Biogeography and community structure of abyssal scavenging Amphipoda (Crustacea) in the Pacific Ocean.

Patel, Tasnim.[1, 2], Robert, Henri.[1], D'Udekem D'Acoz, Cedric.[3], Martens, Koen.[1,2], De Mesel, Ilse.[1], Degraer, Steven.[1,2] & Schön, Isa.[1, 4]

[1] *Royal Belgian Institute of Natural Sciences, Operational Directorate Natural Environment, Aquatic and Terrestrial Ecology, Vautierstraat 29, B-1000 Brussels, Gulledelle 100, 1000 Brussels and 3e en 23e linieregimentsplein, 8400 Oostende, Belgium.*

[2] *University of Ghent, Dept Biology, K.L. Ledeganckstraat 35, B-9000 Ghent, Belgium*

[3] *Royal Belgian Institute of Natural Sciences, Operational Directorate Taxonomy & Phylogeny, Vautierstraat 29, B-1000 Brussels, Belgium.*

[4] *University of Hasselt, Research Group Zoology, Agoralaan Building D, B-3590 Diepenbeek, Belgium.*

Corresponding author: Ms. Tasnim Patel - tpatel@naturalsciences.be

Abstract

In 2015, we have collected more than 60000 scavenging amphipod specimens during two expeditions to the Clarion-Clipperton fracture Zone (CCZ), in the Northeast (NE) Pacific and to the DISturbance and re-COLonisation (DisCOL) Experimental Area (DEA), a simulated mining impact disturbance proxy in the Peru basin, Southeast (SE) Pacific. Here, we compare biodiversity patterns of the larger specimens (> 15 mm) within and between these two oceanic basins. Eight scavenging amphipod species are shared between these two areas, thus indicating connectivity. Overall diversity was lower in the DEA (Simpson Index (D) = 0.62), when compared to the CCZ (D = 0.73) and particularly low, at the disturbance site in the DEA and the site geographically closest to it. Local differences within each basin were observed too. The community compositions of the two basins differ, as evidenced by a Non-Metric Dimensional Scaling (NMDS) analysis of beta biodiversity. Finally, a single species, *Abyssorchomene gerulicorbis* (Shulenberger & Barnard, 1976), dominates the DEA with 60% of all individuals.

Keywords

Introduction

The abyssal deep sea (3000 – 6000 m) represents the largest ecosystem on the planet, with the abyssal seafloor covering approximately 54% of the Earth's solid surface (Rex et al. 1993; Gage & Tyler, 1991). Since it is one of the least investigated ecosystems, there are still extensive gaps in our knowledge of deep-sea fauna (German et al. 2011). Marine research has thus far focused on coastal areas, hydrothermal vents or chemosynthetic habitats, whereas open-ocean abyssal plains have been less extensively investigated (Ramirez-Llodra et al. 2010). This is unsurprising given the challenges of sampling this remote environment, which is impeded by several confounding factors. For example, deep-sea sampling is both financially expensive and labour intensive, and furthermore, constrained by the challenge of deploying equipment at low temperatures (0.01 - 4.0°C) and at high hydrostatic pressures (Sweetman et al. 2017). Therefore, to date very little of the deep sea has been sampled, and the oversampling in the North Atlantic basin has created a biased knowledge base (McClain & Hardy, 2010). Consequently, and owing to the low availability of data on deep-sea biodiversity, and with the inherent risk of under-sampling, it is difficult to estimate species richness in the deep sea.

In the traditional view of the deep sea, the abyss was considered to be homogeneous and many species were thought to have large biogeographical ranges, their dispersal aided by an apparent lack of barriers (Sanders, 1968). This hypothesis was challenged by the discovery of chemosynthetic habitats e.g. hydrothermal vents (Lonsdale, 1977), cold seeps (Paull et al. 1984), seasonal fluctuations in primary productivity (Billett et al. 1983) and erratic whale-falls (Smith et al. 1989). All of this research has demonstrated that the deep sea is an heterogeneous environment and is controlled by many factors, including: Particulate Organic Carbon (POC) flux, water depth, flow regime, current circulation, seafloor topography (Laver et al. 1985) and also historical factors e.g. the opening of ocean basins (i.e. rifting), sea-level rise and fall, and periods of deep-sea anoxia (Smith et al. 2006). All of these can result in a mosaic of different communities (Levin et al. 2001), many of which do not follow a latitudinal gradient (Brandt et al. 2007).

It has also been established that dispersal ability of species on the one hand, and their actual geographic and bathymetric distribution range on the other, are not always linked, and are often dependent on habitat suitability, fragmentation, and ecological flexibility (Lester et al.

90   2007; Liow 2007). Therefore, although the deep seafloor includes some of the largest

91   contiguous features on the planet, the populations of many deep-sea species are spatially

92   fragmented, and may become increasingly so with continued human disturbance (Hilario et

93   al. 2015).

94

95   In the last decade, there has been a bigger demand for exploitation of deep-sea resources e.g.

96   rare earth element (REE) extraction (such as those concentrated in manganese nodule

97   provinces) (Ramirez-Llodra et al. 2011). As a result, ecologists are increasingly asked to

98   assess the ecological risks of these mining activities and to provide sustainable solutions for

99   its mitigation, in order to prevent adverse changes to the deep-sea ecosystem (ISA, 2017).

100

101   Glover et al. (2001) showed that abyssal sediments can contain high biodiversity with more

102   than 100 species of meiofaunal invertebrates (e.g. nematodes, copepods) and protists (e.g.

103   foraminifers) found every square meter. Despite this, our knowledge on the deep-sea

104   ecosystem structure and functioning is still limited, and there is a paucity of data on the

105   distribution, drivers and origins of deep-sea communities at global scales. This is especially

106   true for deep-sea invertebrates, including Amphipoda (Barnard 1961; Thurston 1990).

107

108   Although recent morphological and molecular studies have shed new light on the distribution

109   and habitat niches of certain bentho-pelagic amphipods (e.g. *Eurythenes*) (Havermans, 2016;

110   Narahara-Nakano et al. 2017), there is little published so far on how widespread other

111   amphipod species may be. This lack of information on species richness and ecological

112   uniqueness hampers the answering of crucial questions on recoverability of anthropogenic

113   impacts. Ultimately this impedes ecologists from providing advice on sustainable deep-sea

114   mining practices, thus, underpinning the need for this dedicated deep-sea ecosystem research.

115

116   Here, we present distribution patterns of scavenging deep-sea amphipod communities, with

117   the first comparisons of their biogeography and community structures in two oceanic basins.

118   These two basins are the research areas for simulating/studying the anthropogenic impacts of

119   deep-sea nodule mining.

120

121   We are investigating whether there are differences and similarities in the species

122   compositions of the two basins (e.g. richness, abundances), and further exploit a disturbance

123   experiment to compare the biodiversity of this mining impact proxy to the undisturbed

124 reference areas. We discuss the possible implications of our findings; aiming to use them to

125 formulate recommendations regarding the pending deep-sea mining of manganese nodule

126 activities in the NE Pacific ecosystem.

127 **Material and Methods**

128

129 *Study area*

130

131 We investigated the amphipod communities of two oceanic basins (Figure 1); (i) the Clarion-

132 Clipperton Fracture Zone (CCZ, six million km^2, 7000 km wide), an economically important

133 manganese nodule field in the NE Pacific, comprising several different contractor license

134 areas, (who to date, have exploration licences only), and nine designated Areas of Particular

135 Ecological Interest (APEIs) as designated by the International Seabed Authority (ISA)

136 (Lodge et al, 2014) and (ii) the DISturbance and re-COLonisation (DisCOL) Experimental

137 Area (DEA, 11 km^2, 4 km wide), a mining disturbance proxy (also containing manganese

138 nodules) in the Peru Basin in the SE Pacific. In 1989, the DEA sediment bed was artificially

139 disturbed using a plough-harrow to create 78 track marks (Appendix 1) (Thiel, 1992). These

140 are supposed to simulate the type of disruption which would be caused by a commercial

141 mining operation This baseline study was a new approach in deep-sea risk assessment and is

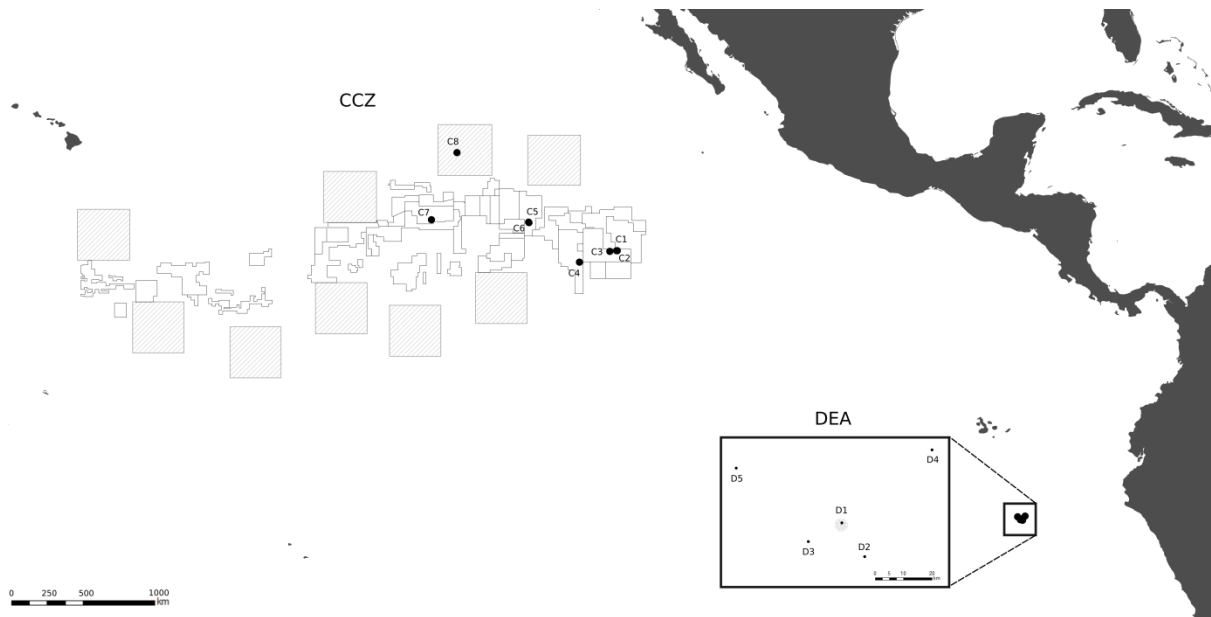142 still ongoing today, providing us with crucial data from this long-term ecological experiment.

143

144

145

146

147

Figure 1: Geographic locations of the two study areas, the Clarion-Clipperton fracture Zone (CCZ) (Northeast Pacific) and the DISturbance and re-COLonisation (DisCOL) Experimental Area (DEA) (Peru Basin, Southeast Pacific). There are nine Areas of Particular Ecological Interest (APEIs) in the CCZ region, which are illustrated by 400 x 400 km^2 grey boxes. White boxes indicate the various contractor license areas in the CCZ. We deployed eight amphipod traps across the CCZ, which is 16000 km^2 and 7000 km wide, and five in the DEA, which encompasses 11 km^2 with a width of 4 km.

