Re-establishment of an abyssal megabenthic community after experimental physical disturbance of the seafloor

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Abstract

The suitability of deep-sea megafauna as indicators of environmental change has been demonstrated by a large-scale and long-term disturbance and recolonisation experiment (DISCOL) established in the deep Peru Basin in 1989. The experiment was designed to show what effects physical disturbances, such as those caused by future commercial deep-sea mining, might have on the seafloor and its inhabitants. A plough-harrow was used to create a large-scale disturbance on the seafloor. It destroyed megafauna within the plough tracks to a large extent and buried the manganese nodules in the area. As a result fauna that lived attached to the nodules disappeared. The soft-bottom community, however, did show signs of recovery in the seven years of the study. The repopulation of the disturbed areas by highly motile and scavenging animals started shortly after the area was ploughed. Seven years later hemisessile animals had returned to the disturbed areas, but the total abundance of soft-bottom taxa was still low compared to the pre-impact study. Nearby reference areas not impacted by the experiment showed natural changes in animal densities during the study. The ploughing activities created a sediment plume that resettled in the surrounding areas. In these not directly impacted areas animal densities declined immediately after the ploughing event, but later appeared to be greater than in the reference areas of the pre-impact study. Possible reasons for this are discussed. © 2001 Published by Elsevier Science Ltd.

1. Introduction

Human industrial activities in the deep sea, e.g. dumping of waste, storage of carbon dioxide, or mining of mineral resources, will have a large impact on the abyssal benthos (Jumars, 1981; Thiel, 1991; Thiel and Schriever, 1994). The deep sea is inhabited by a highly diverse fauna. Our knowledge of the taxonomy and ecology of the abyssal benthos is still poor. There is an urgent

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need for baseline and special environmental studies related to impact assessments of such activities on abyssal communities.

Industrial technologies for manganese nodule mining have already been developed although some technical problems still need to be solved. Knowledge of the impacts created by these devices is largely unknown. At the very least sediment surface structures will be physically changed influencing the structure of benthic communities.

The aim of the DISCOL experiment ('DISturbance and reCOLonization experiment in a manganese nodule area of the deep South Pacific'; Foell et al., 1990, 1992a, b; Schriever, 1990; Schriever and Thiel, 1992; Thiel and Schriever, 1989, 1990) was to observe the long-term re-establishment of the benthic fauna following a large scale, experimental physical disturbance of the seafloor. The experiment was conducted as part of German national deep-sea environmental protection activities (TUSCH, Thiel, 1995; Thiel and Forschungsverbund Tiefsee-Umweltschutz, 1995) and started in 1989 in the Peru Basin, in the tropical south-eastern Pacific Ocean.

A large area of seabed (11 km^2) was ploughed with a specially designed 'plough-harrow' (Thiel and Schriever, 1989). Post-impact studies were conducted immediately after impact, half a year later, and again after three years. Dominant taxa of meio-, macro-, and megafauna were investigated to identify indicator species that characterised the recovery process. Seven years after ploughing, the DISCOL Experimental Area (DEA) was revisited during the ECOBENT project and a similar sampling programme was again conducted (Schriever et al., 1996).

The megabenthos comprises a major fraction of the deep-sea benthic biomass. It plays a key role in abyssal ecosystems (Smith and Hamilton, 1983), and therefore has to be included in environmental studies. Megabenthic organisms are defined as species large enough to be determined on photographs (Grassle et al., 1975; Rex, 1981). They are difficult to study using conventional sampling methods because of their low density, and in areas with manganese nodules the animals are typically badly damaged when collected with trawls (Bluhm et al., 1995).

A great deal of data already exist on the density and diversity of megafauna from manganese nodule sites in the Pacific (Hecker and Paul, 1977; Foell et al., 1986; Pawson, 1988; Foell, 1992; Tilot, 1992; Morgan et al., 1993; Bluhm et al., 1995) and Indian Oceans (Sharma and Rao, 1992). A comparison of these data was presented by Bluhm (1994). Data on megafauna recolonisation within the DISCOL experiment were published in Bluhm et al. (1995). Results of the ECOBENT study, regarding the continuing re-establishment of the community, are presented herein.

2. Material and methods

The DISCOL Experimental Area (DEA) is located close to a German manganese nodule claim. The DEA is a circular area of 10.8 km^2, with its central position at 07°04.4′S and 88°27.6′W. The water depth ranges between 4140 and 4160 m. The abundance of manganese nodules in the DEA before the experiment was about 5–10 kg/m^2. The size of individual nodules varied between 8 and 15 cm in diameter (Thiel and Schriever, 1989).

