25 June 2017

Biogeosciences
Attn..: Matthias Haeckel, Special Issue Associated Editor

Dear Matthias Haeckel,

Please consider our manuscript now entitled "Abyssal plain faunal carbon flow remain depressed 26 years after a simulated deep-sea mining disturbance" for publication in the special issue "Assessing environmental impacts of deep-sea mining – revisiting decade-old benthic disturbances in Pacific nodule areas" of Biogeosciences.

We would like to thank you for handling our manuscript and are grateful for the positive and detailed feedback provided by Peter Jumars (Reviewer #1) and Reviewer #2 for our manuscript "Faunal carbon flows in the abyssal plain food web of the Peru Basin have not recovered during 26 years from an experimental sediment disturbance". The main issues identified by the reviewers considered reporting of precision, estimation of byrozoan biomasses, and naming of sampling sites. We addressed them by reporting all data with 3 significant figures in the text and only 1 decimal in tables. Bryozoan biomass estimates were removed from the table because they were mistakenly reported. In fact, bryozoans were only observed at references sites which were not modelled and not inside or outside plough tracks. We also changed the names to 'outside plough tracks' (previously 'undisturbed site') and 'inside plough tracks' (previously 'disturbed site'). We addressed your editorial comments by correcting the width of the plow harrow to 8 m, provided the PANGAEA DOI for the OFOS images and added the project short name in the acknowledgements. We added the biomass conversion factors mentioned in Tilot's PhD thesis in supplement 2 where we present all conversion factors used in the manuscript and provide the URL access to the digital copy of Tilot's PhD thesis in the references.

We addressed each of the comments of Peter Jumars and Reviewer #2 in detail below.

With these modifications, we hope that the manuscript is now suited for publication in Biogeosciences.

Looking forward to your decision and thank you again for handling our manuscript.


Kind regards,
Tanja Stratmann

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**Detailed responses**

**Reviewer #1**

**Reviewer 1 comment 1:** …the reporting of precision in Tables 1 and 2. Up to six significant figures are given (for Ceriantharia in Table 1), and several of the standard deviations include biomasses below zero. In general, precision for means and deviations should be comparable and should exclude the impossible. The authors seem to have defaulted to an arbitrary two places after an arbitrarily placed decimal point.
**Our response:** We adjusted the Result section 3.1, Table 1 and 2 and report all biomass data with a precision of 3 significant figures in the text and only one decimal place in Table 1. The individual biomasses of organisms in Table 1 are reported as mean ± standard error and percentages are presented as integers in the text and with one decimal place in Table 2. We also corrected the remainder of the manuscript in this respect.

**Reviewer 1 comment 2:** In a more minor but related issue, in Fig. 1 the color scheme makes the error bars very hard to discern.
**Our response:** Also Reviewer #2 (see below) indicated that the error bars are difficult to see. Hence, we decided to remove the error bars from the plot for better visibility and refer to Supplement 1 for the standard deviations.

**Reviewer 1 comment 3:** The approach used to estimate individual biomass of Bryozoa and Hemichordata seems shaky enough that I would recommend doing the calculations with and without those estimates to convince myself that the results are not overly sensitive to their inclusion. Most Bryozoans are colonial, making me wonder what this individual biomass means.
**Our response:** We mistakenly included bryozoans in Table 1 in our initial submission. In the study area bryozoans were only found in the reference sites and, as mentioned in the manuscript (Page 3 line 29), these sites were not modelled. Therefore, we removed bryozoans from Table 1 and from the rest of the manuscript.

All spelling and grammar mistakes that Peter Jumars corrected in the supplement were accepted in the revised manuscript.

**Reviewer #2**

General comments:

**General comment 1:** I feel the naming of sites within the DISCOL experimental area that were not directly ploughed as 'undisturbed' misleading. Although not ploughed, such sites will still likely have experienced disturbance in the form of settlement of re-suspended sediments; a projected impact of deep-sea mining noted by the authors on page 2, line 26 of the manuscript. This is an issue which should be discussed in the manuscript but is not presently recognised.

**Our response:** We agree with referee #2 that the naming we adopted from previous DISCOL publications is misleading and therefore changed it in the revised manuscript to 'inside plough tracks' which corresponds to the former 'disturbed sites' and 'outside plough tracks' corresponding to the previous 'undisturbed sites'.

**General comment 2:** The authors describe the DISCOL experiment as a 'simulated small-scale deep-sea mining experimental disturbance' (Page 2 lines 7-8). However, no nodules were removed during the DISCOL experiment, and in this way, amongst others, DISCOL was not a perfect simulation of disturbance caused by deep-sea mining. How the results of this study may differ if nodules are removed from the sediment deserves discussion.

**Our response:** For epifauna that are dependent on nodules as hard substrate there is no difference between removing the nodule or ploughing it into the sediment surface as in both cases the nodule disappears from the sediment surface. We therefore added the following two sentences: This hypothesis could not be tested directly, because nodules were not removed in this experiment, but only ploughed into the sediment. However, the disappearance of nodules from the sediment surface will have the same effect on sessile epifauna that depend on nodules as hard substrate independently of the method by which the nodules disappeared." Additionally, we describe more specifically which type of disturbance were created during the DISCOL experiment in the Introduction: "A 10.8 km$^2$ circular area (Figure 1) was ploughed diametrically 78 times with an 8 m wide plough-harrow; a treatment which did not remove nodules, but disturbed the surface sediment, buried nodules into the sediment and created a sediment plume (Thiel et al., 1989)."

**General comment 3:** A glaring omission to the LIM analysed in this manuscript is the lack of microbial and meiofaunal data. It is explained in the manuscript that this is because of insufficient data (page 3, lines 10-11). This is understandable, but the impact this lack of microbial and meiofaunal data may have had on the analyses conducted deserves discussion in the 'Model limitations' section of the manuscript.

**Our response:** We agree that the addition of microbial data would increase T.., the sum of carbon flows, but we do not know whether the overall trend (outside plough track vs. inside plough track) would change. Since we cannot adequately discuss this, but only speculate, we decided against a longer discussion in the model section. Furthermore, it is explicitly stated in the title that we modelled only faunal carbon flows.

**General comment 4:** Another limitation of this study is the lack of baseline sampling – a 'Pre-Disturbance' time point. Such a time point would give a better indication of the 'undisturbed' ecosystem state against which all post-disturbance time points could be compared (especially PD0.1). Clearly it is not possible to obtain this data now, but this lack of baseline data requires discussion. At present it is only noted in the legend of figure 6.

**Our response:** We briefly mention this in the introduction ("Therefore, the food-web models presented in this work cover post disturbance 1989 (no adequate pre-disturbance sampling

took place) to 2015 and contain only macrofauna, invertebrate megafauna and fish.") and discuss it in more detail in the 'Model limitation' section: "Pre-disturbance samples and samples from reference sites were not collected for all food-web compartments. We therefore lack a baseline to which the 'outside plough track' food web at $PD_{0.1}$ could be compared to assess the impact that the disturbance effect had on sites outside the plough tracks."

**General comment 5:** Throughout the manuscript, the high values of community metrics obtained for the PD3 time point are noted frequently – highest biomass, highest faunal C ingestion, highest respiration, highest macrofaunal contribution, lowest faeces contribution to total C outflow etc. However, no attempt is made to explain this observation. Similarly, on multiple occasions, 'natural variability' is noted amongst observations. I find it surprising that no attempt has been made to identify the variable(s) that may be driving this variability, even qualitatively. If quantitative analyses to this effect are not possible, the manuscript would still benefit from greater discussion of this natural variability.

**Our response:** The aim of our study was to test Jumars' predictions on ecosystem recovery after deep-sea mining with real data. We therefore do not consider our 'Feeding-type specific differences in recovery' section of the discussion an adequate place to discuss natural variability. However, we address this issue in the 'Model limitations' section now (page 10, lines 11-13): "We cannot identify either whether the high biomasses and as a result higher carbon flows at PD3 were correlated with the begin of the positive (La Niña) phase of the El Niño Southern Oscillation (Trenberth, 1997) which led to an abnormally high POC flux at Station M at the time of $PD_3$ (Ruhl et al., 2008)."

**General comment 6:** Whilst the use of Jumars' (1981) paper to structure the discussion of this manuscript is an excellent idea, I feel that the quality of this discussion could be improved. For example, on page 11, line 28 it is stated that "...Jumars' (1981) predictions for subsurface deposit feeders could not be tested...". In the 'Specific Comments' section, I have given some suggestions of simple analyses which could be used to test Jumars' predictions more effectively.

**Our response:** We appreciate these suggestions and address them below.

**General comment 7:** Finally, whilst the quality of language used in this manuscript is satisfactory, many sentences, particularly in the discussion section could be re-written to improve the flow of the manuscript (e.g. the first sentence of section 4.1).

**Our response:** We improved the manuscript using the detailed textual corrections from Peter Jumars and the later remarks by Reviewer #2. We also modified the first sentence of section 4.1.

Specific comments for the abstract:
**Specific comment 1:** The title is rather long and could be improved to increase the impact of the manuscript. I suggest something like 'Abyssal plain faunal carbon flows remain depressed 26 years after a simulated deep-sea mining disturbance'.

**Our response:** We accept the suggestion of the new title.

**Specific comment 2:** It is not immediately clear upon a first read-through of the abstract that LIM were produced for all points in the time-series, rather than just at PD26 (as the title may suggest). Please make this clearer.

**Our response:** We rephrased the sentence as follows: "We used this unique abyssal faunal time series to develop carbon-based food web models for each point in the time series using the linear inverse model (LIM) approach for sediments subjected to two disturbance levels: 1)

outside the plough tracks, not directly disturbed by plough, but probably suffered from additional sedimentation and 2) inside the plough tracks."

**Specific comment 3:** Percentages – is it possible to give some sense of variability around these values?
**Our response:** It would only be possible to present standard deviations or standard errors for flow values, but not for the biomass at $PD_{26}$, since no replicates are available for megafauna estimates. For consistency, we therefore decided not to report any variability around the percentages in the abstract. However, standard deviations or standard errors are reported in the main text and figures/ tables.

**Specific comment 4:** At nearly 400 words, the abstract would be improved by more a concise wording.
**Our response:** We shortened the abstract following the advice of both reviewers.

Specific comments for the introduction:
**Specific comment 5:** The description of the DISCOL experiment (page 3, paragraph 1) could be clearer. Perhaps a figure illustrating the areas ploughed/not ploughed would help. Also, I feel it would be better for only a short introduction to the DISCOL experiment to be included in the Introduction section, with a more detailed description being reserved for the 'Methods' section.
**Our response:** We added a figure showing the plough tracks inside the DISCOL experimental area, but we like to keep the focus of the 'Methods' section on the food-web models instead of describing the DISCOL experiment in more detail. Moreover, the DISCOL is described in detail in the referenced papers Thiel and Schriever (1989) and Bluhm (2001).

**Specific comment 6 (Page 3, paragraph 2):** It is good to introduce the basics of LIM in the Introduction section. However, the current text is perhaps a little too technical for this section. I suggest moving the more technical aspects of this paragraph to a new paragraph in the Methods section.
**Our response:** We moved the more technical parts of the paragraph to a new subsection in the method part and combined it the former Method section 2.4.

**Specific comment 7:** I would like to see the aims of this study, and perhaps some hypotheses (e.g. based on Jumars (1981)), stated more explicitly at the end of this section.
**Our response:** We rephrased this section and explicitly state three aims of our study.

Specific comments for the methods section:
**Specific comment 8:** It would be useful for the reader to know how many box cores were collected from 'disturbed' and 'undisturbed' sites at every time point, not just the PD26. This could be easily detailed in a table, which could also detail surface area of seabed surveyed for megafauna. Alternatively, the locations of all box cores collected over the 26-year study period could be plotted (colour-coded for date of collection) on the figure I proposed above illustrating the DISCOL experimental mining disturbance regime.
**Our response:** The requested data were already available in our original submission in Supplement 2, but we now also include them in Table 1. We decided, however, against plotting sampling stations on the map because several stations are taken so closely together that symbols would overlap considering the scale of the map.

**Specific comment 9 (Page 4, line 8):** Only three box cores were collected from disturbed sites for PD26. This is a very low level of replication, and something which should be discussed in the 'Model Limitations' section.

**Our response:** We understand this comment, but logistical reasons underlie this low replication. The box corer was not equipped with video guidance and could therefore not be positioned exactly on the 8-m plough tracks. As a result, only three of the boxcores hit the targeted tracks and could be allocated to the category "inside plough tracks". The remaining boxcores in the DISCOL experimental were conservatively assigned to "outside plough tracks". Owing to the ship time available for this type of sampling it was not possible to pursue with further attempts to hit the plough tracks.

**Specific comment 10 (Page 4, paragraph 1):** It seems strange that such an effort was made to analyse the same number of images for 'disturbed' and 'undisturbed' sites for megafauna, but there was no corresponding effort to analyse the same number of box cores for 'disturbed' and 'undisturbed' sites. Was an effort made to standardise megafaunal sampling effort for the other post-disturbance time points to that of PD26?

**Our response:** The low number of box core replicates was addressed above. We did not attempt to standardize megafaunal sampling to other post-disturbance time points because camera systems also differed between the cruises $PD_{0.1}$, $PD_{0.5}$, $PD_3$ and $PD_7$. Additionally, selective sampling which was used during the cruises prior to the $PD_{26}$-cruise make standardization almost impossible and we therefore included also comparisons of samples from the same sampling event, i.e., samples from outside the tracks vs. samples from inside the tracks (e.g. Fig. 6).

**Specific comment 11 (Page 4/5):** Conversion of biomass into carbon content; I would like to know exactly what the conversions used were, if possible. These could be included in a supplementary materials file.

**Our response:** As mentioned in the Methods section 2.2, individual macrofauna organic C values were obtained by direct measurements on an elemental analyzer, so no conversion factors were applied. Conversion factors for megafauna are presented in Supplement 1.

**Specific comment 12 (Page 5, line 20):** No details are given of the conversion used for cnidarian/ poriferan biomass to carbon content. The authors should elaborate on the use of the Tilot (1992) paper.

**Our response:** We report the conversion factors from Tilot's PhD thesis together with the other conversion factors in Supplement 2. Additionally is a digital version of the PhD thesis freely accessible online: http://archimer.ifremer.fr/doc/00000/3754/

**Specific comment 13:** The section detailing biomass to carbon content conversion would be made clearer by greater consistency in the use of the term 'biomass' to mean either the total weight of individuals, or the total carbon weight of individuals.

**Our response:** To improve the understanding of this specific section and other parts of the manuscript, we now refer to a compartment biomass as 'carbon stock' and use the term 'biomass' only for the organic carbon content of individual organisms.

**Specific comment 14 (Page 6, lines 4-9):** What literature was used to determine the coarse feedings guilds assigned to other taxa?

**Our response:** A list with references is provided in Table 2.

**Specific comment 15 (Page 6, lines 7):** It is stated that "...a further detailed classification of the macrofaunal polychaetes..." was made. However, this further detailed classification seems only to additionally subdivide deposit feeding polychaetes into surface/subsurface categories. Could this division not be made with a little effort for all invertebrate macrofauna and mega-fauna?

**Our response:** The subdivision of macrofaunal polychaetes was based on polychaete families for which detailed descriptions are available in Jumars et al. 2015. All other fauna were 'only' identified to higher taxon-level and a more specific classification in feeding types is therefore not possible/ reliable.

**Specific comment 16 (Page 7 line 23 to page 8 line 9):** Why was 'Hedge's d' used here rather than t-tests or their non-parametric equivalent? This should be clarified.

**Our response:** We used the effect size 'Hedges' d', because this is commonly used in meta studies/ analysis to compensate for the fact that we have different sample sizes for different size classes, disturbance levels and sampling events (see e.g. Koricheva, Gurevitch and Mengersen. 2013. Handbook of Meta-analysis in Ecology and Evolution. Princeton University Press).

Specific comments for the results:

**Specific comment 17 (Page 8, lines 21-23):** This comparison of the change in % biomass difference between disturbance treatments from PD0.1 to PD3 is verging on discussion. I suggest moving it to the Discussion section.

**Our response:** We report here solely data on the contributions of specific feeding types to total biomass and we therefore believe that this fits better in the Results than the Discussion.

**Specific comment 18 (Page 8, lines 24-26):** Why is 'absolute weighted Hedge's d $|d+|$' reported here when on page 8, lines 6-9, Hedge's d is explained in a different form? This is confusing for the reader as page 8 lines 6-9 suggests that values greater than ~0.8 represent strong effect sizes, but the results given on page 8 lines 24-26 report small values associated with the metric and the authors describe these as 'indicating a strong experimental effect'.

**Our response:**

Hedges' d is used to compare differences between carbon stocks of the same food-web compartment, e.g., megafauna deposit feeders outside vs. inside plough tracks from $PD_{0.1}$. In contrast, absolute weighted Hedges' d $|d+|$ compares the sum of all carbon stocks from outside vs. inside plough tracks from e.g. $PD_{0.1}$. Hence, the absolute weighted Hedges' d $|d+|$ is the summary statistic of Hedges' d. For a comparison of the effects sizes for each individual compartment (Hedges' d) and summarized over all compartments (absolute weighted Hedges' d), both types of Hedges' d are presented in tables in Supplement 3.

Specific comments for the discussion:

**Specific comment 19 (Page 9, line 28):** Suggest changing "...compared to the undisturbed sediment after 26 years" to "...compared to the undisturbed sediment 26 years after experimental mining disturbance".

**Our response:** We rephrased the sentence as follows: "the sum of all carbon flows in the food web was still significantly lower inside plough tracks compared to outside plough tracks 26 yr after experimental mining disturbance."

**Specific comment 20 (Page 10, lines 1-23):** I feel the authors are somewhat underselling the conclusions of their manuscript by placing a model limitations section so early on in their Discussion. This could be moved to later in the manuscript, perhaps to just before the conclusions.

**Our response:** We considered to move this section, but we do think that this is warranted at the beginning of the Discussion because this allows the reader to put our results that are discussed later on into perspective of the study limitations.

**Specific comment 21 (Page 11, line 7):** I am confused why the authors are discussing changes in fish respiration over long time periods (3 years) at undisturbed sites. The predictions of Jumars (1981) would be better tested by considering changes in respiration at disturbed sites very soon after the disturbance (e.g. PD0.1). I note that no fish were detected at disturbed sites at PD0.1, so simply put, this hypothesis cannot be tested with this data set.

**Our response:** We removed the discussion about respiration during $PD_3$ and concentrate on $PD_{0.1}$ as follows: "The author also predicted that the density of mobile scavengers, such as fish and lysianassid amphipods would rise shortly after the disturbance in response to the increased abundance of dying or dead organisms within the mining tracks. In fact, experiments with baits at PAP and the Porcupine Seabight (NE Atlantic) showed that the scavenging deep-sea fish *Coryphaenoides armatus* intercept bait within 30 min (Collins et al., 1999) and stayed at the food fall for $114\pm55$ min (Collins et al., 1998). Therefore, the absence of fish inside plough tracks during $PD_{0.1}$ and $PD_{0.5}$ could be related to a lack of prey in a potential predator-prey relationship (Bailey et al., 2006). However, because of the relatively small area of plough tracks (only 22% of the 10.8 $km^2$ of sediment were ploughed; Thiel et al., 1989), the low density of deep-sea fish (e.g., between 7.5 and 32 ind. $ha^{-1}$ of the dominant fish genus *Coryphaenoides* sp. at Station M; Bailey, Ruhl and Smith, 2006) and the high motility of fish, this observation is likely coincidental."

**Specific comment 22 (Page 11, line 28):** "Hence, Jumars (1981) predictions for sub-surface deposit feeders could not be tested...". Indeed, it would be easier to test Jumars' predictions if a PD0 time point was available. However, would it not be possible to test whether there is a significant difference in the density of subsurface deposit feeders at PD0.1 between the disturbance categories? Under Jumars' predictions, we would expect the density of sub-surface deposit feeders to be much reduced at 'disturbed' sites relative to 'undisturbed' sites at this time point.

**Our response:** We thank referee #2 for the suggestion how to test Jumars' (1981) predictions for subsurface deposit feeders. We used the Hedges' d and compared its development over time to investigate the recovery of subsurface deposit-feeding polychaetes: "Hence, Jumars' (1981) predictions for sub-surface deposit feeders are difficult to test, provided the natural fluctuations in PolSSDF densities that were used to calculate carbon stock. However, Hedges' d for PolSSDF was |1.47| at PD0.1 and decreased steadily to |0.66| at PD7 (Supplement 3), indicating a very strong experimental effect after the disturbance event and a constant recovery over time."

**Specific comment 23 (Page 11/12, lines 30-6):** The authors state Jumars' prediction that surface deposit feeders will be more drastically impacted by mining activities than sub-surface deposit feeders. However, they do not test this prediction, instead comparing deposit feeder ecosystem functioning to that of 'omnivores, filter- and suspension feeders and carnivores'. Please explain why. It would be possible to investigate the relative changes in surface and sub-surface deposit feeder contributions to ecosystem functioning between 'disturbed' and 'undisturbed' sites.

**Our response:** We combined the sections on surface and subsurface deposit feeders into one section also following the advice given in specific comment 22 and compare these two feeding types.

**Specific comment 24 (Page 12, lines 15-16):** "After 26 years, the relative difference in the filter and suspension feeding respiration rate was still 80%". I assume that this refers to the difference in respiration rate of filter and suspension feeders between the disturbance categories? The current text is ambiguous and could be interpreted as the difference in respiration rate between filter and suspension feeders. It is also unclear whether an 80% difference means that respiration rates at 'disturbed' sites were 80% lower than at 'undisturbed', or that respiration rates at 'disturbed' sites were 80% of those at 'undisturbed'.
**Our response:** We added the following phrase to improve the clarity of the sentence: "suspension feeding respiration rate between outside plough tracks and inside plough tracks".

**Specific comment 25 (Page 12, lines 18-19):** "...indicating a slow recovery of this feeding group". I'd argue that compared to Jumars' predictions this apparent recovery rate is relatively fast!
**Our response:** Indeed, when compared to Jumars' predictions this recovery rate is fast, however, in comparison to other feeding types, the recovery rate is rather slow.

