

Resilience of benthic deep-sea fauna to mining activities

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Abstract :

With increasing demand for mineral resources, extraction of polymetallic sulphides at hydrothermal vents, cobalt-rich ferromanganese crusts at seamounts, and polymetallic nodules on abyssal plains may be imminent. Here, we shortly introduce ecosystem characteristics of mining areas, report on recent mining developments, and identify potential stress and disturbances created by mining. We analyze species' potential resistance to future mining and perform meta-analyses on population density and diversity recovery after disturbances most similar to mining: volcanic eruptions at vents, fisheries on seamounts, and experiments that mimic nodule mining on abyssal plains. We report wide variation in recovery rates among taxa, size, and mobility of fauna. While densities and diversities of some taxa can recover to or even exceed pre-disturbance levels, community composition remains affected after decades. The loss of hard substrata or alteration of substrata composition may cause substantial community shifts that persist over geological timescales at mined sites.

Highlights

► Deep-sea mineral exploration and exploitation licenses have been issued recently. ► Mining will modify the abiotic and biotic environment. ► At directly mined sites, species are removed and cannot resist disturbance. ► Recovery is highly variable in distinct ecosystems and among benthic taxa. ► Community changes may persist over geological time-scales at directly mined sites.

Keywords : Deep ocean, Disturbance, Minerals, Mining, Abyssal plains, Hydrothermal vents, Seamounts, Resilience, Recovery, Benthos

82 Introduction

83

84 Resilience represents a key concept in ecosystem response to disturbance effects. It can be
85 defined as the ability of a system to maintain its overall identity, i.e. the same function and
86 structure, in the face of internal change and external perturbations [1-3]. Resilience relates to
87 a number of processes [4-6]: (1) resistance, as the amount of stress and disturbance that
88 can be absorbed by a system before processes controlling the structure and function of a
89 system change [7], (2) recovery, as the rate an ecosystem returns to pre-disturbance
90 conditions after an disturbance event [8], and (3) reversibility, as whether processes are
91 reversible [8] and if the system is capable returning to the original condition after change [6].
92 Ecosystems that pass a critical threshold or tipping point, marking a drastic change in
93 ecosystem function, are putatively unlikely to recover to the original state [8-10].

94 With increasing interest of companies and countries in deep-sea mining, it is crucial to
95 evaluate the resilience of deep-sea ecosystems to mining disturbance, and thus to assess
96 the potential ecological consequences of extracting mineral resources from the deep sea
97 floor. Three different types of deep-sea mineral resources are being granted for exploration
98 licenses: polymetallic sulphides on active and inactive hydrothermal vents, cobalt-rich
99 ferromanganese crusts on seamounts, and polymetallic nodules on abyssal plains. Targeted
100 ecosystems support different types of biological communities that may be differently
101 impacted from mining activities. Mining activities will impose disturbances with novel nature,
102 strength, stability and spatial and temporal scale on deep-sea ecosystems [11-21].

103 In this review, we aim to evaluate the potential resilience of benthic deep-sea fauna to
104 mining activities at hydrothermal vents, seamounts and abyssal plains. We first set the scene
105 by shortly introducing ecosystem characteristics, recent mining developments, and potential
106 stress and disturbances created by mining. In particular, we (1) estimate to what extent
107 targeted ecosystems may be resistant to mining disturbance, (2) review known recovery
108 rates to small-scale disturbance events that are considered most similar to future mining
109 disturbance (volcanic eruptions at hydrothermal vents; fisheries at seamounts; disturbance
110 experiments designed to mimic nodule mining on abyssal plains), and (3) relate this

111 knowledge (and knowledge gaps identified) to potential reversibility of ecosystem change
112 following mineral mining disturbance.

113

114 **Materials and methods**

115 The study is based on literature review, as well as meta-analyses of empirical and long-term
116 quantitative data assessing the recovery of deep-sea fauna communities following natural or
117 anthropogenic disturbances. For meta-data analyses, we identified impacts most similar to
118 future mining events as: (1) volcanic eruptions that locally eliminate entire communities at
119 hydrothermal vents, (2) bottom-trawl fisheries on seamounts, and (3) disturbance
120 experiments designed to mimic nodule mining at nodule fields on abyssal plains. For the
121 meta-data analyses we included only studies where duration between initial disturbance and
122 post-disturbance measurements was known. When pre-disturbance measurements were
123 unavailable, measurements from close proximity reference areas (control) were used instead
124 (see Appendix A). Percent recovery was plotted against time elapsed since the disturbance
125 impact using the program R [22]. Datasets where the pre-disturbance value was zero, i.e. the
126 respective taxon had not been sampled, are discussed in the manuscript, but were excluded
127 from the analyses.

128 Faunal responses to disturbances reported in the literature are presented in Appendix
129 A, identifying ecosystem type, geographic region, type of impact, comparable potential
130 mining impact, scale of impact, response category (density or diversity), type of response
131 measured (e.g. species richness S , Shannon-diversity H'), taxonomy information (phylum,
132 class, order, family, genus, species), size class (meio-, macro-, megafauna), and mobility
133 (mobile, sessile). The results of the literature search and specific meta-analysis for nodule
134 systems are reported in more detail in Jones et al. [23]. Mobility was included in the analyses
135 as it may be linked to species connectivity and thus recovery potential [24]. Size classes
136 were used in the analyses since meio-, macro- and megafauna communities influence and
137 depend on each other [25], and recent studies have shown that different sized organisms
138 may respond differently to stress and disturbance [26, 27]. We followed the definition of size-
139 classes used in original articles. Megafauna typically included large animals seen with the
140 unaided eye or are visible in seabed photographs. At hydrothermal vents, where fauna is
141 typically large, (adult) macrofauna was classified as fauna larger 1 mm, with no further
142 discrimination into mega- and macrofauna. On nodule fields, where macrofauna is typically
143 small, macrofauna included organisms retained on a 500 μm mesh sieve. Meiofauna was
144 typically classified as fauna smaller than 1 mm. The lower mesh-size used varied from 32 to
145 63 μm (older studies typically used 63 μm). However, Ingole et al. [28] classified all fauna in
146 deep-sea sediments (including nematodes and copepods) as macrofauna, but we
147 reclassified typical meiofauna taxa (nematodes, copepods) as meiofauna.

148 Since the nature of measurements, the number of samples, and sampling technique
149 was often substantially different across studies, we calculated mean percent recovery
150 following a specified period (in years) for each study (Appendix A). Calculation of mean
151 percent recovery was based on mean original values of pre-disturbance conditions and the
152 mean (experimental) values measured post-impact ($100 \times \text{pre disturbance}/\text{after disturbance}$).
153 To account for variability, original values for pre- and post-disturbance and their standard
154 deviation are provided whenever possible in Appendix A and in figures, and are discussed.
155 Mean values of pre-disturbance conditions were interpreted as representing 100% of the
156 original densities or diversities. Consequently, 50% density recovery after one year would
157 imply that mean density value was half the pre-disturbance value one year after disturbance,
158 and 200% density recovery after one year would imply that mean density value was double
159 the pre-disturbance value one year after disturbance.

160 To unravel large scale underlying patterns of recovery in the three different
161 ecosystem types, we tested for differences in mean percent recovery for diversity and
162 density between organism size-classes (meio-, macro-, megafauna), mobilities (sessile,
163 mobile), and localities (different ocean basin of nodule fields) using the one-sided Wilcoxon
164 rank sum test [29]. The non-parametric one-sided Wilcoxon rank sum test tests for
165 differences between each set of pairs of two paired groups, assuming that values of one of
166 the paired groups are larger than the other. The Benjamini-Hochberg correction was used to
167 account for the number of possible comparisons in order to control the expected proportion
168 of false discoveries [30]. Whilst these analyses may identify potential large scale trends in
169 species recovery they cannot account for variability within samples. Where mobility of study
170 organisms comprised mobile as well as sessile taxa, mobility was defined as “mixed”, and
171 data were excluded from mobility analyses.

172

173 **Results and Discussion**

174

175 **1. Ecosystem characteristics**

176

177 **1.1 Polymetallic sulphides, active and inactive hydrothermal vents**

178

179 **1.1.1 Minerals and physical environment**

180 Polymetallic sulphides (Figure 1a), also referred to as seafloor massive sulphides (SMS),
181 form on or below the seabed where hydrothermal vents release mineralized seawater [31-
182 33]. Minerals in hydrothermal fluids precipitate when they come into contact with cold
183 seawater, and form chimney structures (Figure 2a) and/or disperse with the hydrothermal
184 plume through the water. Deposits are patchily distributed at mid-ocean ridges, in back-arc

185 basins, and along submarine volcanic arcs (seamounts). The abundance and content of
 186 sulphides differs between fast- and slow-spreading ridges; whilst lavas commonly disrupt the
 187 flow of hydrothermal fluids and bury sulphide deposits every decades at fast spreading
 188 ridges (e.g. the East Pacific Rise, EPR), eruptions occur on intervals of thousands of years
 189 and deposits are of larger scale at slow spreading ridges (e.g. the Mid Atlantic Ridge (MAR),
 190 the Central Indian Ridge (CIR)) [16, 18].
 191



192
 193 Figure 1. Examples of deep-sea minerals. a. Polymetallic sulphide sample from Edmond vent
 194 field in the Indian Ocean (photo courtesy BGR). b. Cobalt-rich ferromanganese crust from the
 195 Great Meteor seamount chain (photo courtesy EMEPC). c. Polymetallic nodule (size ~ 12 cm
 196 in length) from the Clarion-Clipperton Fracture Zone (photo courtesy of S. Kaiser, SGN)

197
 198 The mineral-rich hydrothermal fluids range in temperature from just a few degrees Celsius to
 199 >400°C [31, 32]. Local fluid flows at active hydrothermal vent sites can reduce and stop
 200 within a few months at fast-spreading ridges such as the EPR [34] or can be stable for
 201 decades on slow-spreading ridges such as the MAR [35]. Vent chimneys and edifices can be
 202 several tens of metres high and are commonly inhabited by specialised communities [17].
 203 The stability at individual sites as well as vent fields exerts a strong influence on the largely
 204 endemic mega- and macrofauna that are dependent on rich *in situ* primary production by
 205 sulphide- and methane oxidizing bacteria [36].
 206

207 **1.1.2 Biological communities at active and inactive vents and in the vent periphery**

208 Fauna associated with polymetallic sulphides at active hydrothermal vents (Figure 2 a, b) are
 209 fueled by rich *in situ* primary production generated via chemosynthesis. Many mega- and
 210 macrofaunal groups have evolved complex physiological or behavioural adaptations to the
 211 extreme environmental conditions in vent habitats [37-39]. Dominant symbiotrophic
 212 megafauna include mussels, snails, shrimps and polychaetes, whereas dominant
 213 macrofauna taxa include limpets, crabs, amphipods and polychaetes [36]. Whilst these fauna
 214 are typically abundant with high biomass, species richness is low [40]. Mega- and
 215 macrofauna show a high level of endemism in biogeographic provinces at both species
 216 (95%) and generic level (76%) [41]. Furthermore, the mega- and macrofauna are commonly

217 endemic to the active vent environment [42]. In contrast to the macrofauna, meiofauna are
218 not exceptionally abundant at the vents, but meiofauna and macrofauna show similar species
219 richness [27, 43-45]. However, vent meiofauna species also occur in the vent periphery, with
220 few species restricted to the vents [46]. Since vents are patchy, transient, and often
221 separated by tens to hundreds of kilometers, connectivity among invertebrate populations is
222 through larval dispersal [26, 47-49].

223 Fauna associated with polymetallic sulphides at inactive vents (Figure 2 c) are little
224 known. Consequently, it is largely unclear whether assemblages that thrive at inactive vents
225 are similar to active vent fauna, are similar to fauna inhabiting hard substrata on non-mineral
226 rich grounds, or are unique [17]. Inactive chimney structures provide substratum for benthic
227 suspension feeders and typically host sponges and cnidarians [50-53]. Some macrofauna
228 and nematode species from active vent sites are also observed at inactive vent sites [54, 55].
229 A comparative study of an active hydrothermal seamount, an inactive hydrothermal
230 seamount with polymetallic sulphides, and a seamount without hydrothermal activity and
231 without mineral deposits, revealed that magnetivity, as a proxy for hydrothermal activity,
232 explained the majority of the variation in megafauna assemblage structures present at the
233 three seamounts [50].

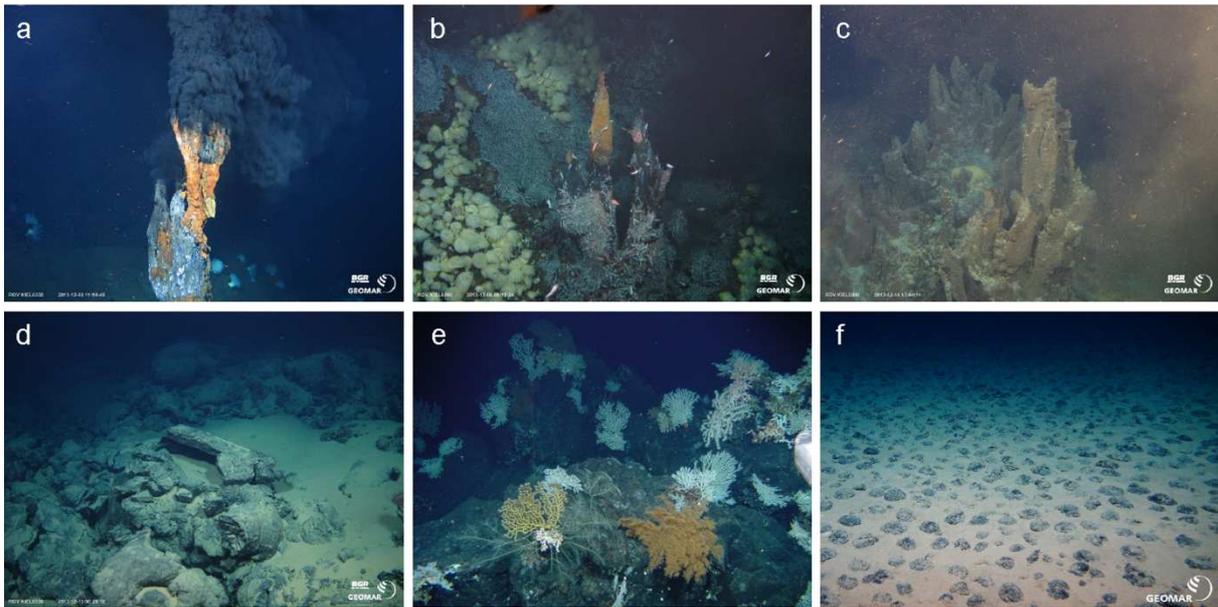
234 There is a paucity of data on fauna from the vent periphery (also termed vent
235 proximate areas, or vent background) but fauna appears to vary with region. Vent peripheral
236 megafauna on the MAR consist of sessile, filter-feeding, long-lived and slow-growing taxa
237 such as sponges, corals and deep-sea crabs [51, 56, 57] (Figure 2 d). Peripheral areas near
238 the Eiffel Tower (Lucky Strike vent field) have high diversity, e.g. of copepods, and also
239 harbour several copepod species typical for active vents. Additionally, juvenile vent fauna
240 have been observed in the vent periphery [45]. Similarly, vent-peripheral areas on the 9°N
241 EPR support juveniles of macrofauna typical of the vent environment, as well as a diverse
242 meiofauna community [27]. Vent-peripheral macrofauna communities in the Lau Basin are
243 largely distinct from active vent communities, with few vent endemic species present [58].
244 Peripheral macrofaunal communities at Eastern Lau Spreading Center and Valu Fa Ridge
245 (ELSC-VFR) harbour mainly zoanthids, anemones, symbiont-containing mussels, brisingid
246 seastars, and polynoids at the northern peripheral sites, whereas sponges, pycnogonids and
247 ophiuroids dominate at southern peripheral sites. Taxonomic richness in these vent-
248 peripheral macrofauna communities is similar to that of active vent communities [59]. In
249 comparison, peripheral assemblages at Scotia Ridge in the Southern Ocean typically
250 comprise asteroids and pycnogonids [60].

