1  **Observations of deep-sea fishes and mobile scavengers from the abyssal DISCOL**
2  **experimental mining area**

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19  **Abstract**

20  Industrial interest in deep-sea mineral extraction began decades ago and today it is at an all-time
21  high, accelerated by global demand for metals. Several seafloor ecosystem disturbance
22  experiments were performed beginning in the 1970's, including the DISturbance and
23  reCOLonization experiment (DISCOL) conducted in the Peru Basin in 1989.  A large seafloor
24  disturbance was created by repeatedly plowing the seafloor over an area of ~10.8 km$^2$. Though a
25  number of studies in abyssal mining regions have evaluated megafaunal biodiversity and
26  ecosystem responses, few have included quantitative and detailed data on fishes or scavengers
27  despite their ecological importance as top predators. We used towed camera transects and baited
28  camera data to evaluate the fish community at the DISCOL site. The abyssal fish community was
29  relatively diverse with 16 taxa dominated by *Ipnops meadi*. Fish density was lower in ploughed
30  habitat during the several years following disturbance but thereafter increased over time in part
31  due to changes in regional environmental conditions. 26 years post disturbance there were no

32    differences in overall total fish densities between reference and experimental areas, but the

33    dominant fish, *I. meadi*, still exhibited much lower densities in ploughed habitat suggesting only

34    partial fish community recovery.  The scavenging community was dominated by eelpouts

35    (*Pachycara* spp), hermit crabs (*Probeebei mirabilis*) and shrimp. The large contribution of

36    hermit crabs appears unique amongst abyssal scavenger studies worldwide. The abyssal fish

37    community at DISCOL was similar to that in the more northerly Clarion Clipperton Zone,

38    though some species have only been observed at DISCOL thus far.  Also, further species level

39    identifications are required to refine this assessment.  Additional studies across the polymetallic

40    nodule provinces of the Pacific are required to further evaluate the environmental drivers of fish

41    density and diversity and species biogeographies, which will be important for the development of

42    appropriate management plans aimed at minimizing human impact from deep-sea mining.

43

## 1. Introduction

The world's oceans are becoming increasingly exploited for their resources, and anthropogenic effects now reach the farthest corners and depths of ocean ecosystems (Ramirez-Llodra et al., 2011). New uses of our oceans are emerging. Industrial interest in deep-sea mineral extraction is at an all-time high, accelerated by global demand for minerals such as cobalt, zinc, copper, nickel, and rare-earth elements, which are enriched in seamount crusts as well as manganese nodules and deposited at hydrothermal vents. Currently, the International Seabed Authority has granted 29 exploration contracts to companies to explore for metals and rare-earth minerals in areas totaling >1,200,000 km$^2$ of seafloor in the Pacific, Atlantic, and Indian Oceans (www.isa.org.jm). Though the current intensity of commercial interest combined with technological innovations will soon lead to exploitation, this idea has a long history. Thus several seafloor ecosystem disturbance experiments were performed beginning in the 1970's (reviewed in Jones et al., 2017).

One of these, the DISturbance and reCOLonization experiment (DISCOL) was conducted in the Peru Basin in 1989. A large experimental seafloor disturbance was created by repeatedly plowing the seafloor. Biological surveys were conducted prior to the disturbance and several times thereafter to monitor seafloor ecosystem recovery (Thiel et al., 2001). Studies of the site seven years after disturbance showed only partial recovery (Thiel et al., 2001;Bluhm, 2001). Similar studies carried out in the north Pacific have also given indications that seafloor communities have not recovered or only partially recovered in periods of 26-37 years following disturbance (Miljutin et al., 2011;Jones et al., 2017;Gollner et al., 2017). This is not surprising given low rates of recruitment and growth common in these ecosystems, and the removal of the hard substrate upon which a large portion of the fauna depends (Amon et al., 2016;Vanreusel et al., 2016;Purser et al., 2017).

Though a number of studies in abyssal mining regions have evaluated megafaunal biodiversity and ecosystem responses, few have included quantitative and detailed data on fishes or scavengers (Leitner et al., 2017). However, many fishes are top predators that can have important influences on communities and ecosystems (Estes et al., 2011;Drazen and Sutton, 2017). Though fishes are mobile and may not suffer immediate mortality from mining, they will be affected by the large sediment plumes created (Oebius et al., 2001) and by the loss of foraging habitat, so they may suffer regionally from local mining activities. Also, top predators can

bioaccumulate metals and other contaminants (Chouvelon et al., 2012;Choy et al., 2009;Bonito et al., 2016) that may be released from the activities of mining. Thus, it is important to characterize the fish community in regions that will likely experience mining in the near future and to begin constructing a biogeography, so that scientists and managers can evaluate potential mining impacts and appropriately locate protected no-mining zones (Wedding et al., 2013).

In 2015 a survey was performed of the DISCOL area using photo and video transecting techniques in a similar manner to the historical surveys of the area conducted into the late 1990s. In addition, archived analogue baited camera images collected shortly after the 1989 disturbance (1989-1992) were digitized and analyzed for fishes and other mobile scavengers, some of which may avoid transecting vehicles (Trenkel et al., 2004;Colton and Swearer, 2010). Our goal was to a) describe the fish and scavenger community in detail for the first time, b) evaluate the fish community response to disturbance and potential recovery, and c) compare the fish and scavenger community to that observed to the north of the equator in the Clarion Clipperton Zone (CCZ) where the majority of abyssal mining exploration licenses have been thus far granted, and where initial pilot mining activities are likely to commence.

## 2. Methods

In 1989 a ~10.8 km² circular region of the Peru basin in the Pacific, the DISCOL experimental area (the DEA), was artificially ploughed, in an effort to simulate the effects of deep-sea mining (Thiel et al., 2001). The study site (7° 04.4' S, 88º 27.60' W) ranges in depth from 4120-4200 m.  Sediments are fine grained clays overlain with heterogeneous cover of manganese nodules, sometimes in high density.  The plough-harrow device was 8 m wide and when deployed, overturned the first 10-15cm of seafloor sediment, ploughing the nodules into the seafloor and removing this hard substrate from the sediment / water interface. The plough was towed in 78 radial transects through the disturbance area with ˜20% of the seafloor directly disturbed by the plough. The most central region of the DEA was the most highly disturbed area crosscut by the majority of plough tows (Fig. 1; Foell et al., 1992).

In 2015 the DISCOL site was revisited and sampled twice (cruises SO242-1 and 2).  The initial cruise was conducted in the summer and primarily conducted detailed acoustic and image-based mapping of the plough tracks using Autonomous Underwater Vehicles and ship based sensors. This initial cruise also towed an epibenthic sled (EBS) several times across the seafloor,

removing the top 20 cm of seafloor in trenches of ~2m x 500 m. These sled deployments were conducted to more accurately simulate the upper sediment removal envisioned as a likely consequence of mining. The second of these cruises focused on the detailed photographic study of the historic and recent disturbances mapped during the first cruise.

For investigation of megafauna, including fishes, the Alfred Wegner Institute (AWI) OFOS LAUNCHER towed camera system was used to conduct photographic transects of the seafloor. The OFOS LAUNCHER is identical to the OFOBS system described in Purser et al. (2018), with the exceptions that the OFOS was not equipped with INS, side scan or forward facing sonar systems. OFOS was flown at a height of ~1.7m above the seafloor and used a 23 megapixel downward looking still camera to take images every 15 seconds, each of which also captured the laser points projected by a tri-laser (50 cm spacing) sizing device. Ship speed was maintained at 0.2-0.4 knots.

Given the high heterogeneity of the seafloor area studied, each image was manually assessed to represent one of a range of disturbance categories. These were 1) 'Reference' areas, not directly within the target circle of seafloor ploughed in 1989 (DEA), 2) 'Undisturbed' areas within the central DEA circle, but not actually impacted by the plough harrow directly, 3) 'Transition' images, within which both the edge of a plough track was visible as well as surrounding seafloor, 4) 'Ploughed' images within which only ploughed seafloor was visible and 5) 'EBS' areas, disturbed a month prior to SO242-2 by the towed epibenthic sled deployed by SO242-1. These five disturbance categories represent increasing levels of physical disturbance.