**Specific comment 26 (Page 12, lines 23-24):** The authors complain here and elsewhere about natural variability in values making it difficult to isolate disturbance-related trends. However, the authors make no effort to identify or even simply discuss the key environmental factors which may be driving this variability.
**Our response:** See our response to general comment 5.

**Specific comment 27 (Page 12, lines 20-28):** This summary paragraph is unnecessary.
**Our response:** We removed the summary paragraph.

**Specific comment 28 (Page 13, lines 5-6):** "In contrast, filter and suspension feeders did not recover at all...". This sentence is too strongly worded. The authors state on page 12, lines 13-15, that "Directly after the initial DISCOL disturbance event, the respiration rate of filter and suspension feeders at the disturbed sediment was only 1% of the respiration rate of this feeding type at the undisturbed sediment" and on page 12, lines 15-16, that "After 26 years, the relative difference in the filter and suspension feeding respiration rate was still 80%". Whilst I agree that the respiration rate of filter- and suspension feeders is still clearly depressed at 'disturbed' sites relative to 'undisturbed', even 26 years post-disturbance, there clearly has been some recovery - perhaps even more so than might be expected! Please re-word this sentence to soften your conclusions.
**Our response:** We rephrase the sentence as follows: "In contrast, filter and suspension feeders recovered less and the relative difference in respiration rate was 79%."

**Specific comment 29 (Page 13, line 7):** The authors state that "...[ecosystem functioning] has not recovered 26 years after the experimental disturbance". However, there is clearly some evidence of recovery. Please could the authors change this statement to "...[ecosystem functioning] has not fully recovered 26 years after the experimental disturbance"?
**Our response:** We rephrased the sentence accordingly.

Specific comments for tables and figures:

**Specific comment 30 (Table 1):** Please explain what 'n' stands for. Is this the number of taxa analysed, or the number of individuals used to estimate taxon-specific biomass etc.?
**Our response:** We added the following sentence to the legend of the table: 'n' refers to the number of individuals used to estimate taxon-specific biomasses.

**Specific comment 31 (Figure 1):** There is a lot of information on this figure, and the overlap in error bars make it especially difficult to read. One option would be to plot each group separately, although this would result in a large number of graphs. Alternatively, this information may be more clearly presented as a table (as per Table 2). Why are there no error bars for the PD26 bars?
**Our response:** This point was also addressed by Peter Jumars (referee #1) and we therefore decided to present the figure without error bars which represent standard deviation and report the standard deviations together with the means in Supplement 2.

**Specific comment 32 (Figure 4):** Why are there no error bars on figure 4a? Are they simply too small to see?
**Our response:** The error bars that symbolize the standard deviations of the flows are indeed very small but were included now in Figure 4a.

Technical corrections for abstract:
**Page 1, line 27:** I, and most others, consider fish as megafauna. Please explain why they are treated separately to the other megafauna.
**Our response:** We separated fish from invertebrate megafauna because of differences in their metabolic rates. To stress that megafauna in our study only includes invertebrate megafauna, we added 'invertebrate' to megafauna throughout the manuscript.

**Page 2, line 12:** The word 'occasionally' is used twice in same sentence.
**Our response:** We removed the second 'occasionally'.

**Page 2, line 20:** Yttrium is typically considered a rare earth element.
**Our response:** We took yttrium out of the list.

**Page 2, line 25:** One could argue that there's not really such a thing as food-rich surface sediments on the deep seafloor.
**Our response:** Though the deep-sea is extremely food-limited, the surface sediments still contain more (and more labile) carbon than subsurface sediment.

**Page 3, line 2:** '10.8 km2 large circular area' – 'large' is not required.
**Our response:** We deleted 'large'.

Technical corrections for methods:
**Page 4, line 21:** 'could' should be used, not 'can'.
**Our response:** We changed the wording accordingly.

Technical corrections for the discussion:
**Page 9, line 23:** Suggest changing 'evolution' for 'change over time'.
**Our response:** We changed the wording accordingly.

**Page 9, line 27:** Put in comma after "...role of the various feeding types in the carbon cycling differs", and after "...was significantly lower".

**Our response:** We added commas accordingly.

**Page 11, line 28:** "Hence, Jumars (1981) predictions..." should be 'Hence, Jumars' (1981) predictions...'.
**Our response:** We changed it accordingly.

**Page 11, line 34:** "...deposit feeders seem to have advantages during the recovery from the DISCOL disturbance experiment...". Relative to whom?
**Our response:** To address specific comments 22 and 23, we removed this part of the text.

Technical corrections for figures and tables:
**Figure 1:** 'Figure 1' is actually referred to in the text after 'figure 2' is. Swap around the order of these figures – i.e. 'figure 2' should be renamed 'figure 1', and vice versa.
**Our response:** We renamed the figures accordingly.

**Figure 2:** Inconsistent spelling of faeces here and throughout the manuscript. Figure legend line 7 "...yellow-dashed arrow indicate..." should be '...yellow-dashed arrow indicates...'. Incorrect use of 'due to' here and throughout the manuscript. Please change to 'because of' or 'as a result of'.
**Our response:** We changed it accordingly.

**Figure 5:** Is it possible to subscript the x-axis post-disturbance times – e.g. PD0.1, for consistency with the rest of the manuscript?
**Our response:** We adjusted the figure accordingly.

# ~~Faunal~~Abyssal plain faunal carbon flows ~~in the abyssal plain food web of the Peru Basin have not recovered during~~remain depressed 26 years ~~from an experimental sediment~~after a simulated deep-sea mining disturbance

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**Abstract**

Future deep-sea mining for polymetallic nodules in abyssal plains will negatively impact the benthic ecosystem, but it is largely unclear whether this ecosystem will be able to recover from mining disturbance and if so, to what extent and at what time scale ~~and to which extent. In 1989, during~~. During the 'DISturbance and reCOLonization' (DISCOL) experiment, a total of 22% of the ~~surface~~seafloor within a 10.8 km$^2$ ~~large~~ circular area of the nodule-rich seafloor in the Peru Basin (SE Pacific) was ploughed in 1989 to bury nodules and mix the surface sediment. This area was revisited 0.1, 0.5, 3, 7, and 26 ~~years~~ yr after the disturbance to assess macrofauna, invertebrate megafauna and fish density and diversity. We used this unique abyssal faunal time series to develop carbon-based food web models for ~~disturbed (sediment inside the plough tracks) and undisturbed (sediment inside the experimental area, but outside the plough tracks) sites. We developed a~~ each point in the time series using the linear inverse ~~model (LIM) to resolve carbon flows between 7 different feeding types within macrofauna, megafauna and fish. The total faunal biomass~~modeling approach for sediments subjected to two disturbance levels: 1) outside the plough tracks, not directly disturbed by plough, but probably suffered from additional sedimentation and 2) inside the plough tracks. Total faunal carbon stock was always higher ~~at the undisturbed sites~~ outside plough tracks compared ~~to the disturbed sites and~~with inside plough

tracks. After 26 years ~~post-disturbance~~, the carbon stock inside the ~~biomass at the disturbed sites~~plough tracks was ~~only~~ 54% of the ~~biomass at undisturbed sites. Fish and sub-surface deposit feeders experienced a particularly large temporal variability in biomass and model-reconstructed respiration rates making it difficult to determine disturbance impacts.~~carbon stock outside plough tracks. Deposit feeders were least affected by the disturbance, with modelled respiration, external predation and excretion ~~levels only~~rates being reduced by only 2.6% ~~in the sediments disturbed 26 years ago~~inside plough tracks compared with ~~undisturbed areas.~~outside plough tracks after 26 yr. In contrast, the respiration rate of filter and suspension feeders was ~~still~~ 79.5% lower in the plough tracks after 26 ~~years when comparing the same sites.~~yr. The 'total system throughput' ($T_{..}$), i.e.~~:~~., the total sum of modelled carbon flows in the food web, was ~~always~~ higher ~~at undisturbed sites~~throughout the time series at outside plough tracks compared ~~to~~with the corresponding ~~disturbed sites~~inside plough tracks and was lowest ~~at disturbed sites~~inside plough tracks directly after the disturbance ($8.63\times10^{-3}\pm1.58\times10^{-5}$ mmol C m$^{-2}$ d$^{-1}$). ~~Therefore,~~Even 26 ~~years~~yr after the DISCOL disturbance, the ~~throughput~~discrepancy of $T_{..}$ between the ~~undisturbed~~outside and the ~~disturbed sediment~~inside plough tracks was still 56%. ~~From these results we conclude that~~Hence, C cycling within the ~~fauna~~faunal compartments of an abyssal plain ecosystem remains reduced 26 ~~years~~yr after physical disturbance, and ~~that~~ a longer period ~~of time~~ is required for the system to recover from such a ~~simulated~~ small-~~-~~scale ~~deep-sea mining experimental~~sediment disturbance experiment.

**1 Introduction**

~~Abyssal plains cover approximately 50% of the world's surface and 75% of the seafloor (Ramirez-Llodra et al., 2010). The abyssal seafloor is primarily composed of soft sediments consisting of fine-grained erosional detritus and biogenic particles (Smith et al., 2008). Occasionally, hard substrate occurs occasionally in the form of clinker from steam ships, glacial drop stones, outcrops of basaltic rock, whale carcasses, and marine litter (Amon et al., 2017; Kidd and Huggett, 1981; Radziejewska, 2014; Ramirez-Llodra et al., 2011; Ruhl et al., 2008). In some soft sediment regions, islands of hard substrate are provided by polymetallic nodules, authigenically formed deposits of metals, which grow at approximate rates of 2 to 20 mm per million years (Guichard et al., 1978; Kuhn et al., 2017). These nodules have the shape and size of cauliflower, cannon balls or potatoes, and are found on the sediment surface and in the sediment at depths between 4000 and 6000 m in areas of the Pacific, Atlantic and Indian Ocean (Devey et al., 2018; Kuhn et al., 2017).~~

~~Polymetallic nodules are rich in metals, such as nickel, copper, cobalt, molybdenum, zirconium, lithium, yttrium and rare earth elements (Hein et al., 2013), and occur in sufficient densities for potential exploitation by the commercial mining industry in the Clarion-Clipperton Fracture Zone (CCFZ; equatorial Pacific), around the Cook Islands (equatorial Pacific), in the Peru Basin (E Pacific) and in the Central Indian Ocean Basin (Kuhn et al., 2017). Extracting these polymetallic nodules during deep-sea mining operations will have severe impacts on the benthic ecosystem, such as the removal of hard substrate (i.e. nodules) and the food-rich surface sediments from the seafloor, physically causing the mortality of organisms within the mining tracks and re-settlement of resuspended particles (Levin et al., 2016; Thiel and Tiefsee-Umweltschutz, 2001). Defining~~

regulations on deep-sea mining requires knowledge on ecosystem recovery from these activities, but to date information on these rates is not extensive (Gollner et al., 2017; Jones et al., 2017; Stratmann et al., 2018; Stratmann et al., in review; Vanreusel et al., 2016). Especially the recovery of ecosystem functions, such as food web structure and carbon (C) cycling, from deep-sea mining is understudied.

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In the Peru Basin (SE Pacific), small-scale deep-sea mining activities were simulated during the 'DISturbance and reCOLonization' experiment (DISCOL) in 1989. A 10.8 km$^2$ large circular area was ploughed diametrically 78 times with a 8 m wide plough harrow to bury the surface nodules into the sediment (Thiel and Schriever, 1989). This experimental disturbance resulted in a heavily disturbed centre and a less affected periphery of the DISCOL area (Bluhm, 2001; Foell et al.,
10  1990; Foell et al., 1992). Over 26 years the region was re-visited five times to assess the Post-Disturbance (PD) situation: directly after the disturbance event, March 1989: (hereafter referred to as 'PD$_{0.1}$'); half a year later, September 1989: 'PD$_{0.5}$'; three years later, January 1992: 'PD$_3$'; seven years later, February 1996: 'PD$_7$'; 26 years later, September 2015: 'PD$_{26}$'. Following the original definition by Bluhm (2001), we denote sites within the DEA (DISCOL Experimental Area), but not directly disturbed by the plough harrow as 'undisturbed sites' and sites that were directly impacted by the plough harrow as
15  'disturbed sites' (Bluhm, 2001). During subsequent visits, densities of macrofauna and megafauna were assessed, but data on meiofauna and microbial communities were only sparsely collected. Therefore, the food web models presented in this work cover a period of 1989 to 2015 and contain macrofauna, megafauna and fish.

Linear inverse modelling (LIM) is an approach that has been developed to disentangle carbon flows between food web
20  compartments for data-sparse systems (Klepper and Van de Kamer, 1987; Vézina and Platt, 1988). It has been applied to assess differences in C and nitrogen (N) cycling in various ecosystems, including the abyssal plain food web at Station M (NE Pacific) under various particulate organic carbon (POC) flux regimes (Dunlop et al., 2016), and a comparison of food web flows between abyssal hills and plains at the Porcupine Abyssal Plain (PAP) in the north-eastern Atlantic (Durden et al., 2017). LIM is based on the principle of mass balancing various data sources (Vézina and Platt, 1988), i.e. faunal biomasses and
25  physiological constraints, that are implemented in the model, either as equality or inequality equations, and these are solved simultaneously (van Oevelen et al., 2010). A food web model almost always includes more inequalities than equalities, i.e. it is mathematically under-determined, which implies that an infinite number of solutions will solve the models. In this case, a likelihood approach can be used to generate a large dataset of possible solutions for the model (van Oevelen et al., 2010), from which the mean and standard deviations for each flow is calculated. Food web models from different sites and/or points in
30  time can be compared quantitatively by calculating network indices, such as the 'total system throughput' ($T..$) that sums all carbon flows in the food web (Kones et al., 2009). Hence, a decrease in the difference of $T..$ between the food webs from undisturbed and corresponding disturbed sites ($\Delta T..$) over time is taken as a sign of ecosystem recovery following disturbance.

~~In this study, benthic food-web models were developed for undisturbed sites and disturbed sites at DISCOL to assess whether faunal biomass and trophic composition of the food webs varied and/or converged between the two sites over time. The model outcomes were compared with conceptual and qualitative predictions on benthic community recovery from polymetallic nodule mining published by Jumars (1981). Additionally, it was investigated how $\Delta T$. developed over time to infer the recovery rate of C flows from experimental deep-sea disturbance in the Peru Basin.~~

Abyssal plains cover approximately 50% of the world's surface and 75% of the seafloor (Ramírez-Llodrà et al., 2010). The abyssal seafloor is primarily composed of soft sediments consisting of fine-grained erosional detritus and biogenic particles (Smith et al., 2008). Occasionally, hard substrate occurs in the form of clinker from steam ships, glacial drop stones, outcrops of basaltic rock, whale carcasses, and marine litter (Amon et al., 2017; Kidd and Huggett, 1981; Radziejewska, 2014; Ramírez-Llodrà et al., 2011; Ruhl et al., 2008). In some soft-sediment regions, islands of hard substrate are provided by polymetallic nodules, authigenically formed deposits of metals, that grow at approximately of 2 to 20 mm per million years (Guichard et al., 1978; Kuhn et al., 2017). These nodules have shapes and sizes of cauliflower florets, cannon balls or potatoes, and are found on the sediment surface and in the sediment at water depths between 4000 and 6000 m in areas of the Pacific, Atlantic and Indian Ocean (Devey et al., 2018; Kuhn et al., 2017).

Polymetallic nodules are rich in metals, such as nickel, copper, cobalt, molybdenum, zirconium, lithium, and rare-earth elements (Hein et al., 2013), and occur in sufficient densities for potential exploitation by commercial mining in the Clarion-Clipperton Fracture Zone (CCFZ; equatorial Pacific), around the Cook Islands (equatorial Pacific), in the Peru Basin (E Pacific) and in the central Indian Ocean basin (Kuhn et al., 2017). Extracting these polymetallic nodules during deep-sea mining operations will have severe impacts on the benthic ecosystem, such as the removal of hard substrate (i.e., nodules) and the food-rich surface sediments from the seafloor, physically causing the mortality of organisms within the mining tracks and resettlement of resuspended particles (Levin et al., 2016; Thiel and Forschungsverbund Tiefsee-Umweltschutz, 2001). Choosing appropriate regulations on deep-sea mining requires knowledge of ecosystem recovery from these activities, but to date information on these rates is not extensive, especially on the recovery of ecosystem functions, such as food-web structure and carbon (C) cycling (Gollner et al., 2017; Jones et al., 2017; Stratmann et al., 2018a, 2018b; Vanreusel et al., 2016).

In the Peru Basin (SE Pacific), a small-scale sediment disturbance experiment was conducted during the 'DISturbance and reCOLonization' experiment (DISCOL) in 1989, which was aimed at mimicking deep-sea mining. A 10.8 km$^2$ circular area (Figure 1) was ploughed diametrically 78 times with an 8 m wide plough-harrow; a treatment which did not remove nodules, but disturbed the surface sediment, buried nodules into the sediment and created a sediment plume (Thiel et al., 1989). This experimental disturbance resulted in a heavily disturbed center and a less affected periphery of the DISCOL area (Bluhm, 2001; Foell et al., 1990, 1992). Over 26 yr, the region was revisited five times to assess the post-disturbance (PD) situation: directly after the disturbance event, March 1989: (hereafter referred to as 'PD$_{0.1}$'); half a year later, September 1989: 'PD$_{0.5}$'; three years later, January 1992: 'PD$_3$'; seven years later, February 1996: 'PD$_7$'; 26 years later, September 2015: 'PD$_{26}$'. During

subsequent visits, densities of macrofauna and invertebrate megafauna were assessed, but data on meiofaunal and microbial communities were collected only sparsely. Therefore, the food-web models presented in this work cover post disturbance 1989 (no adequate pre-disturbance sampling took place in 1989) to 2015, and contain only macrofauna, invertebrate megafauna and fish data.

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Linear inverse modelling is an approach that has been developed to disentangle carbon flows between food-web compartments for data-sparse systems (Klepper and Van De Kamer, 1987; Vézina and Platt, 1988). It has been applied to assess differences in carbon (C) and nitrogen (N) cycling in various ecosystems, including the abyssal-plain food web at Station M (NE Pacific) under various particulate organic carbon (POC) flux regimes (Dunlop et al., 2016), and a comparison of food-web flows

10  between abyssal hills and plains at the Porcupine Abyssal Plain (PAP) in the north-eastern Atlantic (Durden et al., 2017).

The aim of this study was I) to assess whether faunal carbon stock and trophic composition of the food webs varied and/or converged over the time series between outside and inside plough tracks at DISCOL; II) to compare our model outcomes with the conceptual and qualitative predictions on benthic community recovery from polymetallic nodule mining published by

15  Jumars (1981) and III) to infer the recovery rate of C cycling following from a deep-sea sediment disturbance experiment using the network index 'total system throughput' $\Delta T..$, i.e., the sum of all C flows in the food web (Kones et al., 2009), developed over time.

## 2 Methods

### 2.1 Linear inverse model

20  Linear inverse modelling is based on the principle of mass balance and various data sources (Vézina and Platt, 1988), i.e., faunal carbon stock and physiological constraints, that are implemented in the model, either as equalities or inequalities, and they are solved simultaneously. A food-web model with all compartments present in the food web, e.g., the $PD_{26}$ food web model outside plough tracks, consisted of 147 carbon flows with 14 mass balances, i.e., food-web compartments, and 76 data inequalities leading to a mathematically under-determined model (14 equalities vs. 147 unknown flows). Therefore, the linear

25  inverse models (LIMs) were solved with the R package 'LIM' (van Oevelen et al., 2010) in R (R-Core Team, 2017) following the likelihood approach (van Oevelen et al., 2010) to quantify means and standard deviations of each of the carbon flows from a set of 100,000 solutions. This set was sufficient to guarantee convergence of means and standard deviations within a 2.5% deviation.

Food-web models from different sites and/ or points in time were compared quantitatively by calculating $T..$ with the R package

30  'NetIndices' (Kones et al., 2009) for each of the 100,000 model solutions and subsequently summarized as mean ± standard deviation. A decrease in the difference of $T..$ between the food webs from outside and inside plough tracks ($\Delta T..$) over time was taken as a sign of ecosystem recovery following disturbance.