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256 Figure 2. Examples of ecosystems/habitats and associated biological communities potentially
 257 affected by mineral mining. a. Active black smoker (Kaarei; Indian Ocean). b. Vent field
 258 colonized by shrimps, anemones, and mussels (Kaarei; Indian Ocean). c. Inactive vent field
 259 (Edmond; Indian Ocean). d. Pillow lava in vent peripheral areas (adjacent to Sonne; Indian
 260 Ocean). e. Coral gardens on inactive vent/seamount (near Menez Gwen, Atlantic; photo
 261 courtesy of Missão Seahma). f. Nodule field (Clarion-Clipperton Fracture Zone, Pacific).
 262 Photos a-d, f of courtesy of GEOMAR.

263

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266 1.2 Cobalt-rich ferromanganese crusts, seamounts

267

268 1.2.1 Minerals and physical environment

269 Cobalt-rich ferromanganese crusts (Figure 1 b) are formed by the precipitation of metals
 270 dissolved in seawater, grow at rates of 1 to 6 mm per million years, and can form thick
 271 pavements of up to 26 cm thickness [20, 61, 62]. These crusts typically form on exposed
 272 hard rock on seamounts, and especially on guyot plateaus with strong currents that prevent
 273 the accumulation of sediments. Seamounts are underwater mountains of volcanic origin, and
 274 hydrothermal venting may be associated with seamounts, making seamounts a target not
 275 only for crust mining but also for polymetallic sulphide mining [53]. Approximately, 10,000-
 276 33,000 seamounts are arrayed across the ocean floor [63-65]. Like terrestrial mountains,
 277 seamounts exhibit a range of shapes and sizes. Geophysical characteristics of seamounts
 278 accelerate water currents, generate upwelling of nutrients, and create retention of water
 279 masses, thereby increasing local productivity and external flow of organic matter [66-68].

280

281 **1.2.2 Biological communities at seamounts with and without crusts**

282 Seamounts are considered to be hotspots of species richness [69]. High productivity at
283 seamounts supports relatively high biomass of demersal fish populations and large numbers
284 of benthic filter feeders, such as corals and sponges (Figure 2 e) in comparison to adjacent
285 deep continental margins at comparable depths [70, 71]. However, there is little known about
286 the seamount fauna in general, and about crust-associated fauna in particular [72-74]; few
287 seamounts (<1%) have been sampled [67, 72]. Furthermore, studies have focused on
288 megafaunal organisms, with little information available on macro- and meiofauna [75, 76], or
289 on microbiota.

290 Many seamount taxa are long-lived and slow-growing, especially those forming
291 biogenic structures. Individuals of some species may be hundreds to thousands of years old:
292 for example, it may take thousands of years for stony corals to build complex biogenic
293 structures [77]. Seamount faunas can vary greatly even at local (km) spatial scales [72, 73,
294 78]. Variation in community composition and diversity has been related to a number of
295 environmental factors, particularly those linked to depth and seabed structure (e.g.
296 substratum, relief, presence of bio-constructors), as well as current regimes and distance to
297 source populations, amongst others [50, 67, 73].

298 Owing to a paucity of data, it remains uncertain whether fauna associated with crusts
299 differs from similar non-crust areas [73, 74]. However, Schlacher et al. [73] and Morgan et al.
300 [79] identified differences in biodiversity and community structure between seamounts with
301 and without crusts. Nonetheless, it remains unclear whether chemical components of the
302 crusts are dominant drivers of benthic assemblage structure, or whether differences result
303 from contrasting seafloor parameters, such as geographic location, topography and depth-
304 related factors [73].

305

306 **1.3 Polymetallic nodules, abyssal plains**

307

308 **1.3.1 Minerals and physical environment**

309 Polymetallic nodules, also referred to as manganese nodules, are potato-shaped concretions
310 with a size range of 2-8 cm (max. 15 cm) that are composed of manganese oxides and iron
311 oxihydroxides (Figure 1 c, Figure 2 f). Polymetallic nodules grow with average rates of 10 to
312 20 mm per million years. They occur in high abundances on the sediment-covered abyssal
313 plains of all oceans, where sedimentation rates are low (≤ 10 mm kyr⁻¹). Nodules are
314 embedded in the sediment surface. Nodules therefore provide a hard substratum habitat on
315 abyssal plains dominated by sediment. Deep-sea sediments around nodules typically consist
316 of a mixture of siliceous ooze and deep-sea clay and are rich in oxygen [80-82]. The

317 environment is very stable, with low current velocities ($3.8 \pm 2.0 \text{ cm s}^{-1}$) [83, 84]. Well-studied
318 occurrences of manganese nodules are known from the Clarion Clipperton Fracture Zone
319 (CCZ) in the NE equatorial Pacific, the Peru Basin in the SE Pacific, the Cook Island region
320 in the SW Pacific, and in the Central Indian Ocean Basin [85]. The CCZ contains the largest
321 known contiguous occurrence of nodule fields and covers an area of approximately 4 million
322 square kilometers (an area as large as the European Union) [80]. Nodule abundance in the
323 CCZ ranges between 0 and $\sim 30 \text{ kg m}^{-2}$ (based on wet nodule weight) with an average of 15
324 kg m^{-2} [19].

325

326 **1.3.2 Biological communities on nodules and in deep-sea sediments**

327 At higher taxonomic levels, the composition of the soft-sediment fauna around nodules
328 resembles abyssal areas elsewhere. The dominant meiofaunal groups are nematodes,
329 followed by harpacticoid copepods, whilst polychaetes and isopods are the dominant
330 macrofaunal taxa. Typical megafaunal organisms include ophiuroids, holothurians, fish, large
331 komokiaceans and xenophyophore protists [86]. Diversity can be high at both local and
332 regional spatial scales [87-89]. Across the CCZ there are pronounced changes in species
333 composition in some taxa such as polychaetes, isopods, and nematodes [88, 90, 91].
334 Differences among samples are typically driven by a high proportion of rare species (defined
335 as species with only few individuals occurring in samples and/or with a restricted
336 geographical range) [92].

337 Nodule surfaces are often covered with sessile organisms such as sponges,
338 cnidarians and xenophyophores, but crevices are also inhabited by meiofauna, such as
339 nematodes, harpacticoid copepods, tardigrades, and foraminiferan protists [93-97]. Nodule
340 surface and adjacent soft sediment fauna are distinct in a number of protozoan and
341 metazoan taxa [95, 96, 98, 99]. Epifaunal densities are higher in regions with dense nodule
342 seafloor coverage, and epifauna such as alcyonacean and antipatharian corals are virtually
343 absent in nodule-free areas [100]. Many larger epifaunal species appear to be widespread,
344 but these distributions are based predominantly on morphological examination from video
345 and/or still images which provide insufficient resolution for species-level identification.
346 Nonetheless, recent analysis of nodule encrusting foraminiferans revealed that most morpho-
347 species are widely distributed across the CCZ [101]. Remarkably little is known regarding the
348 geographic distribution of the nodule associated fauna, such as whether species are unique
349 to nodules or whether adjacent seamount crusts host these same species.

350

351

352 **2. Mineral Mining**

353

354 **2.1 Licencing in international and national waters**

355 Many deep-sea mineral resources are found in areas beyond national jurisdiction i.e. “The
356 Area” (>200 nautical miles offshore, depending on whether a state has an extended
357 continental shelf), which are managed by the International Seabed Authority (ISA).
358 Contractors may apply for a 15-year exploration contract at the ISA, which gives them
359 exclusive rights to prospect for mineral resources in a specific exploration area. In the case
360 of manganese nodules, a single exploration area covers up to 75 000 km² of seafloor (Figure
361 3), but areas are smaller in the case of polymetallic sulphide or crust exploration comprising
362 3,000 and 10,000 km², respectively [102]. Ocean-wide, 26 exploration contracts have been
363 issued to date. In 2014 alone, the ISA approved seven new mineral exploration licences
364 (<https://www.isa.org.jm/deep-seabed-minerals-contractors>). The first six pioneer contractors
365 ended their 15-year exploration period in 2016. These contractors have applied for
366 exploration extensions for a further 5-year period. Subsequent to the exploration contract,
367 nations/companies may apply for an exploitation licence.

368 Within the Exclusive Economic Zone (EEZ) of a country, mineral resources on the
369 ocean floor are not managed by the ISA, but are instead managed by national regulation.
370 Nations may grant exploration and exploitation licences to companies. Within EEZs, most
371 exploration licenses for deep-sea minerals have been issued by island states in the SW
372 Pacific, Japan, and New Zealand [18, 53]. Nautilus minerals, Bluewater Minerals (Nautilus
373 subsidiary), Neptune Minerals, Bismarck (Neptune subsidiary), Diamond Fields International,
374 Korea Institute of Ocean Science and Technology (KIOST), Japan Oil, Gas & Metals
375 National Corp (JOGMEC) have applied for or have been granted SMS or cobalt-rich crust
376 exploration licences in the South Pacific. The first exploitation license for polymetallic
377 sulphides and for deep-sea minerals in general was granted by Papua New Guinea to the
378 company Nautilus minerals in 2011. Approximately 10 hectares are being considered for
379 mining at Solwara1 [103, 104]. Neptune Minerals has prospecting license applications and
380 granted prospecting licenses covering 175 000 km² in the EEZ of Japan, Papua, New
381 Guinea, Solomon Islands, Vanuatu, Fiji, Tonga and New Zealand
382 (<http://www.neptuneminerals.com/our-business/tenements/>).

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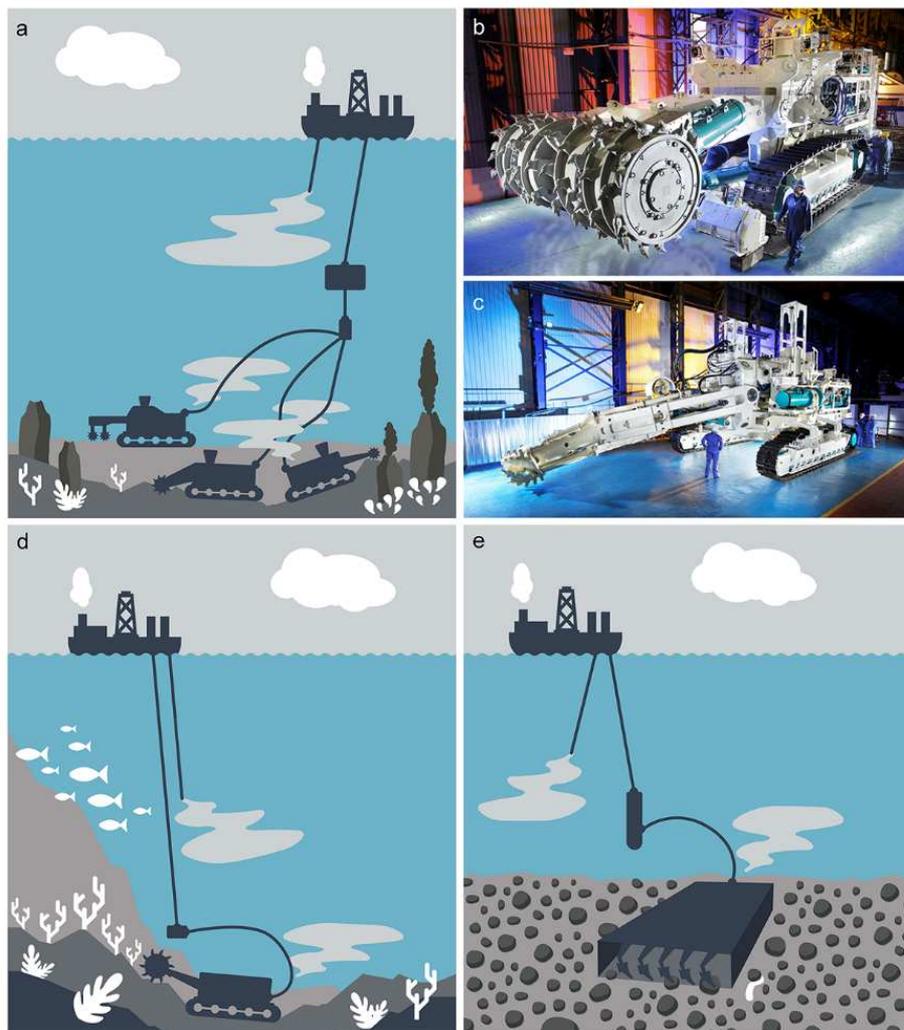
384 **2.2 Mineral Mining operations**

385 The anticipated mining disturbance varies greatly among the different mineral resources and
386 their associated ecosystems. Mining operations will be conducted by machines operating at
387 water depths down to several kilometers. Seabed crawlers for sulphide mining will have
388 auxiliary cutters and bulk cutters to shred mineral deposits (Figure 3 b) and also collecting
389 machines (Figure 3 c). The resulting rock mixture will be transported to a surface support
390 vessel as a slurry by a riser and lifting system (Figure 3 c). Similar conceptual plans exist for

391 mining crusts (Figure 3 d). Machines for nodule collection are not yet available, but several
392 concepts exist and prototypes have been built. Nodule-mining machines are proposed to
393 plough tens of centimeters into the seafloor sediments, mechanically or hydraulically
394 removing the nodules from the sediment. The nodule-sediment mixture will be transported to
395 a surface support vessel as a slurry by a riser and lifting system, where the sediment will be
396 separated from the nodules and returned to the water column through a discharge pipe [105]
397 (Figure 3 e). The nature of mining disturbance will also depend on the technology used, even
398 for the same mineral type. For example, tools proposed for sulphide mining by Nautilus for
399 Solwara 1 are less smothering than methods suggested by the Japan Deep Sea Technology
400 Association (DESTA) [16] (and references therein).

401 The potential size of mined areas may vary greatly among the different mineral
402 resources. For each exploitation license issued by the ISA, nodules may be extracted from
403 300 to 800 square kilometers in a year of mining [106, 107] and ~8500 square kilometers
404 over a 20 year period [11, 16, 108, 109]. In contrast, Nautilus Minerals would target only
405 0.112 km² of seabed during polymetallic sulphide mining at Solwara 1, although it could
406 disrupt connectivity of hydrothermal habitat in the region [16, 110]. Some mining plans, such
407 as those of Nautilus Minerals, propose a patchy removal strategy with a mixture of temporary
408 and quasi-permanent refuge areas [16].

409



410
 411 Figure 3. a. Mining scenario for polymetallic sulphides at hydrothermal vents. b. Bulk cutter
 412 for sulphide mining (photo courtesy Nautilus Minerals). c. Collection machine for sulphide
 413 mining (photo courtesy Nautilus Minerals). d. Mining scenario for cobalt-rich ferromanganese
 414 crusts at seamounts. e. Mining scenario for polymetallic nodules on abyssal plains. All
 415 scenarios show the marine environment, seafloor production tools and sediment plumes,
 416 riser and lifting system to the vessel, and release of mineral washings.

417

418 2.3 Mining threats

419 Mining activities will impose disturbances with novel nature, strength, persistence, and
 420 spatial and temporal scale on deep-sea ecosystems. Direct mining impacts will include
 421 mortality and removal of fauna living on mined substrata, removal of substrata and habitat
 422 loss, habitat fragmentation, habitat modification (i.e. change of mineral and sediment
 423 composition, topography, chemical regimes), and diverse other direct impacts such as sound
 424 and electromagnetic radiation by mining instruments. Indirect impacts comprise the formation
 425 of (potentially toxic) sediment plumes by the activity of crawlers, seabed installations and
 426 risers, and potential release of toxic substances into the water column along the riser system

427 and/or by process material discharged from the ship (return plume) [11-21]. Further details
428 are discussed in the reversibility chapter (3.3).