Sampling

In 2015 (26 years after the first impact in the DEA in 1989), two research expeditions with the "RV Sonne" visited the CCZ (cruise SO239) and revisited the DEA (cruise SO242-1 & SO242-2), to assess if and how the deep-sea faunal communities had recovered within the DEA, and to attempt to quantify their recolonisation potential.

Amphipod samples were taken from the CCZ and DEA using a free-fall lander (120 x 120 x 120 cm), to which four plastic traps were attached (two 20 x 25 x 40 cm traps with four cm openings and two 25 x 40 x 60 cm traps with eight cm openings), baited for each station with an 800 g mixture of mackerel, squid and shrimp. Using this specially designed deep-sea sampling equipment, more than 60000 specimens of scavenging amphipods were collected from the CCZ and the DEA sites.

The baited trap was deployed eight times across the CCZ at a depth range of 4116 - 4932 m (samples C1 - C8), and five times in the DEA at a depth range of 4078 - 4307 m (samples D1 - D5; Figure 1, Table 1). In the CCZ, we sampled within four different contractor license areas (Table 1) to obtain a pre-disturbance baseline, and to then compare it with one of the nine protected APEIs around the CCZ. In contrast, in the DEA, sampling was conducted once within the disturbed area (D1), twice 10 km away (D2, D3) and twice 40 km away (D4, D5) from D1 in four surrounding reference areas (see Figure 1).

Table 1: Station overview.

Codes refer to the codes used in this paper in figures 1, 3, 4, 6 and Table 3. The original station code represents the cruise codes from (SO239 and SO242-1). Depth refers to water depth (m) on deployment.

Deployment Code	Station Code	Depth (m)	Known geological features	Remarks	Residence Time (h:m:s)	Lat	Lon	Nodule Presence
C1	SO239-33	4122	Plains	German license area	100:20:00	11° 51' 29" N	117° 3' 38" W	Yes
C2	SO239-37	4116	Plains	German license area	125:49:00	11° 48' 63" N	117° 0' 96" W	Yes
C3	SO239-63	4354	Plains	German license area	66:07:00	11° 48' 64" N	117° 32' 05" W	Yes
C4	SO239-96	4388	Seamount	Inter Ocean Metals (IOM) license area	63:02:00	11° 2' 98" N	119° 41' 16" W	Yes
C5	SO239-123	4529	Plains	Belgian license area	26:12:00	13° 51' 22" N	123° 15' 30" W	Yes
C6	SO239-139	4516	Plains North/South + seamount to west	Belgian license area	56:33:00	13° 52' 41" N	123° 16' 46" W	Yes
C7	SO239-173	4934	Plains	French license area	79:40:00	14° 3' 20" N	130° 4' 61" W	Yes
C8	SO239-205	4855	Plains	Area of Particular Ecological Interest (APEI)	55:59:00	18° 46' 40" N	128° 20' 17" W	No
D1	SO242/1-8	4146	Plains	Disturbed	44:26:33	7° 2' 26" S	88° 16' 30" W	Yes (disturbed)
D2	SO242/1-30	4307	Plains	Undisturbed Reference	51:11:18	7° 5' 45" S	88° 14' 15" W	Not Known
D3	SO242/1-55	4043	Seamount	Undisturbed Reference	25:09:09	7° 4' 17" S	88° 19' 47" W	No
D4	SO242/1-68	4078	Seamount	Undisturbed Reference	65:20:46	6° 31' 17" S	88° 7' 38" W	No
D5	SO242/1-106	4269	Plains	Undisturbed Reference	47:00:50	6° 33' 4" S	88° 26' 52" W	Not Known

Processing

On recovery of the lander, all traps were disconnected and placed in pre-cooled (4 °C) buckets of filtered seawater. All specimens were washed on board in a dedicated cool-climate laboratory (4 °C), morphologically pre-sorted and fixed in molecular grade (95%) ethanol, before being stored at -20 °C.

Detailed sorting and identifications were performed using the morphological species concept (Futuyama, 1998) and the keys of Schulenberger & Barnard (1976) and Barnard & Karaman (1991), to separate the samples into taxonomic "morphotypes". The larger fraction (> 15 mm length) has been identified to the lowest possible taxonomic resolution. Species not assigned with certainty are denoted here by as affiliated species (e.g. *genus* aff. *species*) or conferred species (e.g. *genus* cf. *species*).

Of the 60,000 specimens, those with a size of less than 15 mm length were excluded from the analysis because these were mostly juveniles and their morphological differences were not sufficiently pronounced to allow an accurate identification to the species or even genus level. Some pelagic amphipods were collected accidentally and omitted. Finally, genera containing multiple (and as yet) unidentified species have been summarised as "spp."

Statistical analyses

Our null hypothesis (H_0) here is that there are no differences in the amphipod biodiversity of the two basins. To test this hypothesis, we firstly calculated the alpha biodiversity of the two basins using the Simpson Index (D) (Simpson, 1949) (Appendix 4). Rarefaction was run on the longer than 15 mm fraction using default parameters. Individual-based curves were generated using the rarefy function of the vegan package in R 2.3.0 (R Core Team, 2013; Gotelli, 2001) to compare species richness across all thirteen sampling stations and to test for the completeness of sampling.

Secondly, to compare the beta biodiversity, we estimated the variability of the community compositions between sites. The Bray-Curtis dissimilarity metric (Bray & Curtis, 1957), was used to calculate differences between community compositions based on species densities, and the results were then visualised in 2D using a Non-Metric Dimensional Scaling (NMDS)

261   plot. The ANOSIM function in the vegan package of R (R Core Team, 2013; Taguchi & Ono,

262   2005) was used to test the statistical significance of the differences in species compositions

263   between the two study areas.
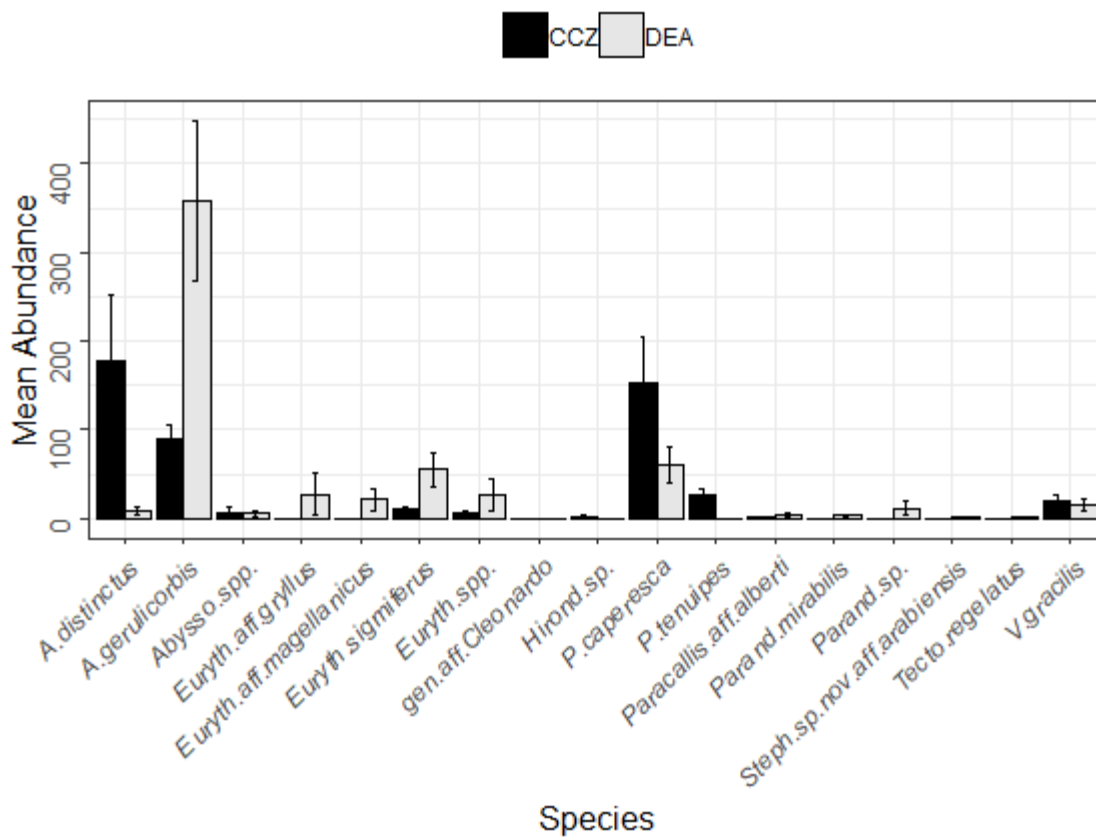
264

265

Results

Basin biodiversity

In total, 6916 scavenging amphipods (> 15 mm) were collected from the thirteen trap deployments in the two study areas, representing a total of seventeen morphotypes (Figure 2). In the CCZ, we collected 3932 individuals, which represent ten morphotypes. Five of these have been identified to the species level: *Abyssorchomene distinctus* (Birstein & Vinogradov, 1960), *Abyssorchomene gerulicorbis* (Shulenberger & Barnard, 1976), *Eurythenes sigmiferus* (d'Udekem d'Acoz & Havermans, 2015), *Paralicella caperesca* (Shulenberger & Barnard, 1976) and *Paralicella tenuipes* Chevreux, 1908. Two are affiliated to a species (*Paracallisoma* aff. *alberti* and *Valettietta* cf. *gracilis*) and the remaining three are at least affiliated to a genus (Table 2). The 2984 individuals from the DEA represent fifteen morphotypes. Six of these have been identified to the species level: *Abyssorchomene distinctus* (Birstein & Vinogradov, 1960), *Abyssorchomene gerulicorbis* (Shulenberger & Barnard, 1976), *Eurythenes sigmiferus* (d'Udekem d'Acoz & Havermans, 2015), *Paralicella caperesca* (Shulenberger & Barnard, 1976), *Parandaniexis mirabilis* Schellenberg, 1929 and *Tectovalopsis regelatus* Barnard & Ingram, 1990. A further five which have been affiliated to a species: *Eurythenes* aff. *gryllus*, *Eurythenes* aff. *magellanicus*, *Paracallisoma* aff. *alberti*, *Stephonyx* sp. nov. aff. *arabiensis* and *Valettietta* cf. *gracilis* and the remaining four identified to at least an affiliated genus (Table 2).

There are eight morphotypes shared between the basins: *Abyssorchomene distinctus* (Birstein & Vinogradov, 1960), *Abyssorchomene gerulicorbis* (Shulenberger & Barnard, 1976), *Abyssorchomene* spp., *Eurythenes sigmiferus* (d'Udekem d'Acoz & Havermans, 2015), *Eurythenes* spp., *Paracallisoma* aff. *alberti*, *Paralicella caperesca* (Shulenberger & Barnard, 1976) and *Valettietta* cf. *gracilis* (Figure 2).