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## 2.2 Data availability

~~Macrofauna, megafauna and fish density data (mean±std; ind. m$^{-2}$) for the first four cruises (PD$_{0.1}$ to PD$_2$) were extracted from the original papers (Bluhm, 2001 annex 2.8; Borowski, 2001; Borowski and Thiel, 1998) and methodological details can be found in those papers. In brief, macrofauna samples (>500 µm size fraction) were collected with a 0.25 m$^{-2}$ box-corer and~~
5 ~~densities of megafauna and fish were assessed on still photos and videos taken with a towed "Ocean Floor Observation System" (OFOS) underwater camera system. During the PD$_{26}$ cruise (RV Sonne cruise SO242-2; Boetius, 2015), macrofauna were collected with a square 50 × 50 × 60 cm box-corer (disturbed sites: n = 3; undisturbed sites: n = 7) and the upper 5 cm of sediment was sieved on a 500 µm sieve (Greinert, 2015). All organisms retained on the sieve were preserved in 96% un-denaturated ethanol on board (Greinert, 2015) and were sorted and identified ashore to the same taxonomic level as the previous~~
10 ~~cruises under a stereomicroscope. Megafauna and fish density during the PD$_{26}$ cruise was acquired by deploying the OFOS (Boetius, 2015). Every 20 s, the OFOS automatically took a picture of the seafloor at an approximate altitude of 1.5 m above the seafloor (Boetius, 2015; Stratmann et al., in review) resulting in 1,740 images of plough marks (disturbed sites) and 6,624 images from undisturbed sites (Boetius, 2015). A subset of 300 pictures from the disturbed sites (surface area: 1,440.6 m$^2$) and 300 pictures from the undisturbed sites (surface area: 1,420.4 m$^2$) were randomly selected from the original~~
15 ~~set of pictures and annotated using the open-source annotation software PAPARA(ZZ)I (Marcon and Purser, 2017). Megafauna were identified to the same taxonomic levels as for the previous megafauna studies conducted within the DEA (Bluhm, 2001), whereas fish were identified to genus level using the CCZ species atlas (www.ccfzatlas.com).~~

Macrofauna, invertebrate megafauna and fish density data (mean ± std; ind. m$^{-2}$) for the first four cruises (PD$_{0.1}$ to PD$_7$) were
20 extracted from the original papers (Borowski and Thiel, 1998; Bluhm, 2001 annex 2.8; Borowski, 2001), and methodological details can be found in those papers. In brief, macrofaunal samples (> 500 µm size fraction) were collected with a 0.25 m$^{-2}$ box-corer (number of samples is reported in Table 1), and densities of invertebrate megafauna and fish were assessed on still photos and videos taken with a towed "Ocean Floor Observation System" (OFOS) underwater camera system (extent of total surveyed area is reported in Table 1). During the PD$_{26}$ cruise (RV Sonne cruise SO242-2; Boetius, 2015), macrofauna were
25 collected with a square 50 × 50 × 60 cm box-corer (outside plough tracks: n = 7; inside plough tracks: n = 3), and the upper 5 cm of sediment were sieved on a 500 µm sieve (Greinert, 2015). All organisms retained on the sieve were preserved in 96% un-denaturated ethanol on board (Greinert, 2015) and were sorted and identified ashore under a stereomicroscope to the same taxonomic level as the previous cruises. Invertebrate megafauna and fish density during the PD$_{26}$ cruise were acquired by deploying the OFOS (Boetius, 2015). Every 20 s, the OFOS automatically took a picture from approximately 1.5 m above the
30 seafloor (Boetius, 2015; Stratmann et al., 2018b) resulting in 1,740 images of plough marks (inside plough tracks) and 6,624 images from outside plough tracks (Boetius, 2015). A subset of 300 pictures from inside plough tracks (surface area: 1,441 m$^2$) and 300 pictures from the outside plough tracks (surface area: 1,420 m$^2$) were randomly selected from the original set of pictures and annotated using the open-source annotation software PAPARA(ZZ)I (Marcon and Purser, 2017).

Invertebrate megafauna were identified to the same taxonomic levels as for the previous megafauna studies conducted within the DISCOL experimental area (DEA) (Bluhm, 2001), whereas fishes were identified to genus using the CCZ species atlas (www.ccfzatlas.com).

5 The above-mentioned density data collected for macrofauna, invertebrate megafauna and fish were used to build food–web models to resolve carbon fluxes; hence, all faunal density data ~~needed~~required conversion into carbon units before they ~~can~~could be used in the food–web model. Converting density data to carbon ~~biomass values~~stocks was challenging in the current study, as few to no conversion factors for deep-sea fauna are available in the literature. Below, we describe the approach that we used to tackle this ~~hurdle~~problem for macrofauna, invertebrate megafauna and fish.

10 ~~In case~~

Measuring the carbon content of a macrofaunal specimen~~, measuring the carbon content~~ requires its complete combustion, which means that the specimen cannot be kept as ~~voucher specimen in scientific collections. The macrofauna~~a voucher. Macrofaunal samples collected for this study are part of the Biological Research Collection of Marine Invertebrates (Department of Biology & Centre for Environmental and Marine Studies, University of Aveiro, Portugal) and were therefore

15 not sacrificed. Instead, we used the C conversion factors of ~~macrofauna~~macrofaunal specimens previously collected within the framework of a pulse-chase experiment in the Clarion-Clipperton Zone (CCZ, NE Pacific), in which a deep-sea benthic lander (3 incubation chambers à $20 \times 20 \times 20$ cm) was deployed at water depths between 4050 and 4200 m ~~(Sweetman et al., in review).~~(Sweetman et al., in review). The upper 5 cm of the sediment of the incubation chambers ~~was~~were sieved on ~~300~~a 500 µm sieve and preserved in 4% buffered formaldehyde ~~solution~~. Ashore, the samples were sorted and identified under a

20 dissecting microscope~~,~~ and the ~~biomass~~ carbon content of individual freeze-dried, acidified specimens was determined with ~~at~~a Thermo Flash EA 1112 elemental ~~analyser~~analyzer (EA; Thermo Fisher Scientific, USA) to give the individual ~~carbon content~~biomass in mmol C ind$^{-1}$. ~~The macrofauna~~Macrofaunal density data (ind. m$^{-2}$) from all cruises were converted to ~~macrofauna biomass~~macrofaunal carbon stocks (mmol C m$^{-2}$) by multiplying each taxon-specific density (ind. m$^{-2}$) with the mean~~,~~ taxon-specific~~,~~ individual biomass value for macrofauna (mmol C ind$^{-1}$; Table ~~1~~2). Subsequently, the ~~biomass~~carbon

25 stock data of all taxa with the same feeding type (Table ~~1~~2) were summed to calculate the ~~biomass~~carbon stock of each macrofaunal compartment (mmol C m$^{-2}$; Supplement ~~1, Figure 2).~~ 2, Figure 2).

~~The megafauna density data (ind. m$^{-2}$) of the time series was converted to biomass (mmol C m$^{-2}$) by multiplying the taxon-specific density with a taxon-specific mean biomass per megafauna specimen (mmol C ind$^{-1}$; Table 1). To determine this~~

30 ~~taxon-specific biomass per megafauna specimen, size measurements were used as follows. The 'AUV Abyss' (Geomar Kiel) equipped with a Canon EOS 6D camera system with 8-15 mm f4 fisheye zoom lens and 24 LED arrays for lightning (Kwasnitschka et al., 2016) flew approximately 4.5 m above the seafloor at a speed of 1.5 m s$^{-1}$ and took one picture every second (Greinert, 2015). Machine vision processing was used to generate a photo-mosaic (Kwasnitschka et al., 2016). A subsample covering an area of 16,206 m$^{2}$ of the mosaic was annotated using the web-based annotation software 'BIIGLE 2.0'~~

~~(Langenkämper et al., 2017). The length of all megafauna taxa for which data were available from previous cruises was measured using the approach presented in Durden et al. (2016). Briefly, depending on the taxon, either body length, the diameter of the disk, or the length of an arm were measured on the photo-mosaic and converted into biomass per individual (g ind⁻¹) using the relationship between measured body dimensions (mm) and preserved wet weight (g ind⁻¹) (Durden et al., 2016). Subsequently, the preserved wet weight (g ind⁻¹) was converted to fresh wet weight (g ind⁻¹) using conversion factors from Durden et al. (2016) and to organic carbon (g C ind⁻¹ and mmol C ind⁻¹) using the taxon-specific conversion factors presented in Rowe (1983). For the taxa Cnidaria and Porifera no conversion factors were available. Therefore, taxon-specific individual biomass values were extracted from a study from the CCZ (Tilot, 1992). The individual biomass of Bryozoa and Hemichordata were calculated as the average biomass of an individual deep-sea megafauna organism (B, mmol C ind⁻¹) at 4100 m depth following from the ratio of the regression for total biomass and abundance by Rex et al. (2006):~~

$$B = \frac{10^{(-0.734-0.00039\times\text{depth})}}{10^{(-0.245-0.00037\times\text{depth})}}. \tag{1}$$

The invertebrate megafaunal density data (ind. m⁻²) of the time series was converted to carbon stocks (mmol C m⁻²) by multiplying the taxon-specific density with a taxon-specific mean biomass per invertebrate megafaunal specimen (mmol C ind⁻¹; Table 2). To determine this taxon-specific biomass per invertebrate megafaunal specimen, size measurements were used as follows. The 'AUV Abyss' (Geomar Kiel) equipped with a Canon EOS 6D camera system with 8-15 mm f4 fisheye zoom lens and 24 LED arrays for lightning (Kwasnitschka et al., 2016) flew approximately 4.5 m above the seafloor at a speed of 1.5 m s⁻¹ and took one picture every second (Greinert, 2015). Machine-vision processing was used to generate a photo-mosaic (Kwasnitschka et al., 2016). A subsample covering an area of 16,206 m² of the mosaic was annotated using the web-based annotation software 'BIIGLE 2.0' (Langenkämper et al., 2017). Lengths of all invertebrate megafaunal taxa for which data were available from previous cruises were measured using the approach presented in Durden et al. (2016). Briefly, depending on the taxon, either body length, the diameter of the disk, or the length of an arm was measured on the photo mosaic and converted into biomass per individual (g ind⁻¹) using the relationship between measured body dimensions (mm) and preserved wet weight (g ind⁻¹) (Durden et al., 2016). Subsequently, the preserved wet weight (g ind⁻¹) was converted to fresh wet weight (g ind⁻¹) using conversion factors from Durden et al. (2016) and to organic carbon (g C ind⁻¹ and mmol C ind⁻¹) using the taxon-specific conversion factors presented in Rowe (1983) (a detailed list with all conversion factors is presented in Supplement 2). For the taxa Cnidaria and Porifera no conversion factors were available. Therefore, taxon-specific individual biomass values were extracted from a study from the CCZ (Tilot, 1992). The individual biomass of Hemichordata was calculated as the average biomass of an individual deep-sea invertebrate megafaunal organism (B, mmol C ind⁻¹) at 4100 m depth following from the ratio of the regression for total biomass and abundance by Rex et al. (2006):

$$B = \frac{10^{(-0.734-0.00039\times\text{depth})}}{10^{(-0.245-0.00037\times\text{depth})}}. \tag{1}$$

Following the approach applied to the macrofauna dataset, individual ~~biomasses~~ carbon stocks of taxa with similar feeding types (Table ~~1~~2) were summed to determine ~~the biomass~~ carbon stocks of ~~the~~ invertebrate megafauna food-web compartments (mmol C m⁻²; Supplement ~~1; Figure 1).~~ 1; Figure 2).

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Individual biomass of fish was calculated using the allometric relationship for *Ipnops agassizii*:

wet weight = a × length$^b$,  (2)

~~where a = 0.0049 and b = 3.03 (Froese and Pauly, 2017; Froese et al., 2014), as *Ipnops* sp. was the most abundant deep-sea~~
5 ~~fish observed at the DEA (60% of total fish density at undisturbed and 40% of total fish density at disturbed sites). The length~~
~~(mm) of all *Ipnops* sp. specimens was measured on the annotated 600 pictures (300 pictures from undisturbed site, 300 pictures~~
~~from disturbed site) in PAPARA(ZZ)I (Marcon and Purser, 2017) using three laser points captured in each image (distance~~
~~between laser points: 0.5 m (Boetius, 2015)). The wet weight (g) was converted to dry weight and subsequently to carbon~~
~~content (mmol C ind$^{-1}$) using the taxon-specific conversion factors presented in Brey et al. (2010).~~

10 ~~2.2~~where a = 0.0049 and b = 3.03 (Froese et al., 2014; Froese and Pauly, 2017), as *Ipnops* sp. was the most abundant fish
observed at the DEA (60% of total fish density outside plough tracks and 40% of total fish density inside plough tracks). The
length (mm) of all *Ipnops* sp. specimens was measured on the annotated 600 pictures (300 pictures from outside plough tracks,
300 pictures from inside plough tracks) in PAPARA(ZZ)I (Marcon and Purser, 2017) using three laser points captured in each
image (distance between laser points: 0.5 m; Boetius, 2015). The wet weight (g) was converted to dry weight and subsequently
15 to carbon content (mmol C ind$^{-1}$) using the taxon-specific conversion factors presented in Brey et al. (2010).

**2.3 Food-~~ ~~web structure**

~~The faunal biomass was~~Faunal carbon stocks were further divided into feeding guilds in order to define ~~the~~ food-~~ ~~web
compartments of the model. Fish (Osteichthyes) were classified as scavenger/ predator and ~~invertebrate~~ macrofauna and
invertebrate megafauna were divided into filter/suspension feeders (FSF), deposit feeders (DF), carnivores (C) and omnivores
20 (OF) ~~(Figure 2).~~(Figure 3; Table 2.). Since feeding types are well described for polychaetes ~~(Jumars et al., 2015)~~(Jumars et al.,
2015), we made a further detailed classification of the macrofaunal polychaetes into suspension feeders (PolSF), surface
deposit feeders (PolSDF), subsurface deposit feeders (PolSSDF), carnivores (PolC), and omnivores (PolOF).

External carbon sources that were considered in the model included suspended detritus in the water column (Det_w), labile
25 (lDet_s) and semi-labile detritus (sDet_s) in the sediment. Suspended detritus was considered a food source for polychaete,
macrofaunal and invertebrate megafaunal suspension feeders. Labile and semi-labile sedimentary detritus was a source for
deposit-feeding and omnivorous polychaetes, macrofauna and invertebrate megafauna. Omnivores and carnivores of each size
class preyed upon organisms of the same and smaller size classes, i.e~~.~~., MegC and MegOF preyed upon MegDF, MegFSF,
MacFSF, MacDF, MacC, MacOF, PolSDF, PolSSDF, PolSF, PolOF, and PolC. Furthermore, MacC, PolC, MacOF, and PolOF
30 preyed upon MacFSF, MacDF, PolSDF, PolSSDF, and PolSF. Fish preyed upon all fauna and the carcass pool. This carcass
pool consisted of all fauna (macrofauna, invertebrate megafauna and fish) that died in the food web and was also ~~the~~a food
source of omnivores.

9

Carbon losses from the food web were respiration to dissolved inorganic carbon (DIC), predation on macrofauna, invertebrate megafauna and fish by pelagic/ benthopelagic ~~fish~~fishes, scavenging on carcasses by pelagic/ benthopelagic scavengers and ~~faeces~~feces production by all faunal compartments.

### 2.~~3~~4 Literature constraints

~~The carbon~~Carbon flows between faunal compartments are constrained ~~by the implementation of~~in all models by various minimum and maximum process rates and conversion efficiencies ~~as inequalities in all models, which are described here~~. Assimilation efficiency (AE) is calculated as:

$$AE = (I-F) / I, \tag{3}$$

~~where I is the ingested food and F are the faeces (Crisp, 1971). The min-max range was set from 0.62 to 0.87 for macrofauna and polychaetes (Stratmann et al., in prep.), from 0.48 to 0.80 for megafauna (Stratmann et al., in prep.) and from 0.84 to 0.87 for fish (Drazen et al., 2007).~~

~~Net growth efficiency (NGE) is defined as:~~

~~NGE = P / (P + R),~~ (4)

~~with P being secondary production and R being respiration (Clausen and Riisgård, 1996). The min-max ranges are set to 0.60 to 0.72 for macrofauna and polychaetes (Clausen and Riisgård, 1996; Navarro et al., 1994; Nielsen et al., 1995), from 0.48 to 0.60 for megafauna (Koopmans et al., 2010; Mondal, 2006; Nielsen et al., 1995) and from 0.37 to 0.71 for fish (Childress et al., 1980). The secondary production P (mmol C m⁻²) is calculated as:~~

where I is the ingested food and F is the feces (Crisp, 1971). The min-max range was set from 0.62 to 0.87 for macrofauna, including polychaetes (Stratmann et al., in prep.), from 0.48 to 0.80 for invertebrate megafauna (Stratmann et al., in prep.) and from 0.84 to 0.87 for fish (Drazen et al., 2007).

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$$P = P/B\text{-ratio} \times \text{~~biomass,~~ carbon stock} \tag{5}$$

~~with the P/B ratios for macrofauna and polychaetes (8.49 × 10⁻⁴ to 4.77 × 10⁻³ d⁻¹; (Stratmann et al., in prep.)), megafauna (2.74 × 10⁻⁴ to 1.42 × 10⁻² d⁻¹; (Stratmann et al., in prep.)) and fish (6.30×10⁻⁴ d⁻¹; (Collins et al., 2005; Randall, 2002)). The respiration rate R (mmol C m⁻²) was calculated as:~~

with the P/B-ratios for macrofauna, including polychaetes ($8.49 \times 10^{-4}$ to $4.77 \times 10^{-3}$ d$^{-1}$; Stratmann et al., in prep.), invertebrate megafauna ($2.74 \times 10^{-4}$ to $1.42 \times 10^{-2}$ d$^{-1}$; Stratmann et al., in prep.) and fish ($6.30 \times 10^{-4}$ d$^{-1}$; Collins et al., 2005; Randall, 2002). The respiration rate R (mmol C m$^{-2}$) was calculated as:

R = bsFR × ~~biomass~~carbon stock,

(6)

~~where bsFR is the biomass-specific fauna respiration rate (d$^{-1}$) and ranges were fixed between $7.12 \times 10^{-5}$ to $2.28 \times 10^{-2}$ d$^{-1}$ for macrofauna and polychaetes (Stratmann et al., in prep.), $2.74 \times 10^{-4}$ to $1.42 \times 10^{-2}$ d$^{-1}$ for megafauna (Stratmann et al., in prep.) and $2.3 \times 10^{-4}$ and $3.6 \times 10^{-4}$ d for fish (Mahaut et al., 1995; Smith and Hessler, 1974).~~

~~**2.4 Linear inverse model solution and network index**~~

~~A food web model with all compartments present in the food web, like e.g. the PD$_{26}$ food web model for the undisturbed site, consists of 147 carbon flows with 14 mass balances, i.e. food-web compartments, and 76 data inequalities leading to a mathematically under-determined model (14 equalities vs. 147 unknown flows). Therefore, the LIMs were solved with the R package 'LIM' (van Oevelen et al., 2010) in R (R Core Team, 2016) following the likelihood approach (van Oevelen et al., 2010) to quantify the mean and standard deviations of each of the carbon flows from a set of 100,000 solutions. This set was sufficient to guarantee the convergence of mean and standard deviation within a 2.5% deviation.~~

~~The network index 'total system throughput' ($T..$) was calculated with the R package 'NetIndices' (Kones et al., 2009) for each of the 100,000 model solutions and subsequently summarized as mean ± standard deviation.~~

where bsFR is the biomass-specific faunal respiration rate (d$^{-1}$), and ranges were fixed between $7.12 \times 10^{-5}$ to $2.28 \times 10^{-2}$ d$^{-1}$ for macrofauna, including polychaetes (Stratmann et al., in prep.), $2.74 \times 10^{-4}$ to $1.42 \times 10^{-2}$ d$^{-1}$ for invertebrate megafauna (Stratmann et al., in prep.) and $2.3 \times 10^{-4}$ and $3.6 \times 10^{-4}$ d for fishes (Mahaut et al., 1995; Smith and Hessler, 1974).

**2.5 Statistical analysis**

~~Statistical differences between compartment biomasses of the undisturbed vs. disturbed sites for the same sampling event (PD$_{0.1}$, PD$_{0.5}$, PD$_3$, and PD$_7$; PD$_{26}$ was omitted due to a lack of megafauna replicates) were assessed by calculating Hedge's d (Hedges and Olkin, 1985a), which is especially suitable for small sample sizes (Koricheva et al., 2013):~~

~~d=($\bar{Y}$~~Statistical differences between individual compartment carbon stocks from outside vs. inside plough tracks for the same sampling event (PD$_{0.1}$, PD$_{0.5}$, PD$_3$, and PD$_7$; PD$_{26}$ were omitted because of a lack of invertebrate megafaunal replicates) were assessed by calculating Hedges' $d$ (Hedges and Olkin, 1985a), which is especially suitable for small sample sizes (Koricheva et al., 2013):

$$d = (\bar{Y}^{E} - \bar{Y}^{C}) / (((n^{E} - 1) (s^{E})^2 + (n^{C} - 1) (s^{C})^2) / (n^{E} + n^{C} - 2))^{0.5} \times J$$

(7)

with × J=                                                    (7)

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with $J = 1 - (3 / (4(n^E + n^C - 2) - 1))$,

(8)

where $\bar{Y}^E$ is the mean of the experimental group (i.e. the biomass at disturbed sites., carbon stock from inside plough tracks of a particular year), $\bar{Y}^C$ is the mean of the control group (i.e. the biomass at undisturbed sites., carbon stock from inside plough tracks of the respective year), $s^E$ and $s^C$ are the standard deviations with corresponding groups, $n^E$ and $n^C$ are the sample sizes of the corresponding groups. The variance of Hedge'sHedges' $d$ $\sigma_d^2$ (Koricheva et al., 2013)(Koricheva et al., 2013) is estimated as:

$$\sigma_d^2 = ( = (n^E + n^C)() / (n^E n^C)+) + d^2 / ( / (2 (n^E + n^C)).$$

(9)

The weighted Hedge's d and the estimated variance (Hedges and Olkin, 1985b) of the total biomass of all compartments of the same sampling event were calculated as:
The weighted Hedges' $d$ and estimated variances (Hedges and Olkin, 1985b) of the sum of all carbon stocks of the same sampling event were calculated as:

$$d+= + = sum (d_i / \sigma_{di}^2)() / sum (1/ / \sigma_{di}^2),$$

(10)

with $\sigma_{d+}^2 = = 1/ / sum (1/ / \sigma_{di}^2)$.

Following Cohen (1988)'sCohen's (1988) rule of thumb for effect sizes, Hedge'sHedges' $d = | = |0.2|$ signifies a small experimental effect, implying that the biomasscarbon stocks of the food-web compartments isare similar between the disturbedoutside and undisturbed sites.inside plough tracks. When Hedge'sHedges' $d = | = |0.5|$, the effect size is medium, hence there is moderate difference, and when Hedge'sHedges' $d = | = |0.8|$, the effect size is large, i.e.:. there is a large difference between the biomasscarbon stocks of the compartments between sites.from outside and inside plough tracks.

The network index $T..$ was compared between the undisturbed and disturbed sites of the same sampling event by assessing the fraction of the $T..$ values of the 100,000 model solutions of the undisturbed food web that were larger than the $T..$ values of the 100,000 model solutions of the disturbed food web. When this fraction is >0.95, the difference in 'total system throughput' between the two food webs from the same sampling event is considered significantly different (van Oevelen et al., 2011), indicating that thewas compared between the outside and inside plough tracks of the same sampling event by assessing the fraction of the $T..$ values of the 100,000 model solutions of the outside plough track food web that were larger than the $T..$ values of the 100,000 model solutions of the outside plough track food web. When this fraction is > 0.95, the difference in 'total system throughput' between the two food webs from the same sampling event is considered significantly different (van Oevelen et al., 2011), indicating that carbon flows in the food web from that specific sampling event have not recovered from the experimental disturbance.