429

430

431 **3. Estimating resilience of deep-sea ecosystems**

432

433 **3.1 Resistance**

434 To date, large-scale commercial mineral mining has not taken place. Very likely, the removal
435 of minerals will kill fauna inhabiting mineral deposits. However, the capacity for populations
436 of deep-sea species to stay essentially unchanged despite disturbances (resistance *sensu*
437 [111]) associated with deep-sea mining remains uncertain. Resistance (natural ability to
438 remain unaffected by a force) may apply to species response to sound/vibration and
439 electromagnetic radiation produced by mining operations. Shallow-water marine mammals,
440 fish, and invertebrates are physiologically sensitive to acoustic disturbance [112] with
441 potential for ecological effects such as alteration in natural behaviour, reduction in
442 communication ranges, reduction in foraging ability, prevention of predator avoidance,
443 complete habitat avoidance, and death [113, 114]. These physiological and behavioral
444 effects can alter the ecology of marine systems [115]. However, the effects of these potential
445 stressors on deep-sea fauna are poorly constrained: data on sound/vibration and/or
446 electromagnetic radiation impact at deep-sea vents, seamounts or nodule fields are few and
447 uninformative in a deep-sea mining context. For example, high-intensity illumination
448 associated with Human-Occupied Vehicles (HOVs) and Remotely Operated Vehicles (ROVs)
449 has been implicated in photoreceptor damage in shrimp that aggregate on black smokers at
450 Mid-Atlantic Ridge vents [11]. The structure and light-sensitive visual pigment (rhodopsin) of
451 thoracic eyes in adult vent shrimp suggests that they are adapted to detecting the dim light
452 generated by high-temperature venting as a near-field remote-sensing means of avoiding
453 thermal stress and mortality. The initial description of these photoreceptors identified
454 degradation inferred to result from light exposure [116] and it was suggested that cellular
455 machinery to support recovery from light damage disappears during ontogeny [117]. The
456 behavioral consequences of light-damaged photoreceptors in vent shrimp are unknown, but
457 there is no evidence of impacts on shrimp populations repeatedly exposed to high-intensity
458 illumination [118]. However, these shrimp populations are only intermittently exposed to high-
459 intensity illumination, which may not be representative of exposures that will occur during
460 mineral exploitation. Further, the significant variation in visual ecology among deep-sea taxa
461 [119] is likely to influence resistance. Consequently, extrapolating resistance potential to
462 radiation caused by deep-sea mineral exploitation processes to other taxa is not yet possible.

463 Mining will produce sediment plumes on the sea floor, as well as producing discharge
464 sediment plumes in the water column, following mineral washing and fractioning procedures
465 on board of the support vessels. Plumes will disperse beyond the area of direct mining
466 impact. The concept of resistance applies to communities living in these indirectly impacted
467 areas that may cover larger areas than the directly mined area. Sulphide test mining at the
468 Solwara 1 site off Papua New Guinea, indicated increased sedimentation (up to 500 mm)
469 within 1 km of the discharge site, with some material potentially dispersing up to 10 km away
470 [16, 110]. Natural sedimentation rates at vents are much lower, ranging for example from ~1-
471 2 mm per year in Guaymas basin [120] to ~ 0.0025-0.03 mm per year at Juan de Fuca [121].
472 On abyssal plains and seamounts, natural sedimentation rates are in the order of only
473 several mm per thousand years [122]. Yet, it remains unclear if and to what extent deep-sea
474 communities may be resistant to particle plumes generated by mineral extraction and
475 resuspension of sediments.

476 Environmental impact assessment of the deep-water oil and gas exploitation industry
477 indicates that both increased sedimentation and toxicant exposure have significant ecological
478 effects that can extend to more than 5 km from the point source (see [123] and references
479 cited therein). However, impacts depend on both the magnitude and composition of the
480 released material which differs significantly both within and between the deep-sea oil and
481 gas industry and the deep-sea mineral industry, preventing direct inferences of resistance to
482 deep-sea mining impacts.

483 Particle plumes generated by mineral mining may physically smother benthic
484 organisms, clogging gas exchange and feeding structures [123]. Seafloor coverage by a 3
485 mm thick layer of drill cuttings can significantly affect infaunal communities [124]. However,
486 significant quantitative impacts on meiofaunal abundance and community composition have
487 also been observed beyond the extent of observable drill cuttings deposition [125].
488 Resistance to sedimentation generated by mineral extraction processes is likely to vary
489 based on the ecology of individual species, for example depending on whether taxa are
490 epifauna or infauna, errant or sessile, suspension feeders, filter feeders, deposit feeders, or
491 necrophages (see [123] and references cited therein).

492 Shifts in density, biomass, and diversity of benthic assemblages in response to
493 offshore oil and gas exploitation have also been linked to increased toxicant concentrations
494 [126-129]. However, sulfide mineral metal bioavailability and toxicity data are currently only
495 available from laboratory studies with shallow-water fauna [110, 130], which may be
496 unrepresentative of deep-adapted fauna [131]. Mineral particles have high metal
497 concentrations and deep-sea sediments are typically metal enriched [12]. Metal
498 concentrations present in mineral particle plumes appear less toxic than the corresponding
499 concentration of dissolved metals [130] thus the oxidation/reduction processes during mining

500 operations will significantly affect toxicant bioavailability. Mineral dissolution rates depend on
501 the composition of mineral deposits and are also sensitive to redox conditions [132],
502 therefore toxicant bioavailability will be site specific with spatial and temporal variability.
503 Further, toxicant bioavailability may also be influenced by the ecology of individual species,
504 depending on e.g. whether taxa are epifauna or infauna, errant or sessile, suspension
505 feeders, filter feeders, deposit feeders, or necrophages [133]. For example, the ability of
506 species to tolerate (and resist) potentially toxic particles is likely higher at active vents, which
507 are already under the influence of the putatively toxic hydrothermal fluid and plumes [37],
508 than at inactive vents and in the wider deep sea, where taxa are not typically exposed to
509 such toxicants.

510 Deep-sea hydrothermal vent organisms appear to have developed enhanced defence
511 pathways to respond to the presence of high concentrations of dissolved metals released at
512 hydrothermal vents. Induction of antioxidant, biotransformation enzymes, or metal-binding
513 proteins that are able to remove the reactive oxygen species formed by molecular reactions
514 with toxic metals, or detoxification of metals by sequestering them in a non-bioavailable form
515 and/or by eliminating the metal, have been observed in hydrothermal vent fauna at
516 ecologically relevant metal concentrations at *in situ* temperature and hydrostatic pressure
517 [134, 135]. These responses represent an energetic commitment with potential
518 consequences for reproductive capacity and population survival [136]. However,
519 extrapolation from resistance in experimental exposures to resistance in the environment
520 remains challenging: ecological processes and interactions must be understood before
521 experiments in laboratories, micro- or meso-cosms can be related reliably to natural
522 conditions [137]. Further, the physical and chemical composition of the particle plume
523 generated by mineral extraction is likely to differ significantly from the hydrothermal vent fluid
524 and plume, as may the duration of exposure to the chemical mixtures presented by mineral
525 extraction processes, impeding inferences regarding potential resistance to toxicological
526 exposures among vent fauna.

527 The structure and functioning of benthic assemblages at vents, and to a lesser extent
528 at seamounts, are highly dependent on key foundation species [67, 138] and may quickly
529 collapse if the resistance of these species is exceeded. Large sessile suspension feeders,
530 common at inactive vents and on seamounts, also thrive in high particle loads, although they
531 may be sensitive to burial, distinct particle size and shapes, and toxic compounds [53, 139,
532 140]. As natural sedimentation rates are extremely low on abyssal plains, the abyssal fauna
533 are likely least tolerant to enhanced particle load and sedimentation. Although we expect that
534 such species are to some level resistant to mining plumes, current knowledge is insufficient
535 to predict the extent of resistance.

536

537

538 **3.2 Recovery after small-scale disturbance events**

539

540 **3.2.1 Hydrothermal vents**541 **Active vents**

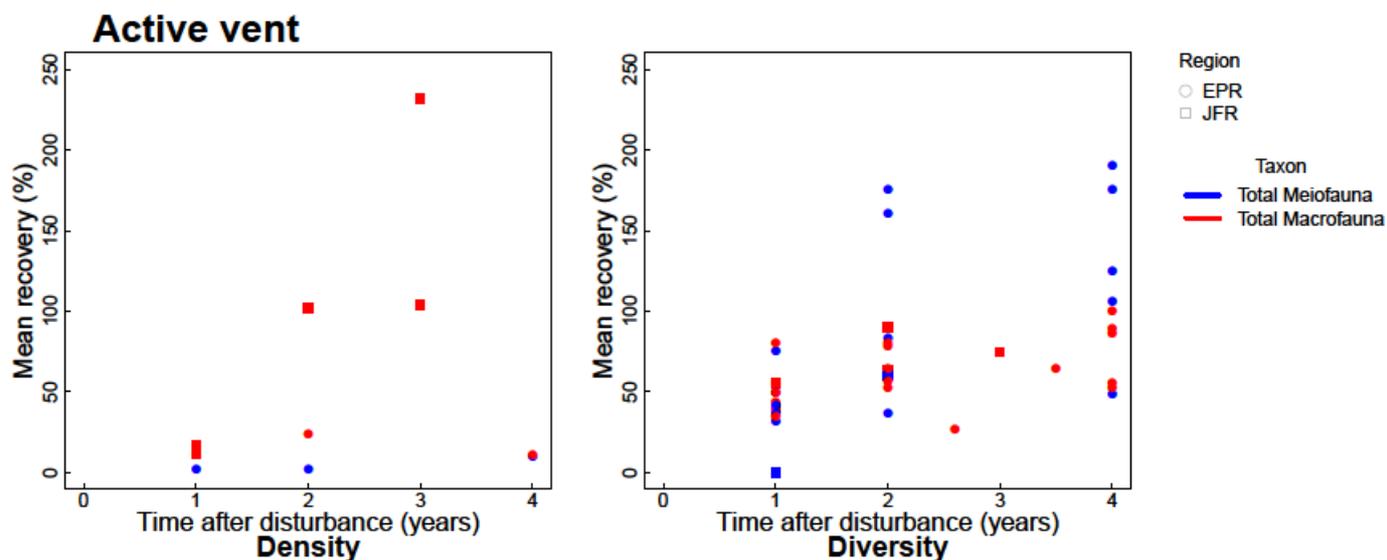
542 Active vents exhibit distinct biogeographic faunal patterns and natural background
543 disturbance regimes, suggesting region-dependent recovery at slow- and fast-spreading
544 centers. In the last three decades, faunal recovery following volcanic eruption events were
545 documented after the 1993 and 1998 eruptions on the intermediate-spreading Juan de Fuca
546 Ridge (JFR) on Co-Axial Segment and Axial Volcano [141, 142], and after the 1991 and
547 2006 eruptions on the fast-spreading 9°N vent field on the East Pacific Rise (EPR) [26, 143].

548 At Juan de Fuca, mean mega- and macrofaunal densities reached and even
549 exceeded pre-eruption values after 2 years (17% mean recovery after 1 year; 290% mean
550 recovery after 2 years) (Figure 4, Appendix A). Biomass showed a similar recovery response
551 (12% after 1 year; 102% after 2 years, Appendix A). Meio- and macrofauna abundances at
552 the EPR also recovered relatively quickly, with no significant differences in abundances
553 across all tubeworm sites relative to pre-eruption data [26]. Similarly, Wilcoxon tests revealed
554 no significant increase in mean percent recovery over years. Comparing meio- and
555 macrofauna recovery data across Juan de Fuca and the EPR revealed that macrofauna
556 densities recovered more quickly than meiofauna ($p < 0.01$; Figure 5; Figure 6). At single vent
557 sites, such as at Tica at the EPR, recovery of abundance was slow, with mean macrofauna
558 abundance reaching only 11-24% and mean meiofauna abundance reaching 2-9% 1 to 4
559 years after eruption (Appendix A). However, abundance standard deviation was very high
560 both pre- and post-eruption at this site (Gollner et al. 2015; Figure 5). For example,
561 abundances at the Tica site varied significantly with 3125 ± 1261 macrofauna and $2255 \pm$
562 3455 meiofauna ind. per 64 cm^2 before the eruption, and with 342 ± 209 macro- and $213 \pm$
563 224 meiofauna ind. per 64 cm^2 four years after eruption. The natural high variability of
564 abundances ranging several orders of magnitude, combined with low quantitative sampling
565 (three samples per site and time), make it impossible to detect potential significant
566 differences pre- and post-eruption. More extensive sampling is needed to understand natural
567 variability at active vents.

568 Mean percent recovery of faunal diversity significantly increased from 1 to 2 years
569 after eruption ($p = 0.013$), from 1 to 4 years ($p = 0.013$) after eruption, but not from 2 to 3
570 years ($p > 0.05$), 2 to 4 years ($p > 0.05$), or 3 to 4 years ($p > 0.05$) (see data Appendix A).
571 Total mega- and macrofauna species richness at the Juan de Fuca vents reached 75% of
572 the pre-disturbance species pool three years after the 1998 eruption [141], and 90% two
573 years after the 1993 eruption [142]. At the EPR, total mega- and macrofauna species

574 richness reached 69% of pre-disturbance values 4.6 years after the 1991 eruption [143].
 575 After the EPR 2006 eruption, the recovery reached 55% for macrofauna and 48% for
 576 meiofauna species after 4 years [26] (for data see Appendix A), with 39% of the macro- and
 577 42% of meiofaunal species returned. In addition, several new species appeared in the
 578 region, including some early colonizers that were dominant in the first post-eruption years
 579 [26]. Species richness at Tica vent site reached 52% of pre-eruption values for macrofauna,
 580 and 106% for meiofauna after 4 years (Appendix A). At this site and time, the physical-
 581 chemical parameters of vent fluids were comparable to values measured pre-eruption [26].
 582 The fast recovery of meiofauna at Tica site shows that distinct size classes (in this case
 583 meiofauna) may recover more quickly than others. However, Wilcoxon rank tests revealed no
 584 significant differences between meio- and macrofauna diversity recovery rates, and also no
 585 differences between the EPR and JFR region (Figure 6). The observations at Tica site in
 586 comparison to regional observations highlight that single sites may not capture regional
 587 recovery; instead several vent sites need to be studied. Similar patterns of recovery were
 588 observed using several diversity parameters (observed species richness, expected number
 589 of species, Shannon's H', Pielou's J') (Appendix A). The variability of diversity values within
 590 sites was not exceptionally high, with similar range pre- and post-eruption overall (Figure 5,
 591 Appendix A).

