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

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Abstract

In 2015, we have collected more than 60,000 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. We further provide evidence that disturbance proxies seem to negatively affect scavenging amphipod biodiversity, as illustrated by a reduced alpha biodiversity in the DEA (Simpson Index (D) = 0.62), when compared to the CCZ (D = 0.73) and particularly of the disturbance site in the DEA and the site geographically closest to it. Community compositions of the two basins differs, as evidenced by a Non-Metric Dimensional Scaling (NMDS) analysis of beta biodiversity. The NMDS also shows a further separation of the disturbance site (D1) from its neighbouring, undisturbed reference areas (D2, D3, D4 and D5) in the DEA. A single species, *Abyssorchomene gerulicorbis* (Shulenberger & Barnard, 1976), dominates the DEA with 60% of all individuals.

Keywords

JPIO Ecological Aspects of Deep-sea mining, Clarion Clipperton Fracture Zone, CCZ, DisCOL Experimental Area (DEA), Amphipoda.

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).

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95 In the last decade, there has been an 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).

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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. In spite of 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).

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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.

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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.

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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**

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129 *Study area*

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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 claim

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.

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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 claim 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.

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 recolonization 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 60,000 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

174   - D5; Figure 1, Table 1). In the CCZ, we sampled within three different contractor claim

175   areas (Table 1) to obtain a pre-disturbance baseline, and to then compare it with one of the

176   nine protected APEIs around the CCZ. In contrast, in the DEA, sampling was conducted once

177   within the disturbed area (D1), twice 10 km away (D2, D3) and twice 40 km away (D4, D5)

178   from D1 in four surrounding reference areas (see Figure 1).

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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 SO232-1). Depth refers to water depth (m) on deployment. Nodule presence/absence information is known only for stations D3 and D4.

Deployment Code	Original Station Code	Depth (m)	Known geological features	Remarks	Residence Time (h:m:s)
C1	SO239-33	4122	Plains	German claim	100:20:00
C2	SO239-37	4116	Plains	German claim	125:49:00
C3	SO239-63	4354	Plains	German claim	66:07:00
C4	SO239-96	4388	Seamount	Inter Ocean Metals (IOM) claim	63:02:00
C5	SO239-123	4529	Plains	Belgian claim	26:12:00
C6	SO239-139	4516	Plains North/South + seamount to west	Belgian claim	56:33:00
C7	SO239-173	4934	Plains	French claim	79:40:00
C8	SO239-205	4855	Plains	Area of Particular Ecological Interest (APEI)	55:59:00
D1	SO242/1-8	4146	Plains	Disturbed	44:26:33
D2	SO242/1-30	4307	Plains	Undisturbed Reference	51:11:18
D3	SO242/1-55	4043	Seamount No nodules	Undisturbed Reference	25:09:09
D4	SO242/1-68	4078	Seamount No nodules	Undisturbed Reference	65:20:46
D5	SO242/1-106	4269	Plains	Undisturbed Reference	47:00:50

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 cool-climate laboratory (4°C), morphologically pre-sorted and fixed in molecular grade (95%) ethanol, before being stored at -20°C.

Detailed sorting and identification was performed using the morphological species concept (Futuyama, 1998) and the keys of Lowry & Killagen (2014) and Schulenberger & Barnard (1976), 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*).

Specimens 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 was 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)

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

250   2005) was used to test the statistical significance of the differences in species compositions

251   between the two study areas.

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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 (Tables 2a and 2b). 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 (Tables 2a and 2b).

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).

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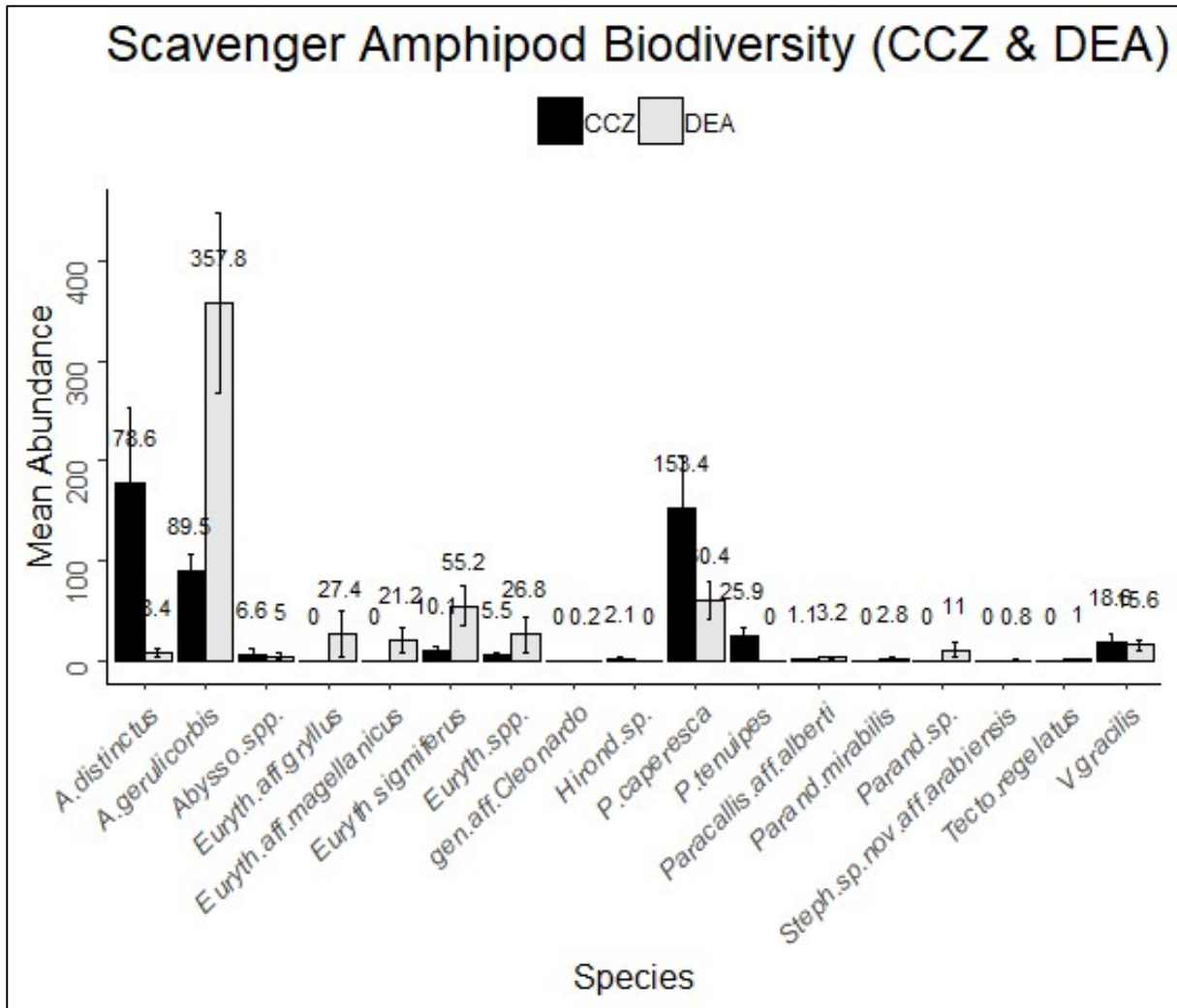
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290 **Figure 2**: **Histogram showing the species assemblage for the scavenging community in**

291 **the Clarion-Clipperton fracture Zone (CCZ) (black) and the DisCOL Experimental**

292 **Area (DEA) (grey)**. The abundances of 17 morphotypes are shown.