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## 3 Results

### 3.1 Food-web structure and trophic composition

Total faunal ~~biomass was~~ carbon stocks were always higher ~~at the undisturbed sites~~outside plough tracks as compared to ~~the disturbed sites from~~inside plough tracks during the same sampling year ~~(Figure 1,~~(Figure 2, Supplement 1), and ranged from a minimum of 5.4~~5~~55±1.2~~7~~3 mmol C m$^{-2}$ (PD$_{0.1}$) to a maximum 22.~~33±3.4~~0±3.4 mmol C m$^{-2}$ (PD$_3$) ~~at the undisturbed sites~~outside plough tracks and from ~~a~~ minimum of 1.3~~6~~4±1.2~~4~~2 mmol C m$^{-2}$ (PD$_{0.1}$) to ~~a~~ maximum 15.~~82±1.99~~8±2.0 mmol C m$^{-2}$ (PD$_3$) ~~at the disturbed sites. At~~ inside plough tracks. During PD$_{0.1}$ the total faunal ~~biomass at the disturbed sites~~carbon stock inside plough tracks was only 25% of the total faunal ~~biomass at the undisturbed sites~~carbon stock outside plough tracks, whereas ~~at~~during PD$_3$ the total faunal ~~biomass at the disturbed sites~~carbon stock inside plough tracks was 71% of the total faunal ~~biomass at the undisturbed sites. At~~ carbon stock outside plough tracks. During PD$_{26}$, the faunal ~~biomass at the disturbed sites~~carbon stock inside plough tracks was 54% of the ~~biomass at the undisturbed sites.~~carbon stock outside plough tracks. The absolute weighted ~~Hedge's~~Hedges' $d$ |d$_+$| of all faunal compartment ~~biomasses~~carbon stocks for PD$_{0.1}$ to PD$_7$ ranged from 0.0~~53~~53±0.0~~19 at~~02 during PD$_{0.5}$ to 0.0~~75~~75±0.0~~19~~02 during PD$_3$ (Supplement ~~2~~3), indicating a ~~strong~~moderate experimental effect and therefore that ~~biomasses~~carbon stocks of all faunal ~~compartment did not~~compartments failed to recover over the period ~~analysed~~analyzed (PD$_{0.1}$ to PD$_7$).

The faunal ~~biomass at both the undisturbed~~carbon stocks outside and ~~disturbed sites~~inside plough tracks from PD$_{0.1}$ to PD$_7$ ~~was~~were dominated by deposit feeders (from 63% ~~at undisturbed PD$_{0.1}$~~outside plough tracks to 83% ~~at disturbed~~inside plough tracks during PD$_{0.5}$ and ~~disturbed PD3) (Figure 3).~~inside plough tracks during PD$_3$) (Figure 4). In contrast, ~~at the undisturbed sites of~~outside plough tracks during PD$_{26}$, ~~the~~ filter- and suspension feeders had the largest contribution to total faunal ~~biomass was from filter- and suspension feeders~~ carbon stock (44%), whereas deposit feeders only contributed 35%. ~~At the disturbed sites of~~Inside plough tracks during PD$_{26}$, deposit feeders had the highest ~~biomass~~carbon stock (61%), followed by carnivores (19%) and filter- and suspension feeders (14%).

### 3.2 Carbon flows

~~The total~~Total faunal C ingestion (mmol C m$^{-2}$ d$^{-1}$) ranged from 8.6~~3~~6×10$^{-3}$±1.5~~8~~6×10$^{-5}$ ~~at the disturbed sites at~~inside plough tracks during PD$_{0.1}$ to 1.4~~7~~5×10$^{-1}$~~±~~± 8.5~~5~~6×10$^{-4}$ ~~at the undisturbed sites at~~outside plough tracks during PD$_3$ and was always lower ~~at the disturbed sites~~inside plough tracks compared to ~~the undisturbed sites (Figure 4A~~outside plough tracks (Figure 5A; Supplement ~~3~~ 4). The ingestion consisted mainly of ~~the~~ sedimentary detritus (labile and semi-labile) that contributed between ~~56.97% (undisturbed sites~~57% (outside plough tracks, PD$_{26}$) and ~~99.50% (disturbed sites~~100% (inside plough tracks, PD$_{0.1}$) to the total carbon ingestion.

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Faunal respiration (mmol C m$^{-2}$ d$^{-1}$) ranged from 6.~~0~~20×10$^{-3}$±6.~~7~~58×10$^{-5}$ (~~disturbed sites~~inside plough tracks, PD$_{0.5}$) to 3.~~9~~29×10$^{-2}$±3.~~6~~97×10$^{-4}$ (~~undisturbed sites~~outside plough tracks, PD$_3$). During the ~~twenty-six years~~26 yr after the DISCOL experiment, modelled faunal respiration was always higher ~~at undisturbed sites as compared to disturbed sites (Table 2, Figure 4).~~outside plough tracks than inside plough tracks (Table 3, Figure 5B). Over time, non-polychaete macrofauna contributed least to total faunal respiration ~~(Table 2),~~(Table 3), except ~~at the disturbed sites of~~inside plough tracks during PD$_{0.5}$ and at both sites ~~of~~during PD$_3$. During this PD$_3$ sampling campaign, macrofauna contributed ~~49.97% at the undisturbed sites~~50% outside plough tracks and 58.~~35% at the disturbed sites~~% inside plough tracks to ~~the~~ total faunal respiration. Polychaetes respired between ~~18.59~~19% of the total fauna respiration ~~at the undisturbed sites at~~outside plough tracks during PD$_{26}$ and 77.~~61~~78% of ~~the~~ total ~~fauna~~faunal respiration ~~at the disturbed sites at~~inside plough tracks during PD$_{0.5}$. ~~The megafauna respiration~~Invertebrate megafaunal contribution to respiration was highest ~~at~~during PD$_{26}$, ~~where~~when they respired 64.95~~65~~% of the total faunal respiration ~~at the disturbed sites~~inside plough tracks and 78.67~~79~~% of the total faunal respiration ~~at the undisturbed sites.~~outside plough tracks. The contribution of fish to total faunal respiration was always <2%. Besides respiration, ~~faeces~~feces production contributed between 20.~~07% at disturbed~~% inside plough tracks during PD$_3$ and ~~34.65% at disturbed~~35% outside plough tracks during PD$_{0.1}$ to total carbon outflow from the food web ~~(Figure 4).~~(Figure 5). The contribution of the combined outflow of predation by external predators and scavengers on carcasses to the total C loss from the food web ranged from 50.~~48% at disturbed~~% inside plough tracks during PD$_7$ to 65.~~33% at disturbed~~% inside plough tracks during PD$_{0.1}$.

The fraction of $T..$ values that were larger for the food webs ~~at the undisturbed sites than for the disturbed sites from~~outside plough tracks than inside plough tracks during the same sampling event was 1.0 at PD$_{0.1}$, PD$_{0.5}$, PD$_3$, PD$_7$ and PD$_{26}$. No decreasing trend in $\Delta T..$ over time was visible ~~(Figure 5),~~(Figure 6), in fact, the largest $\Delta T..$ were calculated for PD$_3$ (7.~~87~~9×10$^{-2}$±~~1.97~~2.0×10$^{-3}$ mmol C m$^{-2}$ d$^{-1}$) and PD$_{26}$ (7.~~67~~7×10$^{-2}$±9.41×10$^{-4}$ mmol C m$^{-2}$ d$^{-1}$).

**4 Discussion**

This study assessed the ~~evolution~~change over time of ~~the~~ food-web structure and ~~the~~ ecosystem function 'faunal C cycling' in an abyssal~~,~~ nodule-rich~~,~~ soft-sediment ecosystem ~~following~~after an experimental sediment disturbance. ~~By comparing a~~From the 26-year time-series ~~over 26 years with food web models (undisturbed vs. disturbed sites),~~ we show that ~~the~~ total faunal ~~biomass at the disturbed site~~carbon stock inside plough tracks was still only about half of ~~the~~ total faunal ~~biomass at the undisturbed sites 26 years after the disturbance.~~carbon stock outside plough tracks. Furthermore, the role of the various feeding types in the carbon cycling ~~differs and~~differed by feeding type. In all, the 'total system throughput' $T..$, i.e.~~,~~ the sum of all carbon flows in the food web, was still significantly lower ~~at the disturbed sediment~~inside plough tracks as compared to ~~the undisturbed sediment~~outside plough tracks 26 yr after ~~26 years~~the experimental mining disturbance.

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**4.1 Model limitations**

Our results are unique as it allowed for the first time to assess the recovery of C cycling in benthic deep-sea food webs from a small-scale sediment disturbance in polymetallic nodule rich areas. However, the models come with limitations. The standard procedures to assess megafauna densities have evolved during the 26 years of post-disturbance monitoring. The OFOS system
5   used 26 years after the initial DISCOL experiment took pictures automatically every 20 s from a distance of 1.5 m above the seafloor (Boetius, 2015; Stratmann et al., in review). By contrast, the OFOS system used in former cruises was towed approximately 3 m above the seafloor and pictures were taken selectively by the operating scientists (Bluhm and Gebruk, 1999). Therefore, the procedure used in the former cruises very likely led to an overestimation of rare and charismatic megafauna, and probably to an underestimation of dominant fauna and organisms of small size (<3 cm) for $PD_{0.1}$ to $PD_2$ as
10   compared to $PD_{26}$.

Previous cruises to the DEA focused on monitoring changes in faunal density and diversity, but not on changes in biomass. Hence, a major task in this study was to find appropriate conversion factors to convert density into biomass. However, no individual biomass data for macrofauna taxa were available for the Peru Basin, so we used data from sampling stations of similar water depths in the eastern Clarion-Clipperton Zone (CCZ, NE Pacific; Sweetman et al., in review). As organisms in
15   deep-sea regions with higher organic carbon input are larger than their counterparts from areas with lower organic carbon input (McClain et al., 2012), using individual biomass data from the CCZ, a more oligotrophic region than the Peru Basin (Haeckel et al., 2001; Vanreusel et al., 2016) might have led to an underestimation of the biomass for macrofauna. However, this has likely limited impact on the interpretation of the comparative results within the time series, because the same methodology was applied throughout the time series dataset. Moreover, the determination of megafauna biomass was also difficult as no
20   size measurements were taken from megafauna individuals during the $PD_{0.1}$ to $P_{D7}$ cruises. Consequently, it was not possible to detect differences in size classes between disturbed and undisturbed sediments or recruitment events in e.g. echinoderms (Ruhl, 2007) following the DISCOL experiment. Instead, we used fixed conversion factors for the different taxa for the entire time series.

**4.2 Feeding-type specific differences in recovery**

25   Eight years before the experimental disturbance experiment was conducted at the DISCOL area, Jumars (1981) qualitatively predicted the response of different feeding types in the benthic community to polymetallic nodule removal. Although several seabed test mining or mining simulations were performed since then (Jones et al., 2017), no study compared or verified these conceptual predictions on feeding-type specific differences in recovery from deep-sea mining. As few comparative studies are available, we compare here our food-web model results with those of the conceptual model predictions for scavengers, surface
30   and subsurface deposit feeders and suspension feeders by Jumars (1981).

15

Jumars (1981) predicted that organisms inside the mining tracks would be killed either by the fluid shear of the dredge/ plough or by abrasion and increased temperatures inside the rising pipe with a mortality rate of >95%. In contrast, the impact on mobile and sessile organisms in the vicinity of the tracks would depend on their feeding type (Jumars, 1981).

The author also predicted that the density of mobile scavengers, such as fish and lysianassid amphipods would rise shortly
5   after the disturbance in response to the increased abundance of dying or dead organisms within the mining tracks. Indeed, when plotting the respiration of fish (in mmol C $m^{-1} d^{-1}$) normalized to the fish respiration at the undisturbed sediment at $PD_{0.1}$ over time, the respiration for the undisturbed sediment increased steeply until $PD_3$ and dropped subsequently (Figure 6). However, experiments with baits at PAP and the Porcupine Seabight (NE Atlantic) showed that the scavenging deep-sea fish *Coryphaenoides armatus* intercept bait within 30 min (Collins et al., 1999) and stayed at the food fall for 114±55 min (Collins
10   et al., 1998). Hence, it is very likely that this rise in fish respiration at the undisturbed sediment 0.5 years after the DISCOL is a result of natural variability as opposed to the predicted rise in scavenger density and/ or biomass caused by the mining activity. At the disturbed sediment, no fish were detected at $PD_{0.1}$ or $PD_{0.5}$, which could be related to lack of prey in a potential predator-prey relationship (Bailey et al., 2006). However, because of the relatively small area of disturbed sediment (only 22% of the 10.8 $km^2$ of sediment were ploughed (Thiel and Schriever, 1989)), the low density of deep-sea fish (e.g. between 7.5
15   and 32 ind. $ha^{-1}$ of the dominant fish genus *Coryphaenoides* sp. at Station M (Bailey et al., 2006)) and the high motility of fish, this observation may be coincidental.

Jumars (1981)Our results are unique, as they allowed us for the first time to assess recovery of C cycling in benthic deep-sea food webs from a small-scale sediment disturbance in polymetallic nodule-rich areas. However, the models proposed here come with limitations. Pre-disturbance samples and samples from reference sites were not collected for all food-web
20   compartments. A notable omission is the lack of data for microbes and meiofauna throughout the times series, hence our C cycling models only resolve C cycling by macro- and megafaunal compartments. Another omission is the lack of a baseline to which the 'outside plough track' food web at $PD_{0.1}$ could be compared to assess the impact that the disturbance effect had on sites outside the plough tracks. Hence, we cannot determine whether the high biomass and carbon flows at $PD_3$ were due to the onset of the positive (La Niña) phase of the El Niño Southern Oscillation (Trenberth, 1997), a phenomenon which is known
25   to lead to a comparatively high POC export flux in the Pacific Ocean (e.g. Station M; Ruhl et al., 2008).

Standard procedures to assess invertebrate megafaunal and fish densities have evolved during the 26 yr of post-disturbance monitoring. The OFOS system used 26 yr after the initial DISCOL experiment took pictures automatically every 20 s from a distance of 1.5 m above the seafloor (Boetius, 2015; Stratmann et al., 2018b). By contrast, the OFOS system used in former cruises was towed approximately 3 m above the seafloor, and pictures were taken selectively by the operating scientists (Bluhm
30   and Gebruk, 1999). Therefore, the procedure used in the former cruises very likely overestimated rare and charismatic invertebrate megafauna, and probably underestimated dominant fauna and organisms of small size (<3 cm) for $PD_{0.1}$ to $PD_7$, as compared to $PD_{26}$.

Previous cruises to the DEA focused on monitoring changes in faunal density and diversity, but not on changes in carbon stock. Hence, a major task in this study was to find appropriate conversion factors to convert density into carbon stocks.

However, no individual biomass data for macrofaunal taxa were available for the Peru Basin, so we used data from sampling stations of similar water depths in the eastern Clarion-Clipperton Zone (CCZ, NE Pacific; Sweetman et al. in prep.). As organisms in deep-sea regions with higher organic carbon input are larger than their counterparts from areas with lower organic carbon input (McClain et al., 2012), using individual biomass data from the CCZ, a more oligotrophic region than the Peru

5  Basin (Haeckel et al., 2001; Vanreusel et al., 2016), might have underestimated carbon stocks for macrofauna. However, this potential bias has likely limited impact on the interpretation of the comparative results within the time series, because the same methodology was applied throughout. Moreover, the determination of invertebrate megafaunal carbon stocks were also difficult, as no size measurements were taken from invertebrate megafaunal individuals during the $PD_{0.1}$ to $P_{D7}$ cruises. Consequently, it was not possible to detect differences in size classes between inside and outside plough tracks or recruitment

10  events in, e.g., echinoderms (Ruhl, 2007) following the DISCOL experiment. Instead, we used fixed conversion factors for the different taxa for the entire time series.

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Jumars (1981) predicted that organisms inside the mining tracks would be killed either by the fluid shear of the dredge/ plough

20  or by abrasion and increased temperatures inside the rising pipe with a mortality rate of > 95%. In contrast, the impact on mobile and sessile organisms in the vicinity of the tracks would depend on their feeding type (Jumars, 1981).

The author also predicted that the density of mobile scavengers, such as fish and lysianassid amphipods would rise shortly after the disturbance in response to the increased abundance of dying or dead organisms within the mining tracks. In fact, experiments with baits at PAP and the Porcupine Seabight (NE Atlantic) showed that the scavenging deep-sea fish

25  *Coryphaenoides armatus* intercept bait within 30 min (Collins et al., 1999) and stayed at the food fall for 114±55 min (Collins et al., 1998). Therefore, the absence of fish inside plough tracks during $PD_{0.1}$ and $PD_{0.5}$ could be related to a lack of prey in a potential predator-prey relationship (Bailey et al., 2006). However, because of the relatively small area of plough tracks (only 22% of the 10.8 $km^2$ of sediment were ploughed; Thiel *et al.*, 1989), the low density of deep-sea fish (e.g., between 7.5 and 32 ind. $ha^{-1}$ of the dominant fish genus *Coryphaenoides* sp. at Station M; Bailey, Ruhl and Smith, 2006) and the high motility

30  of fish, this observation is likely coincidental.

Jumars (1981) predicted that, on a short term, subsurface deposit feeders outside the mining tracks would be the least impacted feeding type, because of their relative isolation from the re-settled sediment, and their relative independence of organic matter

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on the sediment surface, whereas subsurface deposit feeders inside the mining tracks would experience high mortality. For the long-term recovery, the author pointed to the dependence of subsurface deposit feeders on bacterial production in the sediment covered with re-~~resettled sediment. In our food~~ settled sediment. Moreover, this newly settling sediment would alter both sediment composition and food concentration in the sediment. As the total rate of sediment deposition would increase both

5  inside and beyond mining tracks, Jumars (1981) anticipated that surface deposit feeders would endure stronger impacts from deep-sea mining activities compared with sub-surface deposit feeders.

In our food-web model, sub-surface and surface deposit feeders were grouped into the deposit feeder category, except for polychaetes, for which we kept the surface-subsurface distinction. ~~The biomass of PolSSDF fluctuated by one order of magnitude over the 26-year time series and had high biomass values at the undisturbed PD$_{0.1}$ site, the disturbed PD$_3$ sites and~~

10  ~~at both sites at PD$_7$. The normalized respiration of PolSSDF also showed strong fluctuations at the undisturbed and disturbed sites over time (Figure 6) indicating a large natural variability or variable sampling results. Such temporal dynamics in deep-sea macrofauna were detected at Station M, where the density of several dominating metazoan macrofauna increased eight months after a peak in POC flux was measured at 50 and 600 m above the seafloor (Drazen et al., 1998). Hence, Jumars (1981) predictions for sub-surface deposit feeders could not be tested, provided the natural fluctuations in PolSSDF densities that~~

15  ~~were used to calculate biomass~~The carbon stock of PolSSDF fluctuated by one order of magnitude over the 26 yr time series and had high carbon stock values outside plough tracks during PD$_{0.1}$, inside plough tracks during PD$_3$ and inside and outside plough tracks during PD$_7$. Hence, Jumars' (1981) predictions for sub-surface deposit feeders are difficult to test, but Hedges' *d* for PolSSDF was |1.47| at PD$_{0.1}$ and decreased steadily to |0.66| at PD$_7$ (Supplement 3), indicating a very strong experimental effect after the disturbance event and a logarithmic recovery over time. In comparison, the recovery of surface deposit feeders

20  might be delayed, owing to potential unfavorable food conditions as Stratmann et al. (2018b) hypothesized in a study about holothurian densities at the DISCOL experimental area.

~~Jumars (1981) anticipated that surface deposit feeders would suffer more strongly from deep-sea mining activities compared to sub-surface deposit feeders because the rate of sediment deposition would increase inside and beyond mining tracks, with this newly settling sediment altering the sediment composition and food concentration in the sediment. Indeed, the recovery~~

25  ~~of holothurian densities at the DEA was probably delayed owing to unfavourable food conditions (Stratmann et al., in review). Nevertheless, deposit feeders seem to have advantages during the recovery from the DISCOL disturbance experiment. When comparing the contribution of deposit feeders from all size classes (macrofauna, polychaetes, megafauna) to respiration, predation by external predators and faeces production to the contribution of omnivores, filter- and suspension feeders and carnivores, their contribution was always higher at the disturbed site compared to the undisturbed site of the same sampling~~

30  ~~event. However, owing to the overall lower biomass inside the disturbed area compared to the undisturbed area, the absolute carbon respiration (in mmol C m$^{-2}$ d$^{-1}$) remained lower for deposit feeders at the disturbed site compared to the corresponding undisturbed site, even after 26 years when this difference was 2.6%.~~

~~Jumars (1981) expected that the suspension feeders outside the mining tracks would be negatively affected during the presence of the sediment plumes and/ or as long as their filtration apparatus was clogged by sediment. This "clogging" hypothesis could~~

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not be tested here, because the models did not resolve these unknown changes in faunal physiology, but could only assess carbon cycling differences associated with differences in biomass. Furthermore, Jumars (1981) anticipated that the recovery of nodule-associated organisms, such as filter and suspension feeding Porifera, Antipatharia or Ascidiacea (Vanreusel et al., 2016) would require more than 10,000 years, owing to the slow growth rate of polymetallic nodules (Guichard et al., 1978; Kuhn et al., 2017) and the removal and/ or burial of the nodules. Directly after the initial DISCOL disturbance event, the respiration rate of filter and suspension feeders at the disturbed sediment was only 1% of the respiration rate of this feeding type at the undisturbed sediment. After 26 years, the relative difference in the filter and suspension feeding respiration rate was still 80%. Part of this difference at PD$_{26}$ resulted from the presence of a single specimen of Alcyonacea with a biomass of 4.71 mmol C m$^{-2}$ at the undisturbed site. However, even if we ignore this Alcyonacea specimen in the model, the respiration of suspension and filter feeding in the disturbed site would still be 71% lower compared to the undisturbed site, indicating a slow recovery of this feeding group.