Two morphotypes were found only in the CCZ (*Hirondellea* sp. & *Paralicella tenuipes* Chevreux, 1908, and seven morphotypes were found only in the DEA (*Eurythenes* aff. *gryllus*, *Eurythenes* aff. *magellanicus*, gen. aff. *Cleonardo*, *Parandania* sp., *Parandaniexis mirabilis* Schellenberg, 1929, *Stephonyx* sp. nov. aff. *arabiensis*, and *Tectovalopsis regelatus* Barnard & Ingram, 1990 (Table 2).

Figure 2: **Histogram showing the species assemblage for the scavenging community in the Clarion-Clipperton fracture Zone (CCZ) (black) and the DisCOL Experimental Area (DEA) (grey).** The abundances of 17 morphotypes are shown.

305
306
307
308
309
310
311
312
313
314
315

Table 2: Distribution and abundances of morphotypes across the Clarion-Clipperton fracture Zone (CCZ) and DisCOL Experimental Area (DEA). Green = shared, Orange = DEA only, Blue = CCZ only.

Taxa	C1	C2	C3	C4	C5	C6	C7	C8	D1	D2	D3	D4	D5
Abyssorchomene distinctus	629	312	180	170	64	47	2	25	9	3	25	0	5
Abyssorchomene gerulicorbis	73	47	48	107	71	65	184	121	351	143	522	178	595
Abyssorchomene spp.	0	0	50	0	0	3	0	0	5	20	0	0	0
Eurythenes aff. *gryllus*									119	0	9	0	9
Eurythenes aff. *magellanicus*									0	0	59	0	47
Eurythenes sigmiferus	9	3	35	11	12	5	0	6	30	61	127	36	22
Eurythenes spp.	6	3	2	0	0	20	1	12	0	91	3	39	1
gen. aff. *Cleonardo*									1	0	0	0	0
Hirondellea .sp.	0	2	0	0	0	0	5	10					
Paracallisoma aff. *alberti*	0	0	0	0	0	2	1	6	10	4	0	1	1
Paralicella caperesca	104	4	114	152	255	75	63	460	86	108	80	21	7
Paralicella tenuipes	22	0	14	42	43	9	19	58					
Parandania sp.									5	2	42	5	1
Parandaniexis mirabilis									11	0	3	0	0
Stephonyx sp. nov. aff. *arabiensis*									0	4	0	0	0
Tectovalopsis regelatus									5	0	0	0	0
Valettietta cf. *gracilis*	75	11	29	3	2	5	1	23	2	29	17	1	29

337 *Sampling completeness*

338

339 Due to differences in allocated ship-times (CCZ cruise being 52 days and the DEA cruise

340 being 29 days), the trap deployments were not identical, making it necessary to check the

341 effect of the different deployment times. The resulting Catch Per Unit Effort (CPUE) plot

342 (Figure 3,) shows that there is no statistically significant correlation between the length of

343 time the trap was at the seafloor and total number of amphipods caught ($p = 0.551$).

344
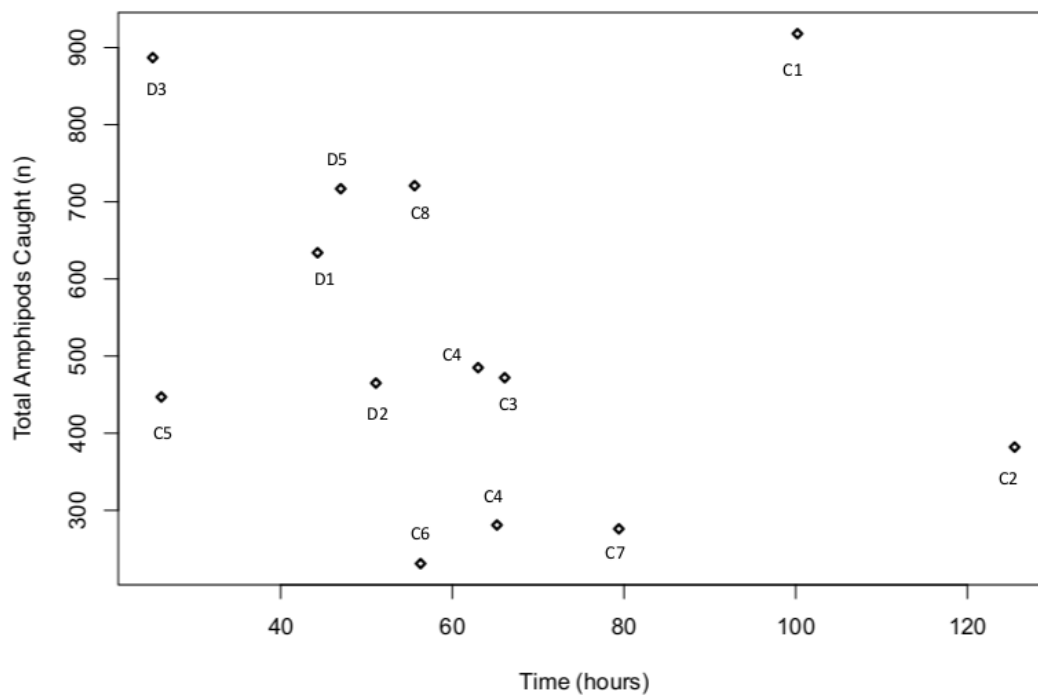
345

346 **Figure 3: Catch Per Unit Effort (CPUE) illustrating the correlation between sampling**

347 **time and number of individuals collected.** Only the longer than 15mm fraction was

348 included here.

349

350

351

352

353

354

355

356

357

358   The rarefaction results (Figure 4) show that the curves for nine stations reach a plateau,

359   indicating that sampling effort was sufficient to assess diversity levels. These include all CCZ

360   stations except C7. In contrast, four of the five curves for the DEA (stations D1, D2, D4 and

361   D5) are unsaturated. A higher number of different species were collected at D1 and D2,

362   however many of these were singletons or doubletons, with *A. gerulicorbis* dominating at

363   both disturbed stations.

364
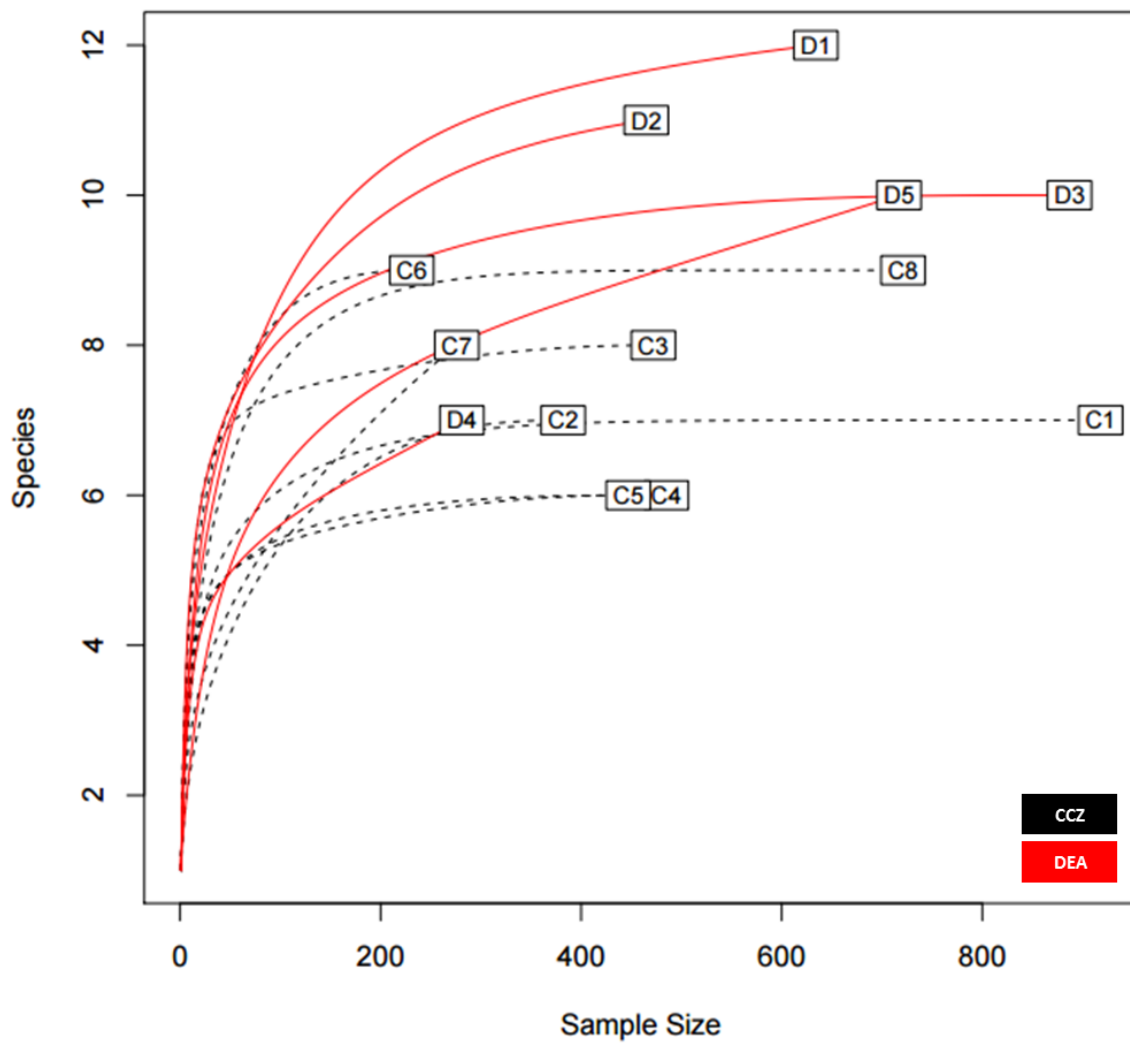
365

366   **Figure 4: Species rarefaction curves for each of the 13 trap stations across both areas,**

367   **the Clarion-Clipperton fracture Zone and the DisCOL Experimental Area.** Only

368   individuals longer than 15 mm were considered here.

369

370

371

372   *Biodiversity*

373

374   Figures 5a and b show that the scavenging community in the CCZ is dominated by three

375   species, *A. distinctus* (Birstein & Vinogradov, 1960) (36%)*, A. gerulicorbis* (Shulenberger &

376   Barnard, 1976) (18%) and *Paralicella caperesca* (Shulenberger & Barnard, 1976) (31%)*,*

377   whereas*,* in contrast, the DEA scavenging community is dominated by a single species, *A.*

378   *gerulicorbis* (Shulenberger & Barnard, 1976), accounting for almost 60% of all specimens.

379   The Simpson Index (*D*) for the entire CCZ area is (with 0.73), higher than the 0.62 that was

380   calculated for the whole of the DEA area (Table 3). The biodiversity of each individual

381   station was further explored (Table 3). In the CCZ, the lowest biodiversity was found at C3

382   and C6 (*D* = 0.23) and the highest at C2 (*D* = 0.67), respectively. In the DEA, the lowest

383   biodiversity of *D* = 0.36 was found at station D1 (the site of the actual disturbance) and just

384   south of the disturbance site at D2 (0.21), while the highest biodiversity was observed at D5

385   (*D* = 0.61) (Table 3).