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Table 2a: Overview of morphotypes across the Clarion-Clipperton fracture Zone (CCZ) and DisCOL Experimental Area (DEA).

	Clarion-Clipperton fracture Zone	DisCOL Experimental Area
Total unique morphotypes collected	17 (10 found in the CCZ, 15 found in the DEA)	
Species possibly unique to this basin	2	7
Shared species between basins	8	

Table 2b: 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

317 *Sampling completeness*

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

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

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

322 (Figure 3,) shows that there is no relationship between the length of time the trap was at the

323 seafloor and total number of amphipods caught. There is a moderate but statistically

324 insignificant negative correlation with increasing deployment times ($R = -0.05$, $p = 0.551$).

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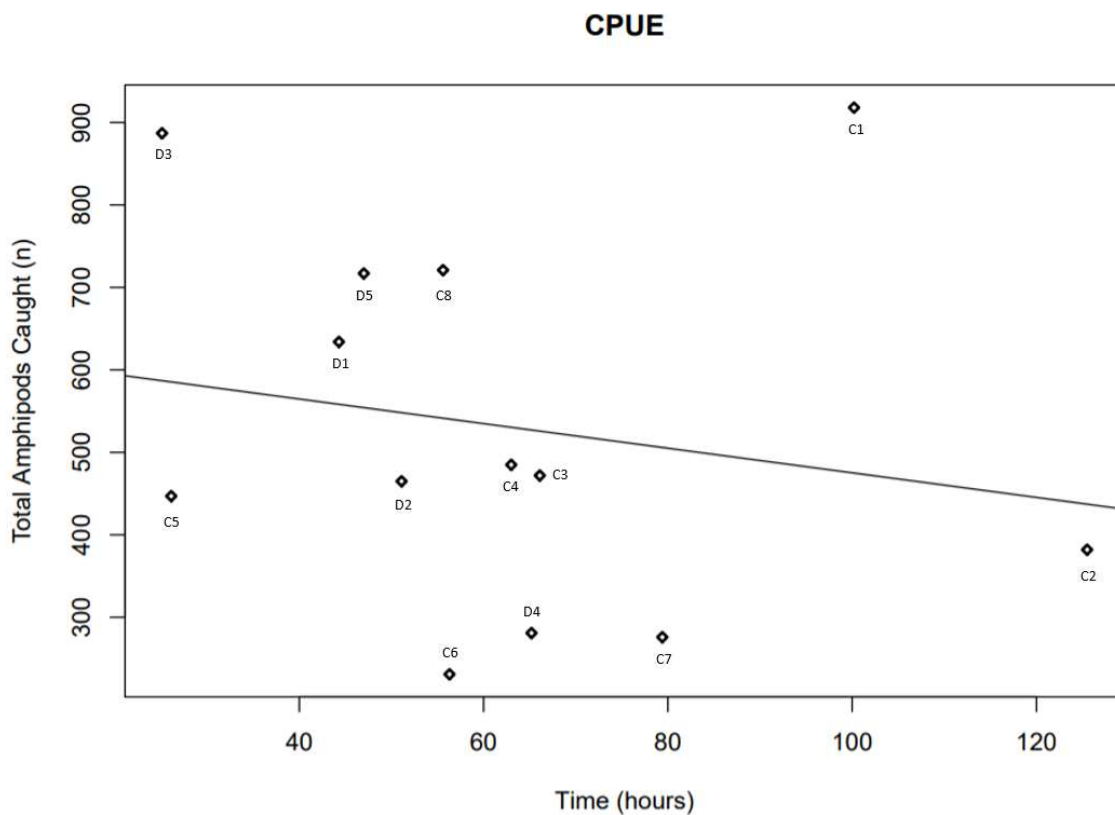
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327 **Figure 3: Catch Per Unit Effort (CPUE) illustrating the correlation between sampling**

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

329 included here.

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

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

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

339 D5) are unsaturated.

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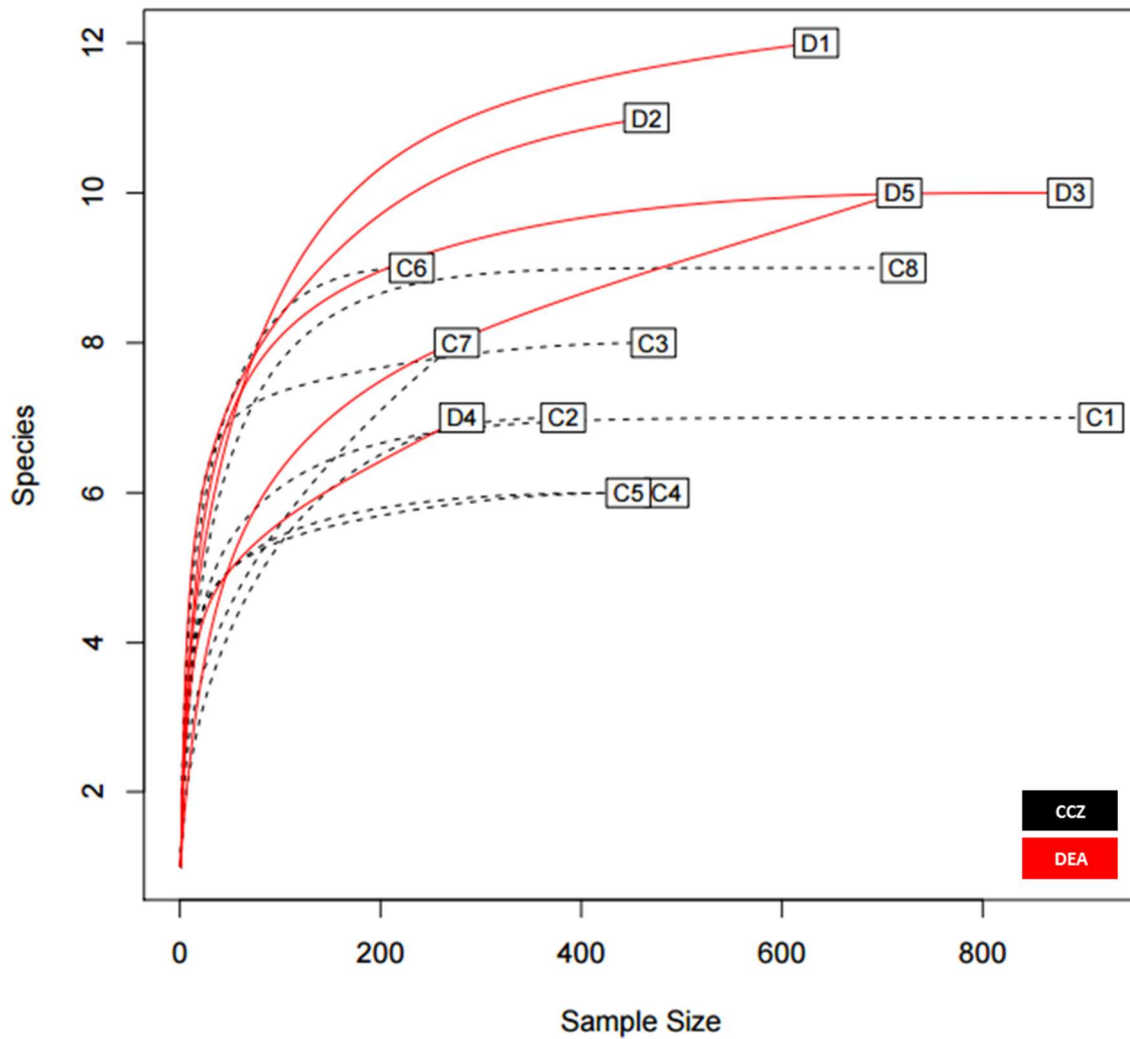
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342 **Figure 4: Species rarefaction curves for each of the 13 trap stations across both areas,**