The plough-harrow was towed on diammetric courses through the centre of the DEA a total of 78 times, so that the inner circle of the DEA was disturbed to a larger degree than the outer ring. This was confirmed by the results of a combined video and side-scan sonar analysis (Bluhm et al.,

1995). During DISCOL and ECOBENT the DEA was sampled five times:

1. during the pre-impact study, February 1989
2. directly after the disturbance, March 1989
3. half a year later, September 1989
4. after three years, January 1992, and
5. after seven years, February 1996.

The megabenthos was studied using the photo/video system OFOS (Ocean Floor Observation System; Bluhm, 1993). OFOS was towed approximately 3–3.5 m above the seafloor (Bluhm et al., 1995). It was equipped with real-time black and white television coupled with a 'photo-on-command' still photography camera loaded with Kodak Ektachrome 200 film. The towing speed varied between 0.5 and $1.3\,\text{kts}^{-1}$.

The results of the analyses of 23 OFOS transects have been published with a detailed description and discussion of the image analyses methodology (Bluhm et al., 1995). For this study, OFOS transects 7, 9 and 10 were ignored because they were made at a time when not all ploughing had been completed. Five ECOBENT transects were added to the DISCOL data. A total of 14,000 slides and 6000 min of video recordings were used in this study (Table 1), representing approximately 700,000 m^2 of the seafloor (Table 2).

The entire DISCOL database had to be recalculated because animal densities calculated by Bluhm et al. (1995) were overestimated due to a software error. In particular the data from the third post-impact study and to a lesser extent those of the second post-impact study were affected. To enhance the quality of the results of the image analyses, the slides and video recordings taken concurrently were re-examined in this study. The new correction factors applied to the video density data are now considered to be accurate.

There was insufficient time to repeat image analyses of the photographs and video recordings, and the number of animal categories found in the pre-impact study should be lower than in the fourth post-impact study due to the increasing experience of the author in identifying taxa during the experiment. To eliminate this problem, the highest taxonomic level was used to compare data from the different expeditions since this was determinable in all cases.

The photographic observations allowed the seabed to be defined according to the following scheme depending on the degree of impact:

'Undisturbed areas': areas within the DEA not directly influenced by the plough-harrow, but which showed various levels of resedimentation of sediment plumes created by the disturber.
'Disturbed areas': areas within the DEA directly disturbed by the plough-harrow. The sediment surface was disrupted by the disturber and covered by a thin layer of resettled sediment. Only a few manganese nodules remained on the sediment surface. Most were ploughed under.
'Reference areas': areas outside the DEA not affected by the disturber.

These definitions are modified from those published in Bluhm et al. (1995) to allow better comparisons to be made with the meio- and macrofauna investigations (Ahnert and Schriever,

Table 1
Analysed OFOS images

Expedition OFOS deployment	Slides used	Video recordings duration (min)
DISCOL 1/1 (pre-impact study)		
2	518	236
3	551	236
4	243	136
5	717	364
6	561	238
8	556	344
DISCOL $\frac{1}{2}$ (first post-impact study, 0 years after the ploughing)		
12	375	206
13	471	231
15	659	305
16	724	146
17	505	215
DISCOL 2 (second post-impact study, 0.5 years after ploughing)		
19	140	62
21	517	225
22	763	240
23	546	211
24	572	229
DISCOL 3 (third post-impact study, 3 years after ploughing)		
30	757	176
31	769	345
32	456	188
33	715	267
ECOBENT (fourth post-impact study, 7 years after ploughing)		
36	481	270
37	199	90
38	483	271
41	509	636
42	730	234
Total	13,517	6101

2001; Borowski, 2001; Vopel and Thiel, 2001). The 'reference area' referred to in these studies was a location 3.2 nautical miles south of the DEA and was not examined by OFOS.

Density calculations were made by counting animals in each of the locations defined and relating the counts to the area surveyed. There was considerable variability in the area covered depending on the length of the video recordings and visibility of the seafloor (Table 2). Due to the

Table 2
Areas monitored by the OFOS (m^2)

Deployment no.	Total (m^2)	Reference (m^2)	Undisturbed (m^2)	Disturbed (m^2)
2	32,000	32,000		
3	37,174	37,174		
4	22,881	22,881		
5	53,125	53,125		
6	24,414	24,414		
8	38,435	38,435		
12	21,486		13,953	4700
13	23,437		20,014	1978
15	36,902		18,640	3974
16	14,043		8542	
17	22,920		14,971	4987
19	10,937		7003	
21	37,262		25,883	4612
22	34,966		17,788	6328
23	34,289	29,681	2868	768
24	37,305	37,207		
30	10,366	3819	3471	1381
31	22,972	5786	11,668	3208
32	13,236	1551	3783	718
33	18,606		13,535	1366
36	39,458	4416	24,277	3628
37	12,532	12,532		
38	33,384	7268	15,103	3716
41	47,746	14,345	17,678	5174
42	27,920	11,545	7478	3495
Total	707,794	336,179	226,656	50,032

absence of true replicates, the data were adjusted by summarising megafauna abundance of the single areas defined and relating the values to the total area observed. From the statistical point of view, this integrated approach limited sample statistics to only a few parameters and did not allow the testing of hypotheses.