386

387

388

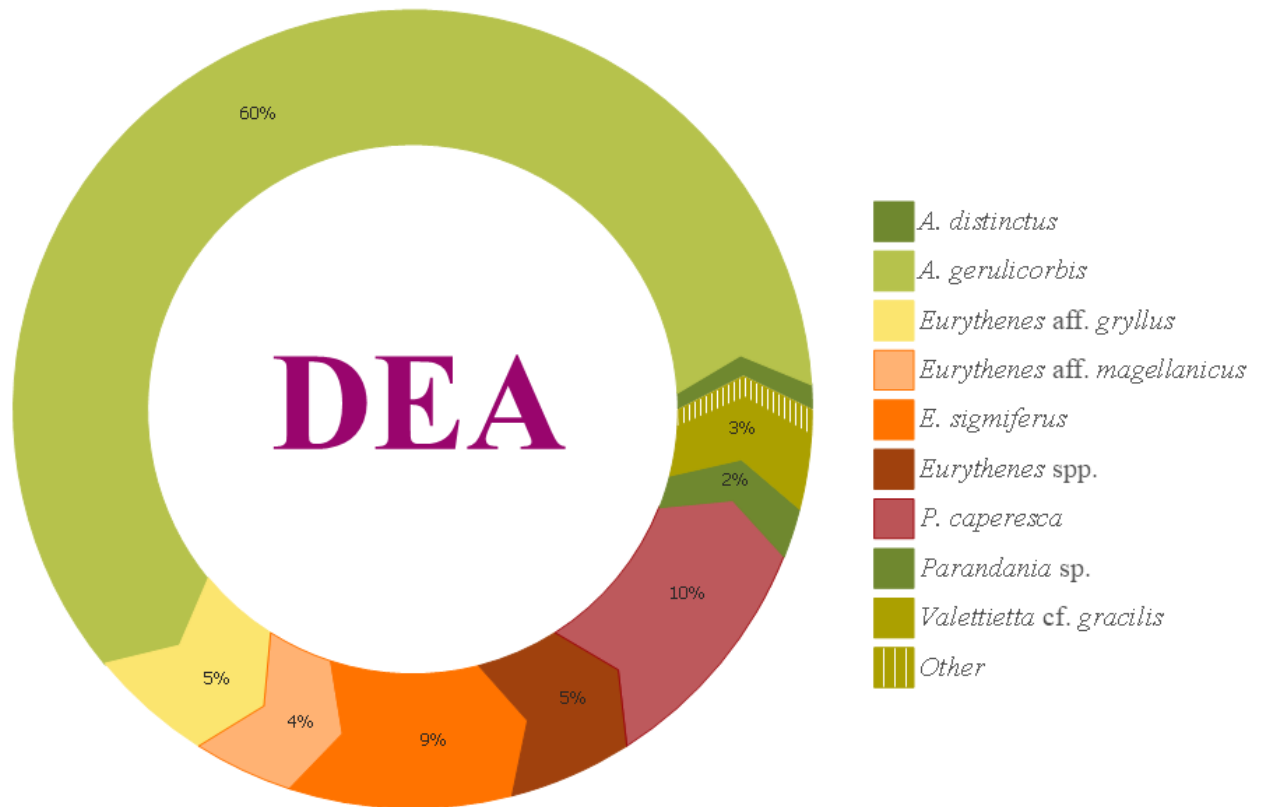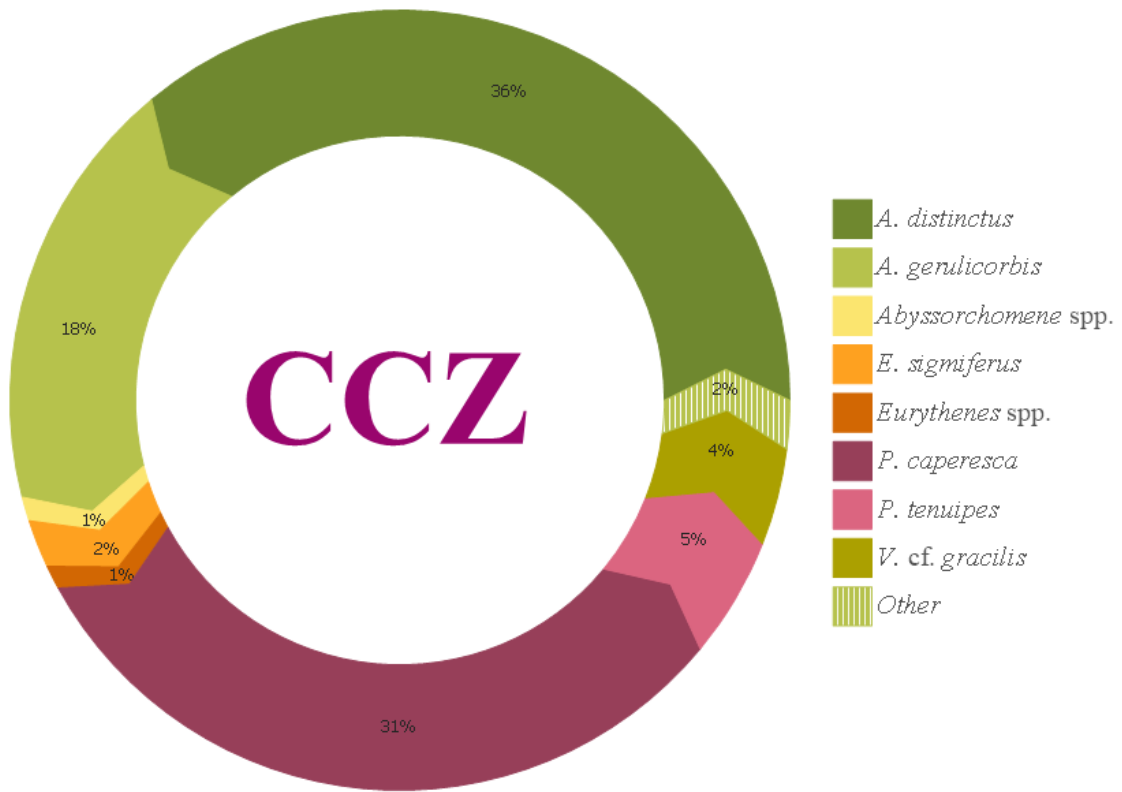389

390

391

392

393

394

395

396

397

398

399

400

401

402

403

CCZ

Legend:
- A. distinctus
- A. gerulicorbis
- Abyssorchomene spp.
- E. sigmiferus
- Eurythenes spp.
- P. caperesca
- P. tenuipes
- V. cf. gracilis
- Other

36%, 18%, 1%, 2%, 1%, 31%, 5%, 4%, 2%

DEA

Legend:
- A. distinctus
- A. gerulicorbis
- Eurythenes aff. gryllus
- Eurythenes aff. magellanicus
- E. sigmiferus
- Eurythenes spp.
- P. caperesca
- Parandania sp.
- Valettietta cf. gracilis
- Other

60%, 5%, 4%, 9%, 5%, 10%, 2%, 3%

404

Figures 5a and b: Relative species abundances in the Clarion-Clipperton fracture Zone and the DisCOL Experimental Area. These abundances represent the longer than 15mm subsample of the scavenging amphipod community.

Table 3: Comparison of biodiversity calculated using the Simpson Index (*D*), for the Clarion-Clipperton fracture Zone and DisCOL Experimental Area, and *D* for each station is shown for further comparisons within these areas.

| Site	Simpson Index (D)
Clarion-Clipperton fracture Zone	0.73
DisCOL Experimental Area	0.62
C1	0.41
C2	0.68
C3	0.23
C4	0.27
C5	0.38
C6	0.23
C7	0.45
C8 (APEI)	0.44
D1 (disturbed)	0.36
D2 (ref 1, close to disturbed)	0.21
D3 ref 2	0.38
D4 ref 3	0.44
D5 ref 4	0.61

428 *Species composition*

429

430 The NMDS shows that the communities of the two basins are dissimilar (ANOSIM: $p =$

431 0.002); Figure 6). The disturbed area in the DEA (D1) is showing a clear difference to the

432 four reference areas (D2 - 5). When the communities between the two basins are compared,

433 D2 appears to be most similar to the CCZ community, and more specifically to C6, C7 and

434 C8. The reliability of the data ranking is supported by a low stress value of 0.01.

435
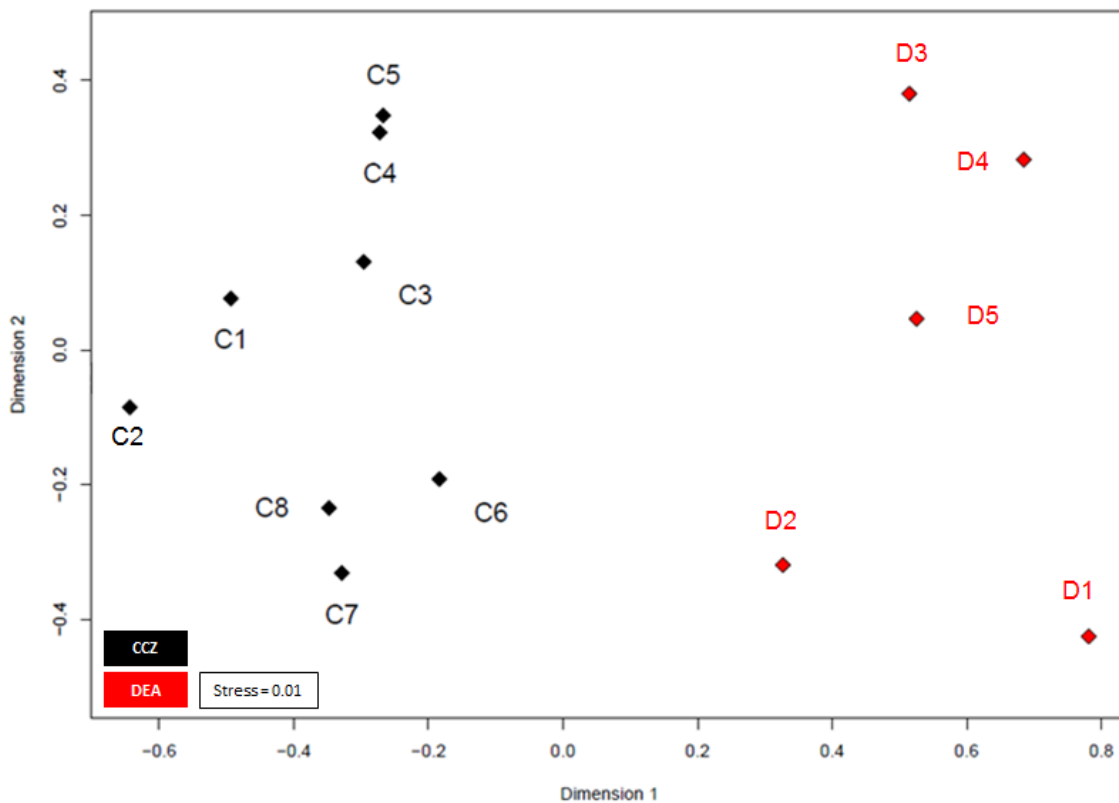
436

437 **Figure 6: NMDS plot** showing the beta biodiversity (dis/similarities) for each of the thirteen
438 amphipod trap sampling stations associated with the two basins, Clarion-Clipperton fracture
439 Zone (CCZ) (black) and the DisCOL Experimental Area (DEA) (red). Data are supported by
440 a low stress value of 0.01.