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

344 individuals longer than 15 mm were considered here.

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Biodiversity

Figures 5a and b show that the scavenging community in the CCZ is dominated by three species, *A. distinctus* (Birstein & Vinogradov, 1960) (36%), *A. gerulicorbis* (Shulenberger & Barnard, 1976) (18%) and *Paralicella caperesca* (Shulenberger & Barnard, 1976) (31%), whereas, in contrast, the DEA scavenging community is dominated by a single species, *A. gerulicorbis* (Shulenberger & Barnard, 1976), accounting for almost 60% of all specimens. The Simpson Index (D) for the entire CCZ area is (with 0.73), higher than the 0.62 that was calculated for the whole of the DEA area (Table 3). The biodiversity of each individual station was further explored (Table 3). In the CCZ, the lowest biodiversity was found at C3 and C6 ($D = 0.23$) and the highest at C2 ($D = 0.67$), respectively. In the DEA, the lowest biodiversity of $D = 0.36$ was found at station D1 (the site of the actual disturbance) and just south of the disturbance site at D2 (0.21), while the highest biodiversity was observed at D5 ($D = 0.61$) (Table 3).

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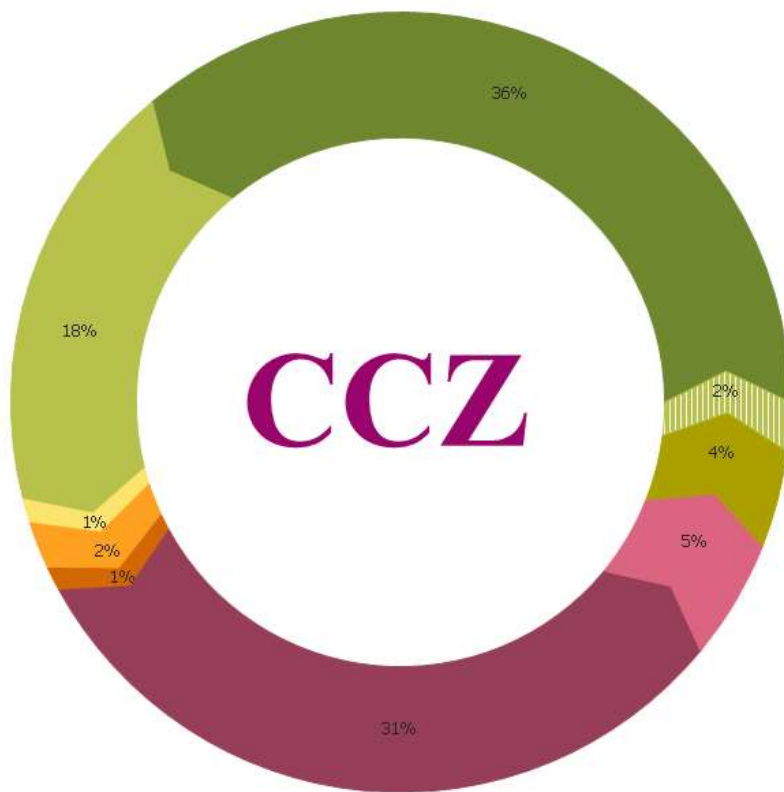
383   **Figures 5a and b: Relative species abundances in the Clarion-Clipperton fracture Zone**

384   **and the DisCOL Experimental Area**. These abundances represent the longer than 15mm

385   subsample of the scavenging amphipod community.

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

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

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395 *Species composition*

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397 The NMDS shows that the communities of the two basins are clearly separated (ANOSIM: *p*

398 = 0.002); Figure 6). The disturbed area in the DEA (D1) is showing a clear difference to the