To summarize the comparison of modelled potential recovery of the different feeding types with the predictions by Jumars (1981), scavenging and predatory fish at the undisturbed sediment followed first the predicted density pattern, though this might also have been related to natural variability. After three years, however, the fish contribution to carbon cycling was lower than expected from the predictions. Owing to an apparently strong natural variability in polychaete subsurface deposit feeder biomass, the recovery prognosis for subsurface deposit feeders could not be tested. Furthermore, it could not be assessed whether surface deposit feeders were more strongly affected by the mining activity than subsurface deposit feeders. In general, the time series analysis showed that deposit feeders likely benefited from the disturbance experiment in comparison to other feeding types. Confirming Jumars (1981) prediction, the activity of filter and suspension feeders in the food web did not recover within 26 years.

Jumars (1981) expected that the suspension feeders outside the mining tracks would be negatively affected during the presence of the sediment plumes and/ or as long as their filtration apparatus was clogged by sediment. This "clogging" hypothesis could not be tested here, because the models did not resolve these unknown changes in faunal physiology, so we could only assess carbon cycling differences associated with differences in carbon stocks. Furthermore, Jumars (1981) anticipated that the recovery of nodule-associated organisms, such as filter and suspension feeding Porifera, Antipatharia or Ascidiacea (Vanreusel et al., 2016) would require more than 10,000 years, owing to the slow growth rate of polymetallic nodules (Guichard et al., 1978; Kuhn et al., 2017) and the removal and/ or burial of the nodules. This hypothesis could not be tested directly, because nodules were not removed in this experiment, but only ploughed into the sediment. However, the disappearance of nodules from the sediment surface will likely have the same effect on sessile epifauna that depend on nodules as hard substrate independently of the method by which the nodules disappeared. Immediately after the initial DISCOL disturbance event, the respiration rate of filter and suspension feeders inside plough tracks was only 1% of the respiration rate of this feeding type outside plough tracks. After 26 yr, the total respiration rate of filter- and suspension feeders inside plough tracks was still 80% lower than in the outside plough tracks. Part of this difference at PD$_{26}$ resulted from the presence of a single specimen of Alcyonacea with a biomass of 4.71 mmol C m$^{-2}$ outside plough tracks. Even if we ignore this Alcyonacea specimen in the

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model, the respiration of suspension and filter feeding inside plough tracks would still be 71% lower compared to outside plough tracks, indicating a slow recovery of this feeding group.

## 5 Conclusion

Deep-sea mining will negatively impact ~~the~~abyssal benthic ~~ecosystem of abyssal~~ ecosystems. It is therefore important to be able to estimate how long ~~the~~ recovery of the ecosystem after a deep-sea mining operation will take. This study used the linear inverse modelling technique to compare the carbon flows between different food-web compartments ~~at undisturbed~~outside and ~~disturbed sites~~inside plough tracks at the DISCOL experimental area in the Peru Basin over a period of 26 ~~years~~ yr. Even after 26 ~~years, the~~ yr, total faunal ~~biomass~~carbon stock and ~~the~~ total food-web activity (i.e~~.~~., summed carbon cycling) ~~at the disturbed sites~~inside plough tracks was only approximately half (54% and 56% respectively) of ~~the~~ total faunal ~~biomass~~carbon stock and food-web activity ~~at the undisturbed sites.~~outside plough tracks. Deposit feeders were the least impacted by the sediment disturbance, with less than 3% relative difference in total carbon loss (i.e~~.~~., respiration, external predation and feces production) between ~~undisturbed~~outside and ~~disturbed sites~~inside plough tracks after 26 ~~years~~ yr. In contrast, filter and suspension feeders ~~did not recover at all~~recovered less and the relative difference in respiration ~~rate~~rates between inside and outside plough tracks was 79%. Overall, ~~it can be concluded that~~ ecosystem ~~functioning~~function (as measured by total carbon cycling) within the macrofauna, invertebrate megafauna and fish has not fully recovered 26 ~~years~~ yr after the experimental disturbance.

## Data availability

~~Data~~Conversion factors used to calculate taxon-specific megafaunal biomasses data on ~~biomass~~carbon stocks of the different food-web compartments are presented in Supplement- 1. Stocks of the various food-web compartments are presented in Supplement 2. Data on ~~Hedge's~~Hedges' *d*, the corresponding standard deviations, weighted ~~Hedge's~~Hedges' *d*, and weighted standard deviation are presented in Supplement-2 3. The mean and standard deviations calculated for each carbon flux over 100,000 iterations for all food webs from ~~the undisturbed~~outside and ~~disturbed site~~inside plough tracks for all time steps is presented in Supplement-3 4. All OFOS images associated with this article are available ~~from~~at the PANGAEA storage archive. (https://doi.pangaea.de/10.1594/PANGAEA.890634).

## Authors contribution

TS went through the published literature for data input to the model, LL, AP, YM, CR, AR, MRC, ESL, AKS, DOBJ and KK contributed data, TS and DvO developed the food web models, TS and DvO wrote the manuscript with input from all co-authors.

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**References**

~~Amon, D. J., Hilario, A., Arbizu, P. M., and Smith, C. R.: Observations of organic falls from the abyssal Clarion-Clipperton Zone in the tropical eastern Pacific Ocean, Mar. Biodivers., 47, 311-321, 2017.~~
~~Bailey, D. M., Ruhl, H., and Smith, K.: Long-term change in benthopelagic fish abundance in the abyssal northeast Pacific Ocean, Ecology, 87, 549-555, 2006.~~
~~Bluhm, H., and Gebruk, A.: Holothuroidea (Echinodermata) of the Peru Basin-Ecological and Taxonomic Remarks Based on Underwater Images, Mar. Ecol., 20, 167-195, 1999.~~
~~Bluhm, H.: Re-establishment of an abyssal megabenthic community after experimental physical disturbance of the seafloor, Deep-Sea Res. II, 48, 3841-3868, 2001.~~
~~Boetius, A.: RV SONNE Fahrtbericht/Cruise Report SO242-2: JPI OCEANS Ecological Aspects of Deep-Sea Mining, DISCOL Revisited, Guayaquil-Guayaquil (Equador), 28.08.-01.10. 2015., 2015.~~
~~Borowski, C., and Thiel, H.: Deep-sea macrofaunal impacts of a large-scale physical disturbance experiment in the Southeast Pacific, Deep-Sea Res. II, 45, 55-81, 1998.~~
~~Borowski, C.: Physically disturbed deep-sea macrofauna in the Peru Basin, southeast Pacific, revisited 7 years after the experimental impact, Deep-Sea Res. II, 48, 3809-3839, 2001.~~
~~Brey, T., Müller-Wiegmann, C., Zittier, Z. M., and Hagen, W.: Body composition in aquatic organisms—a global data bank of relationships between mass, elemental composition and energy content, J. Sea Res., 64, 334-340, 2010.~~
~~Childress, J. J., Taylor, S. M., Cailliet, G. M., and Price, M. H.: Patterns of growth, energy utilization and reproduction in some meso-and bathypelagic fishes off southern California, Mar. Biol., 61, 27-40, 1980.~~
~~Clausen, I., and Riisgård, H.: Growth, filtration and respiration in the mussel Mytilus edulis: no evidence for physiological regulation of the filter-pump to nutritional needs, Mar. Ecol. Prog. Ser., 141, 37-45, 1996.~~
~~Cohen, J.: Statistical power analysis for the behavioral sciences, 2nd ed. ed., Lawrence Erlbaum Associates, Publishers, Mahwah, NJ, 1988.~~
~~Collins, M., Priede, I. G., Addison, S., Smith, A., and Bagley, P. M.: Acoustic tracking of the dispersal of organic matter by scavenging fishes in the deep-sea, Hydrobiologia, 371/372, 181-186, 1998.~~
~~Collins, M., Bailey, D., Ruxton, G., and Priede, I.: Trends in body size across an environmental gradient: a differential response in scavenging and non-scavenging demersal deep-sea fish, Proc. R. Soc. B, 272, 2051-2057, 2005.~~
~~Collins, M. A., Priede, I. G., and Bagley, P. M.: In situ comparison of activity in two deep-sea scavenging fishes occupying different depth zones, Proc. R. Soc. Lond. B Biol. Sci., 266, 2011-2016, 1999.~~

21

Crisp, D.: Energy flow measurements, in: Methods for the study of marine benthos, 1 ed., edited by: Holme, N. A., and McIntyre, A. D., Blackwell Scientific Publications, Oxford, 284-367, 1971.

Devey, C. W., Augustin, N., Brandt, A., Brenke, N., Köhler, J., Lins, L., Schmidt, C., and Yeo, I. A.: Habitat characterization of the Vema Fracture Zone and Puerto Rico Trench, Deep-Sea Res. II, 2018.

5  Drazen, J. C., Baldwin, R. J., and Smith Jr, K. L.: Sediment community response to a temporally varying food supply at an abyssal station in the NE Pacific, Deep-Sea Res. II, 45, 893-913, 1998.

Drazen, J. C., Reisenbichler, K. R., and Robison, B. H.: A comparison of absorption and assimilation efficiencies between four species of shallow-and deep-living fishes, Mar. Biol., 151, 1551-1558, 2007.

Drazen, J. C., and Sutton, T. T.: Dining in the deep: the feeding ecology of deep-sea fishes, Ann. Rev. Mar. Sci., 9, 337-366, 2017.

10  Dunlop, K. M., van Oevelen, D., Ruhl, H. A., Huffard, C. L., Kuhnz, L. A., and Smith, K. L.: Carbon cycling in the deep eastern North Pacific benthic food web: Investigating the effect of organic carbon input, Limnol. Oceanogr., 61, 1956-1968, 2016.

Durden, J. M., Bett, B. J., Horton, T., Serpell-Stevens, A., Morris, K. J., Billett, D. S., and Ruhl, H. A.: Improving the estimation of deep-sea megabenthos biomass: dimension to wet weight conversions for abyssal invertebrates, Mar. Ecol. Prog. Ser., 552, 71-79, 2016.

Durden, J. M., Ruhl, H. A., Pebody, C., Blackbird, S. J., and van Oevelen, D.: Differences in the carbon flows in the benthic food webs of

15  abyssal hill and plain habitats, Limnol. Oceanogr., 62, 1771-1782, 10.1002/lno.10532, 2017.

Foell, E., Thiel, H., and Schriever, G.: DISCOL: a long-term, large-scale, disturbance-recolonization experiment in the abyssal eastern tropical South Pacific Ocean, Offshore Technology Conference, 1990, 1990.

Foell, E., Thiel, H., and Schriever, G.: DISCOL: a long-term, large-scale, disturbance-recolonization experiment in the abyssal eastern tropical South Pacific Ocean. , Min. Eng., 44, 90-94, 1992.

20  Fox, R., Barnes, R. D., and Ruppert, E. E.: Invertebrate Zoology: A Functional Evolutionary Approach, 7 ed., Brooks/ Cole Thompson Learning, Belmont, California, 2003.

Froese, R., Thorson, J. T., and Reyes, R.: A Bayesian approach for estimating length-weight relationships in fishes, J. Appl. Ichthyol., 30, 78-85, 2014.

FishBase  www.fishbase.org, access: 2018/02/21, 2017.

25  Gage, J. D., and Tyler, P. A.: Deep-sea biology: a natural history of organisms at the deep-sea floor, Cambridge University Press, 1991.

Gollner, S., Kaiser, S., Menzel, L., Jones, D. O., Brown, A., Mestre, N. C., van Oevelen, D., Menot, L., Colaço, A., and Canals, M.: Resilience of benthic deep-sea fauna to mining activities, Mar. Environ. Res., 129, 76-101, 10.1016/j.marenvres.2017.04.010, 2017.

Greinert, J.: RV SONNE Fahrtbericht/ Cruise Report SO242-1 - JPI OCEANS Ecological Aspects of Deep-Sea Mining - DISCOL Revisited, GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, Kiel, 290, 2015.

30  Guichard, F., Reyss, J. L., and Yokoyama, Y.: Growth rate of manganese nodule measured with 10Be and 26Al, Nature, 272, 155-156, 10.1038/272155a0, 1978.

Haeckel, M., König, I., Riech, V., Weber, M. E., and Suess, E.: Pore water profiles and numerical modelling of biogeochemical processes in Peru Basin deep-sea sediments, Deep-Sea Res. II, 48, 3713-3736, 2001.

Hedges, L. V., and Olkin, I.: Estimation of a single effect size: Parametric and nonparametric methods, in: Statistical methods for meta-

35  analysis, Academic Press, Inc., Orlando, 75-106, 1985a.

Hedges, L. V., and Olkin, I.: Parametric estimation of effect size from a series of experiments, in: Statistical methods for meta-analysis, Academic Press, Inc., Orlando, 107-145, 1985b.

Hein, J. R., Mizell, K., Koschinsky, A., and Conrad, T. A.: Deep-ocean mineral deposits as a source of critical metals for high-and green-technology applications: Comparison with land-based resources, Ore Geol. Rev., 51, 1-14, 2013.

40  Jones, D. O., Kaiser, S., Sweetman, A. K., Smith, C. R., Menot, L., Vink, A., Trueblood, D., Greinert, J., Billett, D. S., Martinez Arbizu, P., Radziejewska, T., Singh, R., Ingole, B., Stratmann, T., Simon-Lledo, E., Durden, J. M., and Clark, M. R.: Biological responses to disturbance from simulated deep-sea polymetallic nodule mining, PloS One, 12, e0171750, 10.1371/journal.pone.0171750, 2017.

Jumars, P. A.: Limits in predicting and detecting benthic community responses to manganese nodule mining, Mar. Min., 3, 213-229, 1981.

Jumars, P. A., Dorgan, K. M., and Lindsay, S. M.: Diet of worms emended: an update of polychaete feeding guilds, Ann. Rev. Mar. Sci., 7,

45  497-520, 2015.

Kidd, R., and Huggett, Q.: Rock debris on abyssal plains in the northeast Atlantic-a comparison of epibenthic sledge hauls and photographic surveys, Oceanol. Acta, 4, 99-104, 1981.

Klepper, O., and Van de Kamer, J.: The use of mass balances to test and improve the estimates of carbon fluxes in an ecosystem, Math. Biosci., 85, 37-49, 1987.

50  Kones, J. K., Soetaert, K., van Oevelen, D., and Owino, J. O.: Are network indices robust indicators of food web functioning? A monte carlo approach, Ecol. Model. , 220, 370-382, 2009.

Koopmans, M., Martens, D., and Wijffels, R. H.: Growth efficiency and carbon balance for the sponge Haliclona oculata, Mar. Biotechnol., 12, 340-349, 2010.

Koricheva, J., Gurevitch, J., and Mengersen, K.: Handbook of meta-analysis in ecology and evolution, Princeton University Press, Princeton,

55  2013.

Kuhn, T., Wegorzewski, A., Rühlemann, C., and Vink, A.: Composition, Formation, and Occurrence of Polymetallic Nodules, in: Deep-Sea Mining, Springer, 23-63, 2017.

Kwasnitschka, T., Köser, K., Sticklus, J., Rothenbeck, M., Weiß, T., Wenzlaff, E., Schoening, T., Triebe, L., Steinführer, A., and Devey, C.: DeepSurveyCam—a deep ocean optical mapping system, Sensors, 16, 164, 2016.

5  Langenkämper, D., Zurowietz, M., Schoening, T., and Nattkemper, T. W.: BIIGLE 2.0-Browsing and Annotating Large Marine Image Collections, Front. Mar. Sci., 4, 83, 2017.

Levin, L. A., Mengerink, K., Gjerde, K. M., Rowden, A. A., Van Dover, C. L., Clark, M. R., Ramirez-Llodra, E., Currie, B., Smith, C. R., Sato, K. N., Gallo, N., Sweetman, A. K., Lily, H., Armstrong, C. W., and Brider, J.: Defining "serious harm" to the marine environment in the context of deep-seabed mining, Mar. Policy, 74, 245-259, 2016.

10 Mahaut, M.-L., Sibuet, M., and Shirayama, Y.: Weight-dependent respiration rates in deep-sea organisms, Deep-Sea Res. I, 42, 1575-1582, 1995.

Marcon, Y., and Purser, A.: PAPARA (ZZ) I: An open-source software interface for annotating photographs of the deep-sea, SoftwareX, 6, 69-80, 2017.

McClain, C. R., Allen, A. P., Tittensor, D. P., and Rex, M. A.: Energetics of life on the deep seafloor, PNAS, 109, 15366-15371, 2012.

15 Menzies, R. J.: On the food and feeding habits of abyssal organisms as exemplified by the Isopoda, Int. Rev. Hydrobiol., 47, 339-358, 1962.

Mondal, S. K.: Effect of temperature and body size on food utilization in the marine pearl oyster Pinctada fucata (Bivalvia: Pteridae), Indian J. of Mar. Sci., 35, 43-49, 2006.

Navarro, E., Iglesias, J. I. P., Ortega, M. M., and Larretxea, X.: The Basis for a Functional Response to Variable Food Quantity and Quality in Cockles Cerastoderma edule (Bivalvia, Cardiidae), Physiol. Zool., 67, 468-496, 1994.

20 Nielsen, A. M., Eriksen, N. T., Iversen, J. J. L., and Riisgard, H. U.: Feeding, growth and respiration in the polychaetes Nereis diversicolor (facultative filter-feeder) and N. virens (omnivorous) – a comparative study, Mar. Ecol. Prog. Ser., 125, 149-158, 10.3354/meps125149, 1995.

R-Core-Team: R: A language and environment for statistical computing R Foundation for Statistical Computing, Vienna, 2016.

Radziejewska, T.: Characteristics of the sub-equatorial North-Eastern Pacific Ocean's abyss, with a particular reference to the Clarion-Clipperton Fracture Zone, in: Meiobenthos in the sub-equatorial Pacific abyss, Springer, Heidelberg, 13-28, 2014.

25 Ramirez-Llodra, E., Brandt, A., Danovaro, R., De Mol, B., Escobar, E., German, C., Levin, L., Arbizu, P., Menot, L., and Buhl-Mortensen, P.: Deep, diverse and definitely different: unique attributes of the world's largest ecosystem, Biogeosciences, 7, 2851-2899, 2010.

Ramirez-Llodra, E., Tyler, P. A., Baker, M. C., Bergstad, O. A., Clark, M. R., Escobar, E., Levin, L. A., Menot, L., Rowden, A. A., and Smith, C. R.: Man and the last great wilderness: human impact on the deep sea, PLoS One, 6, e22588, 2011.

30 Randall, R.: Using allometry with fish size to estimate production to biomass (P/B) ratios of salmonid populations, Ecol. Freshw. Fish, 11, 196-202, 2002.

Rex, M. A., Etter, R. J., Morris, J. S., Crouse, J., McClain, C. R., Johnson, N. A., Stuart, C. T., Deming, J. W., Thies, R., and Avery, R.: Global bathymetric patterns of standing stock and body size in the deep-sea benthos, Mar. Ecol. Prog. Ser., 317, 1, 2006.

Rowe, G. T.: Biomass and production of the deep-sea macrobenthos, in: Deep-Sea Biology, edited by: Rowe, G. T., The Sea, John Wiley & Sons, Inc., New York, 1983.

35 Ruhl, H. A.: Abundance and size distribution dynamics of abyssal epibenthic megafauna in the northeast Pacific, Ecology, 88, 1250-1262, 2007.

Ruhl, H. A., Ellena, J. A., and Smith, K. L.: Connections between climate, food limitation, and carbon cycling in abyssal sediment communities, P. Natl. Acad. Sci. USA, 105, 17006-17011, 2008.

40 Smith, A. B., and Stockley, B.: The geological history of deep-sea colonization by echinoids: roles of surface productivity and deep-water ventilation, Proc. R. Soc. B, 272, 865-869, 2005.

Smith, C. R., De Leo, F. C., Bernardino, A. F., Sweetman, A. K., and Arbizu, P. M.: Abyssal food limitation, ecosystem structure and climate change, Trends Ecol. Evol., 23, 518-528, 2008.

Smith, K., and Hessler, R.: Respiration of benthopelagic fishes: in situ measurements at 1230 meters, Science, 184, 72-73, 1974.

45 Stratmann, T., Mevenkamp, L., Sweetman, A. K., Vanreusel, A., and van Oevelen, D.: Has phytodetritus processing by an abyssal soft-sediment community recovered 26 years after an experimental disturbance?, Front. Mar. Sci., 5, 10.3389/fmars.2018.00059, 2018.

Stratmann, T., Soetaert, K., Wei, C.-L., and van Oevelen, D.: Global patterns of energy partitioning within the seafloor ecosystems show longitudinal and depth gradient, Global Ecol. Biogeogr., in prep.

Stratmann, T., Voorsmit, I., Gebruk, A., Brown, A., Purser, A., Marcon, Y., Sweetman, A. K., Jones, D. O., and van Oevelen, D.: Recovery of Holothuroidea population density, community composition and respiration activity after a deep-sea disturbance experiment, Limnol. Oceanogr., in review.

Sweetman, A. K., Smith, C. R., Shulse, C. N., Maillot, B., Lindh, M., Church, M. J., Meyer, K., van Oevelen, D., Stratmann, T., and Gooday, A. J.: Key role of bacteria in the short-term cycling of carbon at the abyssal seafloor, Limnol. Oceanogr., in review.

Thiel, H., and Schriever, G.: Cruise report DISCOL 1, Sonne-Cruise 61, Institut für Hydrobiologie und Fischereiwissenschaft der Universität Hamburg, Hamburg, 1989.

Thiel, H., and Tiefsee-Umweltschutz, F.: Evaluation of the environmental consequences of polymetallic nodule mining based on the results of the TUSCH Research Association, Deep-Sea Res. II, 48, 3433-3452, 2001.

Tilot, V.: La structure des assemblages mégabenthiques d'une province à nodules polymétalliques de l'Océan Pacifique tropical Est, PhD, Department de l'Environnement Profund, Direction des Recherches Oceaniques, IFREMER/ Centre de Brest, Universite de Bretagne occidentale, Plouzane, 1992.