441

442

Discussion

An unexplored ecosystem

Although the most recent and comprehensive analysis of the Animal diversity of the World's oceans estimates a total of less than a million species over all depths (Appeltans et al. 2012), it is not currently known how many species inhabit the deep sea. Over 7000 marine amphipod species have been found below 2000 m. These numbers are reduced to 173 known species, 87 genera and 37 families at depths below 3000 m, and 100 known species, 66 genera and 31 families are known to occur below 4000 m (Vader 2005; Brandt et al, 2012).

Lysianassoidea and their biogeography

The superfamily Lysianassoidea constitutes an important part of the abyssal amphipod fauna. Also, in our sampling, lysianassoid amphipods were collected in large numbers (99% of the samples taken in both basins). As a superfamily, they comprise 23% of all the species found below 2000 m, 35% of the species found below 3000 m and 31% of the species found below 4000 m (Brandt et al. 2012).

Many species in the Lysianassoidea occur in multiple abyssal basins, and some even have worldwide distributions (Thurston 1990). Despite the Ocean Biogeographic Information System (OBIS) database containing 615,650 records of Amphipoda, many of these are shelf or pelagic species, with very few records from the CCZ and DEA (OBIS, 2017). Here, we provide additional data for the known bathymetric range of the seven amphipods which we have identified to species level (*Abyssorchomene distinctus* (Birstein & Vinogradov, 1960)*, Abyssorchomene gerulicorbis* (Shulenberger & Barnard, 1976)*, Eurythenes sigmiferus* (d'Udekem d'Acoz & Havermans, 2015)*, Paralicella caperesca* (Shulenberger & Barnard, 1976)*, Paralicella tenuipes* Chevreux, 1908, *Parandaniexis mirabilis* Schellenberg, 1929 and *Tectovalopsis regelatus* Barnard & Ingram, 1990 (Table 2). In addition, we have found two possibly new species of *Eurythenes*, previously not known from these basins which we plan to analyse further in the future.

While we only sampled *Hirondellea* sp. and *Paralicella tenuipes* Chevreux, 1908 in the CCZ, *Eurythenes* aff. *gryllus*, *Eurythenes* aff. *magellanicus*, *gen.* aff. *Cleonardo, Parandania* sp.,

475 *Parandaniexis mirabilis* Schellenberg, 1929*, Stephonyx* sp. nov. aff. *arabiensis,* and

476 *Tectovalopsis regelatus* Barnard & Ingram, 1990 only in the DEA, we cannot conclude based

477 on the current data only if these species are unique to their respective basins without

478 confirming these distribution patterns with additional sampling campaigns.

479

480 Despite the sampling campaign in the CCZ being twice as long as the DEA, the number of

481 individuals/species collected does not correlate positively with deployment effort. We posit

482 that this is rather an effect of abiotic and organic factors, such as the productivity-driven

483 gradients in the CCZ, which decrease from East-West and from North-South (Hannides &

484 Smith, 2003), and also the productivity differences between the both basins.

485

486 ***Biodiversity within basins***

487

488 Figures 5a & b show clearly that the DEA scavenging community has reduced abundances of

489 all species including *A. distinctus* (Birstein & Vinogradov, 1960) (1%) and *P. caperesca*

490 (Shulenberger & Barnard, 1976) (7%), and is now dominated by a single species, *A.*

491 *gerulicorbis* (Shulenberger & Barnard, 1976), accounting for 60% of the DEA community.

492 This indicates an interesting resilience and flexibility in the latter species. Similar patterns

493 have been observed in Potter Cove (Seefeldt et al. 2017), where following glacial retreat, a

494 change in sedimentation rates led to the dominance of a single amphipod scavenging species,

495 *Cheirimedon femoratus* (Pfeffer, 1888)*.*

496

497 The assemblages of the two basins have some overlap in their biodiversity (as is exemplified

498 by the eight shared morphotypes). However, the sampling stations and the two basins as a

499 whole are heterogeneous in their species compositions.

500

501 Thus, we can observe some negative influence (possibly attributed to the disturbance in the

502 DEA) on the scavenging amphipod community. This reduced biodiversity is reflected in the

503 higher Simpson Index (D) for the CCZ (0.73) as compared to the DEA ($D = 0.62$; Table 3).

504

505 To explore whether this reduced diversity in the DEA was truly a result of the simulated

506 disturbance, D was also calculated for each sampling station within each basin (Table 3).

507 In the CCZ, the APEI (C8) shows a moderate level of biodiversity ($D = 0.44$), indicating that

508 it is not optimally placed for representing the biodiversity of the scavenging amphipod

509 community of the CCZ. Additionally, this pre-existing lower biodiversity (in comparison to

510 the contractor license areas), indicates that the APEI may not serve well as a refugium for

511 amphipods post-disturbance. However, due to the fact that only one of the eight APEIs have

512 been investigated thus far, this APEI along with the remaining eight APEIs would need to be

513 (re-) sampled.

514

515 Within the DEA, the lowest biodiversities are observed at the site of the disturbance (D1) and

516 south of it (D2; Table 3), indicating that the reduced biodiversity in the DEA could indeed be

517 caused by the simulated disturbance in 1989 (Thiel, 1992).

518

519 The highest abundances in the DEA were collected from station D5 ($n = 717$); this station

520 also has the highest Simpson Index within the DEA ($D = 0.61$) (Table 3). Side-scan sonar

521 imaging shows a seamount range to the North West (NW) of the disturbed area (D1)

522 (Appendix 3). Although the relief change is only 150m, the range extends laterally for several

523 kilometres hampering dispersal across barriers such as sills, canyons and ridges (Smith, et al.

524 2006; Blankenship et al. 2006; Etter et al. 2011). However, recent studies have shown that

525 due to their mobile nature, geographic isolation alone would not pose a true barrier to bentho-

526 pelagic amphipod species (Havermans, 2016; Ritchie et al. 2017), and thus, cannot explain

527 why such a high number of large scavenging individuals was collected at station D5.

528

529 *Community similarities*

530

531 Scavenging amphipods are resilient and dispersive, but most importantly, they are highly

532 mobile (Ingram and Hessler 1983; Lörz et al. 2018). Often driven by their search for erratic

533 deposited feeding opportunities (Smith et al. 1989), they are probably less constrained by

534 local environmental abiotic conditions and seafloor topography.

535

536 Beta diversity can be regarded as the dissimilarities in species composition between spatially

537 different communities. As an indication for beta biodiversity, the NMDS (Figure 6) shows a

538 significant separation in the similarity index between the two basins (ANOSIM $p = 0.002$).

539 However, despite the dispersive and resilient nature of scavenging amphipods, their

540 biodiversity could have been affected by the disturbance experiment as evidenced by the

541 NMDS (Figure 6), where the disturbed area (D1) and the area closest to it (D2) show a

542 different Bray-Curtis Index to the remaining three reference sites (D3, D4 and D5).

543   In the CCZ, stations C1, C2, C3, C4 and C5 show a different Bray-Curtis Index in

544   comparison to stations C6, C7 and C8 (Figure 6). The CCZ is a geomorphologically very

545   heterogeneous region, with seamounts of 200 m altitude running from North to South. A

546   barrier of this height would be expected to affect sedimentation rates, nodule presence and

547   currents. Furthermore, the difference in depth from the eastern edge (3950 m) and the western

548   edge (5150 m) is more than 1200 m. These combined factors very likely give rise to different

549   trends in species composition (Glover, et al. 2016). However, since it has been established

550   that bentho-pelagic amphipods are less sensitive to such barriers (Havermans, 2016), at this

551   stage, other biotic (e.g. the productivity gradient) and abiotic factors causing this separation

552   cannot be excluded as alternative explanations.

553

554   *Dispersal and connectivity*

555

556   Whilst the NMDS (Figure 6) illustrates a visual separation of the two basins, there is also

557   some similarity in the amphipod fauna between the two areas, (as is obvious by the eight

558   shared species), indicating that the dispersal extent for these eight species might range up to

559   at least 3000 km. However, this hypothesis will need to be confirmed with subsequent

560   molecular analyses.

561

562   Abyssal amphipods have been shown to be able to travel actively at speeds of almost 4

563   cm/sec (Laver, 1985), even at temperatures as low as 3°C (Kankaanpää et al. 1995). It is

564   obvious that they are sufficiently strong to swim up weak currents since they can be found

565   several hundred meters above the seafloor searching pelagically for mates (e.g. *Eurythenes*

566   *gryllus* occurring up to 1800 m above the seafloor) (Thurston 1990; Havermans et al. 2013)

567   or following food-falls (Baldwin and Smith 1987).

568

569   However, it is apparent that the dispersal of abyssal amphipods is not always contingent on

570   current direction, but also on passive dispersal. Amphipods can also be carried passively over

571   long distances by stronger currents e.g. (the circumpolar current of the Southern Ocean)

572   (Laver et al. 1985), but even weaker deep-sea currents have been suggested as a mechanism

573   for deep-sea dispersal of amphipods (e.g. *Eurythenes gryllus* (Schüller and Ebbe 2007)). This

574   coupled with their ability to follow odour-plumes (Ide et al. 2006; Premke, 2003),

575   significantly increases the probability and extent of their dispersal (Conlan 1991; Highsmith,

576   1985). Specialist feeding adaptations for several species in our assemblages have been

reported in Havermans & Smetacek, 2018). For example, the semi-tubular flap-like molars of the genera *Hirondellea* and *Eurythenes*, and the distendable foregut (*Abyssorchomene*) and midgut (*Paralicella*). It is not clear from our study in the absence of Particulate Organic Carbon (POC) data for the areas of the trap deployments whether the biogeography of these specialised feeders is linked to the productivity gradients in these two basins. The lack of a clear dispersal pattern is obvious from Figure 6, where station D2 is the station plotted closest with the CCZ basin in terms of species composition despite station D5 being geographically the shortest distance away from the CCZ.

Recent research on *Eurythenes gryllus* has demonstrated that it thrives in every ocean with a wide (pelagic – hadal) depth range. However, assumptions that individual morphotypes of this species belong to the same genetic lineage have been challenged (Havermans et al. 2013 & Havermans, 2016). Ritchie et al. (2016) demonstrated with microsatellite markers heterozygote deficiency in *Paralicella tenuipes* Chevreux, 1908, which they attributed to cryptic diversity. It is likely that some of the eight shared species between the two basins are cryptic species, which will be tested by ongoing molecular research.