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

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

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

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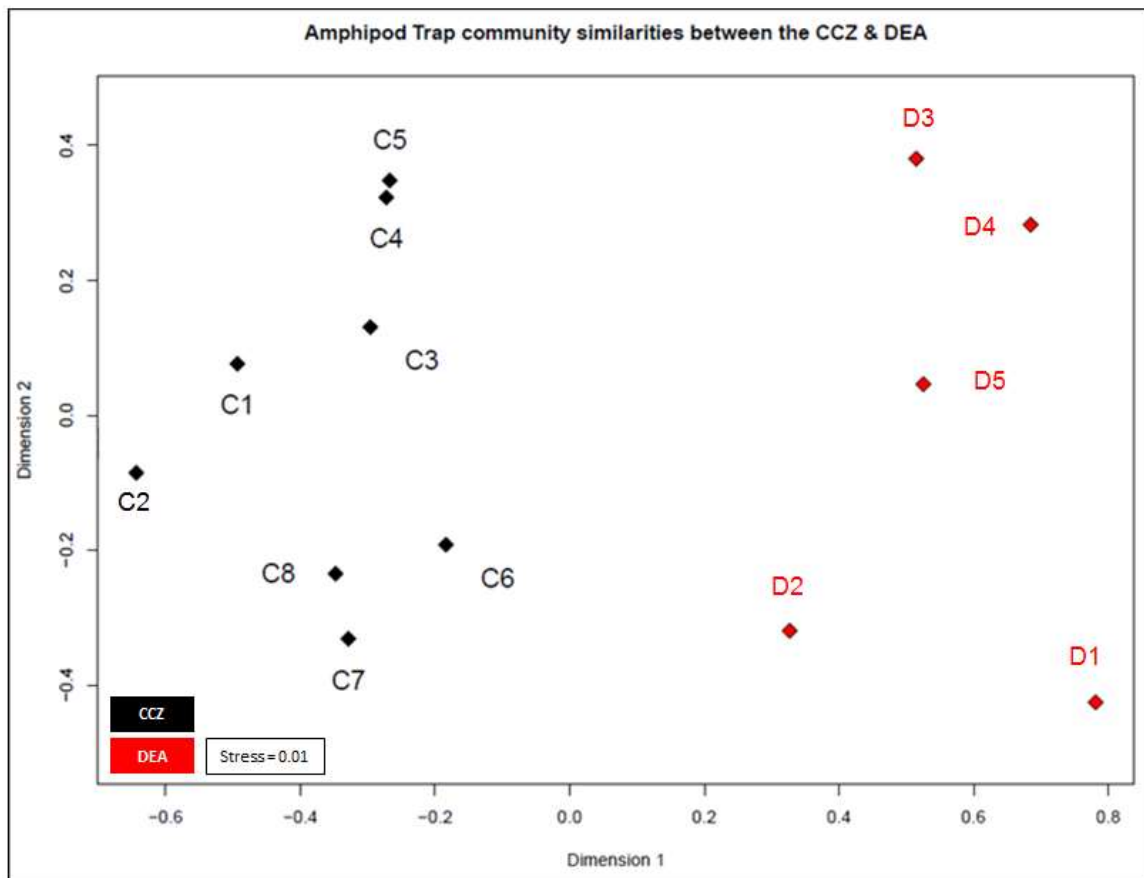
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404 **Figure 6 : NMDS plot** showing the beta biodiversity (dis/similarities) for each of the thirteen
405 amphipod trap sampling stations associated with the two basins, Clarion-Clipperton fracture
406 Zone (CCZ) (black) and the DisCOL Experimental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

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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. Regarding amphipods, only 328 benthic, demersal and benthopelagic species, belonging to 144 genera and 39 families. 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) & *Tectovalopsis* regelatus (Barnard & Ingram, 1990) (Table 2b). 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*, P*arandania* sp., *Parandaniexis mirabilis* (Schellenberg, 1929)*, Stephonyx* sp. nov. aff. *arabiensis,* and *Tectovalopsis regelatus* (Barnard & Ingram, 1990) only in the DEA, we cannot conclude based on the current data only if these species are unique to their respective basins without confirming these distribution patterns with additional sampling campaigns.

Despite the sampling campaign in the CCZ being twice as long as the DEA, the number of individuals/species collected does not correlate positively with deployment effort. We posit that this is rather an effect of abiotic and organic factors, such as the productivity-driven gradients in the CCZ, which decrease from East-West and from North-South (Hannides & Smith, 2003).

Biodiversity within basins

Figures 5a & b show clearly that the DEA scavenging community has reduced abundances of all species including *A. distinctus* (Birstein & Vinogradov, 1960) (1%) and *P. caperesca* (Shulenberger & Barnard, 1976) (7%), and is now dominated by a single species, *A. gerulicorbis* (Shulenberger & Barnard, 1976), accounting for 60% of the DEA community. This indicates an interesting resilience and flexibility in the latter species. Similar patterns have been observed in Potter Cove (Seefeldt et al. 2017), where following glacial retreat, a change in sedimentation rates led to the dominance of a single amphipod scavenging species, *Cheirimedon femoratus* (Pfeffer, 1888).

The assemblages of the two basins have some overlap in their biodiversity (as is exemplified by the eight shared morphotypes). However, the sampling stations and the two basins as a whole are heterogeneous in their species compositions.

Thus, we can observe some negative influence (possibly attributed to the disturbance in the DEA) on the scavenging amphipod community. This reduced biodiversity is reflected in the higher Simpson Index (D) for the CCZ (0.73) as compared to the DEA ($D = 0.62$; Table 3).

To explore whether this reduced diversity in the DEA was truly a result of the simulated disturbance, D was also calculated for each sampling station within each basin (Table 3).

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

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

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

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

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

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

482   (re-) sampled.

483

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

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

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

487

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

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

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

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

492   kilometres (SO242-1 Cruise report, 2016) hampering dispersal across barriers such as sills,

493   canyons and ridges (Smith, et al. 2006; Blankenship et al. 2006; Etter et al. 2011). However,

494   recent studies have shown that due to their mobile nature, geographic isolation alone would

495   not pose a true barrier to bentho-pelagic amphipod species (Havermans, 2016; Ritchie et al.

496   2017), and thus, cannot explain why such a high number of large scavenging individuals was

497   collected at station D5.

498

499   ***Community similarities***

500

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

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

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

504   local environmental abiotic conditions and seafloor topography.

505

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

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

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

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

510   biodiversity appears to have been affected by the disturbance experiment as evidenced by the

511   NMDS (Figure 6), where the disturbed area (D1) and the area closest to it (D2) are separated

512   from the remaining three reference sites (D3, D4 and D5).

513

514   In the CCZ, stations C1, C2, C3, C4 and C5 form one cluster in the NMDS (Figure 6), and

515   stations C6, C7 and C8 a second cluster. The CCZ is a geomorphologically very

516   heterogeneous region, with seamounts of 200 m altitude running from north-south. A barrier

517   of this height would be expected to affect sedimentation rates, nodule presence and currents.

518   Furthermore, the difference in depth from the eastern edge (3950m) and the western edge

519   (5150 m) is more than 1200 m. These combined factors very likely give rise to different

520   trends in species composition (Glover, et al. 2015). However, since it has been established

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

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

523   cannot be excluded as alternative explanations.

524

525   ***Dispersal and connectivity***

526

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

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

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

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

531   molecular analyses.

532

533

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

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

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

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

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

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

540

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

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

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

(Laver et al. 1985), but even weaker deep-sea currents have been suggested as a mechanism for deep-sea dispersal of amphipods (e.g. *Eurythenes gryllus* (Schüller and Ebbe 2007)). This coupled with their ability to follow odour-plumes (Ide et al. 2006; Premke, 2003), significantly increases the probability and extent of their dispersal (Conlan 1991; Highsmith, 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 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 clustering closest with the CCZ basin in terms of species composition despite the fact that station D5 is 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 the connectivity of the eight species we observed as being shared between the CCZ and DEA (based on traditional morphological methods), can be explained by the presence of one or more cryptic amphipod species, which are being tested in our future 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.