5 van Oevelen, D., Van den Meersche, K., Meysman, F. J., Soetaert, K., Middelburg, J. J., and Vézina, A. F.: Quantifying food web flows using linear inverse models, Ecosystems, 13, 32-45, 2010.

van Oevelen, D., Soetaert, K., García, R., De Stigter, H. C., Cunha, M. R., Pusceddu, A., and Danovaro, R.: Canyon conditions impact carbon flows in food webs of three sections of the Nazaré canyon, Deep-Sea Res. II, 58, 2461-2476, 2011.

10 Vanreusel, A., Hilario, A., Ribeiro, P. A., Menot, L., and Martinez Arbizu, P.: Threatened by mining, polymetallic noduels are required to preserve abyssal epifauna, Sci. Rep., 6, 26808, 10.1038/srep26808, 2016.

Vézina, A. F., and Platt, T.: Food web dynamics in the ocean. I. Best-estimates of flow networks using inverse methods, Mar. Ecol. Prog. Ser., 269-287, 1988.

15

**Table 1.** ~~Taxon-specific biomass per individual (mmol C ind⁻¹) for macrofauna and megafauna including the specific feeding types.~~ Amon, D. J., Hilário, A., Martínez Arbizu, P. and Smith, C. R.: Observations of organic falls from the abyssal Clarion-Clipperton Zone in the tropical eastern Pacific Ocean, Mar. Biodivers., 47, 311–321, doi:10.1007/s12526-016-0572-4, 2017.

Bailey, D. M., Ruhl, H. A. and Smith, K. L.: Long-term change in benthopelagic fish abundance in the abyssal northeast Pacific Ocean, Ecology, 87, 549–555, doi:10.1890/04-1832, 2006.

Bluhm, H.: Re-establishment of an abyssal megabenthic community after experimental physical disturbance of the seafloor, Deep. Res. II, 48, 3841–3868, doi:10.1016/S0967-0645(01)00070-4, 2001.

Bluhm, H. and Gebruk, A. V.: Holothuroidea (Echinodermata) of the Peru Basin - ecological and taxonomic remarks based on underwater images, Mar. Ecol., 20, 167–195, doi:10.1046/j.1439-0485.1999.00072.x, 1999.

Boetius, A.: RV SONNE SO242/2. Cruise Report/Fahrtbericht. DISCOL revisited. Guayaquil: 28 August 2015 - Guayaquil: 1 October 2015. SO242/2: JPI Oceans Ecological Aspects of Deep-Sea Mining., Bremen., 2015.

Borowski, C.: Physically disturbed deep-sea macrofauna in the Peru Basin, southeast Pacific, revisited 7 years after the experimental impact, Deep. Res. II, 48, 3809–3839, doi:10.1016/S0967-0645(01)00069-8, 2001.

Borowski, C. and Thiel, H.: Deep-sea macrofaunal impacts of a large-scale physical disturbance experiment in the Southeast Pacific, Deep. Res. II, 45, 55–81, doi:10.1016/S0967-0645(97)00073-8, 1998.

Brey, T., Müller-Wiegmann, C., Zittier, Z. M. C. and Hagen, W.: Body composition in aquatic organisms - A global data bank of relationships between mass, elemental composition and energy content, J. Sea Res., 64, 334–340, doi:10.1016/j.seares.2010.05.002, 2010.

Childress, J. J., Taylor, S. M., Cailliert, G. M. and Price, M. H.: Patterns of growth, energy utilization and reproduction in some meso- and bathypelagic fishes off Southern California, Mar. Biol., 61, 27–40, 1980.

Clausen, I. and Riisgård, H. U.: Growth, filtration and respiration in the mussel *Mytilus edulis*: No evidence for physiological regulation of the filter-pump to nutritional needs, Mar. Ecol. Prog. Ser., 141, 37–45, doi:10.3354/meps141037, 1996.

Cohen, J.: Statistical power analysis for the behavioral sciences, 2nd ed., Lawrence Erlbaum Associates, Publishers, Mahwah, NJ., 1988.

Collins, M. A., Priede, I. G., Addison, S., Smith, A. and Bagley, P. M.: Acoustic tracking of the dispersal of organic matter by scavenging fishes in the deep-sea, Hydrobiologia, 371/372, 181–186, doi:10.1023/A:1017083107914, 1998.

Collins, M. A., Priede, I. G. and Bagley, P. M.: *In situ* comparison of activity in two deep-sea scavenging fishes occupying different depth zones, Proc. R. Soc. B Biol. Sci., 266, 2011–2016, doi:10.1098/rspb.1999.0879, 1999.

Collins, M. A., Bailey, D. M., Ruxton, G. D. and Priede, I. G.: Trends in body size across an environmental gradient: A differential response in scavenging and non-scavenging demersal deep-sea fish, Proc. R. Soc. B Biol. Sci., 272, 2051–2057, doi:10.1098/rspb.2005.3189, 2005.

Crisp, D.: Energy flow measurements, in Methods for the Study of Marine Benthos, edited by N. A. Holme and A. D. McIntyre, pp. 284–367, Blackwell Scientific Publications, Oxford., 1971.

Devey, C. W., Augustin, N., Brandt, A., Brenke, N., Köhler, J., Lins, L., Schmidt, C. and Yeo, I. A.: Habitat characterization of the Vema Fracture Zone and Puerto Rico Trench, Deep. Res. II, 148, 7–20, doi:10.1016/j.dsr2.2018.02.003, 2018.

Drazen, J. C. and Sutton, T. T.: Dining in the deep: The feeding ecology of deep-sea fishes, Ann. Rev. Mar. Sci., 9, 337–366, doi:10.1146/annurev-marine-010816-060543, 2017.

Drazen, J. C., Reisenbichler, K. R. and Robison, B. H.: A comparison of absorption and assimilation efficiencies between four species of shallow- and deep-living fishes, Mar. Biol., 151, 1551–1558, doi:10.1007/s00227-006-0596-6, 2007.

Dunlop, K. M., van Oevelen, D., Ruhl, H. A., Huffard, C. L., Kuhnz, L. A. and Smith, K. L.: Carbon cycling in the deep eastern North Pacific benthic food web: Investigating the effect of organic carbon input, Limnol. Oceanogr., 61, 1956–1968, doi:10.1002/lno.10345, 2016.

Durden, J. M., Bett, B. J., Horton, T., Serpell-Stevens, A., Morris, K. J., Billett, D. S. M. and Ruhl, H. A.: Improving the estimation of deep-sea megabenthos biomass: Dimension to wet weight conversions for abyssal invertebrates, Mar. Ecol. Prog. Ser., 552, 71–79, doi:10.3354/meps11769, 2016.

Durden, J. M., Ruhl, H. A., Pebody, C. A., Blackbird, S. J. and van Oevelen, D.: Differences in the carbon flows in the benthic food webs of abyssal hill and plain habitats, Limnol. Oceanogr., 62, 1771–1782, doi:10.1002/lno.10532, 2017.

Foell, E. J., Thiel, H. and Schriever, G.: DISCOL: A long-term, large-scale, disturbance-recolonization experiment in the abyssal eastern tropical south Pacific Ocean, , 497–503, 1990.

Foell, E. J., Thiel, H. and Schriever, G.: DISCOL: A long-term, large-scale disturbance-recolonization experiment in the

abyssal eastern tropical South Pacific Ocean, Mar. Eng., 90–94, 1992.

Fox, R., Barnes, R. D. and Ruppert, E. E.: Invertebrate Zoology: A functional evolutionary approach, Brooks/ Cole Thompson Learning, Belmont, California., 2003.

Froese, R. and Pauly, D.: FishBase, [online] Available from: www.fishbase.org (Accessed 21 February 2018), 2017.

Froese, R., Thorson, J. T. and Reyes, R. B.: A Bayesian approach for estimating length-weight relationships in fishes, J. Appl. Ichthyol., 30, 78–85, doi:10.1111/jai.12299, 2014.

Gage, J. D. and Tyler, P. A.: Deep-sea biology: A natural history of organisms at the deep-sea floor, Cambridge University Press, Cambridge, UK., 1991.

Gollner, S., Kaiser, S., Menzel, L., Jones, D. O. B., Brown, A., Mestre, N. C., van Oevelen, D., Menot, L., Colaço, A., Canals, M., Cuvelier, D., Durden, J. M., Gebruk, A. V., Egho, G. A., Haeckel, M., Marcon, Y., Mevenkamp, L., Morato, T., Pham, C. K., Purser, A., Sanchez-Vidal, A., Vanreusel, A., Vink, A. and Martínez Arbizu, P.: Resilience of benthic deep-sea fauna to mining activities, Mar. Environ. Res., 129, 76–101, doi:10.1016/j.marenvres.2017.04.010, 2017.

Greinert, J., Ed.: RV Sonne Fahrtbericht/ Cruise Report SO242-1. JPI OCEANS Ecological aspects of deep-sea mining. DISCOL revisited, GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, Kiel., 2015.

Guichard, F., Reyss, J.-L. and Yokoyama, Y.: Growth rate of manganese nodule measured with [10]Be and [26]Al, Nature, 272, 155–156, doi:10.1038/272155a0, 1978.

Haeckel, M., König, I., Riech, V., Weber, M. E. and Suess, E.: Pore water profiles and numerical modelling of biogeochemical processes in Peru Basin deep-sea sediments, Deep. Res. I, 48, 3713–3736, 2001.

Hedges, L. V. and Olkin, I.: Estimation of a single effect size: Parametric and non parametric methods, in Statistical Methods for Meta-Analysis, pp. 75–106, Academic Press, Inc., Orlando., 1985a.

Hedges, L. V. and Olkin, I.: Parametric estimation of effect size from a series of experiments, in Statistical Methods for Meta-Analysis, pp. 107–145, Academic Press, Inc., Orlando., 1985b.

Hein, J. R., Mizell, K., Koschinsky, A. and Conrad, T. A.: Deep-ocean mineral deposits as a source of critical metals for high- and green-technology applications: Comparison with land-based resources, Ore Geol. Rev., 51, 1–14, doi:10.1016/j.oregeorev.2012.12.001, 2013.

Jones, D. O. B., Kaiser, S., Sweetman, A. K., Smith, C. R., Menot, L., Vink, A., Trueblood, D., Greinert, J., Billett, D. S. M., Martínez Arbizu, P., Radziejewska, T., Singh, R., Ingole, B., Stratmann, T., Simon-Lledó, E., Durden, J. M. and Clark, M. R.: Biological responses to disturbance from simulated deep-sea polymetallic nodule mining, PLoS One, 12, e0171750, doi:10.1371/journal.pone.0171750, 2017.

Jumars, P. A.: Limits in predicting and detecting benthic community responses to manganese nodule mining, Mar. Min., 3, 213–229, 1981.

Jumars, P. A., Dorgan, K. M. and Lindsay, S. M.: Diet of worms emended: An update of polychaete feeding guilds, Ann. Rev. Mar. Sci., 7, 497–520, doi:10.1146/annurev-marine-010814-020007, 2015.

Kidd, R. B. and Huggett, J.: Rock debris on abyssal plains in the Northeast Atlantic: A comparison of epibenthic sledge hauls and photographic surveys, Oceanol. Acta, 4, 99–104, 1981.

Klepper, O. and Van De Kamer, J. P. G.: The use of mass balances to test and improve the estimates of carbon fluxes in an ecosystem, Math. Biosci., 85, 37–49, doi:10.1016/0025-5564(87)90098-8, 1987.

Kones, J. K., Soetaert, K., van Oevelen, D. and Owino, J. O.: Are network indices robust indicators of food web functioning? A Monte Carlo approach, Ecol. Modell., 220, 370–382, doi:10.1016/j.ecolmodel.2008.10.012, 2009.

Koopmans, M., Martens, D. and Wijffels, R. H.: Growth efficiency and carbon balance for the sponge *Haliclona oculata*, Mar. Biotechnol., 12, 340–349, doi:10.1007/s10126-009-9228-8, 2010.

Koricheva, J., Gurevitch, J. and Mengersen, K.: Handbook of Meta-Analysis in Ecology and Evolution, Princeton University Press, Princeton., 2013.

Kuhn, T., Wegorzewski, A. V., Rühlemann, C. and Vink, A.: Composition, formation, and occurrence of polymetallic nodules, in Deep-Sea Mining, edited by R. Sharma, pp. 23–63, Springer International Publishing, Cham., 2017.

Kwasnitschka, T., Köser, K., Sticklus, J., Rothenbeck, M., Weiß, T., Wenzlaff, E., Schoening, T., Triebe, L., Steinführer, A., Devey, C. W. and Greinert, J.: DeepSurveyCam — a deep ocean optical mapping system, Sensors, 16, doi:10.3390/s16020164, 2016.

Langenkämper, D., Zurowietz, M., Schoening, T. and Nattkemper, T. W.: BIIGLE 2.0 - Browsing and annotating large marine image collections, Front. Mar. Sci., 4, 1–10, doi:10.3389/fmars.2017.00083, 2017.

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Levin, L. A., Mengerink, K. J., Gjerde, K. M., Rowden, A. A., Van Dover, C. L., Clark, M. R., Ramírez-Llodrà, E., Currie, B., Smith, C. R., Sato, K. N., Gallo, N., Sweetman, A. K., Lily, H., Armstrong, C. W. and Brider, J.: Defining "serious harm" to the marine environment in the context of deep-seabed mining, Mar. Policy, 74, 245–259, doi:10.1016/j.marpol.2016.09.032, 2016.

5 Mahaut, M.-L., Sibuet, M. and Shirayama, Y.: Weight-dependent respiration rates in deep-sea organisms, Deep. Res. I, 42, 1575–1582, 1995.

Marcon, Y. and Purser, A.: PAPARA(ZZ)I : An open-source software interface for annotating photographs of the deep-sea, SoftwareX, 6, 69–80, doi:10.1016/j.softx.2017.02.002, 2017.

McClain, C. R., Johnson, N. A. and Rex, M. A.: Morphological disparity as a biodiversity metric in lower bathyal and abyssal
10 gastropod assemblages, Evolution (N. Y)., 58, 338–348, 2004.

McClain, C. R., Allen, A. P., Tittensor, D. P. and Rex, M. A.: Energetics of life on the deep seafloor, Proc. Natl. Acad. Sci., 109, 15366–15371, doi:10.1073/pnas.1208976109, 2012.

Menzies, R. J.: On the food and feeding habits of abyssal organisms as exemplified by the isopoda, Int. Rev. der gesamten Hydrobiol. und Hydrogr., 47, 339–358, doi:10.1002/iroh.19620470303, 1962.

15 Mondal, S.: Effect of temperature and body size on food utilization in the marine pearl oyster *Pinctada fucata* (Bivalvia: Pteridae), Indian J. Mar. Sci., 35, 43–49, 2006.

Navarro, E., Iglesias, J. I. P., Ortega, M. M. and Larretxea, X.: The basis for a functional response to variable food quantity and quality in cockles *Cerastoderma edule* (Bivalvia, Cardiidae), Physiol. Zool., 67, 468–496, 1994.

Nielsen, A. M., Eriksen, N. T., Lønsmann Iversen, J. J. and Riisgård, H. U.: Feeding, growth and respiration in the polychaetes
20 *Nereis diversicolor* (facultative filter-feeder) and *N. virens* (omnivorous) - a comparative study, Mar. Ecol. Prog. Ser., 125, 149–158, doi:10.3354/meps125149, 1995.

van Oevelen, D., Van den Meersche, K., Meysman, F. J. R., Soetaert, K., Middelburg, J. J. and Vézina, A. F.: Quantifying food web flows using linear inverse models, Ecosystems, 13, 32–45, doi:10.1007/s10021-009-9297-6, 2010.

van Oevelen, D., Soetaert, K., García, R., de Stigter, H. C., Cunha, M. R., Pusceddu, A. and Danovaro, R.: Canyon conditions
25 impact carbon flows in food webs of three sections of the Nazaré canyon, Deep. Res. II, 58, 2461–2476, doi:10.1016/j.dsr2.2011.04.009, 2011.

R-Core Team: R: A language and environment for statistical computing, [online] Available from: https://www.r-project.org/, 2017.

Radziejewska, T.: Characteristics of the sub-equatorial north-eastern Pacific Ocean's abyss, with a particular reference to the
30 Clarion-Clipperton Fracture Zone, in Meiobenthos in the Sub-Equatorial Pacific Abyss, pp. 13–28, Springer, Berlin, Heidelberg., 2014.

Ramírez-Llodrà, E., Brandt, A., Danovaro, R., De Mol, B., Escobar-Briones, E., German, C. R., Levin, L. A., Martínez Arbizu, P., Menot, L., Buhl-Mortensen, P., Narayanaswamy, B. E., Smith, C. R., Tittensor, D. P., Tyler, P. A., Vanreusel, A. and Vecchione, M.: Deep, diverse and definitely different: Unique attributes of the world's largest ecosystem, Biogeosciences, 7,
35 2851–2899, doi:10.5194/bg-7-2851-2010, 2010.

Ramírez-Llodrà, E., Tyler, P. A., Baker, M. C., Bergstad, O. A., Clark, M. R., Escobar-Briones, E., Levin, L. A., Menot, L., Rowden, A. A., Smith, C. R. and Van Dover, C. L.: Man and the last great wilderness: Human impact on the deep sea, PLoS One, 6, e22588, doi:10.1371/journal.pone.0022588, 2011.

Randall, R. G.: Using allometry with fish size to estimate production to biomass (P/B) ratios of salmonid populations, Ecol.
40 Freshw. Fish, 11, 196–202, doi:10.1034/j.1600-0633.2002.00012.x, 2002.

Rex, M. A., Etter, R. J., Morris, J. S., Crouse, J., McClain, C. R., Johnson, N. A., Stuart, C. T., Deming, J. W., Thies, R. and Avery, R.: Global bathymetric patterns of standing stock and body size in the deep-sea benthos, Mar. Ecol. Prog. Ser., 317, 1–8, doi:10.3354/meps317001, 2006.

Rowe, G. T.: Biomass and production of the deep-sea macrobenthos, in Deep-Sea Biology, edited by G. T. Rowe, John Wiley
45 & Sons, Inc., New York., 1983.

Ruhl, H. A.: Abundance and size distribution dynamics of abyssal epibenthic megafauna in the northeast Pacific, Ecology, 88, 1250–1262, doi:10.1890/06-0890, 2007.

Ruhl, H. A., Ellena, J. A. and Smith, K. L.: Connections between climate, food limitation, and carbon cycling in abyssal sediment communities, Proc. Natl. Acad. Sci., 105, 17006–17011, doi:10.1073/pnas.0803898105, 2008.

50 Smith, A. B. and Stockley, B.: The geological history of deep-sea colonization by echinoids: Roles of surface productivity and

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deep-water ventilation., Proc. R. Soc. B Biol. Sci., 272, 865–869, doi:10.1098/rspb.2004.2996, 2005.

Smith, C. R., De Leo, F. C., Bernardino, A. F., Sweetman, A. K. and Martínez Arbizu, P.: Abyssal food limitation, ecosystem structure and climate change, Trends Ecol. Evol., 23, 518–528, doi:10.1016/j.tree.2008.05.002, 2008.

Smith, K. L. and Hessler, R. R.: Respiration of benthopelagic fishes: *In situ* measurements at 1230 meters, Science (80-. )., 184, 72–73, 1974.

Stratmann, T., Mevenkamp, L., Sweetman, A. K., Vanreusel, A. and van Oevelen, D.: Has phytodetritus processing by an abyssal soft-sediment community recovered 26 years after an experimental disturbance?, Front. Mar. Sci., 5, 1–13, doi:10.3389/fmars.2018.00059, 2018a.

Stratmann, T., Voorsmit, I., Gebruk, A. V., Brown, A., Purser, A., Marcon, Y., Sweetman, A. K., Jones, D. O. B. and van Oevelen, D.: Recovery of Holothuroidea population density, community composition and respiration activity after a deep-sea disturbance experiment, Limnol. Oceanogr., 00, 00–00, doi:10.1002/lno.10929, 2018b.

Stratmann, T., Soetaert, K., Wei, C.-L. and van Oevelen, D.: The role of benthos in the global marine carbon cycle, Global Biogeochem. Cycles, n.d.

Sweetman, A. K., Smith, C. R., Shulse, C. N., Maillot, B., Lindh, M., Church, M. J., Meyer, K. S., van Oevelen, D., Stratmann, T. and Gooday, A. J.: Key role of bacteria in the short-term cycling of carbon at the abyssal seafloor, Limnol. Oceanogr., n.d.

Thiel, H. and Forschungsverbund Tiefsee-Umweltschutz: Evaluation of the environmental consequences of polymetallic nodule mining based on the results of the TUSCH Research Association, Deep. Res. II, 48, 3433–3452, doi:10.1016/S0967-0645(01)00051-0, 2001.

Thiel, H., Schriever, G., Borowski, C., Bussau, C., Hansen, D., Melles, J., Post, J., Steinkamp, K. and Watson, K.: Cruise Report DISCOL 1, Sonne - Cruise 61. Balboa/ Panama - Calloa/ Peru 02.02. - 05.03.1989; Callao/ Peru - Callao/ Peru 07.03. - 03.04.1989, Hamburg., 1989.

Tilot, V.: La structure des assemblages mégabenthiques d'une province à nodules polymétalliques de l'océan Pacifique tropical est, Université de Bretagne Occidentale, 7 July. [online] Available from: http://archimer.ifremer.fr/doc/00000/3754/, 1992.

Trenberth, K. E.: The definition of El Niño, Bull. Am. Meteorol. Soc., 78, 2771–2777, doi:10.1175/1520-0477(1997)078<2771:TDOENO>2.0.CO;2, 1997.

Vanreusel, A., Hilário, A., Ribeiro, P. A., Menot, L. and Martínez Arbizu, P.: Threatened by mining, polymetallic nodules are required to preserve abyssal epifauna, Sci. Rep., 6, 26808, doi:10.1038/srep26808, 2016.

Vézina, A. F. and Platt, T.: Food web dynamics in the ocean. I. Best-estimates of flow networks using inverse methods, Mar. Ecol. Prog. Ser., 42, 269–287, 1988.