Image area captured within each image was determined by measuring the spacing of the laser points in a subset of 3663 images using the PAPARA(ZZ)I software application (Marcon and Purser, 2017). The image area of all remaining images was calculated from the camera altitude (distance to seafloor) using a second order polynomial regression of the laser-based measurements. The average seafloor image area was 5.71 $m^2$. In some instances, the camera was manually triggered to capture images of fishes that would have been missed in between timed images, or to capture a fish at a more suitable angle for identification. Images were manually annotated for fishes (for octopi see Purser et al., (2017) and for all invertebrates and benthic fauna see Marcon et al. submitted) using a variety of published keys. Fish density was estimated by dividing the number of fish viewed in regular timed images by the area photographed. Manually triggered images were not included in density estimates as these would present a

137    positive bias towards images with fish in them. Diversity was evaluated using rarefaction curves

138    (on all images, timed and manually triggered, because this approach only requires positive

139    occurrences) to enable comparisons between habitat types that were not sampled at the same

140    intensity.

141         OFOS transects often crossed several habitat types, so for fish density estimates, the

142    images from each transect were divided into habitat type subsets. Fish density was estimated for

143    each of these by dividing the number of fish viewed in the regularly timed images by the area

144    photographed. For some habitat categories, there were very few images collected during a

145    transect. In this case, we eliminated all the subsets/samples that were unlikely to have seen at

146    least one fish based on the mean density of both large and small samples of 30.6 fish ha$^{-1}$,

147    translating to a threshold sample area of 330 m$^2$. If used in the analysis, these small image sets

148    would either bias the results towards zero estimates if no fish present in the small image set, or

149    towards incorrectly high estimates if a few fish happened to be in the small set of collected

150    images. Fish density was compared between habitat types using a permutational ANOVA on a

151    Euclidean distance matrix to account for uneven sample sizes and non-normal data distribution.

152         Baited cameras are now a widely used tool to census marine fishes (Bailey et al., 2007)

153    because they can attract often sparsely distributed animals to within the census view, including

154    some that might avoid active camera survey tools. Thus, for fully describing diversity and

155    species abundances within a regional fish assemblage, they are indispensable. However, in

156    contrast to transect methods, they are more difficult to use for estimations of accurate animal

157    densities (Priede and Merrett, 1998;Yeh and Drazen, 2011).

158         During the first post disturbance cruise in 1989 and three years later in 1992 (Sonne

159    cruises 61 and 77), free fall baited cameras (freefall baited observing systems - FBOS) were

160    deployed (Brandt et al., 2004). These utilized a Benthos 35mm survey camera and strobe. Bait

161    was attached to a rod or placed in a small clear plastic tube ~1m from the camera, resting on the

162    seafloor. Oblique images of ~1.7m$^2$ of the seafloor were taken every 2 to 5.5 min for ~24 to 55

163    hours, averaging 725 images per deployment. Animals were counted in each image. Metrics

164    extracted from the imagery include the maximum number of each taxa visible in any one image

165    over the camera deployment (MaxN), the time of first arrival for each taxa ($T_{arr}$), and the

166    proportion of images in which a taxa was present for a camera deployment (Yeh and Drazen,

167    2011;Linley et al., 2017;Leitner et al., 2017). Only species that were clearly attracted to the bait

168   were enumerated.  This eliminated species that were photographed as they were simply drifting

169   or crawling through the field of view. Further, many small amphipods were often present at the

170   bait but could not be reliably counted and so are not included. Deployments in 1989 were made

171   within both the reference and disturbance areas, and an analysis of similarity test (ANOSIM) was

172   used to compare community compositions.

173

174   **3. Results**

175   3.1 Photographic transects

176        20 OFOS transects samples were performed resulting in 46 habitat samples (Fig. 1).

177   From these a total of 16733 images were examined with 306 fishes observed in 300 images

178   (Table 1). Fishes were represented by 14 taxa (not including the category "unidentified fishes";

179   Fig. 2). Several groups were distinct but could not be identified to species whereas others were

180   only identifiable to genus or family. The most common species observed was the benthic *Ipnops*

181   cf *meadi* representing 61% of the fish observations. The Ophidiids were the most speciose family

182   observed with 6 operational taxonomic units (OTU), some of which were distinct but could not

183   be identified conclusively.

184        Across the five different habitat types, sampling effort was very uneven.  Within the full

185   data set, images taken of reference area and in unploughed habitat within the experimental area

186   were most abundant (Table 1).  Seafloor images showing the disturbed habitat types (transient,

187   ploughed and epibenthic sled (EBS) tracks) were less numerous.  For all the data combined, as

188   well as for the unploughed habitat type alone, rarefaction curves suggested adequate sampling as

189   an asymptote was beginning to be reached in both cases (Fig. 3).  However, within the other

190   habitat types, rarefaction curves suggested more sampling was required to fully capture the fish

191   diversity.  Thus, the use of estimated species richness was needed for diversity comparisons.

192   Interestingly, the disturbed habitat types had higher rarified diversity (ES 26) than the reference

193   area or neighboring unploughed habitat (Fig. 3).

194        Fish densities were highly variable. Across all sample areas surveyed, seafloor areas

195   imaged ranged from 355 to 7798 $m^2$ and fish density ranged from 0 to 71.4 fish ha$^{-1}$.  Across all

196   samples average fish density was $30.2 \pm 18.2$ fish ha$^{-1}$ (Fig. 4).  Across the habitat types, density

197   did not vary significantly (PERMANOVA, p>0.05). The density of the most common fish, *I.*

198   *meadi*, could also be estimated and ranged from 0 to 68 fish ha$^{-1}$, averaging $18.4 \pm 17.5$ fish ha$^{-1}$

199   across all samples (Fig. 4). Its density was significantly lower in the ploughed habitat type

200   compared to undisturbed and reference habitats.  Only a single *I. meadi* was found in the EBS

201   habitat type (Table 1), but this individual did not occur in a habitat sample of sufficient length for

202   density estimation.  *Ipnops meadi* density in the two samples available for analysis was zero.

203        Our fish density estimates can be compared to those published in Bluhm (2001).

204   Bluhm's time series of densities suggests that there were no fish observed 6 months post

205   disturbance, then fish density increased at year 3 and had returned to pre-disturbance density

206   levels after 7 years (Fig. 5). At this time, ophiuroids, holothurians, fish and hermit crabs were

207   observed in the plough tracks.  We examined this data and the 2015 data for the reference,

208   ploughed and unploughed habitat types, in addition to those presented in Bluhm's original work

209   using a two factor PERMANOVA. Habitat type and time were significant predictors of fish

210   density with lower fish densities in the ploughed habitat ($p<0.01$).  Also, the densities of fish

211   across the three habitat types changed significantly with time since the disturbance (habitat x

212   time, $p<0.05$). Fish density was significantly ($p<0.05$) lower than the other habitat types right

213   after the disturbance, at 3 years post disturbance, and marginally lower at 6 months post

214   disturbance ($p=0.057$). At 7 years the undisturbed habitat type in the DEA had higher fish

215   density than the reference area. At 26 years, as already mentioned, there was no difference

216   between habitats. Fish densities were similar to levels found in the undisturbed habitats and the

217   reference area at 3 years post disturbance but higher than other times (Fig. 5). It was not possible

218   to evaluate the times series data for *I. meadi* as Bluhm (2001) did not publish species specific

219   results.

220

221   3.2 Baited camera observations

222        Six baited camera deployments were conducted, 5 in 1989 and 1 in 1992 (Table 2).  Six

223   taxa of fishes were identified (Fig. 6).  The most abundant (MaxN) in the deployments was the

224   eelpout *Pachycara nazca*.  This species occurred in all 6 deployments, reached a MaxN of 9 in

225   two of the deployments and on average was present in 55% of the images. Individuals of the

226   rattail *Coryphaenoides* sp. were either *C. armatus* or *C. yaquinae,* or both were present but, we

227   could not differentiate them in the photographs.  This taxa was present in all of the deployments

228   but was observed on average in only 2.1% of images, and MaxN was never more than 2.  Several

229   ophidiids and a synaphobranchid eel were also observed.