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 only may not necessarily be rare species and secondly, that there could be as yet undetected biodiversity in the DEA. Therefore, the effects of mining impact could be even more pronounced than we observed in this study. However, as the seafloor environment is subject to seasonal fluctuations (Billett et al. 1983), it is hard to predict exactly what the effects will be at this stage.

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 2b). 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 Particulate Organic Carbon (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 areas should be monitored, along with experiments on different types of food-fall in addition to obtaining side-scan sonar and

611   abiotic data. This will provide a more comprehensive view of the food types required for

612   these species to thrive in the deep sea.

613

614   It is not clear from our results whether substrate type (i.e. nodule/non-nodule) has any effect

615   on the amphipod communities (Smith and Demopoulos, 2003) since this kind of data is only

616   available for stations D3 and D4. To answer this question, resampling of the study areas in

617   combination with an Ocean Floor Observation System (OFOBS) (video/camera) is required.

618

619   Although our study only addresses the scavenging amphipod species longer than 15 mm, we

620   already find indications for a disturbance effect in the DEA. It is obvious that scavenging

621   amphipods are only one of several bentho-pelagic indicator groups. Other truly benthic

622   groups such as sponges or less dispersive amphipods (e.g. collected by epibenthic sledge

623   (EBS)) may demonstrate an even more pronounced impact of mining activities and should be

624   investigated in future studies.

625

626   With the application of molecular techniques to identify cryptic species (Delić et al, 2017),

627   more realistic estimates of biodiversity can be obtained (Schön et al. 2012), improving our

628   current knowledge of the biodiversity of this area. If these improved estimates of biodiversity

629   also include cryptic species, it is possible that the biological impact of manganese nodule

630   mining on amphipod and other deep-sea faunal communities may turn out to be even higher.

631   **Conclusions**

632

633   In summary, this study on the scavenging amphipod community of two abyssal oceanic

634   basins has demonstrated that amphipods are present in high abundances across the CCZ and

635   DEA, with eight shared species and some species possibly being unique to their respective

636   basin.

637   Our results have indicated that the simulated mining experiment probably had an impact on

638   the biodiversity of these scavenging amphipods, as demonstrated by the low D of the DEA

639   overall, at the disturbance site itself (D1), and the 60% dominance of *A. gerulicorbis*

640   (Shulenberger & Barnard, 1976) in this region.

641   Given the scarcity of sampling and industry experience of marine habitats at these depths, the

642   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.

Acknowledgements

The authors would like to acknowledge the Belgian Science and Policy Office (BELSPO) and the German Federal Ministry of Research and Education for funding. We would also like to thank the crew of the Research Vessel "Sonne", the University of Ghent (Ghent, Belgium) and Zohra Elouaazizi (Brussels, Belgium) for help in the lab. This study would not have been possible without their support.

References

665
666

667 Appeltans, W., Boxshall, G., Bouchet, P., Vanhoorneb., Decock, W., Warren, A., Collinsa.,
668   Kroh A., Schmidt−Rhaesa, A., Berta, A., Barber, A., Todaro, A., Gittenberger, A.,
669   Hoeksema, B., Swalla, B., Neuhaus, B., Hayward, B., Self−Sullivan, C., Fransen, C.,
670   Messing, C., Erséus, C., Emig, C., Boyko, C., Mah, C., Millsc., Nielsen, C., Jaume,
671   D., Fautin, D., Domning, D. P., Gibson, D., Lazarus, D., Gordon, D., Opresko, D.,
672   Schwabe, E., Mac−Pherson E., Thuesen, E., Dahdouh−Guebas, F., Anderson, G.,
673   Poore, G., Williams, G., Walker−Smith, G., Read, G., Lambert, G., Paulay, G.,
674   Segers, H., Furuya, H., Bartsch, I.,Van Der Land, J., Reimer, J. D., Vanaverbeke, J.,
675   Saiz−aiz, Saike, J., Sair, J. D.,Pilger, J., Norenburg, J., Kolb, J., Schnabel, K. E.,
676   Meland, K., Fauchald, K., Cheng, L., Van Ofwe−Gen L., Błażewicz−Paszkowycz,
677   M., Rius, M., Curini−Galletti, M., Schotte, M., Tasker, M. L., Angel, M. V., Osawa,
678   M., Longshaw M., Guiry, M., Bailly, N., De Voogd, N., Bruce N., Shenkar, N.,
679   Garcia−Alvarez, O., Mclaughlin, P., Kirk, P., Davie, P., Ng, P. K. L., Schuchert P.,
680   Uetz P., Bock P., Pugh P., Lemaitrer., Kristensen R., Van Soestr., Bray, R., Bamber,
681   R. N., Da Rocha, R. M., Hopcroft R., Stöhr, S., De Grave, S., Gerken, S., Gofas, S.,
682   Tyler, S., Ahyong, S., Wilson, S., Brandao S. N., Koenemann, S., Feist, S., Cairns, S.,
683   Timm, T., Cribb, T., Molodtsova, T., Chan, T.–Y., Iseto, T., Artois, T., Scarabino, V.,
684   Siegel, V., Eschmeyer, W., Hummon, W., Perrin W., Sterrer, W., Hernandez, F.,
685   Mees J., Costello, M. J.: The Magnitude of Global Marine Biodiversity, Curr. Biol.,
686   22, 2189–2202, 2012.

687

688 Baldwin, R. J. & Smith, K. L. Jr.: Temporal variation in the catch rate, length, color, and sex
689   of the necrophagus amphipod, *Eurythenes gryllus*, from the central and eastern North
690   Pacific, Deep Sea Res. (part 1 Oceanogr. Res. Pap.), 34, 425–439, 1987.

691

692 Barnard, J. L.: Gammaridean Amphipoda from depth of 400 to 6000 m, Galathea. Rep., 5,
693   23–128, 1961.

694

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

697

698   Belyaev, G. M.: Deep-Sea Ocean Trenches and Their Fauna. Nauka Publishing House,

699   Moscow, 385 pp, 1989.

700

701   Billett, D. S. M., Lampitt, R. S., Rice, A. L. & Mantoura, R. F. C.: Seasonal sedimentation of

702   phytoplankton to the deep-sea benthos, Nature, 302, 520–522. 1983.

703   Blankenship, L. E. & Levin, L. A.: Extreme food webs: Foraging strategies and diets of

704   scavenging amphipods from the ocean's deepest 5 kilometers, Limnol. Oceanogr., 52,

705   1685–1697, 2007.