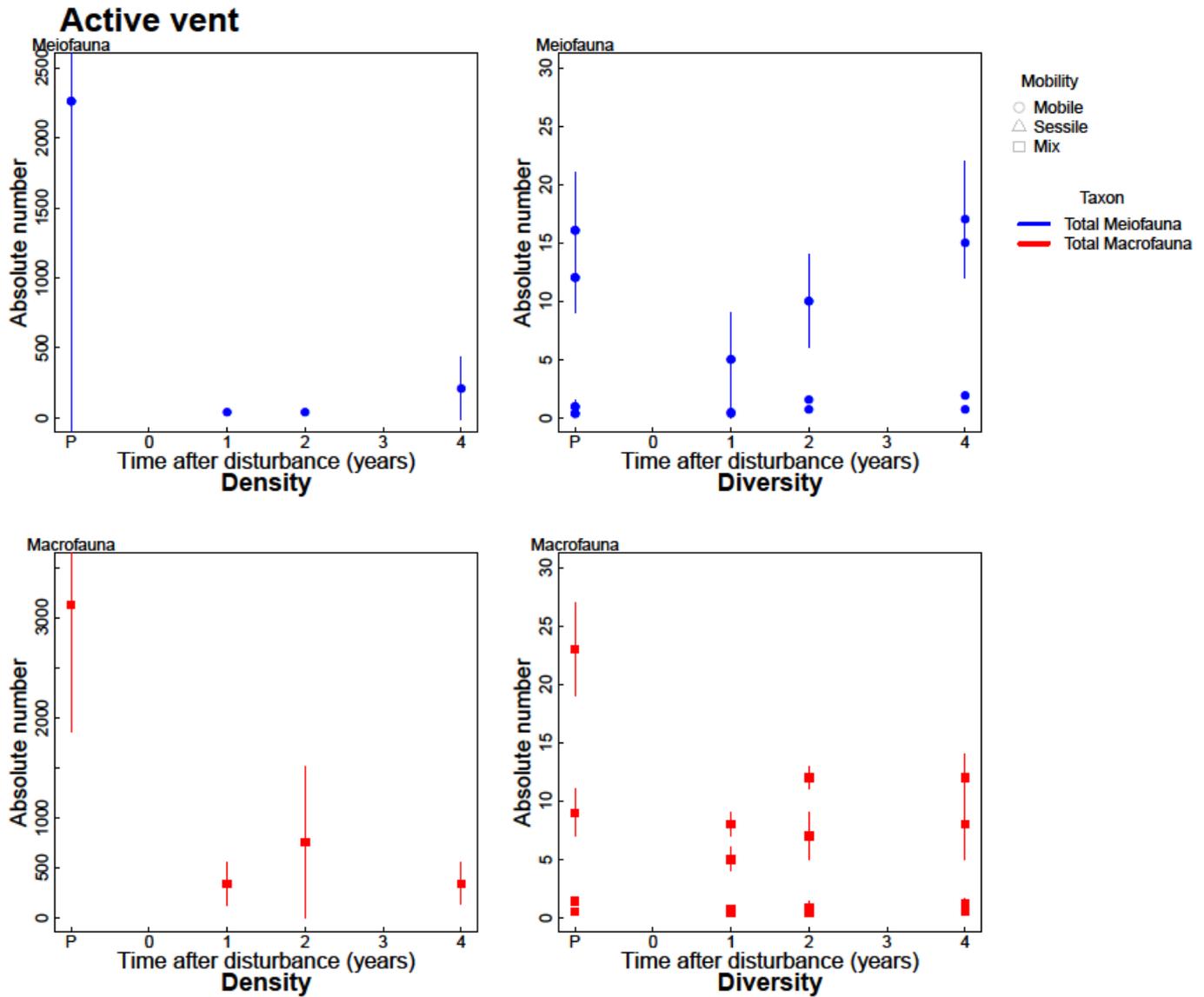
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596 Figure 4. Mean recovery (%) relative to pre-disturbance faunal density and diversity at active
 597 hydrothermal vents. For data see Appendix A. EPR: East Pacific Rise. JFR: Juan de Fuca
 598 Ridge.

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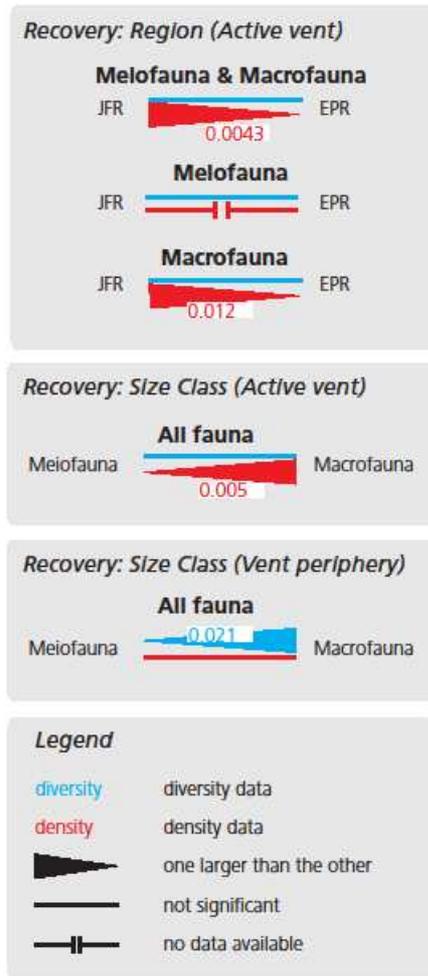
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603 Figure 5. Absolute numbers and standard deviation of density and diversity values measured
604 pre-disturbance (indicated as P) and after disturbance (in years) for meiofauna and
605 macrofauna at active hydrothermal vents. For data and metric see Appendix A. Circles:
606 mobile taxa. Triangle: sessile taxa. Square: mixed taxa (sessile and mobile).

607

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610

611 Figure 6. Results of Wilcoxon rank sum tests for differences in mean recovery (%) relative to
 612 pre-disturbance diversity and density between meio- and macrofauna at active vents at the
 613 East Pacific Rise (EPR) and at the Juan de Fuca (JFR), and in the vent periphery (at EPR).
 614 P-values are given for significant differences.

615

616 At the EPR and at the Juan de Fuca vents community succession patterns following major
 617 disturbance events were attributed to species responses to changes in hydrothermal vent
 618 fluid composition. Typically, vent fluid emissions were high following eruptions but declined
 619 within few years. However, biological interactions and larval dispersal and recruitment also
 620 played important roles in succession processes [26, 54, 138, 141, 143-145]. Interestingly,
 621 post-eruption species (e.g. the limpet *Ctenopelta porifera*) originating from remote areas
 622 invaded disturbed and undisturbed vent sites in the region [138]. As a consequence, large
 623 scale mining may also indirectly influence community composition at neighboring non-mined
 624 vent sites. Meiofauna succession at the EPR was consistent with dispersal potential. Species
 625 with pelagic dispersal demonstrated rapid recovery (e.g. dirivultid copepods) [26, 146],
 626 whereas species lacking pelagic dispersal stages (e.g. nematodes) demonstrated slow and
 627 poor recovery [54]. Species that were highly abundant in the region and inhabited more than

628 one habitat pre-eruption (e.g. diverse vent-sites and the vent periphery) were typically more
629 resilient and returned quickly after the eruption at the EPR [26]. Populations in the vent
630 periphery and at sites where venting recently ceased, as well as at more distant exposed
631 basalt areas, may represent potential source population locations for vent meiofauna
632 recovery [26, 54]. Current observations of vent succession at 9°N on the EPR thus suggest
633 complex recovery dynamics in metacommunities, with species differing in their ability to
634 disperse and with successful colonizers outcompeting poor competitors.

635 There has not yet been a volcanic eruption documented on slow-spreading ridges,
636 resulting in an absence of empirical data. Long-term studies at the Logatchev site (MAR)
637 showed no major successional stages, but a decline in vesicomid clams (probably due to a
638 land slide) and an increase in bathymodiolin mussels, gastropods, and shrimps occurred
639 over a 10 year period [147]. At Lucky Strike (MAR), a 14-year study revealed stable mussel
640 coverage [35]. Overall, the relatively low background disturbance regimes on slow-spreading
641 ridges suggest that recovery after natural and/or anthropogenic disturbances might be slower
642 than at fast-spreading ridges, but this remains conjecture. As with vents on fast-spreading
643 ridges, connectivity and colonization potential will also be essential for recovery processes at
644 slow-spreading ridges.

645 Colonization potential, and therefore recovery potential after disturbance events
646 (either natural or anthropogenic), can be described in the framework of population
647 connectivity [49, 148-152]. Genetic analyses have been performed on various vent meio-,
648 macro-, and megafaunal species (e.g. crustaceans, bivalves, gastropods, polychaetes) in
649 distinct geographical settings (e.g. on the MAR, the EPR, Eastern Lau Spreading Centre,
650 Kermadec back-arc basin and CIR) [153, 154]. Results suggest that gene flow and migration
651 capability between subpopulations is potentially high at both fast- and slow-spreading ridges
652 [48, 146, 155, 156]. A general pattern of high intrapopulation genetic diversity and expansive
653 population growth has emerged among various species from different vent sites [156-158].
654 However, vent organisms studied genetically are typically highly abundant and have pelagic
655 dispersal. No study has yet analyzed patterns of genetic connectivity for vent species that
656 are less abundant and/or lack pelagic dispersal.

657 Underlying mechanisms of high connectivity (migration capability) across the studied
658 active vent species are not fully understood. Data on life history (i.e. reproduction, larval
659 behaviour, juvenile settlement cues) are currently scarce. Life history traits likely play an
660 important role, since they can allow long-term planktonic larval duration and/or rapid
661 population growth, and connectivity between invertebrate populations is often maintained by
662 passive larval drift. However, passive larval drift is influenced by abiotic characteristics such
663 as plume height, or ocean currents [159]. The rate of exchange of individuals between vent
664 fields is likely also influenced by vent field frequency and distance between individual vent

665 sites since typically vent-restricted fauna need to migrate between isolated vent fields to
666 ensure survival. Thus, exchange rates may be higher at closer proximity fast-spreading vent
667 sites compared to more distantly spaced slow-spreading vent sites.

668 To conclude, recovery after natural volcanic eruptions at active hydrothermal vents at
669 fast-spreading centres is highly variable but can be relatively rapid. Vent communities at fast-
670 spreading centres experience frequent volcanic eruptions (at the studied EPR location every
671 ~15 years [160]) and seem to be resilient and adapted to such natural disturbance events.
672 Abundance and biomass values reach pre-disturbance values within a few years. However,
673 very high variability is typically observed, pre- and post-eruption. Diversity values partly reach
674 pre-disturbance values within only a few years, but community composition often remains
675 different, following a sequence of faunal succession. Faunal responses differ among taxa
676 and life history traits. The drivers of vent community resilience are diverse and include
677 availability and composition of hydrothermal fluids as well as biotic controls such as species
678 specific factors of dispersal and connectivity and biotic interactions of competition and
679 predation.

680 However, recovery data were only available for two regions in the East-Pacific that
681 experience frequent volcanic eruptions. Distinct biogeographic faunal patterns, distinct vent
682 site distance and natural background disturbance regimes make it currently impossible to
683 predict recovery rates following volcanic eruptions in other regions, and especially at slow-
684 spreading centres. Further, volcanic eruptions pave over areas which contrasts with the
685 scraping and excavating disturbances that will be imposed by mining machines. Eruptions
686 also do not lead to extensive sediment plumes, as are expected with mining. To what extent
687 changes in substratum surface area and generation of (potentially toxic) sediment plumes
688 may delay or may prevent recovery of vent communities (i.e. disruption of larval dispersal,
689 mortality of larvae, and success of larval settlement) is currently unknown.

690

691 ***Inactive vents***

692 There is currently no data available for recovery at inactive vent sites. Megafauna typically
693 found at inactive vents includes sponges and cnidarians, such as corals [50-53]. Little is
694 known about the age, growth rates, biogeography, or connectivity patterns of inactive vent
695 megafauna. In general, such taxa are considered rather slow-growing and long-lived
696 (hundreds to thousands years) with slow recovery rates [77]. It is yet unclear whether
697 assemblages that thrive at inactive vents are overall partly similar to active vent fauna, are
698 similar to those inhabiting hard-substrate fauna on non-mineral rich grounds, or are unique
699 [17]. A recent study comparing megafauna from active and inactive chimneys off New Zealand
700 found that deposits support unique megafauna assemblages but that species partly overlap
701 [53]. Similarly, a study of a young inactive vent site and active vent sites at the EPR revealed

702 that these environments share some nematode species [54]. The finding of shared species
703 at inactive and active vents suggests that they may provide potential source populations for
704 each other after disturbance events [54]. Consequently, active and inactive sites in each
705 region have to be studied to understand potential recovery after mining disturbance at active
706 and/or inactive vents. Thus it has been suggested that both active and inactive features need
707 to be included within a framework establishing protected areas to mitigate mining impacts at
708 hydrothermal vents [154].

709

710 **Vent periphery**

711 Faunal recovery on basalt in the vent periphery has been studied once, following volcanic
712 eruption disturbances on the 9°N EPR in 2006 [26]. One year post-eruption meio- and
713 macrofauna abundances were similar to pre-eruption abundances, but showed very high
714 variation [26]. Mean recovery of meio- and macrofauna abundances were >100% after one
715 year (Figure 7). Abundances varied highly with 21 ± 28 macrofauna and 113 ± 147 meiofauna
716 ind. per 64 cm^2 before the eruption, and with 566 ± 685 macro- and 1623 ± 2599 meiofauna
717 ind. per 64 cm^2 four years after eruption (Figure 8; Appendix A). Wilcoxon rank tests revealed
718 no significant differences between meio- and macrofauna density recovery rates (Figure 6),
719 and there was no significant increase in percent recovery throughout the years.

720 Total regional macrofauna richness, primarily comprised of juvenile individuals of
721 typical vent species, had recovered to mean 64% of pre-disturbance levels four years after a
722 volcanic eruption (Figure 7). Meiofauna diversity recovered more slowly than macrofauna
723 diversity ($p = 0.021$). Total regional meiofauna richness reached only 28% of pre-eruption
724 values after four years [26]. Many meiofauna species, which were rare prior to the eruption,
725 had not returned. Thus, whilst mean richness recovery was 111% for the macrofauna, mean
726 richness recovery was only 48% for meiofauna after four years. Rare pre-eruption species at
727 individual sites were replaced by common species from the regional species pool. Other
728 diversity measures showed comparable responses. Meiofauna community composition in the
729 vent periphery changed significantly with time (e.g. dominant species one, two, and four
730 years after disturbance were the copepod *Tisbe* sp. nov. 1., the copepod *Amphiascus* sp. 1
731 (aff. *Varians*), and the ostracod *Xylocythere vanharteni*, respectively). Changes were similar
732 to the ones reported for active vent meiofauna and were related to meiofauna species
733 dispersal potential [26]. However, Wilcoxon tests showed that mean percent diversity
734 recovery remained similar in the vent periphery throughout the years (all $p > 0.05$), and
735 diversity did - in contrast to active vents - not increase with years, indicating slower recovery.

736 To conclude, recovery of meiofaunal vent peripheral communities is likely slower than
737 communities at active vents. After four years, only 28% of meiofauna species of the pre-
738 disturbance periphery species pool had returned to the EPR, whereas 42% of meiofauna

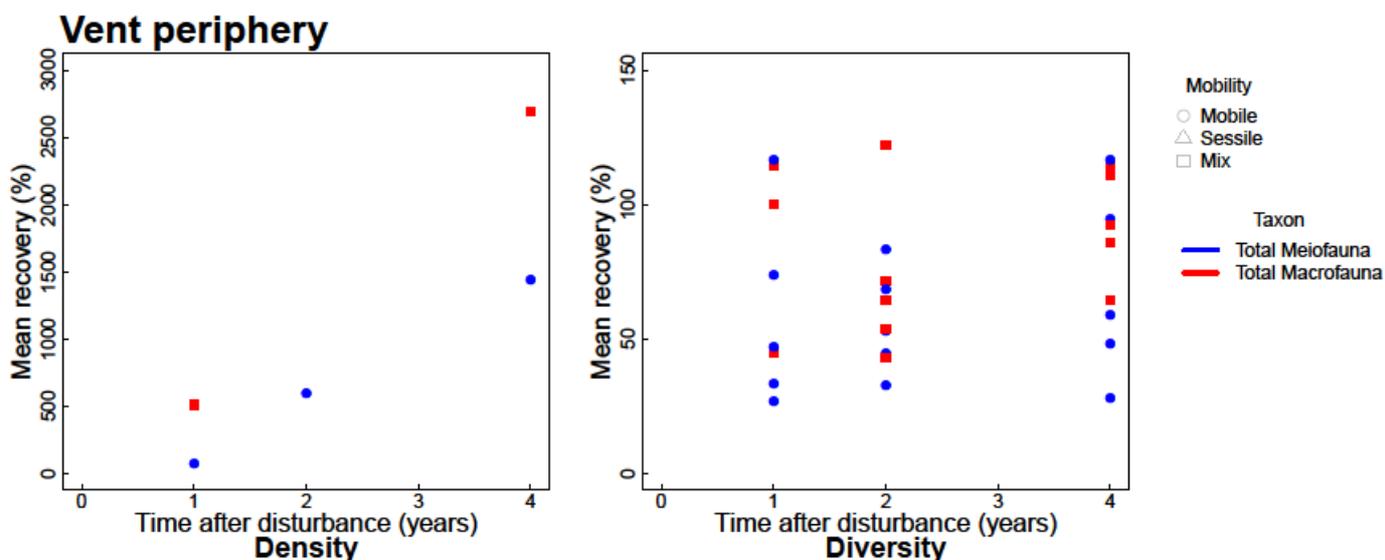
739 species of the pre-disturbance vent species pool had returned to the EPR at active vents
 740 after four years. In contrast, macrofauna recovery of the pre-disturbance species pool was
 741 similar at active vents and in vent peripheral communities. Macrofauna recovery of the pre-
 742 disturbance vent species pool at active vents varied between 75 % (Juan de Fuca, after 3
 743 years), 69 % (EPR, after 4.6 years in 1996), and 42 % (EPR, after 4 years in 2009; not
 744 including new species), whereas macrofauna recovery of the pre-disturbance species pool in
 745 the vent periphery was 64%.