230   The baited camera also attracted 9 taxa of invertebrates (Table 2).  The small shrimp

231   *Hymenopeneus nereus* was present in all of the deployments in relatively large numbers (average

232   MaxN = 9), with up to 15 visible at one time and was present on average in 63% of the images.

233   The hermit crab *Probeebei mirabilis*, was also observed in every deployment but in varying

234   numbers (from 1 to 9) and in 29% of the images.  Penaeid shrimp were also observed in every

235   deployment and were the third most abundant and common scavenging species. Two species

236   were identified, *Cerataspis monstrosus* (identified as *Plesiopeneus armatus* in earlier papers;

237   Leitner et al 2017) and *Benthiscymus* sp.  Frequently, these could not be distinguished as they

238   differ in the shape of the antennal scale and rostrum which were not always clearly visible.

239   Large Munnopsid isopods were seen in all but one deployment but did not remain in the field of

240   view for long. Ophiuroids were not abundant or common, being observed in three deployments

241   as single individuals, but they stayed in the field of view for a long time (high persistence

242   values).

243   Two of the camera deployments in 1989 were made in the disturbance area 6 months post

244   event. In one of these deployments there was no obvious sign of disturbance in the limited field

245   of view. In the other, a plough harrow track was clearly visible (FBOS006; Table 2).  Low

246   numbers of the benthic eelpout, *P. nazca*, were observed during this deployment.  This

247   deployment also had the lowest numbers of the benthic shrimp, *H. nereus*.  However, the

248   community composition did not vary significantly between the 1989 deployments in disturbed

249   and reference areas (ANOSIM, p>0.05).

250   Overall, the diversity observed with the small number of camera deployments was fairly

251   uniform, as evident from the plateau reached in both rarefaction and species accumulation curves

252   (Fig. 7). This was the case for all scavengers and for the fishes alone. The baited cameras

253   observed fewer taxa of fishes compared to the photo transects (Table 1, 2). Many of the fishes

254   observed in the photo transects included less mobile benthic species such as members of the

255   Ipnopidae, Bathysauridae and numerous unidentified ophidiids. However, the baited camera

256   deployments identified two fish species that were not observed in the photo transects, *Barathrites*

257   *iris* and a Synaphobranchid eel, both mobile scavengers.

258

259   **4. Discussion**

260   *4.1 A description of the fish and scavenging community and relationship to past DISCOL studies*

We present some of the first detailed fish assemblage information for the abyssal eastern Pacific where seafloor mining will likely occur. Earlier studies at the DISCOL site presented limited fish assemblage results from the first few years of the experiment and report finding 8 fish taxa with *Ipnops* sp. being the most abundant (Bluhm, 1994). All of the taxa that were observed in these initial investigations were also present in our 2015 survey results, with the exception of *Halosaurus* sp. Moreover, we observed 6 additional taxa in 2015, and together with analysis of the 1989-1992 baited camera deployments, we have observed a total of 16 taxa. Interestingly the earlier camera transect surveys flew the camera system higher off the bottom (3-3.5m vs 1.7m) which is perhaps more appropriate for the survey of larger, mobile fishes. Advances in photographic identification of abyssal fishes across the Pacific and improvements in photographic quality have resulted in the greater detail in the present analysis.

The baited camera deployments provided additional information on the DISCOL fish community and also provided data on scavenging invertebrate fauna. Past taxonomic works have used trapped specimens to document the presence of the eelpouts *P. nasca* and *P. bulbiceps* (Anderson and Bluhm, 1997) and the ophidiid *B. iris* (specimen deposited at the Senckenberg Museum). The physical specimens provide some vouchers for taxa that were identified from photographs. Two taxonomic studies used the baited camera imagery to tentatively identify the ophidiid *Bassozetus nasus* (Nielsen and Merrett, 2000) and large Munnopsid isopods which were thought to belong to the genus *Paropsurus* (Brandt et al., 2004). Bluhm et al (1995) briefly states that *P. mirabilis* and ophiuroids were commonly seen in the baited camera photos, but these results were not given in any detail. We show the eelpouts, the shrimp *H. nereus*, and hermit crabs are indeed common and regular bait attending fauna at this site (see below for comparisons to other abyssal regions).

*4.2 Evaluation of the fish community response to disturbance and potential recovery*

Our results 26 years post disturbance, when compared to earlier sampling, provide some insight into the recovery potential of the fish fauna. The striking result found by Bluhm (2001) was that no fishes were observed in the disturbance area within 6 months of the disturbance; however, we show the presence of fish and scavenging invertebrates at this time from baited camera deployments. Samples sizes were low, but the community seems comparable to that in the reference areas at the same time. It seems likely that the scavengers were attracted from the

larger neighborhood, some possibly from proximate reference or undisturbed areas. This could
occur even if these animals were not commonly residing in the disturbance area due to habitat or
prey community alteration.

Only partial recovery of the fish community has occurred 26 years post disturbance. Total
fish density in the ploughed habitat of the DEA increased over time and in relation to the
reference and undisturbed habitat suggesting recovery. It should be noted that large interannual
changes were evident at the reference site with fish densities peaking 3 years post disturbance
and at high levels again at 26 years (Fig. 5). An increase in megafaunal density over the first 7
years of the experiment was already documented and hypothesized to be the result of increased
phytodetrital food flux and growing populations regionally (Bluhm, 2001). Such variation in
megafaunal abundance is a regular feature of abyssal communities (Kuhnz et al., 2014;Ruhl and
Smith, 2004). Comparisons between habitats at a point in time can provide a more robust means
to assess recovery after plough disturbance (Miljutin et al., 2011). We found no differences in
total fish density between the disturbed and undisturbed habitats at 26 years. Further, diversity
(ES 26) was slightly higher in the disturbed habitat areas, although with relatively small sample
sizes. However, the most common fish *I. meadi*, that makes up more than half of all the fish
observations, had only a third of the density in 26-year-old plough tracks compared to
undisturbed and reference areas, and only one individual was seen in the fresh EBS tracks (Fig.
4). The avoidance of *I. meadi* over plough tracks, shows that even the mobile fish community
has not fully recovered from the disturbance after more than two decades. This species' response
likely relates to its biology as a rather sedentary, small benthic fish that, based on limited data,
feeds on polychaetes, small bivalves, and crustaceans (Nielsen, 1966;Crabtree et al., 1991). Its
prey may not have recovered in the tracks (Jones et al., 2017;Borowski, 2001). Most of the other
fishes observed are benthopelagic and when swimming across a habitat mosaic might as easily
be seen over an old plough track as over other habitat. Even if benthopelagic species tend to
favor undisturbed habitat, this would be difficult to see in the data. Our other benthic species
include the lizardfish *B. mollis* which preys on mobile fishes and shrimps and *B. sewelli*, which
is a larger member of the Ipnopidae, but was too infrequently observed to assess habitat
preferences (Table 1).

Conclusions about fish community recovery over time must be taken with caution. With a
sparsely distributed fauna and the high variability in density, there are limits on statistical power

323  and thus our confidence.  The earlier DISCOL surveys differed in methodology to the current

324  surveys including average altitude of the camera above bottom, image quality, and attention to

325  the fishes. Our diversity estimates may well be higher as a result.  Density estimates could also

326  be affected by these same factors. The most common fish in the surveys, *I. meadi*, is relatively

327  small and despite reflective eyes (Fig. 2) may have been more visible in our 2015 surveys in

328  closer proximity to the seafloor. The influence many of these parameters have had on abundance

329  estimations of fauna in the DISCOL region has been investigated in detail for a region of the

330  DEA which was surveyed several times during the initial 7-year period and again in 2015. In

331  2015, the OFOS was deployed at 1.7 and 4 m in this region, and additionally an AUV was flown

332  at 5 m to image the same region of seafloor. The results from these comparative studies (Purser

333  et al. submitted for this special issue) show the sensitivity of density and diversity indices in the

334  DISCOL area to changes in flight height, illumination, and camera type. Larger megafauna, such

335  as fish, were clearly visible in images collected from higher altitudes, therefore resulting in both

336  higher diversity and abundance estimates for a given transect length than achieved with lower

337  flying camera systems. Certainly, methodology plays a very important role in determining the

338  accuracy of sampling strategies in this ecosystem for determination of these parameters.

