidea. fam. gen. sp. 2; Echinoidea. fam. gen. sp. 7	
	Thin trails	Smooth, concave trails of varying length, up to 2 cm thick. Trails may form linear, meandering or completely random paths	Gastropoda. fam. gen. sp. 1 to Gastropoda. fam. gen. sp. 6; Echinoidea. fam. gen. sp. 6	
	Mounded trails	Smooth, with occasional ploughed features, convex trails of varying length and 3-10 cm thick. Trails may form linear, meandering or completely random paths. Craters appear sometimes in the middle of the trail.	Unknown	
	Resting	Asteroid impressions	Asteroid star-shaped depressions with different dimensions. Diameter ranges from 1 to 15 cm.	Asteroidea. fam. gen. sp. 3, 4, 7, 8, 9
Ophiuroid impressions		Ophiuroid star-shaped depressions	Ophiuroidea. fam. gen. sp. 1 to Ophiuroidea. fam. gen. sp. 3	



613 Circular impressions Circular depressions with a depth of less than 4cm Actiniaria. fam. gen. sp. 1, Actiniaria. fam. gen. sp. 3, Actiniaria. fam. gen. sp. 7

613

614 **Table 3.** Total number of lebensspuren, tracemakers, degrading fauna and fauna
 615 identified through the 8 deep-sea stations at the Kuril Kamchatka area.

616

N=50 (frames per station)	Tracemakers							Lebensspuren				
	Fauna	Degrading fauna	Total	Wasting	Locomotion and feeding	Resting	Dwelling	Total	Wasting	Locomotion and feeding	Resting	Dwelling
Station 3	560	95	91	7	1	81	X	1207	63	84	361	699
Station 4	609	271	250	174	7	70	X	991	257	30	195	509
Station 5	157	27	20	11	10	7	X	974	557	18	37	361
Station 6	750	25	19	9	5	9	X	569	257	36	32	240
Station 8	522	52	36	3	6	27	X	321	77	32	32	178
Station 9	723	119	108	86	6	17	X	2448	2069	25	60	292
Station 10	181	32	13	5	8	4	X	687	278	46	27	328
Station 11	507	169	139	130	2	5	X	2229	1803	50	13	363