SPSS/PC+ Version 4.0 was used to calculate sample statistics. Owing to the small number of OFOS transects for each of the areas defined, the standard deviations and standard errors are not plotted on the figures. Instead, the total data ranges are combined with the arithmetic means. The standard errors and standard deviations however, are given in the tables.

The concept of the 'minimal area' (Weinberg, 1978) relates to the area that has to be sampled to get a representative picture of the species diversity and density at that location. Following the approach of Pfeifer et al. (1996) the minimal area calculations were made using their software package MINAREA (July 1997). For each area defined (see above) the megafauna abundance was calculated for each expedition. From these data, sampling was then simulated and the minimal area was calculated.

Nonmetric multidimensional scaling (MDS; e.g., Kruskal and Wish, 1978) is a method commonly used to classify multivariate data sets in marine research. The first step is to find similarity or distance indices appropriate to the data structure that best fit the differences one would like to detect. The second step is the mirroring of differences between the objects in a low-dimensional space. The results of the non-metric MDS are represented by plots in which two samples are closely related to each other when the spatial distance between them is small.

The Euclidean and Cosine distance measures were used for comparison of the data sets. Cosine distance is defined as: Cosine Distance = 1−Cosine Similarity.

Numerically abundant animals influence the Euclidean distance values while the relative abundance of species is represented by the Cosine similarity. The similarity indices have been constructed simply, and no 'root to root' or other types of data transformation have been used. Both distance measures without any transformations have the advantage that the results are easy to interpret. SPSS/PC + Version 4.0 was used to perform the non-metric MDS. The stress values, calculated after the formula of Kruskal, and the Sheppard diagrams are indications of how well the original differences fit the mirror images. The stress values were low in all calculations (less than 10^{-4}). The Sheppard diagrams are not presented herein, but showed straight increasing lines. Both indicated good approximations to the original data.

The following abbreviations were used in Figs. 3–7 to characterise the data sets:

P	pre-impact study	0	0 years after ploughing; first post-impact study
R	reference area	$\frac{1}{2}$	0.5 years after ploughing; second post-impact study
U	undisturbed area	3	3 years after ploughing; third post-impact study
D	disturbed area	7	7 years after ploughing; fourth post-impact study

e.g. data from disturbed areas three years after ploughing are characterised by 'D3'. Reference records taken directly after the impact (R0) do not exist. The time interval between the pre-impact and first post-impact study was only one month, however, and the pre-impact record (P) therefore can be used as a reference (Bluhm et al., 1995).

3. Results

3.1. Qualitative observation

Details of the plough operations, their impact on the seafloor, the photographic observations, the development of surface structures, and the re-establishment of the epifaunal community during DISCOL are described in detail in Bluhm et al. (1995). Additional information concerning the fourth post-impact study (ECOBENT) is given here.

During the third post-impact study we observed that the plough-harrow tracks were less sharp than previously seen owing to near-bottom currents and faunal activities. Their outlines, however, were still well defined. The same situation was found seven years after impact, although shallow plough marks were now difficult to recognise on the video images. The deeper plough marks had been further smoothed, but otherwise there were no strong differences in the shape of plough marks from those observed after three years.

Ophiuroids, sea cucumbers, fish, and the hermit crab *Probeebei mirabilis* were found frequently in the plough-harrow tracks seven years after the ploughing; a situation comparable to that observed in the third post-impact study. In contrast, however, animals with limited mobility, e.g., anemones and lophenteropneusts (Lemche et al., 1976), as well as asteroids were seen in disturbed areas only after seven years.

3.2. Density data

Eighteen different taxa were identified in the DISCOL and ECOBENT data (Table 3). Specimens that could not be attributed to any particular taxonomic category were classified as 'indeterminable'. Only a few taxa showed high abundances. Fourteen taxa were missing from one or more of the transects.

The taxa were divided into four groups depending on their mean abundances and variances. Group 1 taxa included animals with the highest abundances and variances. In all cases the minimum mean density was greater than zero. The mean abundances decreased from Group 2 to Group 4. The latter group contained only rare taxa.