339        Our results add to a growing body of literature that generally finds little or partial

340  recovery of faunal communities, even decades after simulated mining disturbances. Epifaunal

341  megafauna density was considerably lower in disturbance tracks made 20 and 37 years prior to

342  re-survey during the OMCO experiment in the CCZ (Vanreusel et al., 2016). Meta-analyses of

343  abyssal disturbance experiments in the CCZ suggest that recovery of density and diversity is

344  faster in mobile than sedentary fauna (Gollner et al., 2017;Jones et al., 2017).  For instance, the

345  mobile holothurian community appears to have recovered from disturbance in terms of density

346  and community composition at the DISCOL site after 26 years (Stratmann et al., 2018).  Most

347  holothurians are detrital deposit feeders and their food source settling from above may not be

348  greatly affected by the plough disturbance, whereas some fishes, such as *I. meadi*, likely rely

349  upon epifaunal and infaunal macrofauna for food.  The meiofauna and macrofauna have not

350  recovered completely after 26 years in the CCZ (Miljutin et al., 2011), or after 7 years at the

351  DISCOL site (Borowski, 2001).  Some of the variation in the recovery potential observed

352  between studies is undoubtedly derived from the variation in disturbance type and intensity.  The

353  direct benthic scale of actual nodule mining activities is suggested to be from 300-600 km$^2$ y$^{-1}$

354    for a single mining license (Oebius et al., 2001;Levin et al., 2016). Plumes of sediment from

355    collectors or from discharge of the ore dewatering plume (Rolinski et al., 2001) will greatly

356    expand this area of effect. Therefore, it seems unlikely that the small-scale disturbance

357    experiments, such as DISCOL (~10.8 km$^2$), will be adequate for evaluating the potential effects

358    of full scale nodule mining. Further, the physical disturbance made in all experimental studies to

359    date have not been directly reminiscent of the impacts actual mining will make in terms of

360    volumes of surface sediment removed or displaced, subsequent sediment compaction, or

361    generation of the high resolution topographical changes associated with the ridges and troughs

362    likely to result from tracked mining vehicle movement (Jones et al., 2017;Doya et al., 2017;Jones

363    et al., 2018).

364

365    *4.3 Comparison of the DISCOL fish and scavenger communities to those within the CCZ*

366        Nodule mining is likely to affect very large areas of the seafloor over decades (Wedding

367    et al., 2015). Mobile fishes and other scavengers likely have the greatest ability to migrate away

368    from mining disturbances, but they may be affected regionally through the redistribution of prey

369    resources and sublethal effects from toxic metals or sediment plumes. Consequently, the

370    biogeographies of taxa, even mobile species, are an important input to spatial management

371    approaches (Watling et al., 2013).  The scale of species distributions will help determine where

372    and how large reserve areas should be in order to protect species. Comparison of the present

373    findings in the south Pacific to those in the CCZ polymetallic nodule province to the north,

374    across the equatorial upwelling, provide some insight into the ranges of abyssal fishes and

375    scavengers in this mining relevant region. Past studies frequently combined fish and scavenger

376    taxa into larger functional groups such as megafauna (Jones et al., 2017), but some studies have

377    presented lists of species, which are the focus of the comparison here.

378        A number of the fish taxa observed with camera transects in the CCZ have also been

379    identified in the DISCOL area suggesting large species distributions (Table 3). 10 of the 14 taxa

380    in the DISCOL region are shared with the CCZ. Four taxa were identified from DISCOL that

381    were not previously identified from the CCZ region, none of which were abundant. Four fishes

382    were observed in the various CCZ studies but not at the DISCOL site. A number of abyssal

383    species have pan-Pacific and even global distributions (Priede, 2017). However, we are not

384    suggesting that there is only a single community of fishes and scavengers integrated over 1000's

385  of kilometers. The overlap between the two areas may be artificially high due to the difficulty in

386  identifying species from photographs, particularly those taken from high altitudes, and hence the

387  use of genera and higher taxonomic categories. Further there are some taxa which can easily be

388  confused depending upon image quality. For instance in the DISCOL site we identified the

389  ophidiid, *Porogadus* sp. which has a long whip like tail and narrow body similar to Halosaurs

390  which have been observed in the CCZ (Amon et al., 2017) and in an earlier study at the DISCOL

391  site (Bluhm, 1994). We suspect that with increasing camera resolution and better taxonomic

392  experience, photographic data and its analysis will improve greatly. Also, taxa are much more

393  easily identified in oblique imagery. For instance, Halosaurs have prominent high pectoral fins

394  and a single short dorsal whereas *Porogadus* has a long low dorsal fin all of which are seen in

395  oblique imagery. We suggest the use of both oblique and vertical cameras on the same platforms

396  in future studies. There has been some suggestion that oblique imagery would also alleviate

397  avoidance issues with mobile taxa, but in the one abyssal study that used both oblique and

398  vertical cameras, greater fish density was found in the vertical imagery (Milligan et al., 2016).

399  Finally, collecting physical specimens and genetic data would be a great complement to the

400  camera-based approach. Trawling for fish samples in mining claim areas will be challenging due

401  to the great depth and the abundance of nodules, which can break nets and greatly damage

402  specimens. Baited traps are effective for some of the fauna (Leitner et al., 2017;Linley et al.,

403  2016).

404       The scavenging communities exhibit some interesting differences to those described from

405  the eastern CCZ region and other abyssal Pacific locations. The dominant DISCOL scavengers

406  were the shrimp *H. nereus*, eelpouts *Pachycara* spp., and the hermit crab *P. mirabilis*. The

407  presence of large numbers of hermit crabs at the DISCOL site has been noted in earlier transect

408  studies (Bluhm, 2001), and their large contribution to the scavenging community seems unique

409  amongst abyssal scavenger studies. The most similar finding was a few hermit crabs

410  (*Sympagurus birkenroadi*, MaxN= 2) attending bait from 2000 – 3000m depths off Hawaii (Yeh

411  and Drazen, 2009). The large numbers of *H. nereus* is similar to the community in the eastern

412  CCZ (Leitner et al., 2017). However, the eastern CCZ fishes were dominated by

413  *Coryphaenoides* spp., which were not abundant at the DISCOL site. Overall the DISCOL

414  scavenging community appears more similar to that observed in the western CCZ, which hosted

415  lower numbers of *Coryphaenoides* spp. and greater numbers of ophidiids and shrimp (Leitner et

al., 2017). The differences from east to west in the CCZ have been postulated to be related to the
lower surface productivity in the west. Indeed, more oligotrophic regions have been shown to
shift the dominance of the scavenging fishes from Macrourids to Ophidiids (Linley et al.,
2017;Fleury and Drazen, 2013).  However, the average long term chlorophyll concentration at
the DISCOL site estimated from the MODIS satellite (30x30km box from 2006-2016) is about
1.5 times higher (0.22 mg chl-a m$^{-3}$) than that reported by Leitner et al (2017) in the eastern
CCZ. Whether the community differences observed between the DISCOL and CCZ regions are
the result of variations in overlying productivity, species distributions, or other habitat factors
cannot be discerned until a greater number of baited camera studies are conducted across the
region.

In conclusion, the DISCOL site has a relatively diverse abyssal fish community
dominated by *Ipnops meadi*.  Fish density increased in the ploughed habitat type over time and
became similar to undisturbed habitat types at 26 years post disturbance, but the density of *I. meadi* is still only a third of the undisturbed habitat types indicating only partial recovery of the
fish fauna. The abyssal fish communities observed in the central eastern Pacific at DISCOL and
the more northerly CCZ are similar with many shared taxa.  However, further species level
identifications are required which requires the collection of physical specimens through trawling
or baited traps.  The scavenging community in the DISCOL site is unique in the prevalence of
the hermit crab, *P. mirabilis*, which does not appear in the CCZ in either camera transects or
baited camera deployments.  Not surprisingly, fishes and mobile scavengers appear generally to
have large ranges but also large shifts in community composition across the CCZ (Leitner et al.,
2017) and across the equator. As commercial mining of polymetallic nodule provinces rapidly
progresses, with commercial field trials commencing in the Belgian and German claim areas of
the CCZ in the first months of 2019, gaining a better understanding of these remote ecosystems
is of paramount importance. Until key fauna, such as the various benthic fish species utilizing
these habitats are better known, ensuring that appropriate management plans are developed to
best minimize human impact during mining will be extremely problematic.