746 The discovery of a juvenile subset of typical vent species in the vent periphery
 747 suggests the interconnection of vent periphery and active vent communities. Little is known
 748 about connectivity and dispersal rates in typical peripheral meiofauna species, but nematode
 749 species lack specific planktonic dispersal stages and demonstrate limited dispersal potential
 750 since they are rarely observed in the pelagic. In contrast, typical vent meiofauna species
 751 such as dirivultid copepods disperse via abundant nauplii and copepodites in the pelagic and
 752 are known for their high genetic connectivity [26, 158].

753 The study on vent periphery recovery investigated only areas close to active sites or
 754 recent inactive vent sites (some meters), but there is no information available on recovery
 755 potential of more distant vent peripheral communities. Also, there is no information available
 756 on recovery potential of vent peripheral communities from slow-spreading areas that are
 757 disturbed by volcanic eruptions less frequently.

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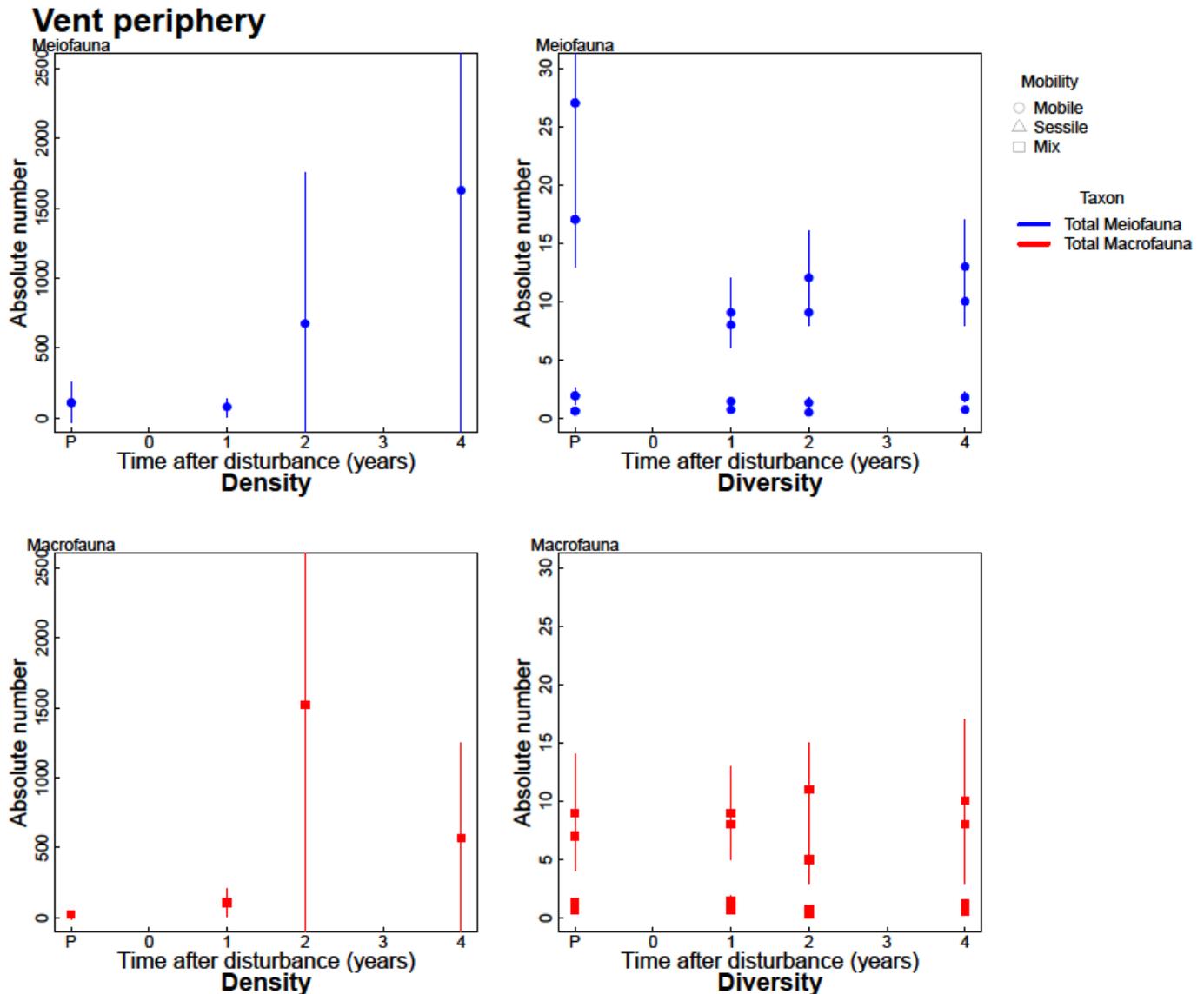
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763 Figure 7. Mean recovery (%) relative to pre-disturbance faunal density and diversity in the
 764 vent periphery. Circles: mobile taxa. Triangle: sessile taxa. Square: mixed taxa (sessile and
 765 mobile).

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773 Figure 8. Absolute numbers and standard deviation of density and diversity values measured
774 pre-disturbance (indicated as P) and after disturbance (in years) for meiofauna and
775 macrofauna in the vent periphery. For data and metric see Appendix A. Circles: mobile taxa.
776 Triangle: sessile taxa. Square: mixed taxa (sessile and mobile).

777

778

779 **3.2.2 Seamounts**

780

781 Fisheries currently impose a severe impact on seamounts, with global catches estimated at
782 ~3 million tonnes per year [77, 161-164]. Unfished seamounts have been observed to
783 support double the overall benthic biomass and species richness than fished seamounts
784 [165]. In particular cold-water corals and other sessile filter feeders, which provide habitat to
785 many other benthic organisms [166-168], are extremely susceptible to bottom trawling [169,
786 170] because they grow extremely slowly (few μm to ~1mm per year) and are long-lived
787 (decades and centuries to millennia) [77, 171, 172]. Knowledge on the coral cover necessary
788 to sustain stony coral communities (and associated species) is scarce. However, most
789 seamounts with high trawling impact have coral cover reduced to below 30-50% of the coral
790 cover estimated as necessary to maintain habitat viability [170].

791 Knowledge on recovery rates following the cessation of bottom trawling are rare, and
792 the uniqueness of seamounts hampers a direct comparison of communities across
793 seamounts to determine recovery rates (e.g. fished vs. unfished) because biological
794 seamount communities experience different environmental conditions and may respond
795 differently to physical disturbance. Thus, only seamounts with similar environmental
796 conditions and in close vicinity can be considered eligible for comparison [173-175].

797 Althaus et al. [173] observed that mean megafauna density recovered to 33%, and
798 mean coral density to only 6% 5-10 years after trawling ceased (Figure 9, Appendix A).
799 However, there were large differences in recovery among taxa, ranging from <5% to up to
800 1100% for anthozoan taxa. Watson and Morato [175] observed 23% recovery in fish
801 densities 15 years after fisheries collapsed and fishing ceased. Williams et al. 2010 [174]
802 distinguished between recovery on hard substratum (coral and rock) and on unconsolidated
803 substratum (sand, gravel rubble). Mean megafauna density recovery was 36% after 5 years
804 and 111% after 10 years on hard substratum, and 167% after 5 years and 143% after 10
805 years on unconsolidated substratum. Similar to Althaus et al. [173], Williams et al. [169]
806 identified large variations among taxa (17% to 800% after 5 years, and 13% to 2600% after
807 10 years on hard substratum; 27% to 2840% after 5 years, and 17% to 1100% after 10 years
808 on unconsolidated substratum; see Appendix A). Standard deviation within taxa was usually
809 not very high (Figure 10, Appendix A), but for many data points replicates were not available.
810 Wilcoxon rank tests revealed no significant differences between mean mobile and sessile
811 megafaunal density recovery (Figure 11). Density recovery was faster on seamounts off
812 Australia than on seamounts off New Zealand when considering only one study, but was
813 faster on seamounts off New Zealand than on seamounts off Australia when considering two
814 studies (Figure 11). There was no significant increase in mean percent recovery throughout
815 the investigated years (all $p > 0.05$).

816 Althaus et al. [173] reported mean megafauna species richness recovery of 32% after
817 5-10 years (Appendix A). Williams et al. [174] presented megafauna recovery data using

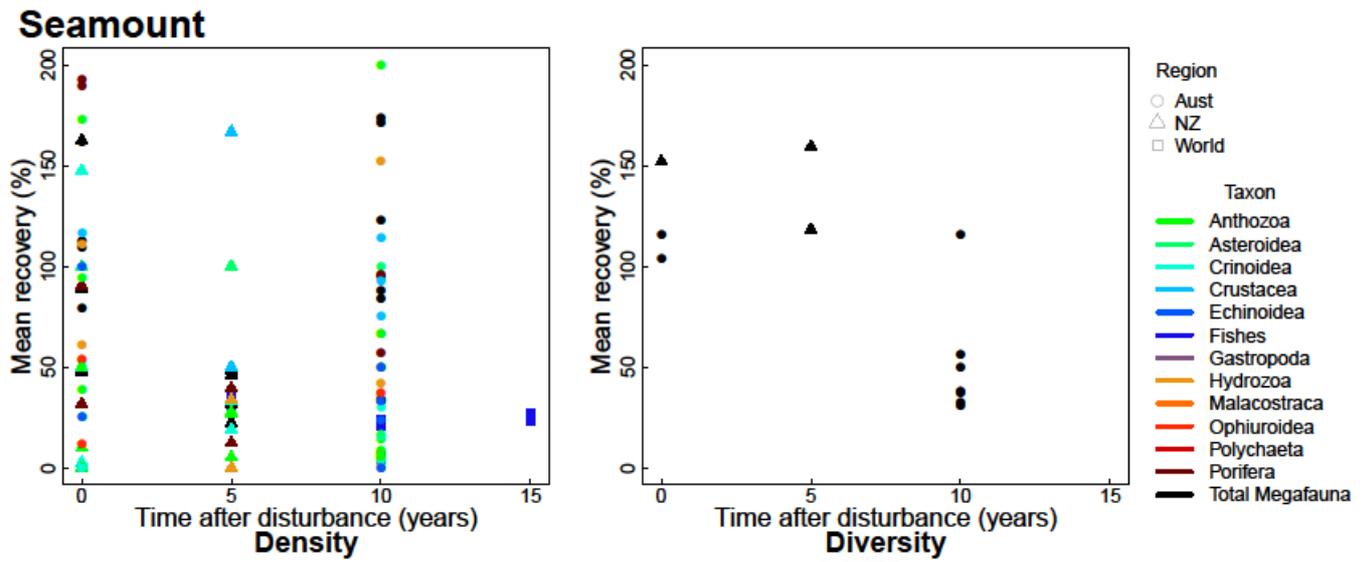
818 Simpson's diversity index that ranged from 129% after 5 years to 198% after 10 years on
819 hard substratum, and from 30% after 5 years to 774% after 10 years on unconsolidated
820 substratum. Wilcoxon rank tests revealed no significant differences between mobile and
821 sessile megafaunal diversity recovery. Mean diversity recovery was greater on seamounts off
822 New Zealand than on seamounts off Australia (Figure 11). However, no significant increase
823 in mean diversity percent recovery was observed throughout the years (all $p > 0.05$).

824 To summarize, data on community recovery following bottom trawling are sparse and
825 available only for fauna large enough to be detected using image analysis. Recovery
826 processes in seamount megafauna show large variations depending on taxa and indicate
827 significant changes in community composition following disturbance. A few individual taxa
828 were found in very high abundance after trawling which may have resulted from resistance to
829 trawling impact or from protection in natural refuges inaccessible to trawls. Alternatively,
830 these highly abundant taxa may represent the early stage of succession after trawling impact
831 [174]. Overall, recovery to original (pre-disturbance) species richness and community
832 composition following fisheries is likely rather slow and is predicted to take decades to
833 centuries since many seamount taxa, especially climax species, are long-lived with slow
834 growth and are potentially geographically isolated [77]. In addition, many species live in
835 association with thickets of a key stone coral (such as *Solenosmilia variabilis*) that have been
836 built over millennia [174]. Data on recovery rates of such associated meio- and macrofauna
837 after trawling do not exist to our knowledge, but resilience may be low where fauna can only
838 live in association with a distinct slow-growing keystone species. Our understanding of
839 ecosystem recovery on seamounts is highly fragmentary and requires further investigation.

840 Impact by trawling fisheries is likely less destructive than mining. A trawl net may
841 bounce along the seabed to some degree, so that the more flexible corals and some
842 occasional individuals may be missed and escape damage. In the case of mining, the entire
843 rock surface will be scraped away so the chance of avoiding removal is much slimmer. In
844 addition, the influence of (potentially toxic) sediment plumes on larval dispersal, survival and
845 settlement success is unknown. Faunal recovery and resilience after mining disturbance is
846 therefore likely to be slower than recovery after trawling.