Group 1: Crustacea, Porifera, Ophiuroidea, and Holothuroidea
Group 2: Actiniaria, Asteroidea, Osteichthyes, and indeterminable
Group 3: Cnidaria (other than Actiniaria, Pennatularia, Gorgonaria, Ceriantharia, and

Table 3
Descriptive statistics of records from the 'reference' areas, combined for all expeditions. (total 18 transects for all taxa)

| Taxon | Mean | Confidence limit | | Median | Mini-mum | Maxi-mum | Variance | Standard deviation | Standard error | Skew-ness | Kur-tosis |
		−95%	+95%								
Porifera	372.45	243.60	501.29	293.30	134.58	1150.65	67134.29	259.10	61.07	1.96	4.24
Cnidaria	13.23	0.91	25.55	3.56	0.00	95.82	613.84	24.78	5.84	2.77	7.71
Actiniaria	39.25	21.10	57.40	28.12	6.41	162.26	1331.90	36.50	8.60	2.55	7.54
Pennatularia	0.83	0.20	1.46	0.00	0.00	3.93	1.61	1.27	0.30	1.59	1.64
Gorgonaria	4.72	2.13	7.32	3.35	0.00	18.07	27.23	5.22	1.23	1.33	1.40
Ceriantharia	1.70	0.04	3.36	0.00	0.00	11.14	11.11	3.33	0.79	2.42	4.99
Anthozoa	1.04	−0.42	2.50	0.00	0.00	10.56	8.57	2.93	0.69	2.87	7.50
Cephalopoda	3.24	1.05	5.43	0.86	0.00	14.69	19.34	4.40	1.04	1.46	1.63
Crustacea	523.79	337.72	709.85	436.28	125.43	1560.09	139996.28	374.16	88.19	1.87	3.23
Polychaeta	6.16	2.02	10.31	3.09	0.00	29.38	69.48	8.34	1.96	1.70	2.66
Asteroidea	18.65	10.01	27.28	12.33	0.00	70.14	301.49	17.36	4.09	2.01	4.20
Ophiuroidea	224.16	165.99	282.32	192.61	69.08	549.77	13680.00	116.96	27.57	1.36	2.41
Echinoidea	3.62	0.48	6.77	1.36	0.00	25.63	39.93	6.32	1.49	2.82	9.01
Holothuroidea	157.41	120.04	194.78	155.51	72.20	348.95	5647.25	75.15	17.71	1.22	1.52
Crinoidea	7.70	2.85	12.54	4.09	0.00	38.45	94.88	9.74	2.30	2.21	5.40
Hemichordata	6.60	3.28	9.92	5.03	0.00	24.18	44.53	6.67	1.57	1.42	1.84
Ascidia	12.42	5.72	19.12	10.49	0.00	44.08	181.61	13.48	3.18	1.01	0.43
Osteichthyes	14.02	4.95	23.08	5.51	0.00	51.45	332.59	18.24	4.30	1.25	0.23
Indet.	47.57	30.82	64.32	38.54	0.00	146.45	1134.52	33.68	7.94	1.43	3.60

Antipatharia), Ascidia, Hemichordata, and Crinoidea

Group 4: Rest (Pennatularia, Gorgonaria, Ceriantharia, Antipatharia, Cephalopoda, Polychaeta, Echinoidea)

3.3. Minimal area

More than 170 different categories of megabenthos were found in the southeastern Pacific manganese nodule area (Bluhm, 1994; Bluhm et al., 1995). Many of them showed only low abundances and frequencies of occurence. Only the most abundant taxa were used to detect temporal changes in the animal community, but even in these fauna their patchy distributions influenced the size of the minimal areas to a high degree.

The minimal areas were greatest for the pre-impact study (P in Table 4A). When all taxa are considered together, the areas monitored by OFOS in most cases exceeded the values of the minimal areas in the reference and undisturbed areas (Table 4A). However, in all the disturbed areas and in the undisturbed area monitored during the third post-impact study (U3), there were insufficient data to characterise the whole megafaunal community. Therefore, the number of taxa were reduced to the 12 most abundant taxa present in the reference areas, consisting of members from Group 1 to 3 (see above). Even with this change, the data collected in the disturbed areas still did not adequately represent the megafaunal community (Table 4B).

The minimal areas were now greatest during the first post-impact study (Table 4B) indicating a large spatial heterogeneity in distributions as a result of the ploughing activities. The minimal areas of the undisturbed areas declined significantly between the first (U0) and the last (U7) post-impact study, i.e. the animals became more evenly distributed with time.