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**Table 1.** Number of box cores ($n_{box\ cores}$) taken for macrofauna sampling outside plough tracks (outside PT) and inside plough tracks (inside PT) directly after the disturbance event in March 1989 ($PD_{0.1}$), 0.5 yr post disturbance (September 1989, $PD_{0.5}$), 3 yr post disturbance (January 1992, $PD_3$), 7 yr post disturbance (February 1996, $PD_7$) and 26 yr post disturbance (September 2015, $PD_{26}$). Number of 'OFOS' tracks ("ocean floor observatory system"; $n_{OFOS\ tracks}$) analyzed to estimate invertebrate megafauna and fish density and total area of seafloor ($m^2$) that was surveyed during each sampling event outside and inside plough tracks.

References: [1](Borowski and Thiel, 1998), [2](Borowski, 2001), [3]this study, [4](Bluhm, 2001).

~~Macrofauna biomass data are based on macrofauna specimen collected in the abyssal plains of the Clarion-Clipperton Zone (NE Pacific) (Sweetman et al., in review). In contrast, megafauna biomass was estimated by converting size-measurements of specific body parts of organisms from DEA that were acquired using photo-annotation into preserved wet weight per organism using the relationships presented in Durden et al. (2016). Subsequently the preserved wet weight was converted into fresh wet weight and biomass following the conversions presented in Durden et al. (2016) and Rowe (1983). Whenever no conversion factors for a specific taxon were reported in Durden et al. (2016) mean taxon specific biomass data per individual were extracted from Tilot (1992) for the CCZ.~~

~~The abbreviation are: C = carnivores, DF = deposit feeders, FSF = filter/ suspension feeders, O = omnivores, PolC = carnivorous polychaete, PolOF = omnivorous polychaete, PolSF = suspension feeding polychaete, PolSDF = surface deposit feeding polychaete, PolSSDF = subsurface deposit feeding polychaete, S = scavengers.~~

~~References: [1](Fox et al., 2003), [2](Menzies, 1962), [3](McClain et al., 2012), [4](Smith and Stockley, 2005), [5](Gage and Tyler, 1991), [7](Jumars et al., 2015), [8](Bluhm, 2001), [9](Drazen and Sutton, 2017)~~

| ~~Size class~~ | Macrofauna~~Taxon~~ | | | Feeding type~~Invertebrate megafauna and fish~~ | ~~n~~ | ~~Biomass (mmol C ind⁻¹) (Mean±Std)~~ | | | |
|---|---|---|---|---|---|---|---|---|---|
| | $n_{box\ cores}$ | | Ref. | $n_{OFOS\ tracks}$ | | Total area surveyed ($m^2$) | | Ref. | |
| | Outside PT | Inside PT | | Outside PT | Inside PT | Outside PT | Inside PT | | |
| ~~Macrofauna~~PD$_{0.1}$ | ~~Bivalvia*2~~ 1 | ~~FSF~~ 7 | ~~1.41 × 10~~³±8.29×10⁻⁴[1, 2] | 4 | 5 | 76,120 | 15,639 | [4] | |

| | Taxon | Feeding mode | n | Value | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| PD$_{0.5}$ | Cumacea[a] 22 | DF[1] 8 | [1,2] 4 | $3.09 \times 10^{-3} \pm 6.22 \times 10^{-4}$ 3 | | | 53,542 | 11,708 | 4 |
| PD$_3$ | Echinoidea[b] 20 | 85% O, 15% DF[1] 9 | 64 | $9.66 \times 10^{-3} \pm 2.84 \times 10^{-2}$ [1,2] | 4 | 4 2 | 32,457 | 6,673 | 4 |
| PD$_7$ | Gastropoda[a] 8 | 90% DF, 10% C[2] 8 | 2 | $8.56 \times 10^{-3} \pm 3.98 \times 10^{-2}$ 2 | 4 | 4 | 64,536 | 16,013 | 4 |
| PD$_{26}$[a] | Isopoda[e] | 93% DF, 7% C[2] | 43 | $1.33 \times 10^{-3} \pm 1.06 \times 10^{-3}$ 3 | | | 1,420 | 1,441 | 3 |
| | Ophiuroidea[b] | C[1] | 64 | $9.66 \times 10^{-3} \pm 2.84 \times 10^{-2}$ | | | | | |
| | Polychaeta[a] | PolSF, PolSDF, PolSSDF, PolC, PolOF[2] | 26 | $1.33 \times 10^{-2} \pm 3.68 \times 10^{-2}$ | | | | | |
| | Scaphopoda[b] | C[1] | 64 | $9.66 \times 10^{-3} \pm 2.84 \times 10^{-2}$ | | | | | |
| | Tanaidacea[a] | DF[1] | 5 | $5.48 \times 10^{-3} \pm 1.04 \times 10^{-2}$ | | | | | |
| Mega-fauna | Actiniaria | FSF[1] | 301 | $2.95 \times 10^{4} \pm 8.75 \times 10^{4}$ | | | | | |
| | Antipatharia | FSF[1] | 3 | $177.30 \pm 68.23$ | | | | | |
| | Ascidiacea[d] | FSF[1] | | $8.30 \times 10^{1}$ | | | | | |
| | Asteroidea | C[1] | 53 | $139.23 \pm 43.56$ | | | | | |
| | Bryozoa[g] | FSF[1] | | 22.38 | | | | | |
| | Cephalopoda | C[1] | 7 | $46.85 \pm 27.88$ | | | | | |
| | Ceriantharia[d] | FSF[1] | | 1923.17 | | | | | |
| | Cnidaria[e] | FSF[1] | | $2.35 \times 10^{1}$ | | | | | |
| | Crinoidea[d] | FSF[1] | | 5.33 | | | | | |
| | Crustacea | C[1,8] | 541 | $2.56 \pm 10.05$ | | | | | |
| | Echinoidea[d] | 15% DF, 85% OF[1] | | 59.17 | | | | | |
| | Alcyonacea[d] | FSF[1] | | 21.67 | | | | | |
| | Hemichordata[g] | DF[5,8] | | 22.38 | | | | | |
| | Holothuroidea[e] | DF[1] | 450 | $154.32 \pm 332.51$ | | | | | |

| | Ophiuroidea | C[1] | 527 | 16.05±10.15 |
|---|---|---|---|---|
| | Pennatularia[d] | FSF[1] | | 21.67 |
| | Polychaeta | PolSF, PolSDF, PolSSDF, PolC, PolOF[2] | 62 | $5.30×10^{-1}±1.20×10^{-2}$ |
| | Porifera[e] | FSF[1] | | 6.74 |
| Fish | Osteichthyes[f] | S, C[9] | 10 | 73.36±41.12 |

[a]Taxon-specific individual biomass; [b]Individual biomass calculated based on all other macrofauna data; [c]Median taxon-specific individual biomass for individuals from the Porcupine Abyssal Plain where Durden et al. (2016) did not have reliable dimension measurements; [d]Mean taxon-specific biomass data per individual were extracted from Tilot (1992) for the CCZ; [e]Individual biomass of *Benthodytes* sp., one of the most abundant holothurian morphotype at the DISCOL site (Stratmann et al., in review); [f]Individual biomass of *Ipnops* sp., the most abundant deep-sea fish at the $PD_{26}$ undisturbed site; [g]Individual biomass calculated for mean benthos megafauna at 4100 m depth based on the biomass-bathymetry and abundance-bathymetry relationships presented in Rex et al. (2006).

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Table 2. During PD$_{26}$, the densities of invertebrate megafauna and fish were estimated on 300 pictures from outside plough tracks and 300 pictures from inside plough tracks that were randomly selected from a 21 OFOS tracks (Boetius, 2015).

**Table 2.** Taxon-specific biomass per individual (mmol C ind$^{-1}$) for macrofauna and invertebrate megafauna including the specific feeding types. Macrofaunal biomass data are based on macrofaunal specimens collected in the abyssal plains of the Clarion-Clipperton Zone (NE Pacific) (Sweetman *et al.*, in review). In contrast, invertebrate megafaunal biomass was estimated by converting size-measurements of specific body parts of organisms from DEA that were acquired using photo-annotation into preserved wet weight per organism using the relationships presented in Durden *et al.* (2016). Subsequently the preserved wet weight was converted into fresh wet weight and biomass following the conversions presented in Durden *et al.* (2016) and Rowe (1983). Whenever no conversion factors for a specific taxon were reported in Durden *et al.* (2016) mean taxon-specific biomass data per individual were extracted from Tilot (1992) for the CCZ. 'n' refers to the number of individuals used to estimate taxon-specific biomasses. A detailed list with exact conversion factors for invertebrate megafauna is presented in Supplement 1.

The abbreviation are: C = carnivores, DF = deposit feeders, FSF = filter/ suspension feeders, O = omnivores, PolC = carnivorous polychaetes, PolOF = omnivorous polychaetes, PolSF = suspension-feeding polychaetes, PolSDF = surface deposit-feeding polychaetes, PolSSDF = subsurface deposit-feeding polychaetes, S = scavengers.

References: [1](Fox et al., 2003), [2](Menzies, 1962), [3](McClain et al., 2004), [4](Smith and Stockley, 2005), [5](Gage and Tyler, 1991), [7](Jumars et al., 2015), [8](Bluhm, 2001), [9](Drazen and Sutton, 2017).

| Size class | Taxon | Feeding type | n | Biomass (mmol C ind$^{-1}$) (Mean±SE) |
|---|---|---|---|---|
| Macro-fauna | Bivalvia[a] | FSF[1] | 7 | $1.4\times10^{-3}\pm3.1\times10^{-4}$ |
| | Cumacea[a] | DF[1] | 2 | $3.1\times10^{-3}\pm4.4\times10^{-4}$ |
| | Echinoidea[b] | 85% O, 15% DF[4] | 64 | $9.7\times10^{-3}\pm3.6\times10^{-3}$ |
| | Gastropoda[a] | 90% DF, 10% C[3] | 2 | $8.6\times10^{-2}\pm2.8\times10^{-2}$ |
| | Isopoda[a] | 93% DF, 7% C[2] | 4 | $1.3\times10^{-3}\pm5.3\times10^{-4}$ |
| | Ophiuroidea[b] | C[1] | 64 | $9.7\times10^{-3}\pm3.6\times10^{-3}$ |
| | Polychaeta[a] | PolSF, PolSDF, PolSSDF, PolC, PolOF[7] | 26 | $1.3\times10^{-2}\pm7.2\times10^{-3}$ |
| | Scaphopoda[b] | C[1] | 64 | $9.7\times10^{-3}\pm3.6\times10^{-3}$ |
| | Tanaidacea[a] | DF[1] | 5 | $5.5\times10^{-3}\pm4.7\times10^{-3}$ |
| Mega-fauna | Actiniaria | FSF[1] | 301 | $3.0\times10^{-1}\pm5.0\times10^{-2}$ |
| | Alcyonacea[d] | FSF[1] | | $2.2\times10^{1}$ |
| | Antipatharia | FSF[1] | 3 | $1.8\times10^{2}\pm3.9\times10^{1}$ |
| | Ascidiacea[d] | FSF[1] | | $8.3\times10^{-1}$ |
| | Asteroidea | C[1] | 53 | $1.4\times10^{2}\pm6.0$ |
| | Cephalopoda | C[1] | 7 | $4.7\times10^{1}\pm1.1\times10^{1}$ |

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| | | | | |
|---|---|---|---|---|
| | Ceriantharia[d] | FSF[1] | | $1.9\times10^3$ |
| | Cnidaria[c] | FSF[1] | | $2.4\times10^{-1}$ |
| | Crinoidea[d] | FSF[1] | | 5.3 |
| | Crustacea | C[1,8] | 541 | $2.6\pm4.3\times10^{-1}$ |
| | Echinoidea[d] | 15% DF, 85% OF[4] | | $5.9\times10^1$ |
| | Hemichordata[g] | DF[5,8] | | $2.2\times10^1$ |
| | Holothuroidea[e] | DF[1] | 450 | $1.5\times10^1\pm1.6\times10^1$ |
| | Ophiuroidea | C[1] | 527 | $1.6\times10^1\pm4.4\times10^{-1}$ |
| | Pennatularia[d] | FSF[1] | | $2.2\times10^1$ |
| | Polychaeta | PolSF, PolSDF, PolSSDF, PolC, PolOF[7] | 62 | $5.3\times10^{-1}\pm1.5\times10^{-3}$ |
| | Porifera[c] | FSF[1] | | 6.7 |
| Fish | Osteichthyes[f] | S, C[9] | 10 | $7.3\times10^1\pm1.3\times10^1$ |

[a]Taxon-specific individual biomass; [b]Individual biomass calculated based on all other macrofauna data; [c]Median taxon-specific individual biomass for individuals from the Porcupine Abyssal Plain where Durden *et al.* ( 2016) did not have reliable dimension measurements; [d]Mean taxon-specific biomass data per individual were extracted from Tilot (1992) for the CCZ; [e]Individual biomass of *Benthodytes* sp., one of the most abundant holothurian morphotype at the DISCOL site (Stratmann et al., 2018b); [f]Individual biomass of *Ipnops* sp., the most abundant deep-sea fish at the $PD_{26}$ outside plough tracks; [g]Individual biomass calculated for mean benthic invertebrate megafauna at 4,100 m depth based on the biomass-bathymetry and abundance-bathymetry relationships presented in Rex *et al.* (2006).

**Table 3.** Faunal respiration rate (mmol C m$^{-2}$ d$^{-1}$) and contribution (%) of the size classes macrofauna, polychaetes, invertebrate megafauna and fish to the respiration ~~for the undisturbed (Undist.)~~ outside plough tracks (outside PT), and ~~disturbed (Dist.) sites~~ inside plough tracks (inside PT) directly after the disturbance event in March 1989 (PD$_{0.1}$), 0.5 ~~years~~ yr post-disturbance (September 1989, PD$_{0.5}$), 3 ~~years~~ yr post-disturbance (January 1992, PD$_3$), 7 ~~years~~ yr post-disturbance (February 1996, PD$_7$), and 26 ~~years~~ yr post-disturbance (September 2015, PD$_{26}$).

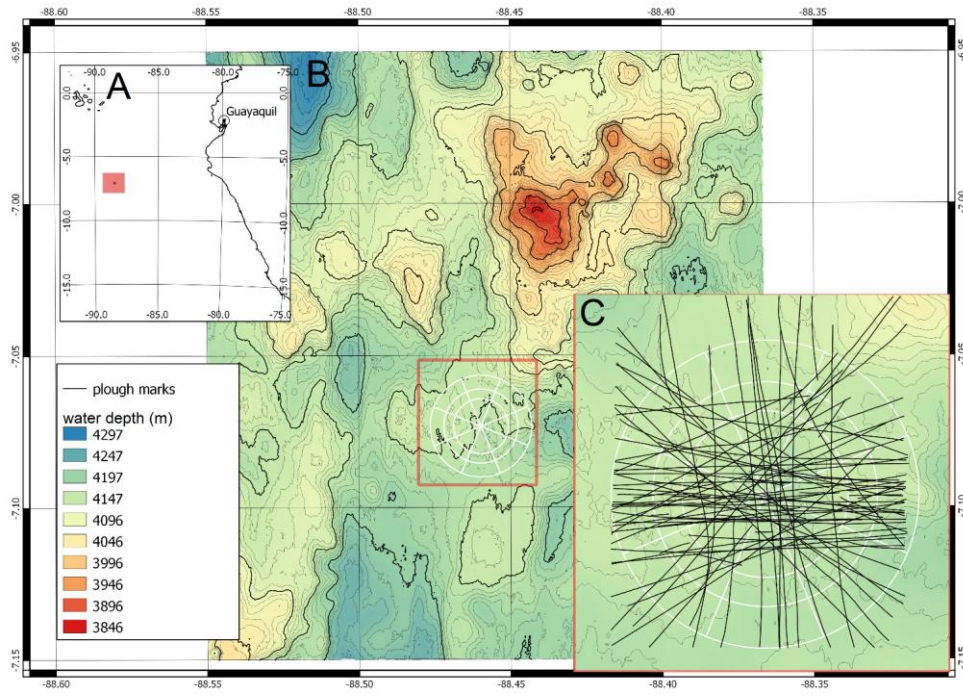| | PD$_{0.1}$ ~~Undist.~~ outside PT | PD$_{0.1}$ ~~Dist.~~ inside PT | PD$_{0.5}$ ~~Undist.~~ outside PT | PD$_{0.5}$ ~~Dist.~~ inside PT | PD$_3$ ~~Undist.~~ outside PT | PD$_3$ ~~Dist.~~ inside PT | PD7 ~~Undist.~~ outside PT | PD7 ~~Dist.~~ inside PT | PD26 ~~Undist.~~ outside PT | PD26 ~~Dist.~~ inside PT |
|---|---|---|---|---|---|---|---|---|---|---|
| Faunal respiration | $1.00\times10^{-2}$ $\pm\,1.12\times10^{-4}$ | $2.77\times10^{-3}$ $\pm\,5.22\times10^{-6}$ | $1.01\times10^{-2}$ $\pm\,5.77\times10^{-5}$ | $6.00\times10^{-3}$ $\pm\,6.78\times10^{-5}$ | $3.99\times10^{-2}$ $\pm\,3.67\times10^{-4}$ | $3.0\times10^{-2}$ $\pm\,2.33\times10^{-4}$ | $2.11\times10^{-2}$ $\pm\,2.55\times10^{-4}$ | $1.55\times10^{-2}$ $\pm\,1.45\times10^{-4}$ | $2.00\times10^{-2}$ $\pm\,1.55\times10^{-4}$ | $1.11\times10^{-2}$ $\pm\,1.00\times10^{-4}$ |
| Macrofauna | 8.66 | 7.33 | 9.77 | 14.34 | 50.0 | 58.34 | 6.55 | 4.55 | 2.66 | 1.12 |
| Polychaeta | 61.56 | 77.88 | 62.67 | 77.66 | 27.01 | 30.00 | 67.01 | 83.55 | 18.55 | 32.44 |
| ~~Megafauna~~ Invertebrate megafauna | 29.45 | 14.89 | 27.01 | 8.00 | 22.03 | 11.55 | 25.78 | 11.66 | 78.67 | 65.0 |
| Fish | $3.00\times10^{-1}$ | 0.00 | $5.23\times10^{-1}$ | 0.00 | $6.44\times10^{-1}$ | $7.78\times10^{-2}$ | $6.66\times10^{-1}$ | $3.55\times10^{-1}$ | $1.77\times10^{-1}$ | 1.44 |

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**Figure 1.1.** A) Location of the DISCOL experimental area (DEA) in the Peru Basin (SE Pacific; red square), B) detailed map of the DEA indicated by the white circle, C) location of all plough tracks (black lines) that were observed by the 'AUV Abyss' (Geomar Kiel) after 26 yr during RV Sonne cruise SO242-1 (Greinert, 2015).
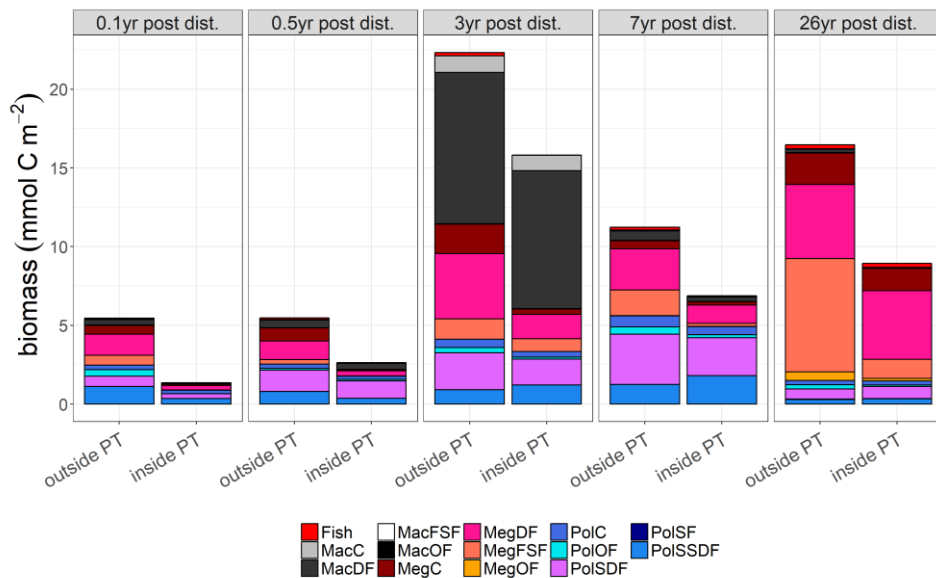
**Figure 2.** Mean ~~biomass~~carbon stocks (mmol C $m^{-2}$) of the food-~~-~~web compartments for ~~the undisturbed~~outside (outside PT) and ~~disturbed sites~~inside (inside PT) the plough tracks at the DISCOL experimental area (Peru Basin, SE Pacific) 0.1 ~~years~~yr post-~~ ~~disturbance (PD$_{0.1}$), for 0.5 ~~years~~yr post-~~ ~~disturbance (PD$_{0.5}$), for ~~three years~~3 yr post-~~ ~~disturbance (PD$_3$), for ~~seven years~~7 yr post-~~ ~~disturbance (PD$_7$), and for 26 ~~years~~yr post-~~ ~~disturbance (PD$_{26}$). ~~The~~For visibility reasons, no error bars ~~represent 1~~are plotted, but mean ± standard ~~deviation.~~deviations of each food-web compartment are presented in supplement 2. The abbreviation are: MacC = macrofauna carnivores, MacDF = macrofauna deposit feeders, MacFSF = macrofauna filter/ suspension feeders, MacO = macrofauna omnivores, MegC = invertebrate megafauna carnivores, MegDF = invertebrate megafauna deposit feeders, MegFSF = invertebrate megafauna filter/ suspension feeders, MegOF = invertebrate megafauna omnivores, PolC = polychaete carnivores, PolOF = polychaete omnivores, PolSDF = polychaete surface deposit feeders, PolSF = polychaete suspension feeders, PolSSDF = polychaete subsurface deposit feeders.
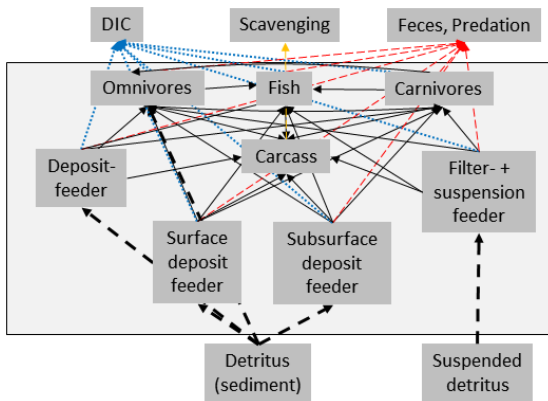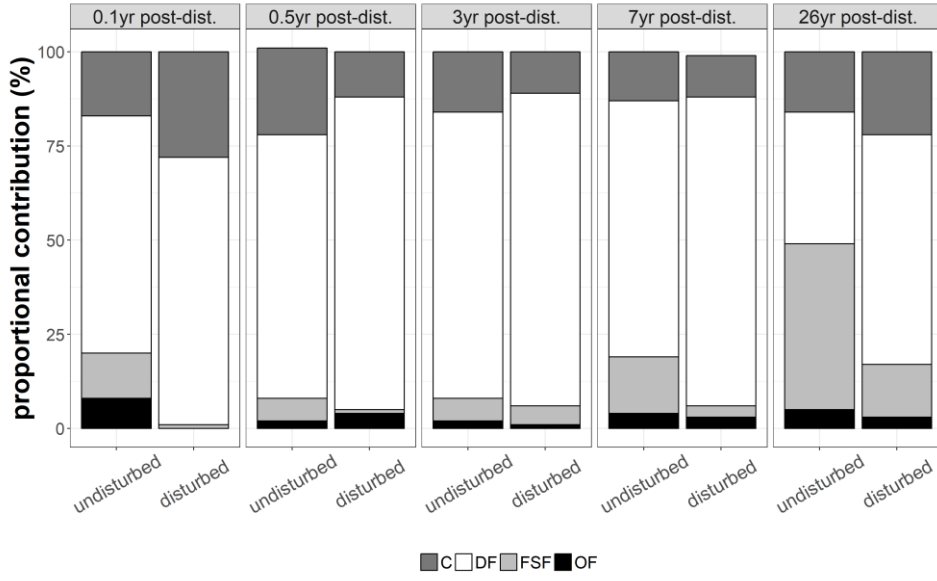
**Figure 2.3.** Simplified schematic representation of the food web structure that forms the basis of the linear inverse model (LIM). All compartments inside the box were part of the food web model, whereas compartments outside the black box were only considered as carbon influx or efflux, but were not directly modelled. In order to simplify the graph, for macrofauna,