847

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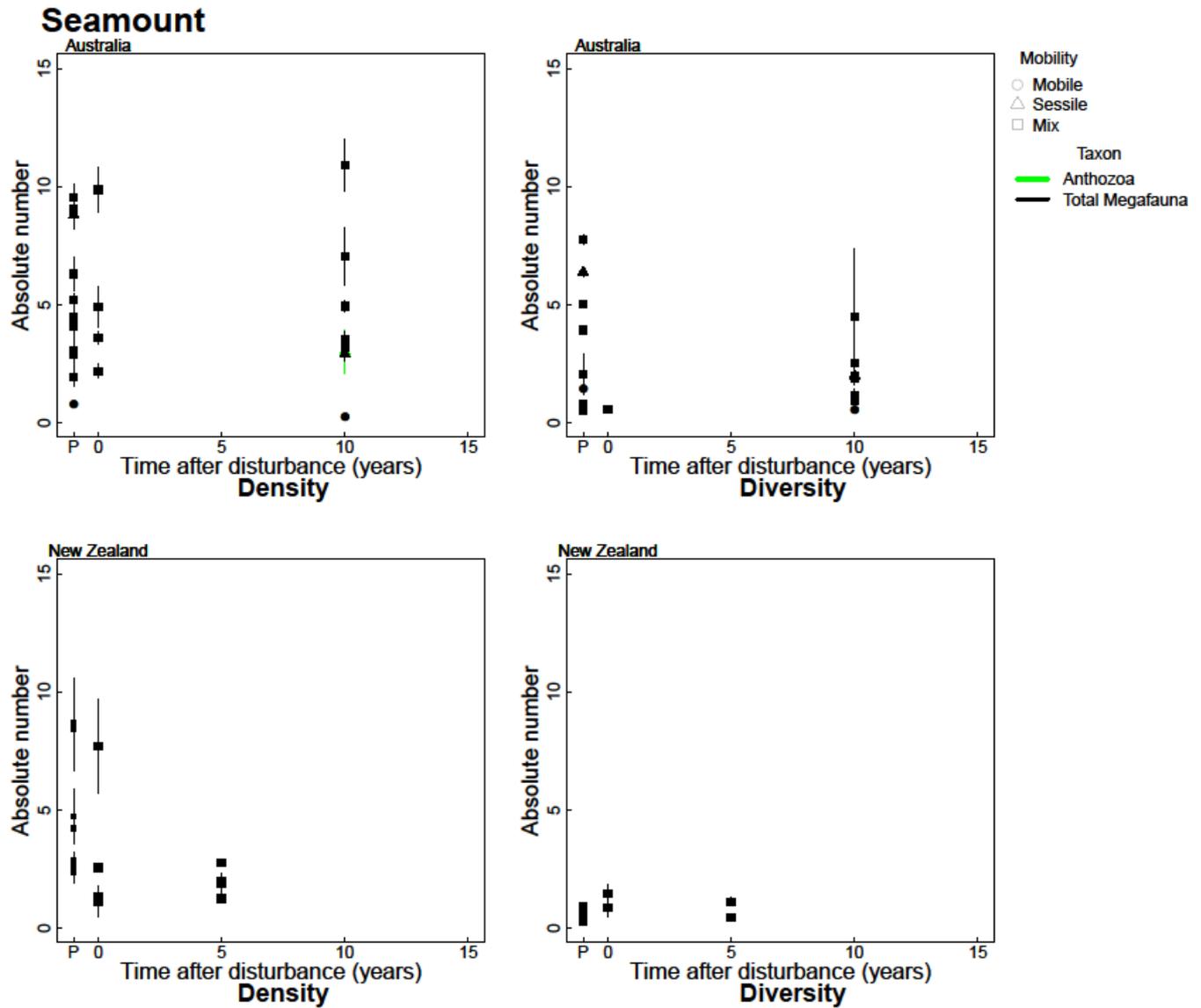
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851 Figure 9. Mean recovery (%) relative to pre-disturbance megafaunal density and diversity at

852 seamounts. For data see Appendix A. Aust: Australia. NZ: New Zealand.

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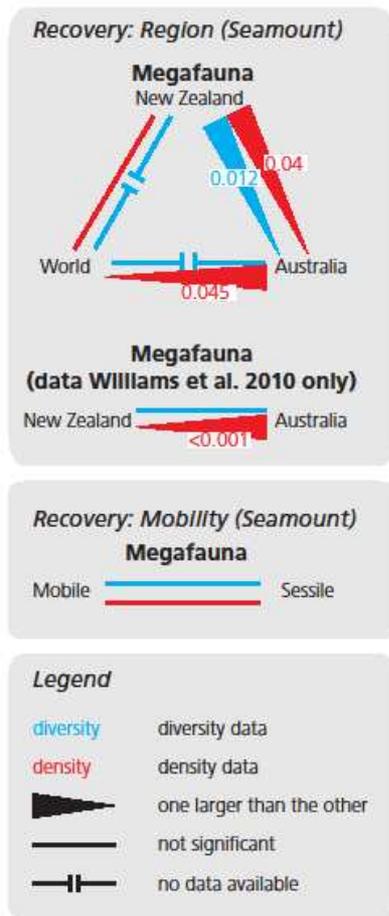
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859 Figure 10. Absolute numbers and standard deviation of density and diversity values
860 measured pre-disturbance (indicated as P) and after disturbance (in years) for megafauna at
861 seamounts. For data and metric see Appendix A.

862



863

864 Figure 11. Results of Wilcoxon rank sum tests for differences in mean recovery (%) relative
 865 to pre-disturbance diversity and density for megafauna at seamounts. P-values are given for
 866 significant differences.

867

868

869 **3.2.3 Nodule fields**

870

871 Since 1970, 11 small-scale disturbance experiments have been conducted to study the
 872 potential effects of nodule mining on the benthos (reviewed by [23]). During these
 873 experiments, disturbance gear was towed over the seafloor, removing or burying nodules.
 874 These experiments were performed in three regions: the Clarion-Clipperton Fracture Zone
 875 (CCZ), Peru Basin, and Central Indian Ocean Basin (CIOB) [23].

876

877 **Peru Basin**

878 During the German "DISturbance and reCOLonization experiment" (DISCOL), a polymetallic
 879 nodule area in the Peru Basin was artificially disturbed in 1989, using a plough harrow to
 880 simulate manganese nodule extraction. The impact by the plough created a ~11 km² patch-

881 mosaic of disturbed tracks and adjacent sites disturbed indirectly by the sediment plume
882 suspended.

883 DISCOL results showed that megafauna densities were still diminished 7 years after
884 disturbance, with minimal recovery [176]. Density recovery was on average only 9% for
885 sessile megafauna, and 49% for the mobile megafauna (see Appendix A). After 26 years,
886 megafauna densities demonstrated high variability in recovery rates among taxa, ranging
887 from only 11% in Anthozoa to 167% in Holothuridea, and major changes in community
888 composition persisting (unpublished data by Purser et al., Appendix A, Figure 12, Figure 13).
889 In contrast, macrofauna density in sediments recovered more quickly, reaching mean
890 recovery of 85% after 7 years [177]. Mean density recovery rates differed among macrofauna
891 taxa, with several taxa reaching ~100% pre-disturbance conditions (polychaetes,
892 tanaidaceans, isopods, scaphopods, echinoids), whilst others showed lower recovery
893 ranging from 15-47% (cumaceans, bivalves, gastropods, ophiuroids) [177, 178] (Appendix A,
894 Figure 12). After 26 years, mean meiofauna densities had recovered to 90% (unpublished
895 data by Mevenkamp, Egho & Vanreusel, Appendix A). However, high variation in densities
896 was observed, particularly in impacted sites. Wilcoxon tests revealed a significant increase in
897 mean percent density recovery from 0.003 years to 0.5 years ($p = 0.05$), 3 years ($p = 0.04$), 7
898 years ($p = 0.04$), and 26 years ($p = 0.05$). No increase was detected not from 0.5 years to 3,
899 7 and 26 years (all $p > 0.05$), from 3 years to 7 and 26 years (all $p > 0.05$), and fro, 7 to 26
900 years ($p > 0.05$).

901 Diversity was studied in less detail during DISCOL, but diversity recovery was on
902 average only 16% for sessile megafauna, and 33% for the mobile megafauna after 7 years
903 [176]. In contrast, mean polychaete diversity had recovered to greater extent of ~80-99%
904 [177, 179] (Appendix A). Diversity recovery after 26 years is currently under investigation.
905 Wilcoxon tests showed no significant increase of mean diversity with years ($p > 0.05$).

906

907 **CCZ**

908 Total mean meiofauna, nematode, copepod and foraminifera densities recovered to pre-
909 disturbance values within two to three years in the CCZ [180-182] (IOM-BIE & JET
910 experiments). Mean macrofauna densities recovered to 93% after one year, with recovery
911 rates ranging from 48% (amphipods) to 108% (polychaetes) [183] (BIE). Mean mobile
912 megafauna densities reached 290% of pre-disturbance values after three years [184] (IOM-
913 BIE) (Appendix A, Figure 12).

914 26 years after the OMCO disturbance experiment, mean total meiofauna densities
915 had recovered to 105% (Appendix A), but taxa responded differently with density recovery
916 ranging from 50% (tantulocarids) to 552% (kinorhynchs) [185] (Appendix A). Nematode
917 abundances were significantly lower 26 years after the disturbance [186] with mean

918 recovery of 73% (Appendix A). The number of meiofauna genera was higher post-
919 disturbance (70 genera) than pre-disturbance (50 genera) [185], but nematode diversity
920 remained significantly lower than pre-disturbance with diversity recovery only 81-94% after
921 26 years [186]. Further, nematode community composition remained significantly different 26
922 years after disturbance [186]. After 37 years, epifauna remained almost absent, indicating
923 that recovery of epifauna is very slow [100].

924 In the CCZ no clear trend of an increase of mean density percent recovery with
925 increasing years past disturbance could be observed. Typically, percent recovery was similar
926 among years past disturbance ($p > 0.05$), with a few exceptions (mean density recovery
927 greater after 0.08 years ($p = 0.03$), 2 years ($p < 0.01$), 3 years ($p < 0.01$) and 26 years ($p =$
928 0.03) compared to after 0.04 years; mean density recovery greater after 3 years than
929 compared to after 0.08 years ($p = 0.03$) and 1 year ($p = 0.01$)).

930

931 ***Indian Ocean***

932 Almost four years after the INDEX disturbance, mean total meio- and macrofauna infauna
933 densities had recovered to ~100%. Recovery differed among taxa, ranging from 27%
934 (harpacticoids) to 290% (gastrotricha) for meiofauna taxa [28, 187, 188] (Appendix A, Figure
935 12). Mean percent density recovery was significantly greater 3.8 years after disturbance than
936 0.08 years after disturbance ($p = 0.05$).

937

938 ***Analyses of recovery in the Peru Basin, CCZ, and Indian Ocean***

939 Analysis of available density and diversity datasets from the Peru Basin (DISCOL), from the
940 CCZ (JET, IOM-BIE, OMCO, BIE), and from the Indian Ocean (INDEX) reveals that absolute
941 recovery and percent density and diversity recovery varied greatly within and among taxa
942 (Figure 12, 13, 14). However, there was a trend across all samples with small and mobile
943 species recovering faster than large and sessile species (Figure 15). Jones et al. [23]
944 observed the same trend. Due to lack of information owing to low taxonomic resolution in
945 some of the original publications, we could not separate our analysis into sediment infauna
946 and nodule epifauna. However, sessile species typically require hard substrate.

947 Mean density recovery was faster for mobile meiofauna than for macrofauna and
948 megafauna. In contrast, there was no difference between mean meio- and macrofauna
949 diversity recovery (Figure 15). However, both meiofauna and macrofauna diversity recovered
950 more quickly than megafauna diversity (Figure 15).

951 Mobile megafauna diversity showed faster recovery than sessile megafauna diversity
952 (Figure 13, 15). The response of megafauna may reflect differences in feeding guilds: mobile
953 species are typically detritus feeders or scavengers (such as ophiuroids, holothurians,
954 polychaetes) whereas sessile species are typically filter-feeding (such as poriferans,

955 anthozoans, cnidarians). Mobile and sessile macrofauna taxa showed similar percent
956 recovery in density (diversity data were not available). Some mobile taxa such as peracarids
957 that are assumed to have limited capacity for dispersal due to brooding reproductive mode,
958 show recovery similar to sessile macrofaunal taxa, suggesting a role for reproductive
959 strategy in recovery potential. Thus low population connectivity in deep-sea species such as
960 polychaetes or isopods [87] implies slow recovery potential after disturbance.

961 To summarize, disturbance experiments designed to mimic polymetallic nodule
962 mining on abyssal plains have provided first insight into recovery processes after small-scale
963 disturbance events on abyssal plains with nodules. Analysis of faunal densities indicates that
964 mobile and smaller organisms tend to have greater recovery potential, sometimes reaching
965 or exceeding pre-disturbance levels following disturbance. However, in some cases
966 meiofauna density had not recovered even 26 years after disturbance [186]. Fewer diversity
967 data were available, and the taxonomic resolution of analyses varied considerably among
968 studies from species to order level. Further, different diversity parameters were used (e.g.
969 number of taxa, Shannon's H, Pielou's J') in different studies. Nonetheless, diversity recovery
970 appears greater for mobile and small organisms, although there were exceptions (e.g.
971 nematode diversity had not recovered after 26 years [186]). In all cases, there was high
972 variance in recovery rates among taxa, preventing prediction of a general pattern of recovery
973 or a sequence of successional stages at nodule fields. Despite this, it is clear that large
974 sessile fauna have very slow recovery after disturbance.

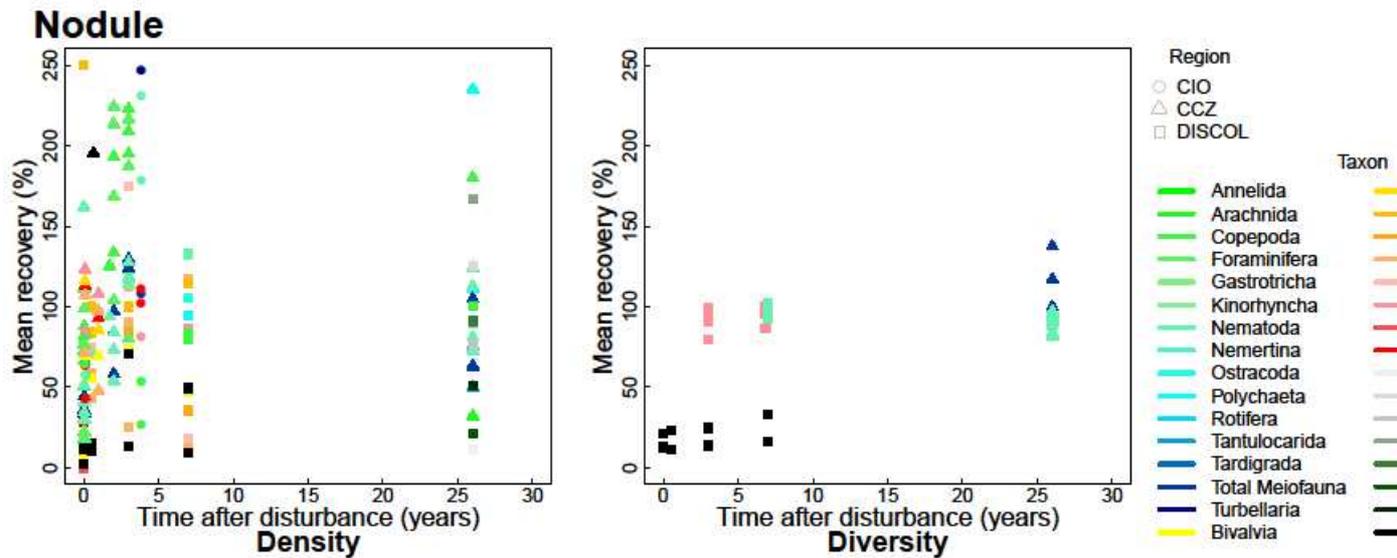
975 Changes in species abundances following small-scale test mining may be linked to
976 multiple factors. Some taxa have exceeded pre-disturbance density values, and may
977 represent opportunistic species [189]. Others showed slow or no recovery. Understanding
978 connectivity may be a key parameter for predicting recovery after large-scale disturbances
979 [87]. Further, substratum availability is essential for the nodule epifauna. Without hard-
980 substratum (nodules), nodule epifauna are unlikely to recover. The response of some fauna
981 may be further linked to biotic controls. Increases in faunal densities after disturbance at
982 DISCOL and in the CCZ may be related to enhanced food (phytodetritus) inputs [176-178,
983 182, 184, 190]. There is a clear need to assess natural community variance over time and
984 spatial scale in order to be able to understand impacts of disturbance.

985 The scale of disturbance experiments was rather small in all cases (several m² to a
986 few km²) in comparison to the disturbance scale anticipated for nodule mining activities (>100
987 km²). Our analyses revealed for example that mean megafauna densities recovered quicker
988 after a smaller-scale disturbance in the CCZ (single track) than after a larger scale
989 disturbance (a few km²) at DISCOL. The underlying reasons for this observation may be
990 diverse (different taxa and regions were observed), but scale of disturbance may have
991 influenced recovery. Mining of large areas could disrupt faunal connectivity and thus prolong

992 or impede recovery. In addition, the effect of (potentially toxic) sediment plumes on e.g. larval
 993 dispersal and recruitment is unknown. Faunal resilience to and recovery from mining-
 994 disturbance is likely to be slower than recovery after small-scale disturbance experiments.