For the reduced data set (Table 4B) the minimal area of the undisturbed areas in the first post-impact study (U0) was larger than that of the pre-impact (P) and reference areas ($R\frac{1}{2}$ to R7) and decreased during the following post-impact studies. Seven years after ploughing (U7) it was again nearly the same as the pre-impact value. The number of taxa in the disturbed areas were less than the number in the reference and undisturbed sites (see below), but even so the minimal area was three to five times greater than that in the pre-impact study (P) despite using fewer taxa.

3.4. Community analyses

Megabenthos from manganese nodule areas are difficult to capture (Bluhm et al., 1995) and only a few specimens could be determined at the species level. The protocols created during image analyses therefore had to use higher levels of taxonomic classification, although the lowest level was used wherever possible, e.g. family, order, or class. The 'animal category' (Bluhm, 1994) employed therefore encompasses a variety of taxonomic levels. These were used for diversity comparisons.

Fig. 1 presents the numbers of animal categories found in the disturbed areas during the experiment. Sessile, as well as hemi-sessile and mobile megafauna, categories declined after the impact, and remained at the same level seven years after ploughing. A similar decrease was observed in animal densities (Fig. 2), but while the densities of sessile animals remained approximately the same throughout the post-impact studies, the densities of mobile megafauna

Table 4
Results of the minimal area calculations for each expedition and type of area, using (A) all taxa and (B) the 12 dominant groups: Porifera, Cnidaria (other than Actiniaria, Pennatularia, Gorgonaria, Ceriantharia, and Antipatharia), Actiniaria, Crustacea, Holothuroidea, Asteroidea, Ophiuroidea, Crinoidea, Hemichordata, Ascidiacea, Osteichthyes, and 'indeterminables'[a]

Area type	Number of taxa	Area monitored (ha)	Minimal area μ (ha)	Std. dev. $\tilde{o}$ of μ	Number of taxa in μ-$\tilde{o}$
(A) (All taxa)					
P	19	20.80	12.49	9.82	18
$R\frac{1}{2}$	18	7.81	1.38	0.98	16
R3	16	1.12	1.01	0.81	14
R7	19	5.01	1.45	1.07	16
U0	18	7.61	4.00	2.96	16
$U\frac{1}{2}$	17	5.35	5.08	3.24	15
U3	19	3.25	4.73	2.93	17
U7	18	6.45	1.80	1.23	16
D0	10	1.56	2.80	2.41	7
$D\frac{1}{2}$	8	1.17	2.46	1.77	6
D3	10	0.67	0.90	0.58	8
D7	13	1.60	2.19	1.38	11
(B) (Twelve dominant groups)					
P	12	20.80	0.51	0.29	10
$R\frac{1}{2}$	12	7.81	0.29	0.17	10
R3	12	1.12	0.14	0.10	10
R7	12	5.01	0.41	0.24	10
U0	12	7.61	3.45	3.10	10
$U\frac{1}{2}$	12	5.35	3.05	3.01	7
U3	12	3.25	0.93	0.89	8
U7	12	6.45	0.68	0.55	10
D0	8	1.56	2.69	2.48	5
$D\frac{1}{2}$	8	1.17	2.46	1.77	6
D3	9	0.67	0.68	0.50	7
D7	11	1.60	1.74	1.22	9

[a] Std. dev, standard deviation. Area type: (R) reference; (U) undisturbed; (D) disturbed area; (P) pre-impact value; (0) 0 years; ($\frac{1}{2}$), 0.5 years; (3) 3 years; and (7) 7 years after ploughing.

almost reached the pre-impact level three years after ploughing. However, a decline in total density was again apparent seven years after the impact.

Fig. 3A shows the results of the non-metric MDS using the Euclidean distance for all taxa found and provides detailed information about temporal change in the megabenthic community. The plot demonstrates relatively high similarities between reference and undisturbed areas. The differences in the composition of the megabenthic communities at the undisturbed areas and during the pre-impact study (P) are comparably small directly after ploughing (U0), but become increasingly different during the experiment until three years after the impact (U3).