706

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

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

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

710

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

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

713   Janussen, D., Kaiser, S., Linse, K., Malyutina, M., Brandao, S., Pawlowski, J. &

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

715   Nature, 447, 307–311, 2007.

716

717   Bray, J. R. & J. T. Curtis.: An ordination of upland forest communities of southern

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

719

720   Brenke, N.: An epibenthic sledge for operations on marine soft bottom and bedrock, Mar.

721   Technol. Soc. J., 39, 10–21, 2005. hdl.handle.net/10.4031/002533205787444015.

722

723   Carmona, L., Malaquias, M. A. E., Gosliner, T. M., Pola, M. & Cervera, J. L. Amphi-Atlantic

724   distributions and cryptic species in Sacoglossan sea slugs, J. Molluscan Stud., 77,

725   401–412, 2011.

726

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

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

729

730   Delić, T., Trontelj, P., Rendoš, M. & Fišer., C.: The importance of naming cryptic species
731   and the conservation of endemic subterranean amphipods. Sci. Rep., 7, 3391, 2017.
732   https://doi.org/10.1038/s41598-017-02938-z

734   Etter, R. J., Boyle, E. E., Glazier, A., Jennings, R. M., Dutra, E. & Chase. M. R.
735   "Phylogeography of a Pan-Atlantic Abyssal Protobranch Bivalve: Implications for
736   Evolution in the Deep Atlantic." Molecular Ecology 20 (4): 829–843, 2011.
737   doi:http://dx.doi.org/10.1111/j.365-294X.2010.04978.x.

739   France, D. & Kocher, T.: Geographic and bathymetric patterns of mitochondrial 16S rRNA
740   sequence divergence among deep-sea amphipods, *Eurythenes gryllus*. Mar. Biol., 126,
741   633–643, 1996.

743   Futuyma, D. J.: Evolutionary Biology, ed. 3. Sinauer Associates, Sunderland MA, 751 pp.,
744   1998.

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

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

754   Glover, A., Paterson, G., Bett, B., Gage, J., Sibuet, M., Sheader, M., Hawkins, L.: Patterns in
755   polychaete abundance and diversity from the Madeira Abyssal Plain, northeast
756   Atlantic. Deep Sea Res. (part 1 Oceanogr. Res. Pap.), 48, 217–236, 2001.

758   Glover, A., Smith, C. R., Paterson, G. J. L., Wilson, G. D. F., Hawkins, L. & Sheader, M.:
759   Polychaete species diversity in the central Pacific abyss: local and regional patterns,
760   and relationships with productivity, Mar. Ecol. Prog. Ser., 240, 157–170, 2002.
761

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

766 Hannides, A., Smith, C. R.: The northeast abyssal Pacific plain. In: Biogeochemistry of
767   Marine Systems, K. B. Black and G. B Shimmield, eds., CRC Press, Boca Raton,
768   Florida, 208-237, 2003.

770 Havermans, C.: Have we so far only seen the tip of the iceberg? Exploring species diversity
771   and distribution of the giant amphipod Eurythenes, Biodiversity, 2016.
772 DOI: 10.1080/14888386.2016.1172257

774 Havermans, C & Smetacek, V. Bottom-up and top-down triggers of diversification: A new
775   look at the evolutionary ecology of scavenging amphipods in the deep sea. Progress in
776   Oceanogprahy, 164, 37-51, 2018.

778 Havermans, C., Sonet, G., d'Udekem d'Acoz, C., Nagy, Z. T., Martin, P., Brix, S., Riehl, T.,
779   Agrawal, S. & Held, C.: Genetic and morphological divergences in the cosmopolitan
780   deep-sea amphipod *Eurythenes gryllus* reveal a diverse abyss and a bipolar species.
781   PLoS ONE, 8, e74218, 2013.

783 Held, C. & Wägele, J. W.: Cryptic speciation in the giant Antarctic isopod *Glyptonotus*
784   *antarcticus* (Isopoda: Valvirfera: Chaetiliidae), Sci. Mar. 69 (Suppl. 2), 175–181,
785   2005.

787 Highsmith, R.: Floating and algal rafting as potential dispersal mechanisms in brooding
788   invertebrates, Mar. Ecol. Prog. Ser., 25, 169–179, 1985.

790 Hilário, A., Metaxas, A., Gaudron, S. M. ,Howell, K. L., Mercier, A., Mestre, N. C., Ross, R.
791   E. ,Thurnherr, A. M. & Young, C.: Estimating dispersal distance in the deep
792   sea:challenges and applications to marine reserves, Front. Mar. Sci., 2, 2015.
793   doi:10.3389/ fmars.2015.00006.

794 Ide, K.,Takahashi, K., Nakano, T., & Minoru, S. & Omori, M. Chemoreceptive foraging in a
795   shallow-water scavenging lysianassid amphipod: Role of amino acids in the location
796   of carrion in Scopelocheirus onagawae. Marine Ecology-progress Series, 2006.
797 MAR ECOL-PROGR SER. 317. 193-202. 10.3354/meps317193.
798
799 International Seabed Authority. A Discussion Paper on Developing a Regulatory Framework
800   for Mineral Exploitation in the Area (Env. Matt.), 1–102, 2017.
801
802 Kankaanpää, H., Laurén, M., Mattson, M. & Lindström, M.: Effects of bleached kraft mill
803   effluents on the swimming activity of Monoporeia affinis (Crustacea, Pmphipoda)
804   lindström, Chemosphere, 31, 4455–4473, 1995.
805
806 Laver, M. B., Olsson, M. S., Edelman, J. L. & Smith K. L. Jr.: Swimming rates of scavenging
807   deep−sea amphipods recorded with a free−vehicle video camera. Deep−Sea Res. II,
808   32, 1135–1142,1985.
809
810 Lester, S. E., Ruttenberg, B. I., Gaines, S. D. & Kinlan B. P.: The relationship between
811   dispersal ability and geographic range size. Ecol. Lett, 10, 745–758, 2007.
812
813 Levin, L. A., Etter, R.J., Rex, M. A., Gooday, A. J., Smith, C. R., Pineda, J., Stuart, C. T.,
814   Hessler, R. R. & Pawson, D.: Environmental influences on regional deep-sea species
815   diversity, Annu. Rev. Ecol. Evol. Syst., 32, 51–93, 2001.
816
817 Liow, L. H.: Does versatility as measured by geographic range, bathymetric range and
818   morphological variability contribute to taxon longevity? Glob. Ecol. Bio., 16, 117–
819   128, 2007.
820
821 Lodge, M., Johnson, D., Le Gurun, G., Wengler, M., Weaver, P. & Gunn, V.: Seabed mining:
822   International Seabed Authority environmental management plan for the Clarion–
823   Clipperton Zone. A partnership approach, Mar. Pol., 49, 66–72, 2014.
824
825 Lonsdale, P.: Clustering of suspension-feeding macrobenthos near abyssal hydrothermal
826   vents at oceanic spreading centers, Deep-Sea Res., 24, 857–863, 1977.