Unfortunately, in the absence of data on deep-sea currents in the study area, especially between the CCZ and DEA, it is not yet possible to fully explain the drivers and mechanisms of amphipod dispersal between these particular basins.

The DisCOL Experimental Area as a proxy

Higher abundances of scavenging amphipods were collected from the CCZ (3932 individuals) as opposed to the DEA (2984 individuals). Yet, we have identified more morphotypes in the DEA (18) than in the CCZ (10), indicating that the DEA is more speciose, and thus, more biodiverse.

However, although the DEA is more speciose many of its morphotypes were collected in low abundances, with several of these being singletons or doubletons (collected from one or two sampling stations only). This is reflected in the rarefaction curves (Figure 4), which indicate thorough sampling in the CCZ with all but station C7 reaching asymptotes. In contrast, four stations in the DEA (D1, D2, D4 and D5) are unsaturated. This pattern suggests firstly, that the less abundant species which are present at fewer stations may not necessarily be rare species and secondly, that there could be as yet undetected biodiversity in the DEA.

Our preliminary (basin-scale) comparison of the scavenging communities of the two study areas shows that even if the DEA is a small-scale disturbance experiment, it is a very diverse area. Thus, the DEA is a well-chosen site for monitoring the impacts of disturbance and instrumental in its role as a proxy to assess impending mining activities in the CCZ.

Future research

At several stations in both basins, we collected amphipods in very high abundances (C1, C8, D3 & D5) (Table 2). Since biotic production is contingent on the sinking flux of particles from the euphotic zone (Sweetman, 2017), the biodiversity differences at each of the thirteen stations could be driven by POC or erratic whale-falls (Smith et al. 1989). However, not all feeding behaviour of scavenging amphipods is based on opportunistic or erratic availability of nutrients (Havermans & Smetacek, 2018). During future sampling campaigns, the POC of these amphipod sampling areas should be monitored, along with experiments on different types of food-fall in addition to obtaining side-scan sonar and abiotic data. This will provide a more comprehensive view of the food types required for these species to thrive in the deep sea.

It is not clear from our results whether substrate type (i.e. nodule/non-nodule) has any effect on the amphipod communities (Smith and Demopoulos, 2003) since these kinds of data are only available for stations D3 and D4. To answer this question, resampling of the study areas in combination with an Ocean Floor Observation System (OFOBS) (video/camera) is required.

Although our study only addresses the scavenging amphipod species longer than 15 mm, we already find indications for a possible disturbance effect in the DEA. It is obvious that scavenging amphipods are only one of several bentho-pelagic indicator groups. Other truly benthic groups such as sponges or less dispersive amphipods (e.g. collected by the EpiBenthic Sledge (EBS)) may demonstrate an even more pronounced impact of mining activities and should be investigated in future studies.

With the application of molecular techniques to identify cryptic species (Delić et al, 2017), more realistic estimates of biodiversity can be obtained (Schön et al. 2012), improving our current knowledge of the biodiversity of this area. If these improved estimates of biodiversity also include cryptic species, it is possible that the biological impact of manganese nodule mining on amphipod and other deep-sea faunal communities may turn out to be even higher.

Conclusions

In summary, this study on the scavenging amphipod community of two abyssal oceanic basins has demonstrated that amphipods are present in high abundances across the CCZ and DEA, with eight shared species and some morphotypes possibly being unique to their respective basin.

Our results have indicated that the simulated mining experiment may have had an impact on the biodiversity of these scavenging amphipods, as demonstrated by the low alpha biodiversity of the DEA overall, at the disturbance site itself (D1), and the 60% dominance of *A. gerulicorbis* (Shulenberger & Barnard, 1976) in this region.

Given the scarcity of sampling and industry experience of marine habitats at these depths, the formulation of effective regulations is challenging (International Seabed Authority, 2017). Nonetheless, our study provides the first results on possible effects of disturbance activities on the abyssal amphipod biodiversity of deep-sea basins.

Sample and data availability

Biological samples pertaining to this manuscript are stored at the Royal Belgian Institute of Natural Sciences, and the data discussed in the manuscript are submitted to PANGEA.

References

Appeltans, W., Boxshall, G., Bouchet, P., Vanhoorneb., Decock, W., Warren, A., Collinsa., Kroh A., Schmidt−Rhaesa, A., Berta, A., Barber, A., Todaro, A., Gittenberger, A., Hoeksema, B., Swalla, B., Neuhaus, B., Hayward, B., Self−Sullivan, C., Fransen, C., Messing, C., Erséus, C., Emig, C., Boyko, C., Mah, C., Millsc., Nielsen, C., Jaume, D., Fautin, D., Domning, D. P., Gibson, D., Lazarus, D., Gordon, D., Opresko, D., Schwabe, E., Mac−Pherson E., Thuesen, E., Dahdouh−Guebas, F., Anderson, G., Poore, G., Williams, G., Walker−Smith, G., Read, G., Lambert, G., Paulay, G., Segers, H., Furuya, H., Bartsch, I.,Van Der Land, J., Reimer, J. D., Vanaverbeke, J., Saiz−aiz, Saike, J., Sair, J. D.,Pilger, J., Norenburg, J., Kolb, J., Schnabel, K. E., Meland, K., Fauchald, K., Cheng, L., Van Ofwe−Gen L., Błażewicz−Paszkowycz, M., Rius, M., Curini−Galletti, M., Schotte, M., Tasker, M. L., Angel, M. V., Osawa, M., Longshaw M., Guiry, M., Bailly, N., De Voogd, N., Bruce N., Shenkar, N., Garcia−Alvarez, O., Mclaughlin, P., Kirk, P., Davie, P., Ng, P. K. L., Schuchert P., Uetz P., Bock P., Pugh P., Lemaitrer., Kristensen R., Van Soestr., Bray, R., Bamber, R. N., Da Rocha, R. M., Hopcroft R., Stöhr, S., De Grave, S., Gerken, S., Gofas, S., Tyler, S., Ahyong, S., Wilson, S., Brandao S. N., Koenemann, S., Feist, S., Cairns, S., Timm, T., Cribb, T., Molodtsova, T., Chan, T.–Y., Iseto, T., Artois, T., Scarabino, V., Siegel, V., Eschmeyer, W., Hummon, W., Perrin W., Sterrer, W., Hernandez, F., Mees, J. and Costello, M. J.: The Magnitude of Global Marine Biodiversity, Curr. Biol., 22, 2189–2202, 2012.

Baldwin, R. J. and Smith, K. L. Jr.: Temporal variation in the catch rate, length, color, and sex of the necrophagus amphipod, Eurythenes gryllus, from the central and eastern North Pacific, Deep Sea Res. Pt. I (Oceanogr. Res. Pap.), 34, 425–439, 1987.

Barnard, J. L.: Gammaridean Amphipoda from depth of 400 to 6000 m, Galathea. Rep., 5, 23–128, 1961.

Barnard, J. L. and Karaman, G.: The Families and Genera of Marine Gammaridean Amphipoda (Except Marine Gammaroids), Rec. Aust. Mus. Suppl. 13., 1–866, 1991.

Billett, D. S. M., Lampitt, R. S., Rice, A. L. and Mantoura, R. F. C.: Seasonal sedimentation of phytoplankton to the deep-sea benthos, Nature., 302, 520–522. 1983.

731

732 Birstein Y.A. and Vinogradov M.E.: Pelagischeskie gammaridy tropischeskoi chasti Ticogo

733   Okeana. [Pelagic Gammaridea of the tropical part of the Pacific Ocean], Trudy

734   instituta okeanologii Akademi nauk SSSR., 34, 165–241, 1960.

735

736 Blankenship, L. E., Yayanos, A. A., Cadien, D. B. and Levin, L. A.: Vertical zonation

737   patterns of scavenging amphipods from the Hadal zone of the Tonga and Kermadec

738   Trenches, Deep-Sea Res. Pt. I., 53, 48–61, doi:10.1016/j.dsr.2005.09.006, 2006.

739

740 Brandt, A., Błazewicz-Paszkowycz, M., Bamber, R. N., Mühlenhardt-Siegel, U., Malyutina,

741   M. V., Kaiser, S., Broyer, C. De. and Havermans, C.: Are there widespread peracarid

742   species in the deep sea (Crustacea: Malacostraca)?, Pol. Polar Res., 33, 139–162,

743   2012.

744

745 Brandt, A., Gooday A. J., Brix S. B., Brökeland, W., Cedhagen, T., Choudhury, M.,

746   Cornelius, N., Danis, B., De Mesel, I., Diaz R. J., Gillan D. C., Ebbe B., Howe J.,

747   Janussen, D., Kaiser, S., Linse, K., Malyutina, M., Brandao, S., Pawlowski, J. and

748   Raupach, M.: The So Deep Sea: First Insights Into Biodiversity And Biogeography,

749   Nature, 447, 307–311, 2007.

750

751 Bray, J. R. and J. T. Curtis.: An ordination of upland forest communities of southern

752   Wisconsin, Ecol. Mono., 27, 325–349, 1957.

753

754 Conlan K. E.: Precopulatory mating behavior and sexual dimorphism in the amphipod

755   Crustacea, Hydrobiologia., 223, 255–282, 1991.

756

757 Delić, T., Trontelj, P., Rendoš, M. and Fišer., C.: The importance of naming cryptic species

758   and the conservation of endemic subterranean amphipods, Sci. Rep., 7, 3391,

759   https://doi.org/10.1038/s41598-017-02938-z, 2017.

760

761 d'Udekem d'Acoz, C. and Havermans, C.: Contribution to the systematics of the genus

762   Eurythenes S. I. Smith in Scudder, 1882 (Crustacea: Amphipoda: Lysianassoidea:

763   Eurytheneidae), Zootaxa., 3971 (1), pp. 180: 67–74, 2015.

764

765 Etter, R. J., Boyle, E. E., Glazier, A., Jennings, R. M., Dutra, E. and Chase. M. R.
766   Phylogeography of a Pan-Atlantic Abyssal Protobranch Bivalve: Implications for
767   Evolution in the Deep Atlantic, Mol. Ecol., 20, 829–843,
768   doi:http://dx.doi.org/10.1111/j.365-294X.2010.04978.x, 2011.

769

770 Futuyma, D. J.: Evolutionary Biology, (Ed.) 3. Sinauer Associates, Sunderland, MA, 751 pp,
771   1998.

772

773 Gage, J. D. and Tyler, P. A.: Deep-Sea Biology: a natural history of organisms at the deep-
774   sea floor, Vol. Cambridge University press, Cambridge, 1991.

775

776 German C. R., Ramirez-Llodra, E., Baker, M. C., Tyler, P. A., and the Chess Scientific
777   Steering Committee.: Deep-Water Chemosynthetic Ecosystem Research during the
778   Census of Marine Life Decade and Beyond: A Proposed Deep Ocean Road Map,
779   PLoS ONE., 6, 1–16, doi:10.1371/journal.pone.0023259, 2011.