In Fig. 3A the disturbed areas form a distinct cluster. The temporal differences are smaller as compared to the undisturbed and reference areas. The largest difference to the pre-impact
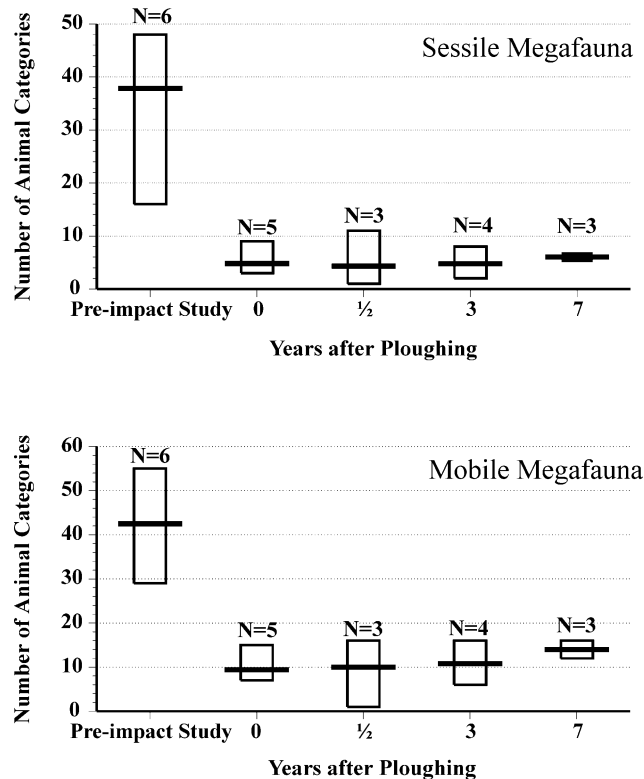
Fig. 1. Disturbed area. Number of animal categories found during the experiment: arithmetic mean, minimum–maximum range and *N*, the number of records used.

situation can be observed directly after the impact (D0). The dissimilarities of the disturbed and the pre-impact records decrease over the course of the experiment.

Using the Cosine distance (Fig. 3B) the undisturbed areas show the least and the disturbed areas the greatest temporal change. The similarities between the undisturbed and reference areas are greatest three years after ploughing. The undisturbed area sampled 0.5 years after the impact $(U\frac{1}{2})$ is similar to the pre-impact situation (P).

Using only the 12 taxa of groups 1, 2 and 3 (see above), results comparable to those presented in Fig. 3 were found.

3.5. Total megabenthos densities

A simple hypothetical model presented by Bluhm et al. (1995) predicted the changes in megafauna densities during the recovery process. Greatest densities of megafauna were expected during the pre-impact study and in the reference areas. In the ploughed area, a majority of the megabenthos was buried or killed by the plough-harrow. The densities therefore should be minimal in these areas and should increase with time. Density values of the 'undisturbed' areas should be similar to those of the 'reference areas'. Both should show different degrees of
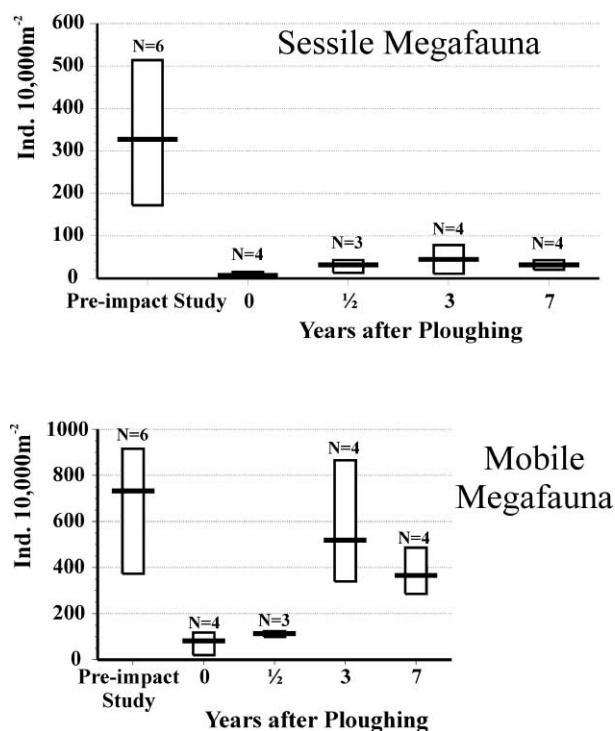
Fig. 2. Disturbed area. Densities (Ind. $10,000\,m^{-2}$): arithmetic mean, minimum–maximum range and N, the number of records used.

resedimentation, which might have an effect on the megabenthos. Presumably during the first stages of the experiment, the effect should be negative because high resedimentation rates would cause problems for filter-feeding animals.

Fig. 4 shows the megafauna density distributions found in the different regions of the DISCOL area. The left-hand bars in all three diagrams represent pre-impact data. With the exception of the 'three years after ploughing' data, the densities of megabenthos remain approximately at the same level in the 'undisturbed' (Fig. 4B) and 'reference areas' (Fig. 4A) throughout the experiment.

Three years after ploughing, the total abundance at undisturbed and reference stations increased to values three to four times higher when compared to the other expeditions. A similar situation is observable within the data of the disturbed areas (Fig. 4C). This is an indication that natural changes also may have influenced megafauna densities during the experiment.