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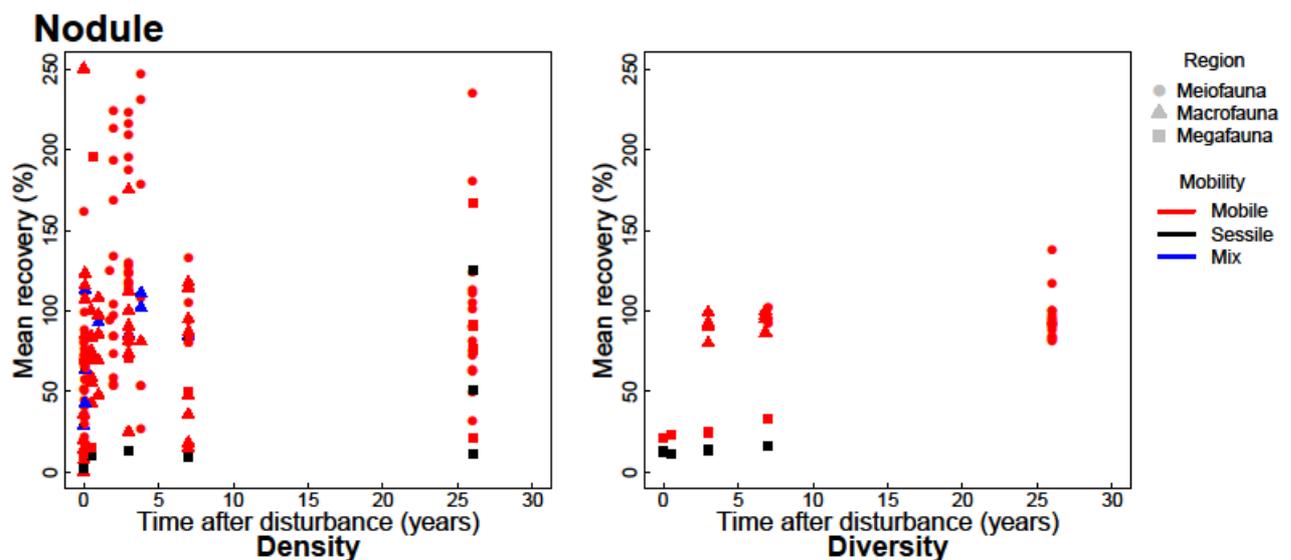
997

998

999 Figure 12. Mean recovery (%) relative to pre-disturbance faunal density and diversity at
 1000 nodule fields. For data see Appendix A. CIO: Central Indian Ocean. CCZ:Clarion Clipperton
 1001 Fracture Zone. DISCOL: "DISturbance and reCOLonization experiment" in Peru Basin.

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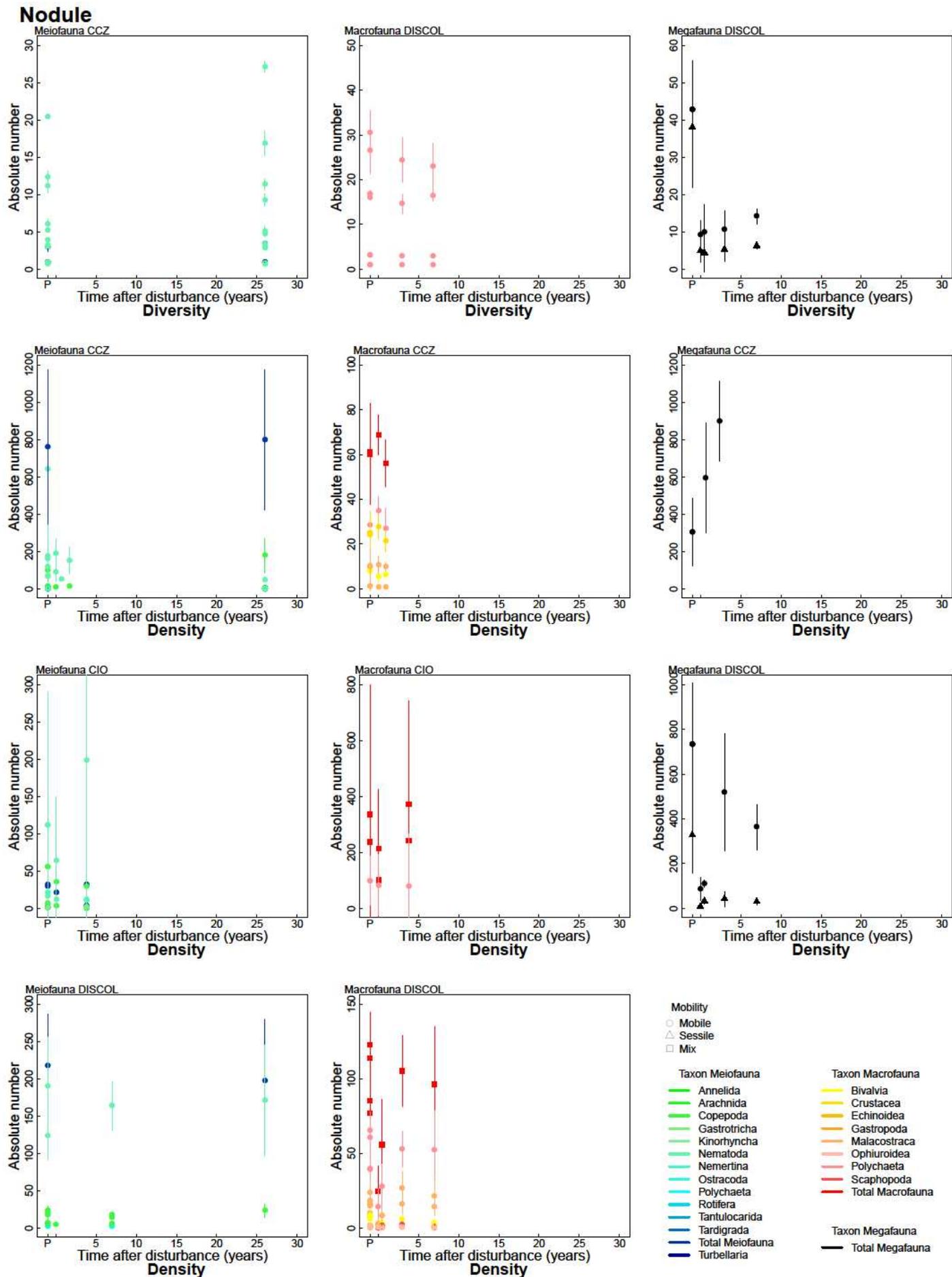


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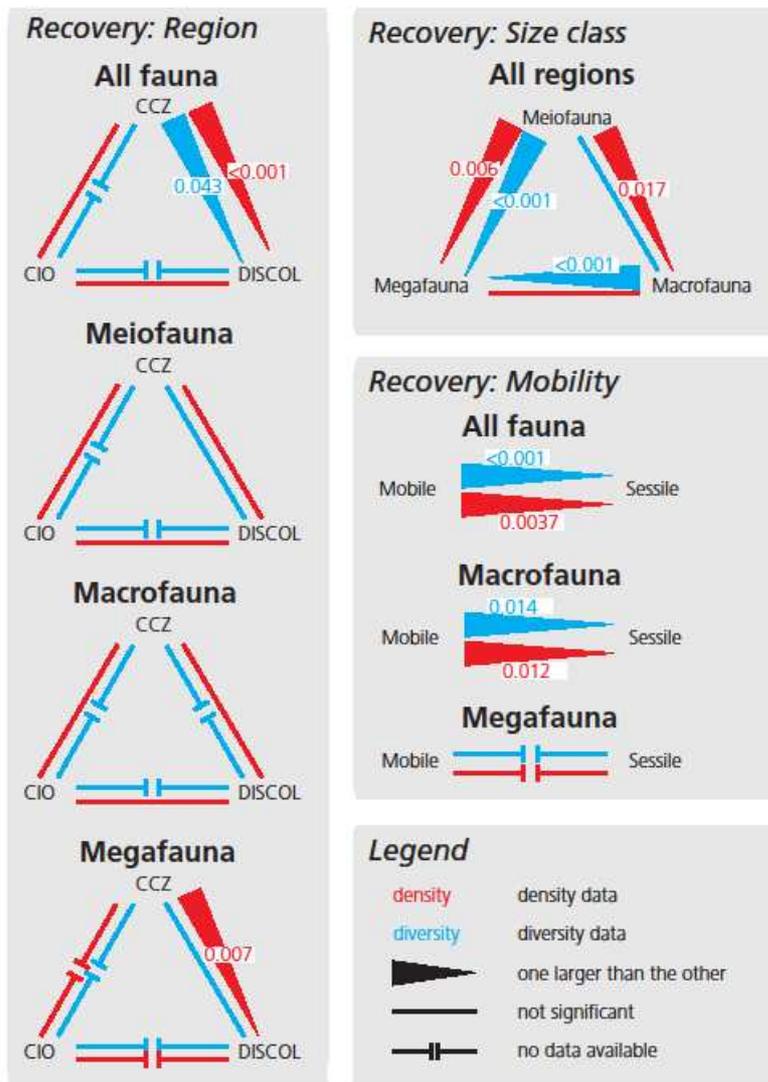
1006 Figure 13. Mean recovery (%) relative to pre-disturbance faunal density and diversity at
1007 nodule fields. For data see Appendix A. Circles: mobile taxa. Triangle: sessile taxa. Square:
1008 mixed taxa (sessile and mobile).
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Figure 14. Absolute numbers and standard deviation of density and diversity values measured pre-disturbance (indicated as P) and after disturbance (in years) for meio-, macro- and megafauna at nodule fields. For data and metric see Appendix A. Circles: mobile taxa. Triangle: sessile taxa. Square: mixed taxa (sessile and mobile). CIO: Central Indian Ocean. CCZ:Clarion Clipperton Fracture Zone. DISCOL: "DISturbance and reCOLonization experiment" in Peru Basin.



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Figure 15. Results of Wilcoxon rank sum tests for differences in mean recovery (%) relative to pre-disturbance diversity and density between meio- and macrofauna at nodule fields according to region, size class and mobility. CIO: Central Indian Ocean. CCZ:Clarion Clipperton Fracture Zone. DISCOL: "DISturbance and reCOLonization experiment" in Peru Basin. P-values are given for significant differences.

1028

1029

1030 3.3 Reversibility after mineral mining impacts

1031 In the context of the United Nations Convention on the Law of the Sea (UNCLOS), the
1032 International Seabed Authority (ISA) must ensure effective protection of the marine
1033 environment on behalf of humankind. In the international legal context this includes that
1034 “serious harm” must be avoided during deep-sea mining. However, the definition of “serious
1035 harm” is challenging in deep ecosystems, where lack of knowledge is the rule rather than the
1036 exception [191]. Mineral mining will modify or remove substrata that organisms inhabit, and
1037 sediment plumes will affect areas beyond mining sites. A key question is whether similar
1038 species or functional groups will recover in modified environments, or if disturbed areas will
1039 shift to altered or depauperate states. Whether processes are reversible and whether the
1040 deep sea system can return to pre-disturbance condition requires investigation [8] [6].

1041 To date, large-scale commercial mineral mining has not taken place. Nonetheless, we
1042 need to understand and predict resilience of communities to these disturbances in order to
1043 be able to define “serious harm” and to propose successful mitigation actions. To estimate
1044 reversibility, it has to be considered that the nature and scale of mining disturbance will be
1045 different to the above described recovery scenarios. Volcanic eruptions pave over areas of
1046 seabed in a single locality. A trawl net may bounce a little along the seabed so that not all
1047 fauna are entirely removed. Experiments that mimic nodule mining typically did not remove
1048 nodules but buried them, and the disturbed area was considerably smaller than expected for
1049 future mining scenarios. The spatial (at most a few km²) and temporal (typically independent
1050 events) scales of disturbances were in significantly more limited than those proposed for any
1051 mining activities, which may range from 100’s to 1000’s km² per nodule mining operation per
1052 year [106], from 10’s to 100’s km² for crust mining [109], and some hectares per polymetallic
1053 sulphide mining operation [103]. The scale of mining operations will result in habitat
1054 fragmentation which may affect reversibility. Large continuous nodule fields will be
1055 fragmented into a system of smaller-sized nodule fields. Naturally patchily distributed active
1056 and inactive hydrothermal vents and seamounts will be further fragmented by large-scale
1057 mining.

1058 Direct mining impacts will include mortality and removal of fauna living on mined
1059 substrata in all targeted ecosystems. Removal of nodules will cause habitat loss for hard
1060 substrata fauna on a geological time scale because nodules reform at rates of mm per million
1061 year. At hydrothermal vents and seamounts mineral rich rocks will be removed, leaving
1062 mineral-poor rocks which prevents thriving of species exclusively relying on mineral rich
1063 crusts. At nodule fields, fauna living in the sediments may be killed by sediment
1064 compression. Sediments below and adjacent to nodules will be compacted by vehicle tracks,

1065 which may result in long-term changes in sediment porewater geochemistry [122]. Potentially
1066 toxic sediment plumes may affect areas beyond the directly mined locality [18-20]. To
1067 estimate the reversibility of mineral mining impacts, geological timescale of habitat/mineral
1068 reformation as well as biological timescale and mode of community recovery need to be
1069 considered.

1070

1071

1072 **3.3.1 Hydrothermal vents and polymetallic sulphides**

1073 **Active vents**

1074 Reversibility of mineral mining impacts at active vents will depend on the frequency and
1075 scale of sulphide mining operations. Assuming that vent fluids do not change dramatically
1076 and that connectivity of species is not disrupted, recovery of active vent communities at fast-
1077 spreading centres may occur within decades. However, large-scale mining may substantially
1078 diminish species populations and could hinder recolonisation by disrupting connectivity of
1079 source populations [11, 49]. The loss of foundation species may hinder the settlement of
1080 associated fauna, and may indicate a tipping point where resilience capacity is exceeded and
1081 the system transitions to a new state. Alternative states at active vents may be dominated by
1082 bacterial mats instead of rich faunal communities.

1083 The loss of topographic features such as black smokers may change settlement
1084 behavior, and thus diversity of fauna [192]. Typically, active black smokers can reform within
1085 several months or years at fast-spreading centres [110], but consequences of large scale
1086 mining on local fluid composition are not known. Sulphide mining at hydrothermal vents may
1087 cause local modification of vent fluid regimes (i.e. flow rates, distribution, chemistry) by
1088 clogging vent fluid channels [11], with severe consequences for active vent communities
1089 which depend on fluid regimes. Low-diversity communities are typically associated with high
1090 temperature venting (i.e. around black smokers), whereas higher diversity is linked to low-
1091 temperature venting [27, 32]. Further, symbiotic foundation species such as tubeworms,
1092 snails, or mussels only thrive in specific vent regimes [32]. Therefore, modification of vent-
1093 fluid regimes could cause local habitat loss or change community composition at active
1094 hydrothermal vents, as well as at sites that are not directly affected by mining [193].

1095 Set-aside areas are suggested as part of environmental management strategies to
1096 mitigate mining effects. Such areas should preserve biodiversity that may be lost at a mine
1097 site and should support connectivity among populations of vent organisms within the region.
1098 Set-aside areas must be suitably connected by the transport of larvae to ensure exchange of
1099 genetic material among remaining populations [49]. Ideally, set-aside areas provide source
1100 populations for the recovery of the mined site [49].