**5. Author Contributions**

JCD and ABL analyzed the data and wrote the manuscript. SM annotated the baited camera

images and assembled the data. AP and YM designed and conducted the camera transect

experiments, quantified image coverage, helped write the manuscript, and generated the map

figure. JG digitized and archived the original baited camera images. All authors read and

commented on the manuscript.

## 6. Competing interests

The authors declare that they have no conflict of interest.

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620 **Table 1**. Numbers of photo transect observations (all images/ timed images only) for fishes in

621 the DISCOL area by habitat type. The percent of images with fishes are calculated from the

622 timed images only.

| OTU | Family | total | reference | undisturbed | transition | ploughed | ebs |
|---|---|---|---|---|---|---|---|
| *Bathysaurus mollis* | Bathysauridae | 13/11 | 2/1 | 5/4 | 2 | 2 | 2 |
| *Bathytyphlops* cf *sewelli* | Ipnopidae | 5 | | 3/3 | | 2 | |
| *Ipnops* cf *meadi* | Ipnopidae | 188/178 | 68/64 | 97/91 | 11 | 11 | 1 |
| Liparidae | Liparidae | 4/3 | 1 | 3/2 | | | |
| *Coryphaenoides armatus/yaquinae* | Macrouridae | 6/5 | | 3/3 | 3/2 | | |
| *Coryphaenoides leptolepis*? | Macrouridae | 1/0 | | 1/0 | | | |
| *Bassozetus* cf *nasus* | Ophidiidae | 6 | 2 | 1 | 2 | 1 | |
| *Bassozetus* sp. B | Ophidiidae | 2 | | 1 | 1 | | |
| *Bathyonus caudalis* | Ophidiidae | 30/26 | 8 | 15/12 | 2 | 3/2 | 2 |
| *Leucicorus* sp. | Ophidiidae | 3/2 | 3/2 | | | | |
| Ophidiid sp. 3 | Ophidiidae | 6 | 1 | 2 | 1 | 2 | |
| Ophidiidae unided | Ophidiidae | 16/14 | 2 | 8/6 | 1 | 5 | |
| *Porogadus* sp. | Ophidiidae | 11 | 4 | 3 | 3 | 1 | |
| *Pachycara spp.* | Zoarcidae | 4/2 | 2/1 | 2/1 | | | |
| unided fish | | 11/10 | 4/3 | 4 | | 2 | 1 |
| **#fish** | | 306/281 | 97/89 | 148/133 | 26/25 | 29/28 | 6 |
| **# OTUs** | | 14 | 10 | 13/12 | 9 | 8 | 3 |
| **# images** | | 16733 | 5964 | 7155 | 1209 | 2055 | 350 |
| **# images with fish** | | 300/275 | 97/89 | 145/130 | 23/22 | 29/28 | 6 |
| **% images with fish** | | 1.6% | 1.5% | 1.8% | 1.8% | 1.4% | 1.7% |

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**Table 2.** Deployment MaxN, persistence (pers.) and $T_{arr}$ for each bait-attending species by camera deployment. *deployment filmed a plough harrow track.

| Deployment | FBOS003 | | | FBOS004 | | | FBOS005 | | | FBOS006* | | | FBOS007 | | | FBOS013 | | | average | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | 2/20/1989 | | | 3/3/1989 | | | 3/16/1989 | | | 3/21/1989 | | | 3/22/1989 | | | 2/16/1992 | | | | |
| Image interval (min) | 5.5 | | | 3.5 | | | 5 | | | 2 | | | 3.5 | | | 3.5 | | | | |
| # images | 729 | | | 791 | | | 681 | | | 683 | | | 718 | | | 734 | | | 723 | |
| Latitude | 7° 2.12' S | | | 7° 1.97' S | | | 7° 4.83' S | | | 7° 4.53' S | | | 7° 4.55' S | | | 7° 4.72' S | | | | |
| Longitude | 88° 26.53' W | | | 88° 28.57' W | | | 88° 21.33' W | | | 88° 26.25' W | | | 88° 27.92' W | | | 88° 27.63' W | | | | |
| General location | Reference area | | | Reference area | | | Reference area | | | Disturbance area | | | Disturbance area | | | Disturbance area | | | | |
| Depth (m) | 4057 | | | 4167 | | | 4076 | | | 4220 | | | 4159 | | | 4170 | | | | |
| | MaxN | Pers. | $T_{arr}$ | MaxN | Pers. | $T_{arr}$ | MaxN | Pers. | $T_{arr}$ | MaxN | Pers. | $T_{arr}$ | MaxN | Pers. | $T_{arr}$ | MaxN | Pers. | $T_{arr}$ | MaxN | Pers. |
| **Fishes** | | | | | | | | | | | | | | | | | | | | |
| *Barathrites iris* | 1 | 0.4% | 5:38 | 1 | 3.0% | 4:54 | | | | 1 | 0.6% | 9:34 | 1 | 0.3% | 15:38 | | | | 1 | 1.1% |
| *Bassozetus* cf *nasus* | 2 | 13% | 39:20 | 1 | 4.9% | 10:48 | | | | 1 | 1.3% | 18:16 | | | | 1 | 21% | 2:31 | 1 | 10% |
| *Coryphaenoides armatus/yaquinae* | 1 | 1.0% | 10:11 | 2 | 7.4% | 1:49 | 2 | 2.3% | 8:05 | 1 | 1.2% | 12:40 | 1 | 0.1% | 2:17 | 1 | 0.8% | 2:52 | 1 | 2.1% |
| *Leucicorus* sp | | | | | | | 1 | 0.4% | 41:40 | | | | | | | | | | 1 | 0.4% |
| *Pachycara* spp. | 9 | 87% | 2:07 | 3 | 21% | 4:23 | 5 | 35% | 11:55 | 3 | 32% | 3:00 | 9 | 74% | 5:53 | 4 | 80% | 6:08 | 6 | 55% |
| Synaphobranchidae | 1 | 2.5% | 37:02 | 1 | 2.9% | 3:37 | 2 | 11% | 23:15 | | | | 1 | 0.1% | 17:23 | 1 | 7.4% | 3:13 | 1 | 4.8% |
| **Crustaceans** | | | | | | | | | | | | | | | | | | | | |
| *Hymenopeneus nereus* | 8 | 65% | 1:23 | 10 | 85% | 1:07 | 8 | 40% | 4:00 | 5 | 62% | 0:54 | 9 | 39% | 0:39 | 15 | 89% | 0:21 | 9 | 63% |
| Total Penaeid shrimp | 3 | 6.9% | 0:11 | 4 | 20% | 1:35 | 2 | 6.0% | 5:55 | 3 | 21% | 1:28 | 2 | 16% | 0:18 | 3 | 24% | 0:21 | 3 | 16% |
| *Cerataspis monstrosus* | 1 | 0.7% | 4:57 | 1 | 0.4% | 15:38 | | | | 1 | 1.0% | 1:28 | 1 | 0.4% | 40:01 | | | | 1 | 0.6% |
| *Benthiscymus* sp. | 2 | 2.2% | 15:02 | 2 | 3.3% | 2:17 | 1 | 0.7% | 8:00 | 2 | 4.4% | 6:16 | 1 | 4.0% | 0:46 | 2 | 3.5% | 2:17 | 2 | 3.0% |
| *Munnidopsis* sp. | | | | 2 | 11% | 10:16 | 1 | 9.4% | 35:10 | 1 | 0.4% | 12:12 | | | | 1 | 7.2% | 36:35 | 1 | 9.3% |
| Munnopsidae | 2 | 4.4% | 11:44 | 1 | 1.6% | 39:02 | 2 | 4.4% | 0:45 | 1 | 0.3% | 19:46 | 1 | 1.0% | 2:20 | | | | 1 | 2.4% |
| Mysidae | | | | 1 | 0.4% | 3:41 | 2 | 1.0% | 10:55 | | | | | | | | | | 1 | 0.6% |
| *Probeebei mirabilis* | 1 | 1.8% | 0:22 | 9 | 32% | 0:00 | 4 | 27% | 2:20 | 3 | 12% | 0:20 | 4 | 30% | 0:11 | 6 | 69% | 0:04 | 5 | 29% |
| **Other taxa** | | | | | | | | | | | | | | | | | | | | |
| Octopoda | 1 | 0.3% | 10:55 | | | | 1 | 2.3% | 23:25 | | | | | | | | | | 1 | 1.3% |
| Ophiuroidea | 1 | 0.7% | 21:55 | | | | | | | | | | 1 | 47% | 4:37 | 1 | 7.8% | 1:31 | 1 | 19% |