Ploughing the seafloor results in a strong impact on the megabenthos as indicated by the low densities found in the plough tracks shortly after impact (Fig. 4C). During subsequent expeditions, an increase of megabenthos abundance was found in the ploughed area. Total densities in disturbed areas were still lower seven years after ploughing when compared to pre-impact values.

The first and second post-impact records supported the hypothetical model. The increase in the total megafauna densities at these times are lower at the undisturbed sites when compared to the
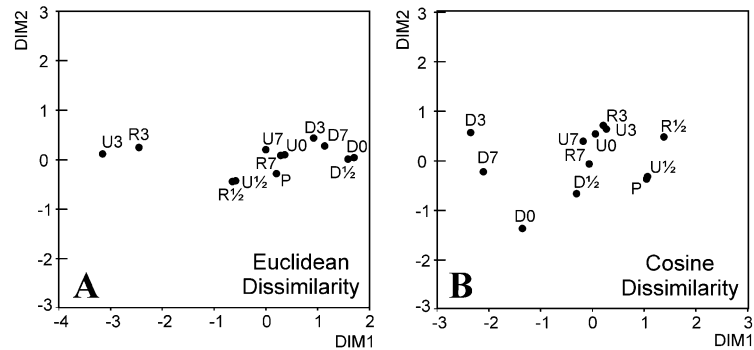
Fig. 3. Nonmetric MDS plots (A: Euclidean and B: Cosine dissimilarities) for all megafauna taxa: (R) reference; (U) undisturbed; (D) disturbed area; (P) pre-impact value; (0) 0 years; ($\frac{1}{2}$) 0.5 years; (3) 3 years; and (7) 7 years after ploughing.

reference areas, indicating that the sediment plume created during the ploughing activities resettled on the seafloor and negatively affected the megabenthos; but three and seven years after ploughing a reverse effect was noted. The mean density values of the undisturbed areas are higher than those of the reference areas, indicating an enhanced 'attractiveness' of the DEA to the megafauna.

3.6. Megafauna taxa

The megafauna found in the image material of the ECOBENT project was typical for the DEA (Bluhm et al., 1995) and for other manganese nodule areas, although there were some differences in the taxonomic compositions between the Clarion–Clipperton Fracture Zone (CCFZ) and the Peru Basin (Bluhm, 1994).

Crustacea, Porifera, Ophiuroidea, and Holothuroidea were the most abundant animal taxa. Sponges are typical hard-bottom community elements and grow on manganese nodules in the DEA. They will be significantly affected by future commercial mining operations because their hard-substrate environment will be reduced.

Crustacea consisted mainly of the hermit crab *Probeebei mirabilis* and to a lesser degree of *Aristaeomorpha*-type shrimps. During image analyses swimming specimens were ignored (Bluhm et al., 1995). Therefore, the shrimps might be underestimated in the abundance data. *P. mirabilis* have high densities in the DEA. This species was not found in the North Pacific manganese nodule claim areas.

Ophiuroids are often difficult to detect in images of the seabed because the majority of these animals occurs within the upper centimetres of sediment. Generally, only the tips of the arms are visible in the photographs, emerging above the sediment. At least two types of Ophiuroids were found in the DISCOL material. A whitish-coloured Ophiuroid was often seen resting under manganese nodules or crawling through the sediment, while an orange-coloured species were frequently observed attached to stalks. It was not possible to identify these brittle stars to species.
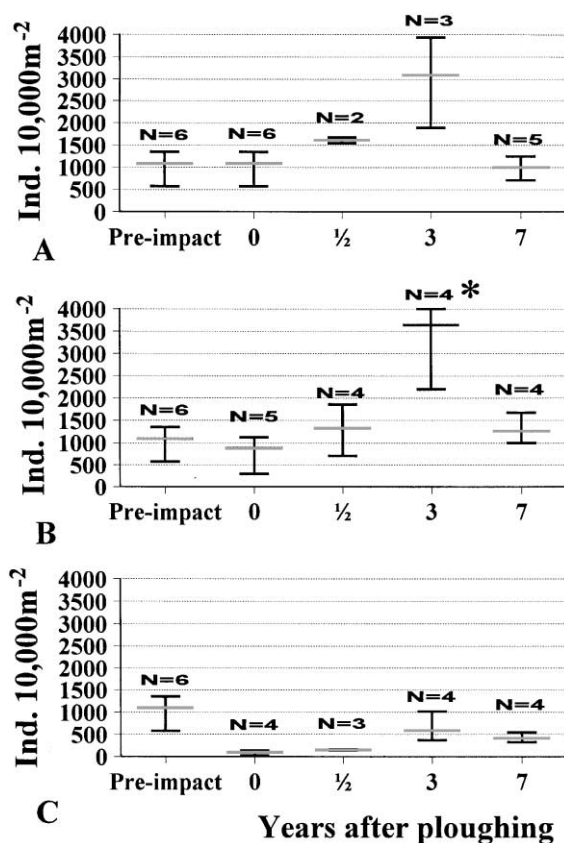
Fig. 4. Megafauna densities [individuals $10,000\,\mathrm{m}^{-2}$] in the: (A) reference; (B) undisturbed; and (C) disturbed areas: arithmetic means, ranges, and N, the number of records used. *Maximum at 6200 Ind. $10,000\,\mathrm{m}^{-2}$