780

781 Glover, A., Dahlgren, T. G., Wiklund, H., Mohrbeck, I. and Smith, C. R.: An end-to-end
782   DNA taxonomy methodology for benthic biodiversity survey in the Clarion-
783   Clipperton Zone, central Pacific abyss, Journal of Marine Science and Engineering.,
784   4, 1–34, doi: 10.3390/jmse4010002, 2016.

785

786 Glover, A., Paterson, G., Bett, B., Gage, J., Sibuet, M., Sheader, M. and Hawkins, L.:
787   Patterns in polychaete abundance and diversity from the Madeira Abyssal Plain,
788   northeast Atlantic, Deep Sea Res. Pt. I (Oceanogr. Res. Pap.)., 48, 217–236, 2001.

789

790 Gotelli, N. J. and Colwell, R., K.: Quantifying Biodiversity: Procedures and Pitfalls in the
791   Measurement and Comparison of Species Richness, Ecol. Lett., 4, 379–91,
792   doi:10.1046/j.1461-0248.2001.00230, 2001.

793

794 Hannides, A. and Smith, C. R.: The northeast abyssal Pacific plain, in: Biogeochemistry of
795   Marine Systems, K. B. Black and G. B Shimmield, edited by: CRC Press, Boca
796   Raton, Florida, 208–237, 2003.

797

798 Havermans, C.: Have we so far only seen the tip of the iceberg? Exploring species diversity
799   and distribution of the giant amphipod Eurythenes, Biodiversity., doi:
800   10.1080/14888386.2016.1172257, 2016.
801
802 Havermans, C and Smetacek, V.: Bottom-up and top-down triggers of diversification: A new
803   look at the evolutionary ecology of scavenging amphipods in the deep sea. Progress in
804   Oceanography., 164, 37–51, 2018.
805
806 Havermans, C., Sonet, G., d'Udekem d'Acoz, C., Nagy, Z. T., Martin, P., Brix, S., Riehl, T.,
807   Agrawal, S. and Held, C.: Genetic and morphological divergences in the
808   cosmopolitan deep-sea amphipod Eurythenes gryllus reveal a diverse abyss and a
809   bipolar species, PLoS ONE., 1–14, 8, e74218, doi:http://dx.doi.org/10.1371/journal.
810   pone.0074218, 2013.
811
812 Highsmith, R.: Floating and algal rafting as potential dispersal mechanisms in brooding
813   invertebrates, Mar. Ecol. Prog. Ser., 25, 169–179, 1985.
814
815 Hilário, A., Metaxas, A., Gaudron, S. M. ,Howell, K. L., Mercier, A., Mestre, N. C., Ross, R.
816   E. ,Thurnherr, A. M. and Young, C.: Estimating dispersal distance in the deep sea:
817   challenges and applications to marine reserves, Front. Mar. Sci., 2, doi:10.3389/
818   fmars.2015.00006, 2015.
819
820 Ide, K., Takahashi, K., Nakano, T., Minoru, S. and Omori, M.: Chemoreceptive foraging in a
821   shallow-water scavenging lysianassid amphipod: Role of amino acids in the location
822   of carrion in Scopelocheirus onagawae. Mar Ecol Prog Ser., 317, 193–202, 2006.
823
824 Ingram, C. L. and Hessler, R. R.: Distribution and behavior of scavenging amphipods from
825   the central North Pacific, Deep-Sea Res., 30, 683–706, 1983.
826
827 International Seabed Authority (ISA).: A Discussion Paper on Developing a Regulatory
828   Framework for Mineral Exploitation in the Area, Env. Matt., 1–102, 2017.
829

830 Kankaanpää, H., Laurén, M., Mattson, M. and Lindström, M.: Effects of bleached kraft mill
831   effluents on the swimming activity of Monoporeia affinis (Crustacea, Amphipoda)
832   lindström, Chemosphere., 31, 4455–4473, 1995.

833

834 Laver, M. B., Olsson, M. S., Edelman, J. L. and Smith K. L. Jr.: Swimming rates of
835   scavenging deep−sea amphipods recorded with a free−vehicle video camera.
836   Deep−Sea Res. II., 32, 1135–1142, 1985.

837

838 Lester, S. E., Ruttenberg, B. I., Gaines, S. D. and Kinlan B. P.: The relationship between
839   dispersal ability and geographic range size, Ecol. Lett., 10, 745–758, 2007.

840

841 Levin, L. A., Etter, R. J., Rex, M. A., Gooday, A. J., Smith, C. R., Pineda, J., Stuart, C. T.,
842   Hessler, R. R. & Pawson, D.: Environmental influences on regional deep-sea species
843   diversity, Annu. Rev. Ecol. Evol. Syst., 32, 51–93, 2001.

844

845 Liow, L. H.: Does versatility as measured by geographic range, bathymetric range and
846   morphological variability contribute to taxon longevity? Glob. Ecol. Bio., 16, 117–
847   128, 2007.

848

849 Lodge, M., Johnson, D., Le Gurun, G., Wengler, M., Weaver, P. and Gunn, V.: Seabed
850   mining: International Seabed Authority environmental management plan for the
851   Clarion–Clipperton Zone. A partnership approach, Mar. Pol., 49, 66–72, 2014.

852

853 Lonsdale, P.: Clustering of suspension-feeding macrobenthos near abyssal hydrothermal
854   vents at oceanic spreading centres, Deep-Sea Res., 24, 857–863, 1977.

855

856 Lörz A-N, Jażdżewska AM, Brandt A.: A new predator connecting the abyssal with the hadal
857   in the Kuril-Kamchatka Trench, NW Pacific. Costello M, ed. PeerJ., doi:
858   10.7717/peerj.4887, 2018

859

860 Narahara-Nakano, Y., Nakano, T. and Tomikawa, K. Deep-sea amphipod genus Eurythenes
861   from Japan, with a description of a new Eurythenes species from off Hokkaido
862   (Crustacea: Amphipoda: Lysianassoidea), Marine Biodiversity., 1867–1616, doi:
863   10.1007/s12526-017-0758-4, 2017.

OBIS (Ocean Biogeographic Information System) - https://obis.org/, last access 12th January
2019.

Paull, C. K., Hecker, B., Commeau, R., Freeman-Lynde, R. P., Neumann, C., Corso, W. P.,
Golubic, S., Hook, J. E., Sikes, E. & Curray, J.: Biological communities at the Florida
escarpment resemble hydrothermal vent taxa, Science, 226, 965–967, 1984.

Pfeffer, G.: Die Krebse von Sud-Georgien nach der Ausbeute der Deutschen Station 1882-83.
2.Teil. Die Amphipoden Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten.
5, 75–142. pls.1–3, 1888.

Premke, K., Muyakshin, S., Klages, M. and Wegner, J.: Evidence for long-range
chemoreceptive tracking of food odour in deep-sea scavengers by scanning sonar
data, J. Exp. Mar. Biol. Ecol., 285, 283–294, 2003.

R Core Team. R: A language and environment for statistical computing. R Foundation for
Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, 2013, http://www.R-
project.org/, last accessed June 25th 2018.

Ramirez-Llodra, E., Brandt, A., Danovaro, R., De Mol, B., Escobar, E., German, C. R.,
Levin, L. A., Martinez Arbizu, P., Menot, L., Buhl-Mortensen, P., Narayanaswamy,
B. E., Smith, C. R., Tittensor, D. P., Tyler, P. A., Vanreusel, A. and Vecchione, M.:
Deep, diverse and definitely different: unique attributes of the world's largest
ecosystem, Biogeosciences., 7, 2851–2899, 2010.

Ramirez-Llodra, E., Tyler, P. A., Baker, M. C., Bergstad, O. A., Clark, M. R. and Escobar,
E.: Man and the last great wilderness: human impact on the Deep Sea, PLoSONE., 6,
doi:10.1371/journal.pone.0022588, 2011.

Rex, M. A., Stuart, C. T., Hessler, R., R., Allen, J. A., Sanders, H. L. and Wilson, G. D. F.:
Global-scale latitudinal patterns of species diversity in the deep-sea benthos, Nature,
365, 636–639, 1993.

897 Ritchie, H., Jamieson, A. J. and Piertney, S. B.: Isolation and Characterization of
898   Microsatellite DNA Markers in the Deep-Sea Amphipod Paralicella tenuipes by
899   Illumina MiSeq Sequencing, Journal of Heredity., 367–371, 2016.
900

901 Sanders H. L.: Marine benthic diversity: a comparative study, Am. Nat., 102, 243–282, 1968.
902

903 Schön I, Pinto R. L., Halse, S., Smith, A. J. and Martens, K.: Cryptic Species in Putative
904   Ancient Asexual Darwinulids (Crustacea, Ostracoda), PLoS ONE., 7, e39844.
905   doi:10.1371/journal.pone.0039844, 2012.
906

907 Schulenberger, E. and Barnard, J. L.: Clarification of the Abyssal Amphipod, Paralicella
908   tenuipes Chevreux, Crustaceana., 31, 267–274, 1976.
909

910 Schüller, M. and Ebbe, B.: Global distributional patterns of selected deep−sea Polychaeta
911   (Annelida) from the Southern Ocean, Deep−Sea Res. II., 54, 1737–1751, 2007.
912

913 Seefeldt, M. A., Weigand, A. M., Havermans, C., Moreira, E. and Held, C.: Fishing for
914   scavengers: an integrated study to amphipod (Crustacea: Lysianassoidea) diversity of
915   Potter Cove (South Shetland Islands, Antarctica). Marine Biodiversity.,
916   https://doi.org/10.1007/s12526-017-0737-9, 2017.
917

918 Simpson, E. H.: Measurement of diversity, Nature., 163, 688, 1949.
919

920 Smith, C. R., Kukert, H., Wheatcroft, R. A., Jumars, P. A. and Deming, J. W.: Vent fauna on
921   whale remains, Nature., 341, 27–28, 1989.
922

923 Smith, C. R. and A.W. J. Demopoulos.: Ecology of the deep Pacific Ocean floor, in:
924   Ecosystems of the World Volume 28: Ecosystems of the Deep Ocean, P. A. Tyler,
925   (Ed.), Elsevier, Amsterdam, pp. 179–218, 2003.
926

927 Smith, C. R., Drazen J. and Mincks, S. L.: Deep-sea Biodiversity and Biogeography:
928   Perspectives from the Abyss. International Seabed Authority Seamount Biodiversity
929   Symposium., 1–13, 2006.
930

931 Sweetman, A. K., Thurber, A. R., Smith, C. R., Levin, L. A., Mora, C., Wei, C.-L., Gooday,
932   A. J., Jones, D. O. B., Rex, M., Yasuhara, M., Ingels, J., Ruhl, H. A., Frieder, C. A.,
933   Danovaro, R., Würzberg, L., Baco, A., Grupe, B. M., Pasulka, A., Meyer, K. S.,
934   Dunlop, K. M., Henry, L.-A. and Roberts, J. M.:Major impacts of climate change on
935   deep-sea benthic ecosystems. Elem Sci Anth, 5., 4, doi:
936   http://doi.org/10.1525/elementa.203, 2017.