5    polychaetes and invertebrate megafauna, only feeding types were presented and no size classes. Solid black arrows represent the carbon flux between food-web compartments and black dashed arrows represent the influx of carbon to the model. Blue-dotted arrows show the loss of carbon from the food web via respiration to DIC. The red dashed arrows indicate the loss of carbon from the food web as faecesfeces and as predation by pelagic/ benthopelagic fish and the yellow-dashed arrow indicateindicates the reduction of the carcass pool due toas a result of scavenging by pelagic/ benthopelagic fish.
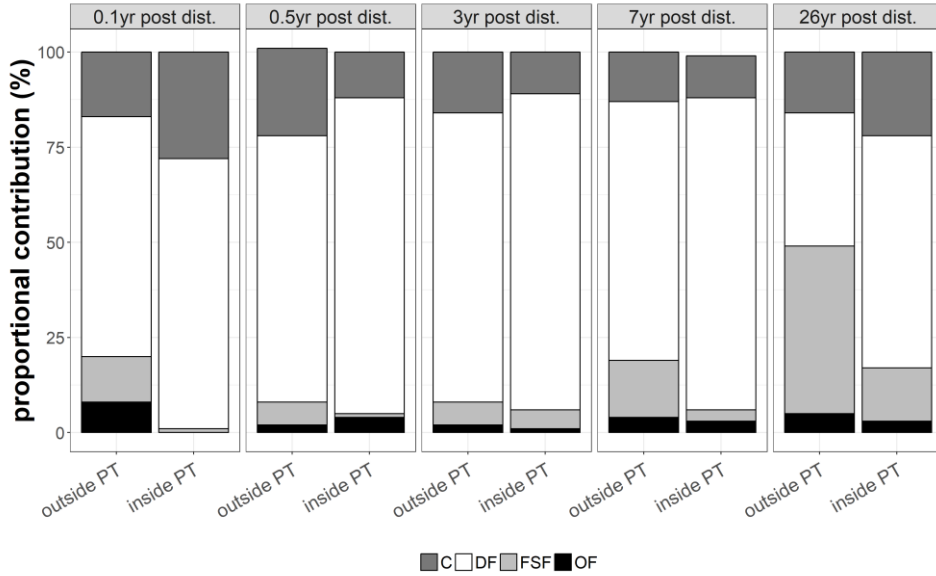
10

proportional contribution (%)

0.1yr post-dist.   0.5yr post-dist.   3yr post-dist.   7yr post-dist.   26yr post-dist.

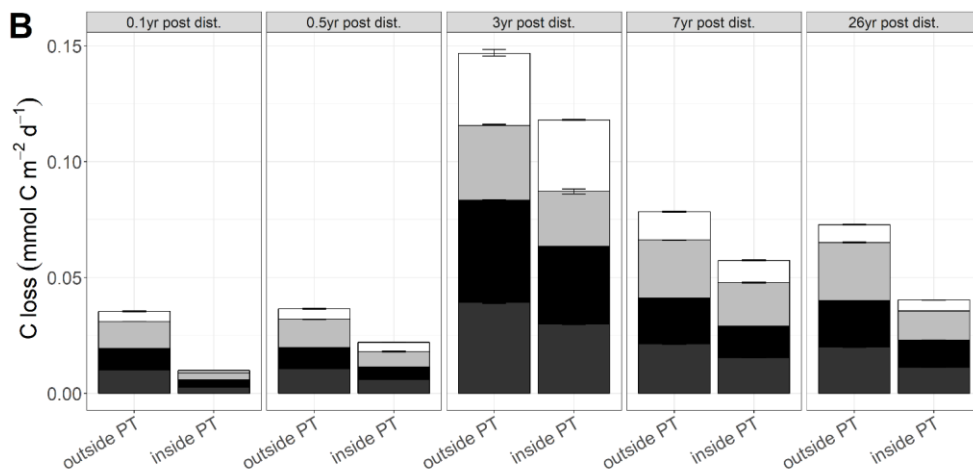undisturbed   disturbed

■ C □ DF ■ FSF ■ OF

**Figure 3.4.** Proportional contribution (in %) of the feeding types C = carnivores, DF = deposit feeders, FSF = filter and suspension feeders, OF = omnivores to the total ~~biomass for the undisturbed~~carbon stocks outside and ~~disturbed sites~~ inside plough tracks in the DISCOL experimental area (Peru Basin, SE Pacific) 0.1 ~~years~~yr post- disturbance ($PD_{0.1}$), for 0.5 ~~years~~yr post- disturbance ($PD_{0.5}$), for 3 ~~years~~yr post- disturbance ($PD_3$), for 7 ~~years~~yr post- disturbance ($PD_7$) and for 26 ~~years~~yr post-disturbance ($PD_{26}$).
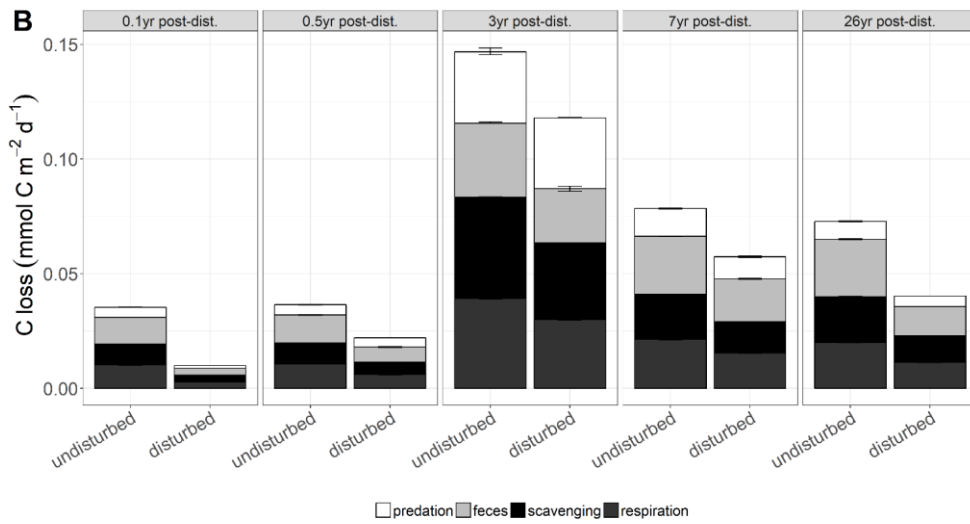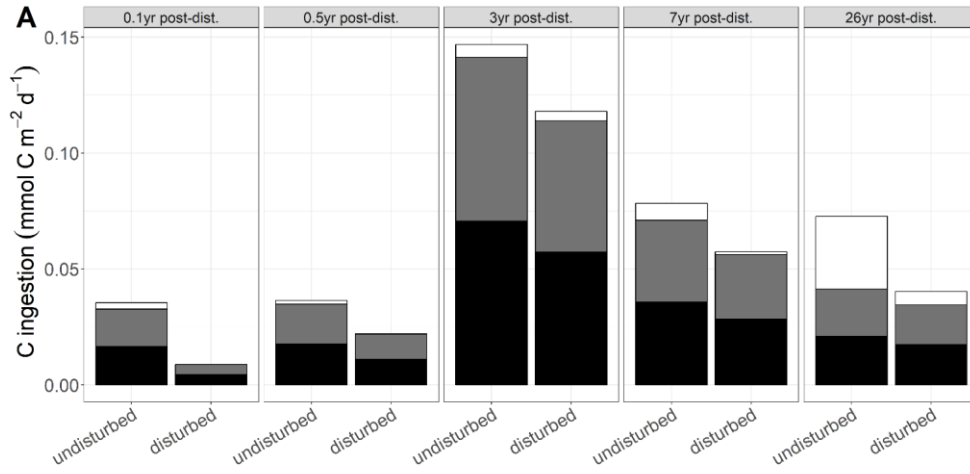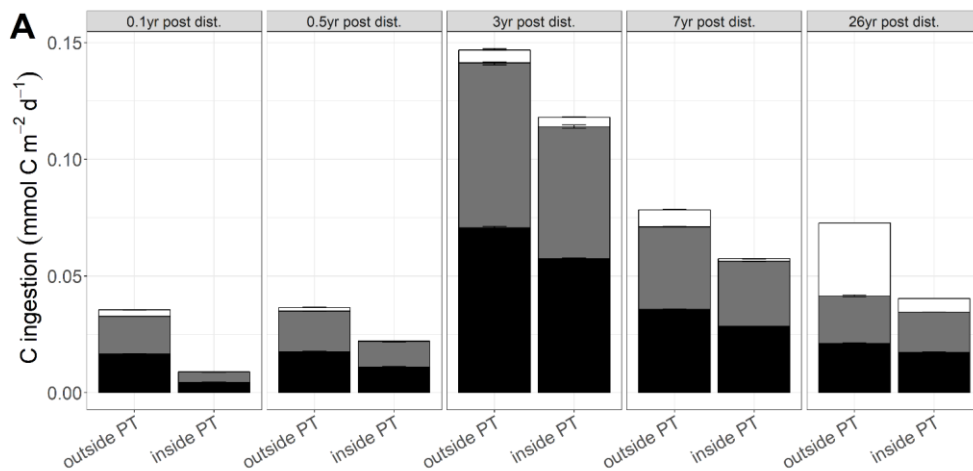
A

C ingestion (mmol C m$^{-2}$ d$^{-1}$)

| 0.1yr post-dist. | 0.5yr post-dist. | 3yr post-dist. | 7yr post-dist. | 26yr post-dist. |

☐ suspended detritus ☐ labile detritus (sediment) ■ semi-labile detritus (sediment)

B

C loss (mmol C m$^{-2}$ d$^{-1}$)

| 0.1yr post-dist. | 0.5yr post-dist. | 3yr post-dist. | 7yr post-dist. | 26yr post-dist. |

☐ predation ☐ feces ■ scavenging ■ respiration

**A**

C ingestion (mmol C m$^{-2}$ d$^{-1}$)

0.1yr post dist. | 0.5yr post dist. | 3yr post dist. | 7yr post dist. | 26yr post dist.

outside PT | inside PT

□ suspended detritus  ▨ labile detritus (sediment)  ■ semi-labile detritus (sediment)

**B**

C loss (mmol C m$^{-2}$ d$^{-1}$)

0.1yr post dist. | 0.5yr post dist. | 3yr post dist. | 7yr post dist. | 26yr post dist.

outside PT | inside PT

□ predation  ▨ feces  ■ scavenging  ■ respiration

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**Figure 4.5.** A) Mean faunal carbon ingestion (mmol C m$^{-2}$ d$^{-1}$) as suspended detritus, sedimentary labile and sedimentary semi-labile detritus ~~for the undisturbed~~outside and ~~disturbed sites the DISCOL experimental area (Peru Basin, SE Pacific)~~inside plough tracks 0.1 ~~years~~yr post-disturbance (PD$_{0.1}$), 0.5 ~~years~~yr post-disturbance (PD$_{0.5}$), 3 ~~years~~yr post-disturbance (PD$_3$), 7 ~~years~~yr post-disturbance (PD$_7$) and 26 ~~years~~yr post-disturbance (PD$_{26}$). B) Mean carbon losses (mmol C m$^{-2}$ d$^{-1}$) from the food webs as predation, ~~faeces~~feces, scavenging on the carcass, and faunal respiration ~~for the undisturbed~~outside and ~~disturbed sites at~~inside plough tracks during PD$_{0.1}$, PD$_{0.5}$, PD$_3$, PD$_7$, and PD$_{26}$. In both figures, the error bars represent 1 standard deviation.
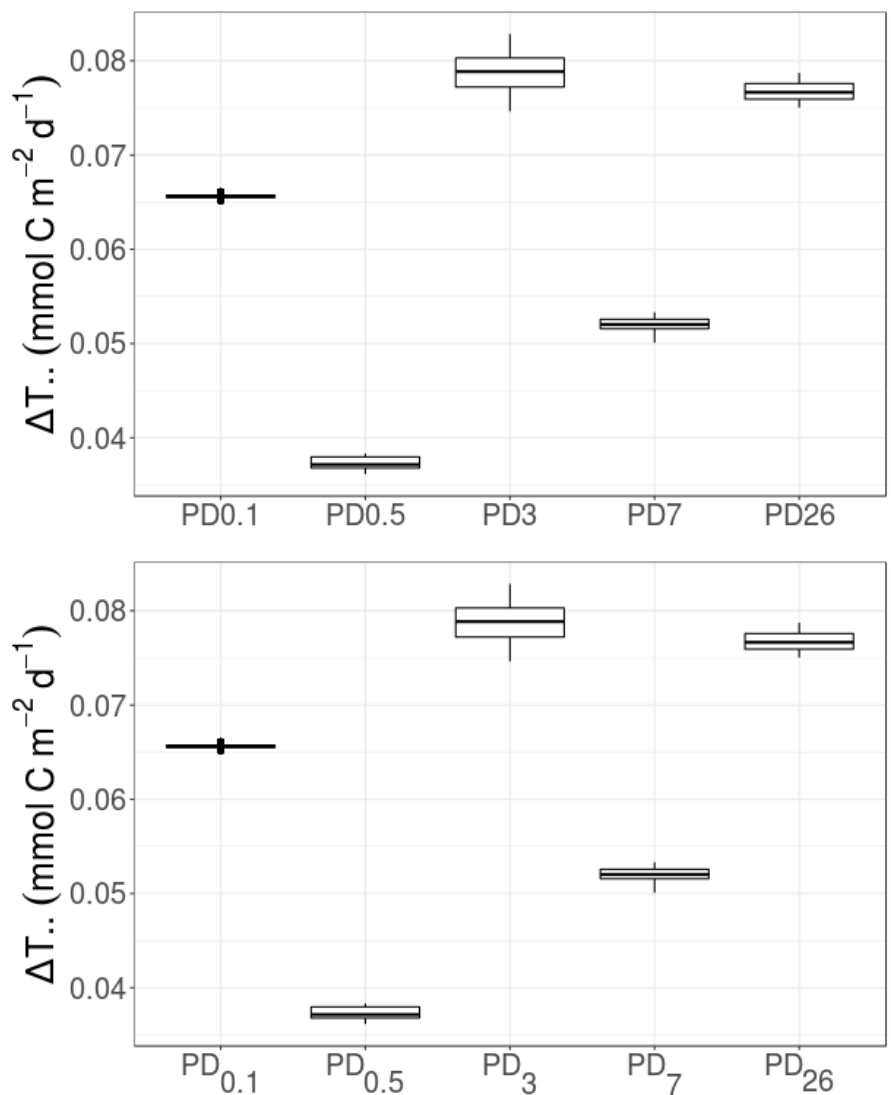
**Figure** ~~5.~~6, Development of $\Delta T..$ (mmol C m$^{-2}$ d$^{-1}$), i.e~~.~~., the difference in 'total system throughput' $T..$ ~~from the undisturbed~~outside plough tracks compared to ~~the disturbed sites~~inside plough tracks, over time. PD$_{0.1}$ corresponds to 0.1 ~~years~~yr post~~-~~disturbance, PD$_{0.5}$ is 0.5 ~~years~~yr post~~-~~disturbance, PD$_3$ is 3 ~~years~~yr post-disturbance, PD$_7$ is 7 ~~years~~yr post-disturbance and PD$_{26}$ is 26 ~~years~~yr post~~-~~disturbance.
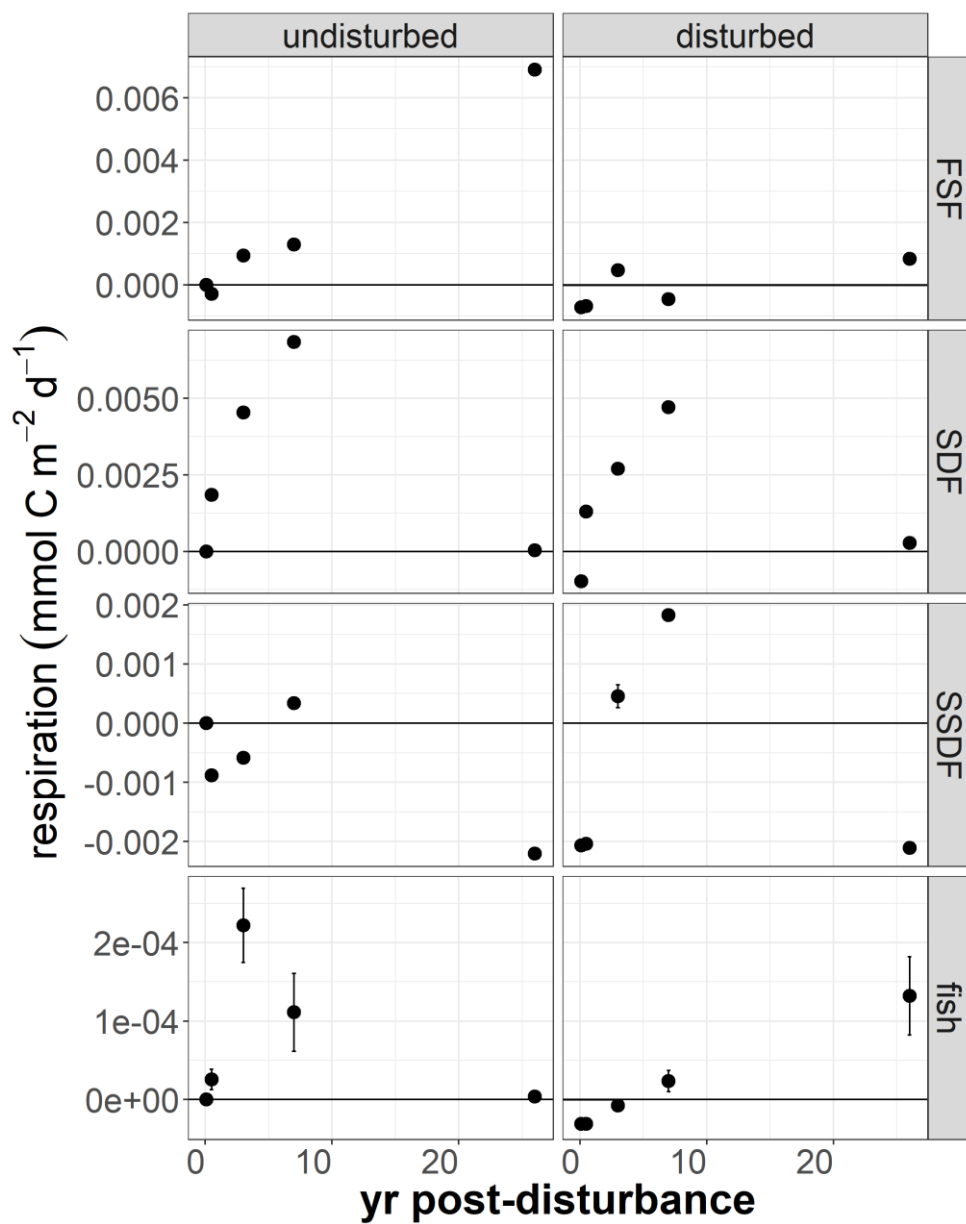
**Figure 6.** Feeding type related differences in the recovery of faunal respiration (mmol C m$^{-2}$ d$^{-1}$) over time following the DISCOL disturbance experiment. Due to a lack of pre-disturbance respiration rates (T$_0$), the respiration rate for each feeding type (filter and suspension feeders=FSF, surface deposit feeders=SDF, subsurface deposit feeders=SSDF, fish) is standardized to the respective feeding type specific respiration rate at the undisturbed sediment of 0.1 years post-disturbance. The respiration rate for filter and suspension feeders includes the respiration of macrofaunal, polychaete and megafaunal filter and suspension

feeders. The surface deposit feeders are the polychaete surface deposit feeders and the subsurface deposit feeders correspond to the polychaete subsurface deposit feeders. Fish are the scavengers and predators.

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