626 **Table 3**. Fish taxa occurrences from DISCOL and abyssal sites of the CCZ. * listed in Bluhm

627 (1994), bc – observed by baited camera only, #only these taxa out of 17 are given in the original

628 reference

| Taxa | Family | This study | (Amon et al., 2017;Amon et al., 2016) | (Pawson and Foell, 1983) | (Radziejewska and Stoyanova, 2000) | (Tilot, 2006)[#] |
|---|---|---|---|---|---|---|
| *Bathysaurus mollis* | Bathysauridae | x | x | x | | x |
| Halosauridae | Halosauridae | * | x | | | |
| *Bathytyphlops sewelli* | Ipnopidae | x | | | | |
| *Ipnops meadi* | Ipnopidae | x | x | x | x | x |
| Liparidae | Liparidae | x | | | | x |
| *Coryphaenoides armatus/yaquinae* | Macrouridae | x | x | x | x | x |
| *Coryphaenoides leptolepis*? | Macrouridae | x | | | | |
| *Barathrites iris* | Ophidiidae | bc | bc | | | x |
| *Bassozetus* sp. | Ophidiidae | x | x | x | | |
| *Bassozetus* sp. B (sp 4 in Amon et al 2017) | Ophidiidae | x | x | | | |
| *Bathyonus caudalis* (sp 5 in Amon et al 2017) | Ophidiidae | x | x | | | |
| *Leucicorus* sp. | Ophidiidae | x | | | | |
| Ophidiid sp. 1 | Ophidiidae | | x | | | |
| Ophidiid sp. 2 | Ophidiidae | | bc | | | |
| Ophidiid sp. 3 | Ophidiidae | x | x | | | |
| Ophidiidae | Ophidiidae | x | | x | | x |
| *Porogadus* sp. | Ophidiidae | x | | | | |
| *Typhlonus nasus* | Ophidiidae | | | x | | x |
| *Histiobranchus bathybius* | Synaphobranchidae | | x | | | |
| Synaphobranchidae | Synaphobranchidae | bc | | | | x |
| *Pachycara* spp. | Zoarcidae | x | x | | | |
| Zoarcidae | Zoarcidae | | x | x | | |

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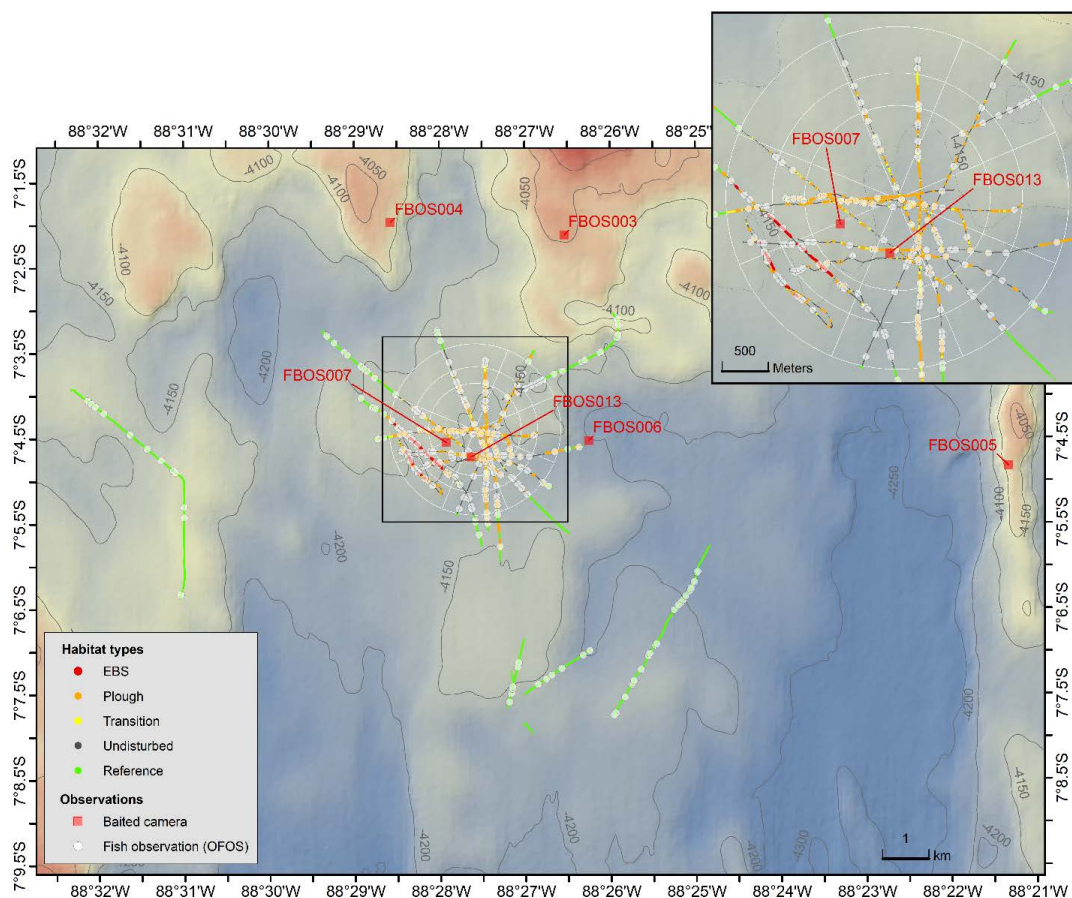
630

631    **Figure Captions**

632

633
634    **Figure 1**. Map of the DISCOL study site showing the distribution of OFOS camera transects

635    (colors indicate the 5 habitat types), the OFOS-based fish observations (white circles), and the

636    location of the baited camera deployments (red squares). The white circular pattern and spokes

637    shows the location and extent of the DEA.