938 Taguchi Y. H. and Oono, Y.: Relational patterns of gene expression via non-metric
939   multidimensional scaling analysis, Bioinformatics., 21, 730–740, 2005.

941 Thiel, H.: Deep-sea Environmental Disturbance and Recovery Potential, Int. Revue ges.
942   Hydrobiol. Hydrogr., 77, 331–339, doi:10.1002/iroh.19920770213, 1992.

944 Thurston, M. H.: Abyssal necrophagous amphipods (Crustacea: Amphipoda) in the northeast
945   and tropical Atlantic Ocean, Prog. Oceanogr., 24, 257–274, doi:10.1016/0079-
946   6611(90)90036-2, 1990

948 Vader, W.: How many amphipods species? 6th International Crustacean Congress, Glasgow,
949   Scotland, 18–22 July 2005, 143, 2005.

Figure captions

Figure 1: Geographic locations of the two study areas, the Clarion-Clipperton fracture Zone (CCZ) (Northeast Pacific) and the DISturbance and re-COLonisation (DisCOL) Experimental Area (DEA) (Peru Basin, Southeast Pacific). There are nine Areas of Particular Ecological Interest (APEIs) in the CCZ region, which are illustrated by 400 x 400 km^2 white boxes. Grey boxes indicate the various contractor license areas in the CCZ. We deployed eight amphipod traps across the CCZ, which is 16,000 km^2 and 7000 km wide, and five in the DEA, which encompasses 11 km^2 with a width of 4 km.

Figure 2: **Histogram showing the species assemblage for the scavenging community in the Clarion-Clipperton fracture Zone (CCZ) (black) and the DisCOL Experimental Area (DEA) (grey)**. The abundances of 17 morphotypes are shown.

Figure 3: Catch Per Unit Effort (CPUE) illustrating the correlation between sampling time and number of individuals collected.

Figure 4: Species rarefaction curves for each of the 13 trap stations across both areas, the Clarion-Clipperton fracture Zone and the DisCOL Experimental Area. Only individuals longer than 15 mm were considered here.

Figures 5a and b: Relative species abundances in the Clarion-Clipperton fracture Zone and the DisCOL Experimental Area. These abundances represent the longer than 15mm fraction of the scavenging amphipod community only.

Figure 6: NMDS plot showing the beta biodiversity (dis/similarities) for each of the thirteen amphipod trap sampling stations associated with the two basins, Clarion-Clipperton fracture Zone (CCZ) (black) and the DisCOL Experimental Area (DEA) (red). Data are supported by a low stress value of 0.01.

989 **Table captions**

990

991 **Table 1: Station overview.** Codes refer to the codes used in this paper in figures 1, 3, 4, 6

992 and Table 3. The original station code represents the cruise codes from (SO239 and SO232-

993 1). Depth refers to water depth (m) on deployment. Nodule presence/absence information is

994 known only for stations D3 and D4.

995 **Table 2:** Overview of morphotypes across the Clarion-Clipperton fracture Zone (CCZ) and

996 DisCOL Experimental Area (DEA).

997

998 **Table 3:** Comparison of biodiversity calculated using the Simpson Index (D), for the Clarion-

999 Clipperton fracture Zone and DisCOL Experimental Area, and D for each station is shown

1000 for further comparisons within these areas.

1001

1002

1003

1004

1005

1006

1007

1008

1009

1010

Appendix/Electronic Supplementary Information (ESM) captions

Appendix 1: Multibeam scan - Showing the location of the 78 track marks created by the plough harrow in the DisCOL Experimental Area to simulate manganese nodule extraction activity (D1)

Appendix 2 – Photograph showing the baited free-fall lander trap designed and deployed by RBINS.

Appendix 3 - Side-scan sonar image of site D5 showing possible seamount barriers. View from NW (top) to SE (bottom). Contours are every 25 m. (Source: GEOMAR, 2015).
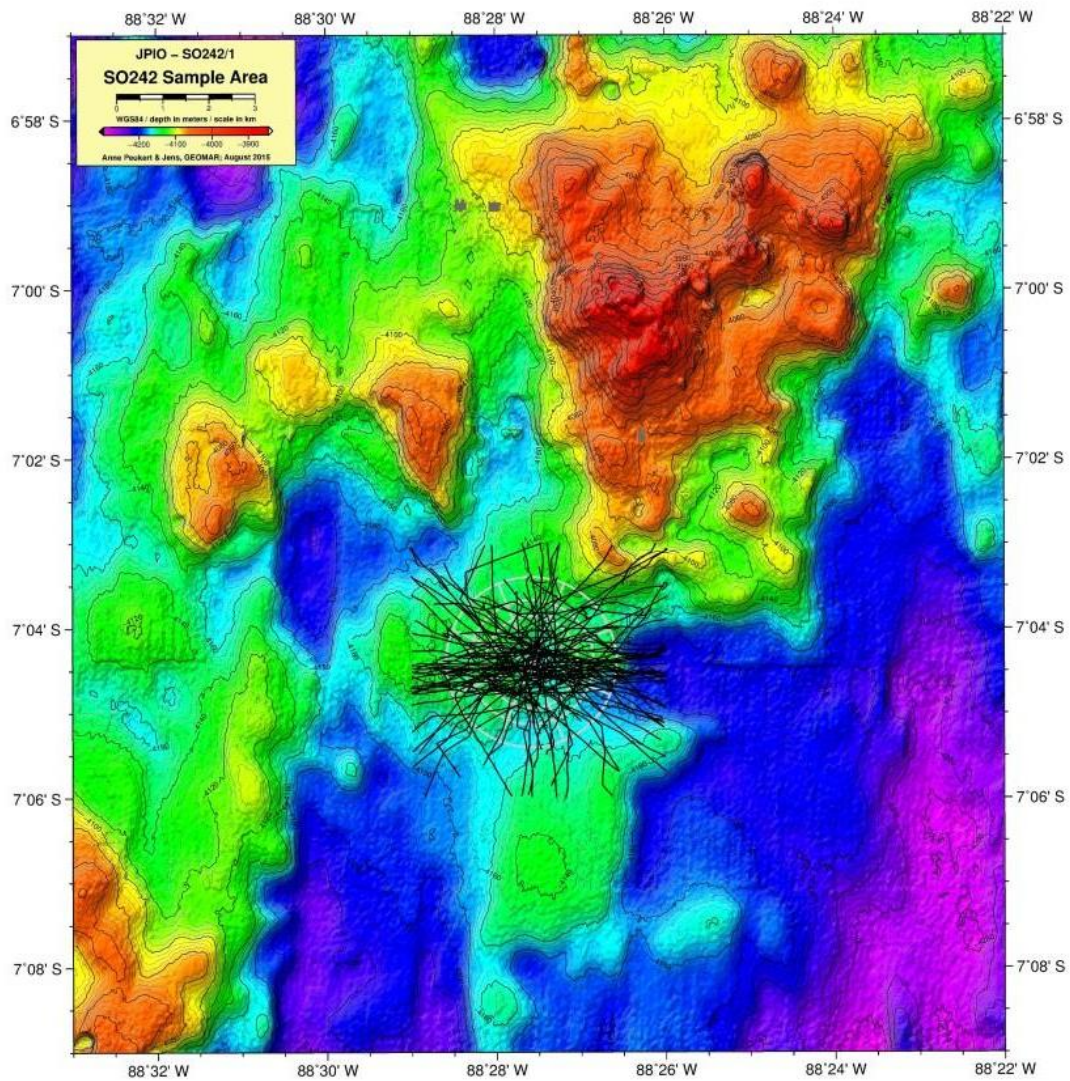
Appendix 4 – Calculation of alpha biodiversity used in this manuscript.

Appendix 1: Multibeam scan - Showing the location of the 78 track marks created by the plough harrow in the DisCOL Experimental Area to simulate manganese nodule extraction activity.
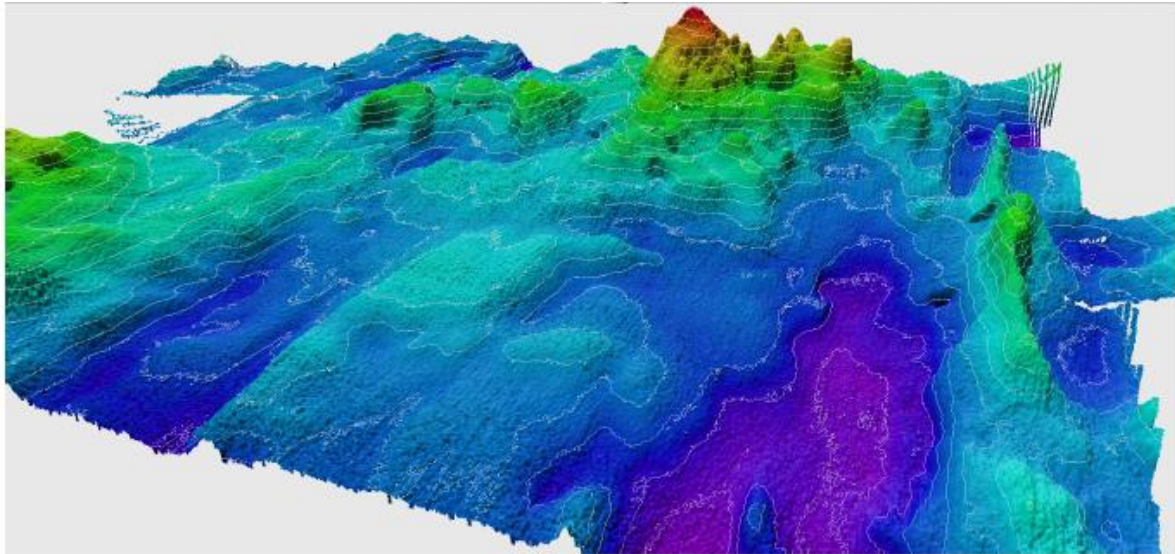
1050 **Appendix 2** – Photograph showing the baited free-fall lander trap designed and deployed by
1051 RBINS.

1052

1053

1054

1055

1056

1057

1058

1059

1060

1061

1062

1063

1064

1065 **Appendix 3** - Side-scan sonar image of site D5 showing possible seamount barriers. View
1066 from NW (top) to SE (bottom). Contours are every 25 m. (Source: GEOMAR, 2015).

1067

1068

1069 _____

1070

1071

1072

1073

1074

1075

1076

1077

1078

1079   **Appendix 4** - Calculation of alpha biodiversity used in this manuscript.

1080   Simpson Index

1081   Simpson Diversity Index (D) = $1 - \dfrac{\sum n(n-1)}{N(N-1)} =$

1082   D = Diversity Index

1083   n = number of individuals in each particular species

1084   N = Total number in community

1085   A high value of D indicates a high species diversity.

1086

1087

1088

1089

1090

1091

1092

1093

1094

1095

1096

1097

1098

1099

1100

1101

1102

1103

1104

1105

1106

1107