827   Lörz A-N, Jażdżewska AM, Brandt A. A new predator connecting the abyssal with the hadal
828   in the Kuril-Kamchatka Trench, NW Pacific. Costello M, ed. PeerJ. 2018;6:e4887.
829   doi:10.7717/peerj.4887.
830
831   Managing Impacts of Deep Sea Resource Exploitation (MIDAS) Summary Report:
832   Biodiversity in the Clarion-Clipperton Zone, 1–2, 2016.
833
834   McClain, C. R. & Hardy, S. M.: The dynamics of biogeographic ranges in the deep sea, Proc.
835   Roy. Soc. B: Bio. Sci., 277, 3533–3546, 2010.
836
837   Narahara-Nakano, Y., Nakano, T. & Tomikawa, K. Deep-sea amphipod genus Eurythenes
838   from Japan, with a description of a new Eurythenes species from off Hokkaido
839   (Crustacea: Amphipoda: Lysianassoidea), Marine Biodiversity, 1867-1616, 2017. Mar
840   Biodiv DOI 10.1007/s12526-017-0758-4
841
842   Paull, C. K., Hecker, B., Commeau, R., Freeman-Lynde, R. P., Neumann, C., Corso, W. P.,
843   Golubic, S., Hook, J. E., Sikes, E. & Curray, J.: Biological communities at the Florida
844   escarpment resemble hydrothermal vent taxa, Science, 226, 965–967, 1984.
845   Premke K, Muyakshin S, Klages M & Wegner J. Evidence for long-range chemoreceptive
846   tracking of food odour in deep-sea scavengers by scanning sonar data. J Exp Mar Biol
847   Ecol, 285:283–294, 2003.
848
849   R Core Team. R: A language and environment for statistical computing. R Foundation for
850   Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, 2013.
851   URL http://www.R-project.org/.
852
853   Ramirez-Llodra, E., Brandt, A., Danovaro, R., De Mol, B., Escobar, E., German, C. R.,
854   Levin, L. A., Martinez Arbizu, P., Menot, L., Buhl-Mortensen, P., Narayanaswamy,
855   B. E., Smith, C. R., Tittensor, D. P., Tyler, P. A., Vanreusel, A. & Vecchione, M.:
856   Deep, diverse and definitely different: unique attributes of the world's largest
857   ecosystem, Biogeosciences, 7, 2851–2899, 2010.
858

859   Ramirez-Llodra, E., Tyler, P. A., Baker, M. C., Bergstad, O. A., Clark, M. R. & Escobar, E.:

860   Man and the last great wilderness: human impact on the Deep Sea, PLoSONE, 6,

861   2011. doi:10.1371/journal.pone.0022588.

862

863   Rex, M. A., Stuart, C. T., Hessler, R., R., Allen, J. A., Sanders, H. L. & Wilson, G. D. F.:

864   Global-scale latitudinal patterns of species diversity in the deep-sea benthos, Nature,

865   365, 636–639, 1993.

866   Ritchie, H., Jamieson, A. J. & Piertney, S. B. Isolation and Characterization of Microsatellite

867   DNA Markers in the Deep-Sea Amphipod Paralicella tenuipes by Illumina MiSeq

868   Sequencing, Journal of Heredity, 367 – 371, 2016.

869

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

871

872   Schön I, Pinto R. L., Halse, S., Smith, A. J. & Martens, K.: Cryptic Species in Putative

873   Ancient Asexual Darwinulids (Crustacea, Ostracoda), PLoS ONE, 7, e39844.

874   doi:10.1371/journal.pone.0039844. 2012.

875

876   Schulenberger, E. & Barnard, J. L.: Clarification of the Abyssal Amphipod, *Paralicella*

877   *tenuipes* Chevreux, Crustaceana, 31, 267–274, 1976.

878

879   Schüller, M. & Ebbe, B.: Global distributional patterns of selected deep−sea Polychaeta

880   (Annelida) from the Southern Ocean, Deep−Sea Res. II, 54, 1737–1751, 2007.

881

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

883

884   Smith, C. R., Kukert, H., Wheatcroft, R. A., Jumars, P. A. & Deming, J. W.: Vent fauna on

885   whale remains, Nature, 341, 27–28, 1989.

886

887   Smith, C. R. & A.W. J. Demopoulos.: Ecology of the deep Pacific Ocean floor. In:

888   Ecosystems of the World Volume 28: Ecosystems of the Deep Ocean, P. A. Tyler,

889   ed., Elsevier, Amsterdam, pp. 179–218, 2003.

890

891   Smith, C. R., Drazen J. & Mincks, S. L.: Deep-sea Biodiversity and Biogeography:
892   Perspectives from the Abyss. International Seabed Authority Seamount Biodiversity
893   Symposium, 1–13, 2006.

894

895   Somero, G. N.: Adaptations to high hydrostatic pressure, Ann. rev. physiol., 54, 57–577.
896   1992.

897

898   Stuart, C., Rex, M. & Etter, R.: Large scale spatial and temporal patterns of deep-sea
899   biodiversity. Ecosystems of the World Volume 28: Ecosys. Deep Oc., P. A. Tyler, ed.,
900   Elsevier, Amsterdam, 295–311, 2003.

901

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

904

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

907

908   Thurston, M. H.: Abyssal necrophagous amphipods (Crustacea: Amphipoda) in the northeast
909   and tropical Atlantic Ocean, Prog. Oceanogr., 24, 257–274, 1990. doi:10.1016/0079-
910   6611(90)90036-2.

911

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

914

915   Wilson, G. D. F., Hessler R.: Speciation in the deep sea, Ann. Rev. Ecol. Syst., 18, 185–207,
916   1987.

917

918   Zardus, J. D., Etter, R. J., Chase, M. R., Rex, M. A. & Boyle, E. E. Bathymetric and
919   geographic population structure in the pan-Atlantic deep-sea bivalve *Deminucula*
920   *atacellana* (Schenck, 1939), Mol. Ecol., 15, 639–651, 2006.

921

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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 claim 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.

954 **Table captions**

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

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

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

959 known only for stations D3 and D4.

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

961 DisCOL Experimental Area (DEA).

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

963 DisCOL Experimental Area (DEA).

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

965 Clarion-Clipperton fracture Zone and DisCOL Experimental Area, and *D* for each station is

966 shown for further comparisons within these areas.

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977   **Appendix/Electronic Supplementary Information (ESM) captions**

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

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

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

986   **Appendix 4** – Calculation of alpha biodiversity used in this manuscript.