638

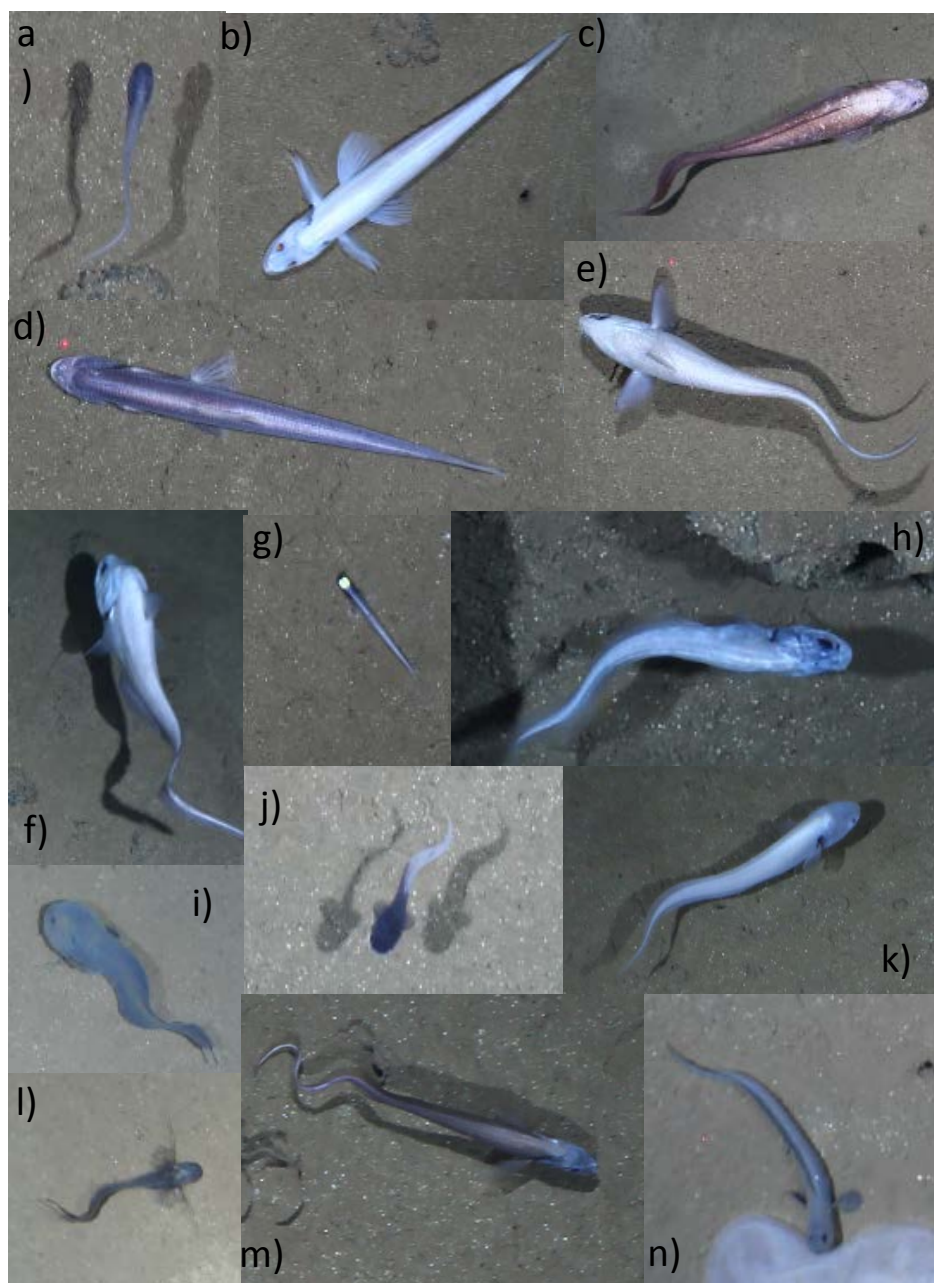



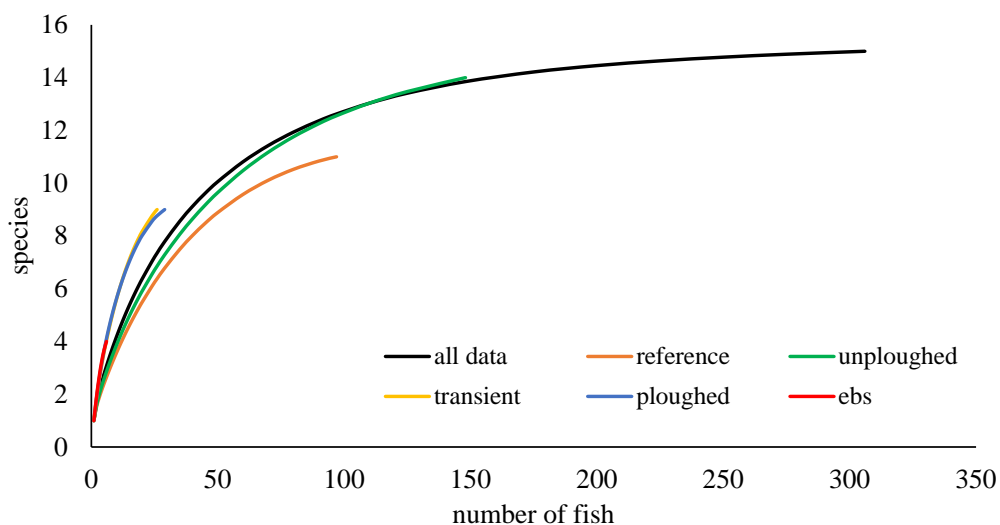
**Figure 2**. Representative images of OTUs identified in the DISCOL region during the 2015

survey. A) *Bassozetus* cf. *nasus* b) *Bathysaurus mollis* c) *Bathyonus* cf. *caudalis* d)

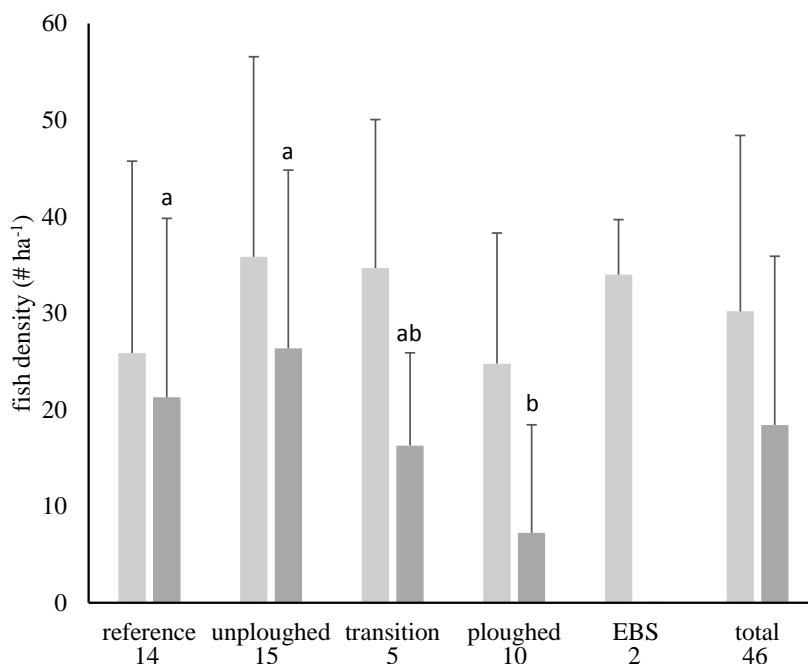
*Bathytyphlops* cf. *sewelli* e) *Coryphaenoides armatus/yaquinae* f) *Coryphaenoides leptolepis* g)

643    *Ipnops* cf. *meadi* h) *Leucicorus* sp. i) Liparidae grey morphotype h) Liparidae bicolor

644    morphotype k) *Bassozetus* sp. B l) Ophidiid sp. 3 m) *Porogadus* sp. n) *Pachycara* cf. *nazca*.

645

646
647     **Figure 3**. Rarefaction curves, estimated species richness as a function of the number of fish

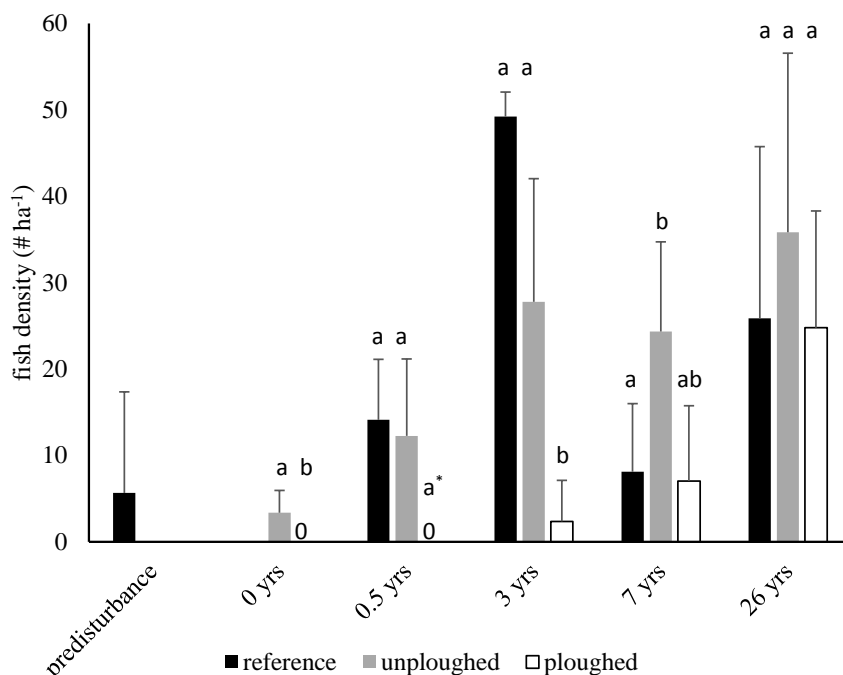
648     observations, for OFOS transects across habitat types.