1101

1102 ***Inactive vents and vent periphery***

1103 The scarce knowledge on species diversity, role of functional groups, species distribution,
1104 connectivity, and settlement behaviour makes it impossible to estimate reversibility potential
1105 at inactive vents and in vent peripheral areas following mining disturbances. Primary
1106 considerations include permanent modification of topography, and change of mineral
1107 composition. Removal of polymetallic sulphide substratum at inactive vents cannot be
1108 reversed due to lack active hydrothermal fluids [16]. Habitat homogeneity (smoothing), or
1109 habitat heterogeneity (roughening) may increase during collection of mineral resources [16,
1110 194]. Substratum will be altered from mineral-rich to mineral-poor rock at inactive vent sites.
1111 Yet it is not known to what extent, if at all, species will be able to settle and grow in such
1112 modified environments. That inactive vents and vent periphery areas harbour unique
1113 communities but also share several species with active vent areas [53, 54, 59] highlights the
1114 importance of including hydrothermally active and inactive areas within networks of protected
1115 areas [53].

1116

1117 **3.3.2 Seamounts**

1118 Habitat structure on seamounts will be changed by removal of upper centimeters of crust,
1119 and functional groups such as 100- or 1000-year old corals and their associated fauna will be
1120 removed, potentially resulting in slow (century-scale) recovery [77]. Loss of crusts may
1121 hinder colonization of substratum specific seamount species or prohibit recovery [50, 192,
1122 195]. Changes in topographic features may affect settlement behaviour [192] and thus
1123 diversity of fauna in the long term. Cumulative effects may be especially severe around
1124 seamounts. Many seamounts are subject to fisheries impacts, and shifting ocean
1125 temperatures, oxygenation, and acidification may adversely affect distant source populations
1126 and thus may hinder recovery [12].

1127 In addition, seamount faunas vary even at local (km) spatial scales [72, 73, 78].
1128 Variation in community composition and diversity has been related to depth and seabed
1129 structure (e.g. relief, substrate type, presence of bio-constructors), as well as current regimes
1130 and distance to source populations, amongst others factors [50, 67, 73]. Connectivity among
1131 seamount populations reveals contrasting patterns among species. Some seamount species
1132 are distributed across large geographic distances (e.g. some corals [67, 196, 197]; fish [198];
1133 harpacticoid copepods [199]), whereas other coral and fish species have much more
1134 restricted distributions [200-202]. Several studies highlight high uniqueness in seamount
1135 fauna [203], but these may simply reflect low sampling effort [67]. There is evidence that
1136 connectivity is directly linked to life history patterns [204]; many seamount fauna appear to
1137 have non-planktotrophic larvae implying restricted dispersal potential [67, 173, 205].
1138 However, there is contrasting evidence that wide geographic distributions exist in putatively

1139 poor dispersers [199, 206]. McClain et al. [207] revealed that more than 70% of species in
1140 the megafaunal assemblages on a North Pacific seamount were cosmopolitan. The
1141 inconsistency of these results may reflect the complex interplay of several ecological and
1142 evolutionary processes shaping seamount systems, or may be linked to the paucity of
1143 genetic studies on seamount species [206].

1144 Biogeography and connectivity of fauna, as well as abiotic characteristics that
1145 influence seamount fauna composition need to be understood and considered in any mining
1146 mitigation concept. Recovery will be slow at seamounts and modifications made by mining
1147 may be too great to allow for return to pre-disturbance community composition and
1148 abundance. Spatial management employing a systematic method to identify Ecologically or
1149 Biologically Significant Areas (EBSA criteria) for protection may help to mitigate mining
1150 effects [208].

1151

1152

1153 **3.3.3 Nodule fields**

1154 Removal of nodules will be associated with local loss of nodule-specific fauna. Fauna relying
1155 on nodules as a hard substratum may remain absent until the substratum recovers, i.e. for
1156 millions of years. Species ranges and source/sink dynamics of the nodule-inhabiting fauna
1157 are unknown and it is unclear whether populations can survive in unaffected refugia. Any
1158 refugia should harbour similar nodule density as mined sites, since epifaunal densities and
1159 nodule coverage are linked. Nodule dense areas harbour more than two times higher
1160 epifaunal densities, and corals are essentially absent in nodule-free areas [100]. It is
1161 currently unknown whether species are endemic to nodules or whether adjacent seamount
1162 crusts host partly the same species as nodules. Future studies should explore whether
1163 adjacent seamounts host potential source populations capable of recolonising impacted
1164 habitats [209] or capable of maintaining connectivity among undisturbed areas. The potential
1165 responses of communities to mitigation and restoration actions, such as deployment of
1166 artificial nodules, are currently unknown.

1167 Sediment-dwelling fauna in mined nodule areas may also experience density
1168 decreases below a critical threshold. Sediments will be compacted by vehicle tracks, which
1169 may result in changes in sediment porewater geochemistry. The organic-rich upper sediment
1170 layer, which is a food source for most sediment feeders, will be removed by the collector
1171 and/or re-suspended. The sediment that redeposits from the plume in the immediate vicinity
1172 of the collector may have an average composition of the topmost 10-25 cm of the sediment
1173 and thus will have an altered chemical composition relative to the pre-disturbance sediment
1174 [122]. Some long-term disturbance experiments reported that sediment-dwelling fauna had
1175 not recovered after almost 30 years, potentially because organisms were unable to penetrate

1176 compacted sediments [186]. However, other studies demonstrated density recovery potential
1177 for some sediment fauna. Nonetheless, nodules grow in areas with low sedimentation rates
1178 (<20 mm per thousand years) [122] and it will therefore take at least several decades to
1179 millennia for sediment layers to recover. Despite this, it remains difficult to estimate whether
1180 sediment compaction and/or extraction of upper sediment layers will affect density and or
1181 diversity of sediment infauna over an extended timescale (decades to centuries), or whether
1182 recovery to the pre-disturbance state is possible.

1183

1184 **3.3.4 Areas adjacent to mining sites**

1185 Enhanced sedimentation caused by mining-generated sediment plumes in areas surrounding
1186 mining sites may harm suspension and deposit feeders, causing depletion of functional
1187 groups and shifts in community composition [210]. On abyssal plains, sedimentation will
1188 modify grain size composition, which can change community composition [211]. Potentially
1189 toxic plumes will impose additional stress on organisms and may eventually become lethal
1190 [136]. Decreasing effective population size, loss of subpopulations, and/or loss of populations
1191 in mined areas may hinder population exchange and diminish genetic diversity in areas
1192 surrounding mining sites [49]. Fauna may be able to resist these stressors partly or may be
1193 able to recover from stressors. However, it is not yet possible to estimate the effect of these
1194 cumulative effects, or predict whether they will result in irreversibility of changes, causing
1195 altered ecosystem states in areas surrounding mining.

1196

1197 **4. Conclusion**

1198 Resilience – the ability of a system to maintain structure and function, in the face of
1199 internal change and external disturbances – is a complex interplay of different processes,
1200 including the resistance of species and communities to alterations, their recovery potential
1201 following disturbance events, and the potential reversibility of ecosystem changes.

1202 The capacity for populations of deep-sea species to stay essentially unchanged
1203 despite stress and disturbances (resistance *sensu* [111]) associated with deep-sea mining
1204 remains uncertain. Our review on resistance revealed that species may be to some level
1205 resistant to (potentially toxic) mining plumes or electromagnetic radiation, but current
1206 knowledge is insufficient to predict the extent of resistance.

1207 We performed meta-analyses on post-disturbance population density and diversity
1208 mean percent recovery, after disturbances most similar to mining: volcanic eruptions at
1209 vents, fisheries on seamounts, and experiments designed to mimic nodule mining on abyssal
1210 plains. Communities can recover to some extent after mining-related disturbance events
1211 since mean percent recovery density and diversity values are above zero (Figure 16). Mean
1212 recovery was highly variable in distinct ecosystems and among benthic taxa and variability

1213 among samples was often very high. In addition, as stated by Jones et al. [23], many past
1214 recovery studies have limitations that reduce their effectiveness in determining responses.
1215 Our results can show some potential large scale trends, but current knowledge is far from
1216 showing the complete picture.

1217 At active vents, an increase in diversity percent recovery was observed with
1218 increasing time past disturbance. Communities at active hydrothermal vents at frequently
1219 naturally-disturbed fast-spreading ridges can recover after such punctual natural disturbance
1220 events and follow a sequence of succession, related to abiotic (e.g. hydrothermal fluid
1221 regime) and biotic (e.g. larval dispersal, predation, competition) factors. We lack data on
1222 recovery potential from communities along slow-spreading ridges with long volcanic eruption
1223 intervals, but suggest that fauna at those communities may recover (much) more slowly.

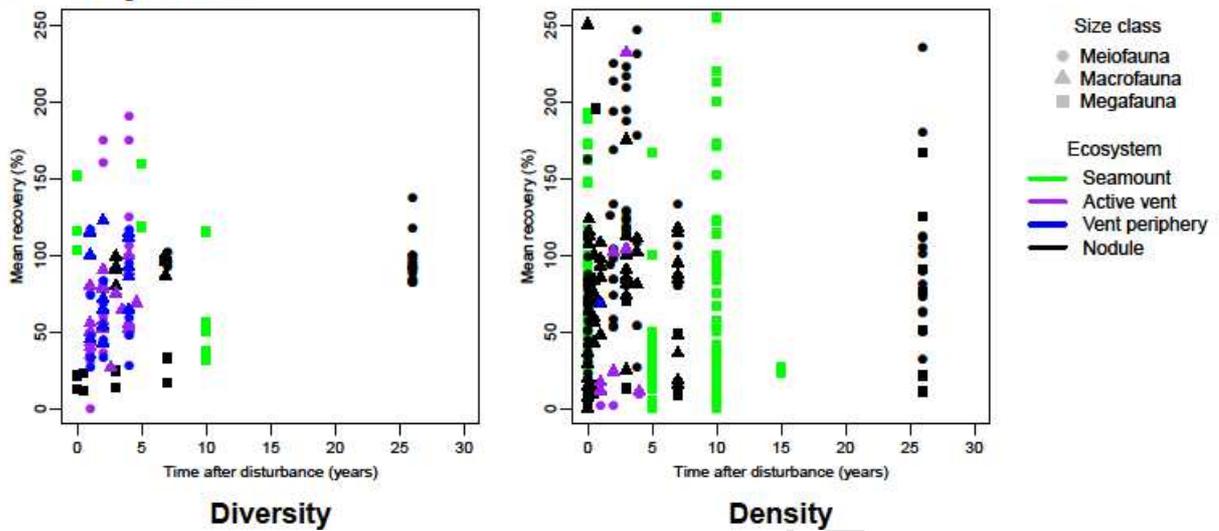
1224 Knowledge on recovery from communities at inactive vents is lacking. In the vent
1225 periphery no significant increase of diversity with increasing time past disturbance was
1226 detected. In general, recovery is expected to be slower compared to active vents since
1227 climax species typically have longer life times (decades to centuries) and a higher proportion
1228 of rare species is present at inactive vents and in the vent periphery.

1229 Recovery of keystone species from seamounts is typically slow. Some species, that
1230 may have survived seamount fisheries trawling or that present the early stages of succession
1231 after disturbance were highly abundant after 5 to 10 years but other pre-disturbance
1232 keystone species such as century old stony corals showed very little sign of recovery. Meta-
1233 analyses revealed no significant increase of mean percent density or diversity recovery with
1234 increasing time past disturbance, pointing to overall slow recovery processes.

1235 Similarly, sessile megafauna associated with nodules showed very slow recovery
1236 after disturbance, whilst small and mobile taxa recovered or exceeded pre-disturbance
1237 densities after a few years. Meta-analyses of mean percent recovery revealed that small
1238 animals typically recover faster than large animals, and that mobile animals typically recover
1239 faster than sessile species. These results are in accordance with Jones et al. [23]. Larger
1240 spatial scale impacts at DISCOL may have prolonged faunal recovery in comparison to
1241 smaller spatial scale impacts in the CCZ.

1242 There are no data available on reversibility after mining impacts, because large-scale
1243 mining has not yet been carried out. Nodule-mining is expected to have large-scale and long-
1244 term impacts, particularly on the resident nodule-encrusting and crevice fauna, and abyssal
1245 plains may shift to altered or depauperate states through removal of and change in substrata.
1246 Similarly, local modification of fluid sources at active vents may result in loss or change of
1247 chemosynthetic communities in exploited areas. Local extinction of keystone species, or loss
1248 of mineral-specific faunas, may cause long-term or even permanent shifts in community
1249 composition at vents and seamounts.

1250

All ecosystems1251
1252

1253 Figure 16. Mean recovery (%) relative to pre-disturbance faunal density and diversity at
 1254 seamounts, active vents, vent periphery, and nodule fields. No recovery data were available
 1255 for inactive vents. For data see Appendix A.

1256

1257 There are significant knowledge gaps with implications for understanding faunal
 1258 recovery and resilience patterns following mining impacts (Table 1). Lack of knowledge
 1259 concerns scales of mining operations, faunal recovery processes after large-scale
 1260 disturbances, spatial and temporal influences on faunal community composition. Cumulative
 1261 impacts may lead to unexpected ecosystem changes and need to be investigated [11].
 1262 Cumulative impacts refer to the interaction of several mining operations within a given area,
 1263 but also to additional non-mining related natural and human impacts such as volcanic
 1264 eruptions (vents), fishing (seamounts), and changes in physical and geochemical ocean
 1265 parameters (e.g. temperature, pH, O₂). In addition, potential community responses to
 1266 mitigation and restoration actions are currently unknown. Substantial community shifts,
 1267 including the loss of species, may persist over geological timescales at directly mined sites
 1268 due to habitat loss (mineral removal). Therefore, spatial environmental management to
 1269 detect and establish set-asides, protected areas of similar seafloor habitat as to be mined
 1270 areas, may be especially important to mitigate species loss and maintain regional biodiversity
 1271 [212]. Future research needs to substantially increase baseline knowledge: effective
 1272 environmental management of deep-sea mining is dependent on data identifying the extent
 1273 of resistance to and capacity to recover from extractive activities in deep-sea benthic
 1274 communities.

1275

1276

1277

1278 Table 1. Short summary of main knowledge gaps and problem that currently hinder a precise
1279 prediction of resilience of benthic deep-sea fauna to mining activities, and potential solutions
1280 to diminish knowledge gaps.

1281

1282

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1303 **7. References**

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Knowledge gap	Problem	Potential Solution
Mining operations	Unknown spatial and temporal scale and nature of mining operations	Provide expected scales and conditions of mining operations
Sediment plumes	Unknown scale of sediment plume (particle size, toxicity, dispersion, temperature)	Provide expected scales and conditions of sediment plumes
Recovery processes	Observed recovery patterns are from small-scale disturbance studies and different areas	Perform test-mining to investigate effects
Lack of methodological standardization	Lack hinders intercalibration of data sets even within same regions	Develop detailed standardized sampling protocols (sample number, size, area, timeframe)
Lack of samples from parts of license areas	Impedes estimation of how representative existing data are	Standardized sampling in license areas
Lack of samples from potential protected areas	Impedes whether recolonization can take place from designated preservation areas	Standardized sampling in potential protected areas
Faunal variability across spatial and temporal scales	Difficulty to define pre-disturbance conditions and monitor change	Standardized sampling before and after (test) mining, obtain long-term datasets
Undescribed species/lack of genetic data	Hinders comparison between data sets and evaluation of species range sizes	Describe species including genetic codes (material deposits)
Biogeography and endemism of fauna	Areas that may host source populations are often unknown	Study biogeography and endemism (also outside areas of mining interest)
Limited taxon sampling	Biased data on biogeography, connectivity and recovery potential	Study species of different sizes and life traits
Reproductive biology and settlement cues	Larvae and adults likely respond different to stress and disturbance	Study biology of species
Resistance of deep-sea species to toxicity	Resistance of deep-sea species to toxic plumes may not be estimated based on shallow-water species	Study effects of toxicity on deep-sea species and shallow-water species to determine suitability of shallow-water taxa as ecotoxicological proxies for deep-sea taxa
Cumulative effects	Cumulative effects may reduce resilience and may act synergistically	Consider cumulative effects