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1004   plough harrow in the DisCOL Experimental Area to simulate manganese nodule extraction
1005   activity.

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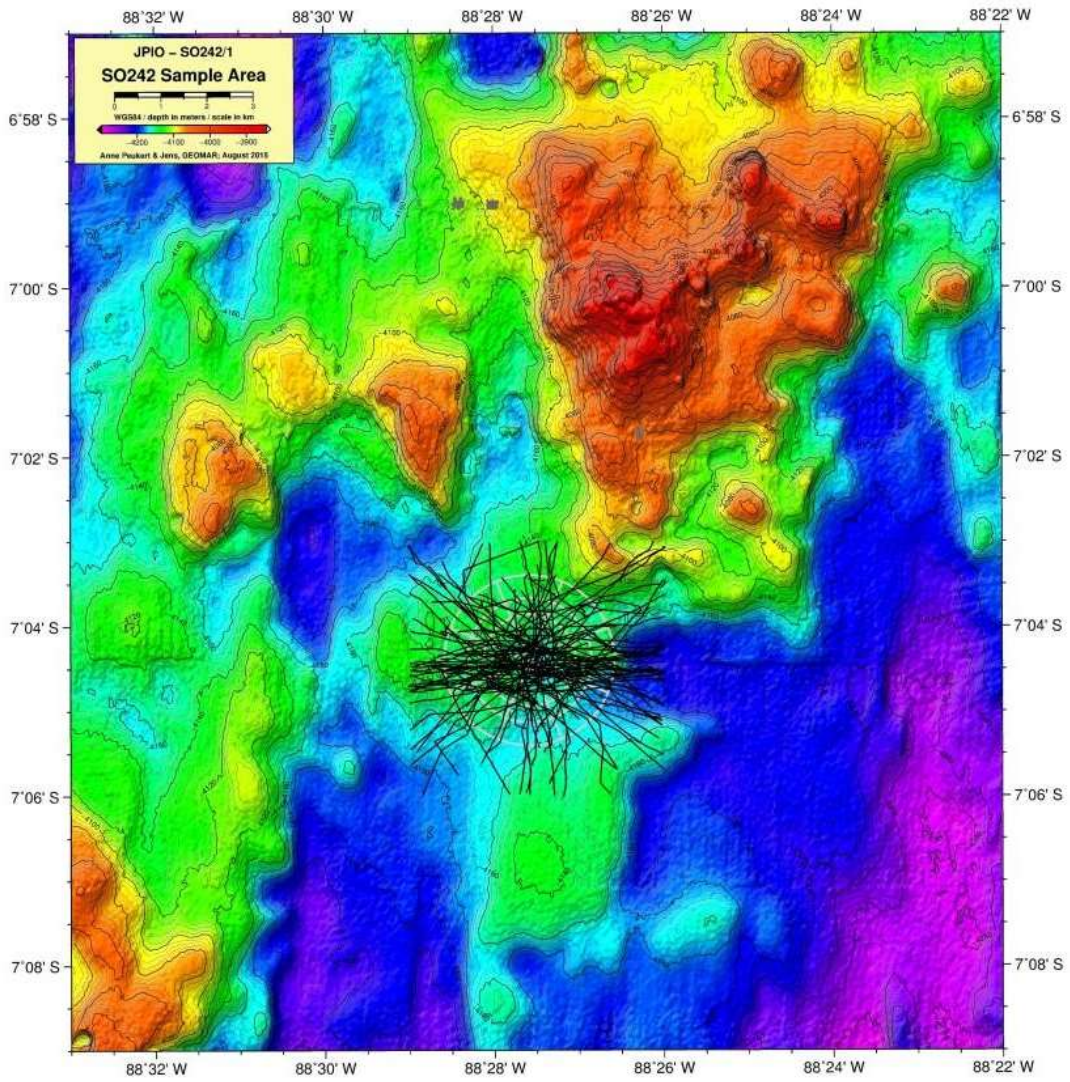
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1015   **Appendix 2** – Photograph showing the baited free-fall lander trap designed and deployed by
1016   RBINS.

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1030 **Appendix 3** - Side-scan sonar image of site D5 showing possible seamount barriers. View
1031 from NW (top) to SE (bottom). Contours are every 25 m. (Source: GEOMAR, 2015).

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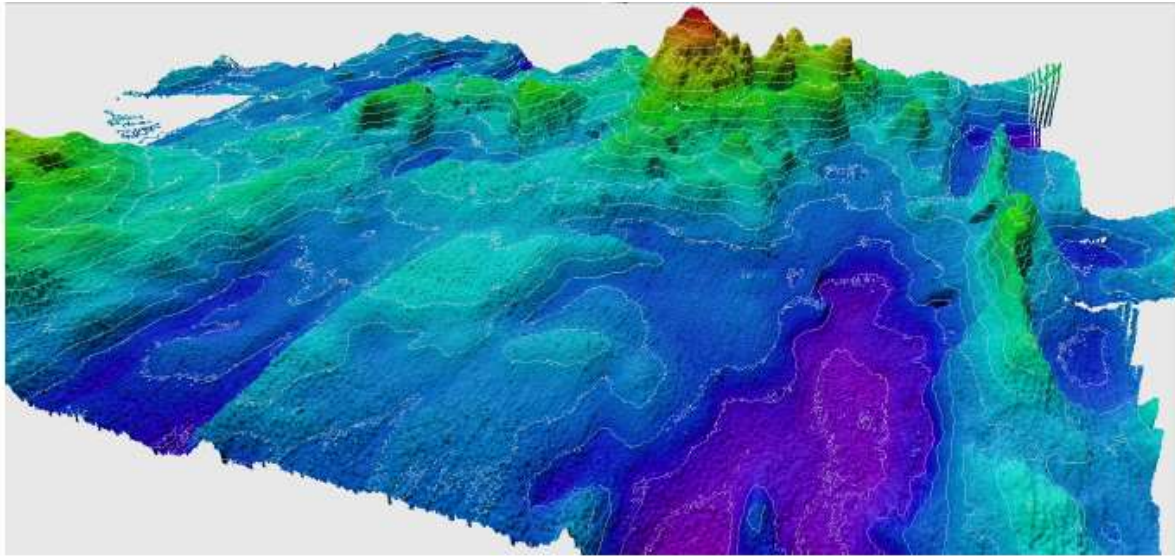
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1044 **Appendix 4** - Calculation of alpha biodiversity used in this manuscript.

1045 Simpson Index

1046 Simpson Diversity Index (D) = $1 - \dfrac{\sum n(n-1)}{N(N-1)} =$

1047 D = Diversity Index

1048 n = number of individuals in each particular species

1049 N = Total number in community

1050 A high value of D indicates a high species diversity.

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