649

650
651     **Figure 4**. Total fish (light grey) and *I. meadi* (dark gray) density (mean and standard deviation)

652     from the 2015 OFOS transects by habitat type (timed images only) and for the entire dataset.

653    The number of separate transects for each habitat type is given under its name.  Letter symbols

654    for each habitat indicate significant differences in *I. meadi* density (p<0.05).

655

656
657    **Figure 5**. Fish density (mean and standard deviation) from predisturbance (1989) to 26 years

658    post disturbance (2015) in the reference area and in the ploughed and unploughed habitats of the

659    DEA. Data from predisturbance to 7 years post disturbance are from Bluhm (2001). Letter

660    symbols for each time indicate significant differences between habitat types (p<0.05). At 0.5 yrs

661    the asterisk indicates a marginal significant difference (p = 0.057).

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663
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665
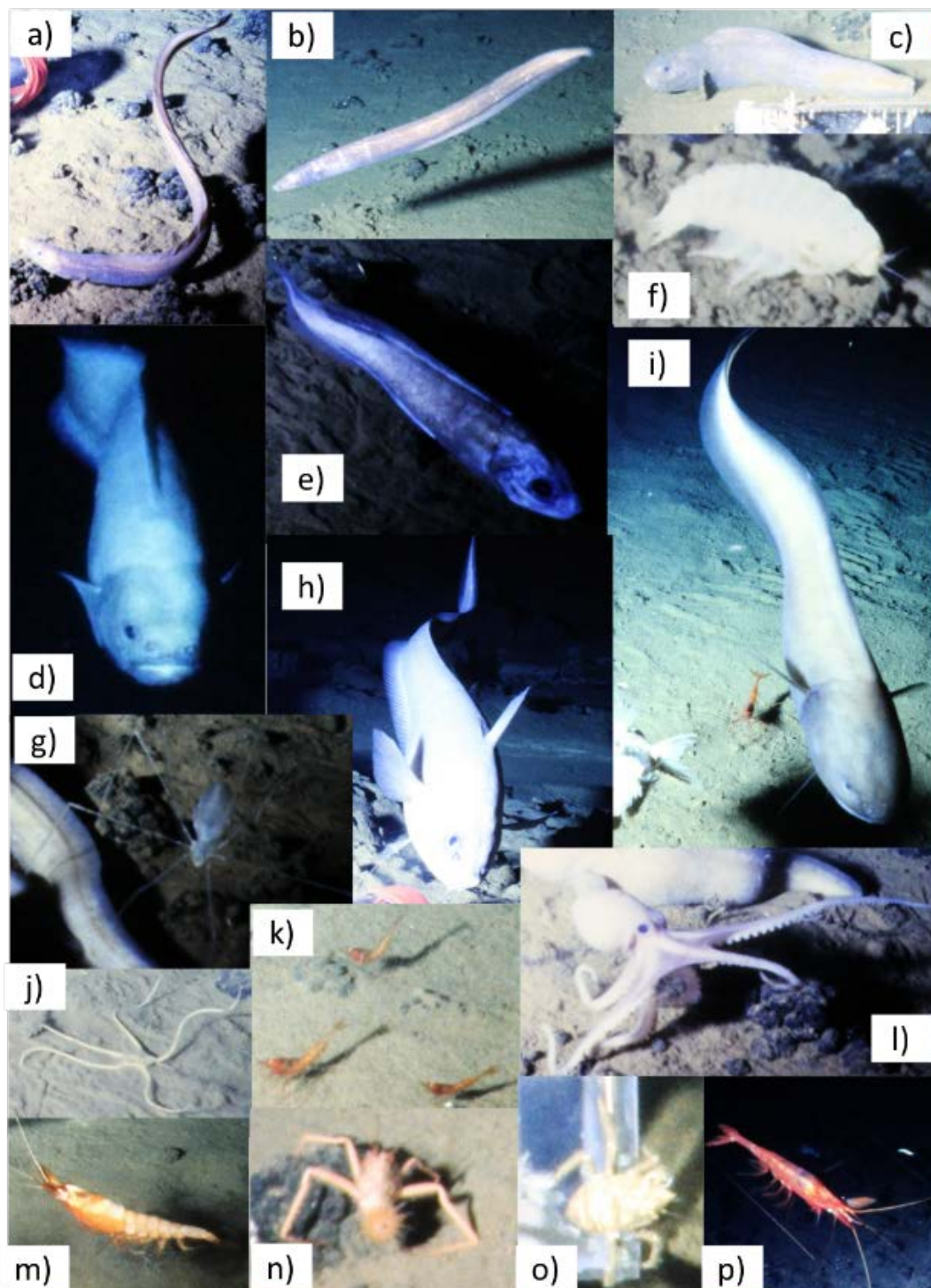
**Figure 6**. Representative images of OTUs identified using baited cameras in the DISCOL

region. A) *Illypohis* sp. B) Synaphobranchidae C) *Pachycara nazca* D) *Barathrites iris* E)

*Leucicorus* sp. F) Large amphipod likely *Eurythenes* sp. G) Munnopsidae H) *Coryphaenoides* sp.

I) *Bassozetus* c.f. *nasus* J) Ophiuroidea K) *Hymenopeneus nereus* L) Octopoda (*Vulcanoctopus*

sp.) M) *Benthiscymus* sp. N) *Probeebei mirabilis* O) *Munnidopsis* sp P) *Cerataspis monstrosus*
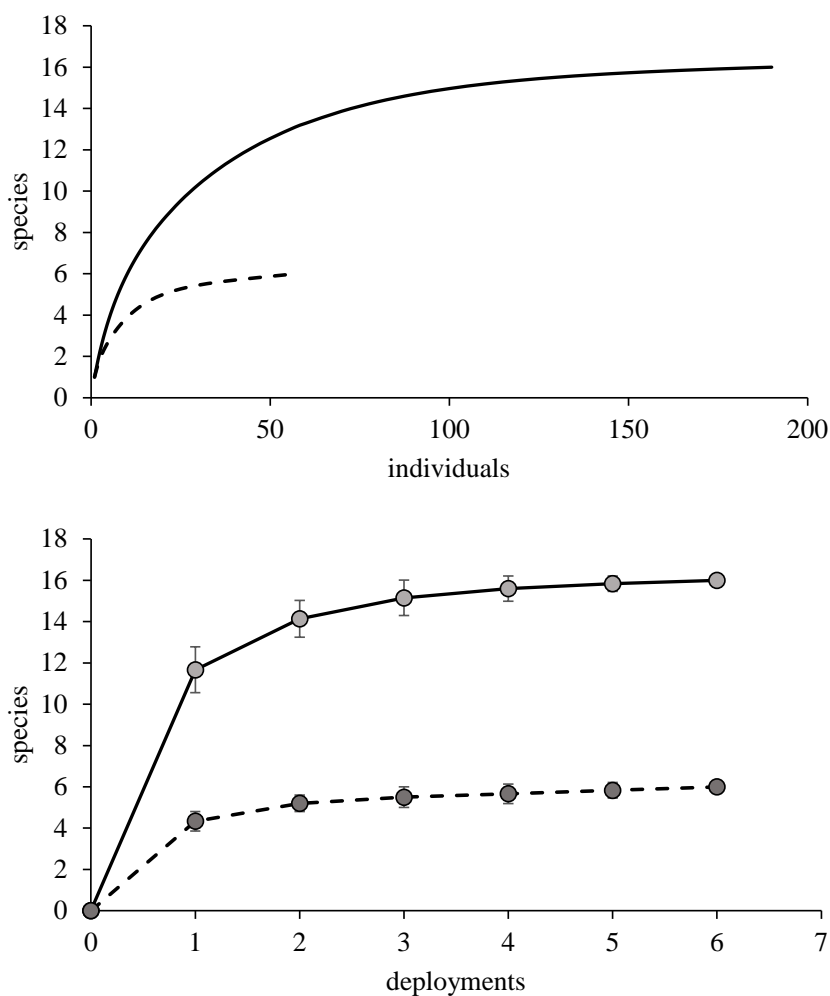
**Figure 7.** a) Rarefaction and b) species accumulation curves for baited camera observations.

Solid lines represent all data and dashed lines are fishes only (both based on MaxN data).