The Holothuroidea observed on the photographs have been described (Bluhm and Gebruk, 1999), and a few specimens were taken in the DISCOL trawl material. This taxon appears frequently in the images.

Within the Actiniaria some larger specimens were observed rolling on the seafloor (Foell and Pawson, 1986) within the plough tracks. Some species of Actiniaria appear to have limited mobility and are able to leave less desirable locations for new areas.

A number of fish are present including *Ipnops* sp. (fam. Ipnopidae). These fish rest for hours on the seafloor, but should be able to escape the moving plough-harrow. In addition zoarcids (Anderson and Bluhm, 1997), synaphobranchids, ophidiids, and macrourids were also observed in the DEA.

Ascidia, Cnidaria, and Crinoidea have limited or no mobility and fragile body structures. In the disturbed areas these taxa were absent or showed low densities in the post-impact studies (see below). The Lophenteropneusta (Lemche et al., 1976) and different stages of their decaying faecal loops were observed frequently in the images; the life cycle of this taxon is still unknown. A high percentage of the image material was classified as 'Indeterminable'.

3.7. Densities of functional groups

The mobility, feeding strategy and preferred substratum was determined for each taxon. The heterogeneous group of 'indeterminable specimens' was excluded from this examination. Where different feeding strategies occur within a higher taxon, the most common category was chosen to represent the group.

Feeding guilds: The results of the non-metric MDS for carnivorous, deposit, omnivorous and suspension feeding guilds are presented in Fig. 5. The term 'omnivore' was used to characterise animals with a variety of feeding strategies.

The cosine distance matrix for the carnivore abundance data exhibits a distinct cluster for the reference stations, in which no other station was found. The disturbed area (D0) sampled immediately after ploughing was found to have the largest dissimilarity to the reference cluster. The undisturbed stations show a similar temporal development compared to the disturbed ones. The largest similarities to the reference cluster can be found at the undisturbed areas half a year ($U\frac{1}{2}$) and three years (U3) after ploughing. The undisturbed and disturbed area of the ECOBENT expedition (U7 and D7) are located close together, but show large dissimilarities to the pre-impact situation (P). This indicates a shift in species composition during the experiment.

Unlike the results of the cosine plot, the undisturbed and reference stations in the non-metric MDS plot using Euclidean distance show a similar temporal development. The disturbed stations are very similar and form a cluster in the outlying area of the plot. The temporal variation is greatest within the reference area owing to the distant position of the reference area three years after ploughing (R3) and the minimum variation within the disturbed areas. The reference area of the ECOBENT expedition (R7) plotted next to the pre-impact station (P), indicating comparable abundance distributions.

The undisturbed and reference stations of the non-metric MDS for the deposit feeding guild using the cosine distance matrix starting half a year after impact show a similar temporal development. The development of the disturbed stations is different although the disturbed station of the ECOBENT expedition (D7) finally plotted next to the reference station. Both show only small dissimilarities to the pre-impact station, and the taxa distribution of the reference station of ECOBENT (R7) is similar when compared to the pre-impact record.

The stations of the non-metric MDS with the Euclidean distance show a one-dimensional distribution. The disturbed stations have comparable abundance compositions and, therefore, group in a cluster in the left outlying area of the plot. The reference and undisturbed areas of each expedition are very similar and exhibit similar temporal development. Despite their large spatial variability, the similarities to the pre-impact station are high when compared to the disturbed stations.

Two clusters are detectable in the non-metric MDS plot (cosine distance) for the omnivores. With the exception of the undisturbed area sampled directly after impact, the records of the pre-impact (P), first, and second post-impact records form a cluster that does not include any other records. This indicates a change in the community structures between the second and the third post-impact studies. The different areas defined showed comparable taxonomic compositions during each expedition.

When calculating the Euclidean distance another picture can be found: the disturbed areas form a cluster in the right outlying area of the plot. The temporal developments of the undisturbed
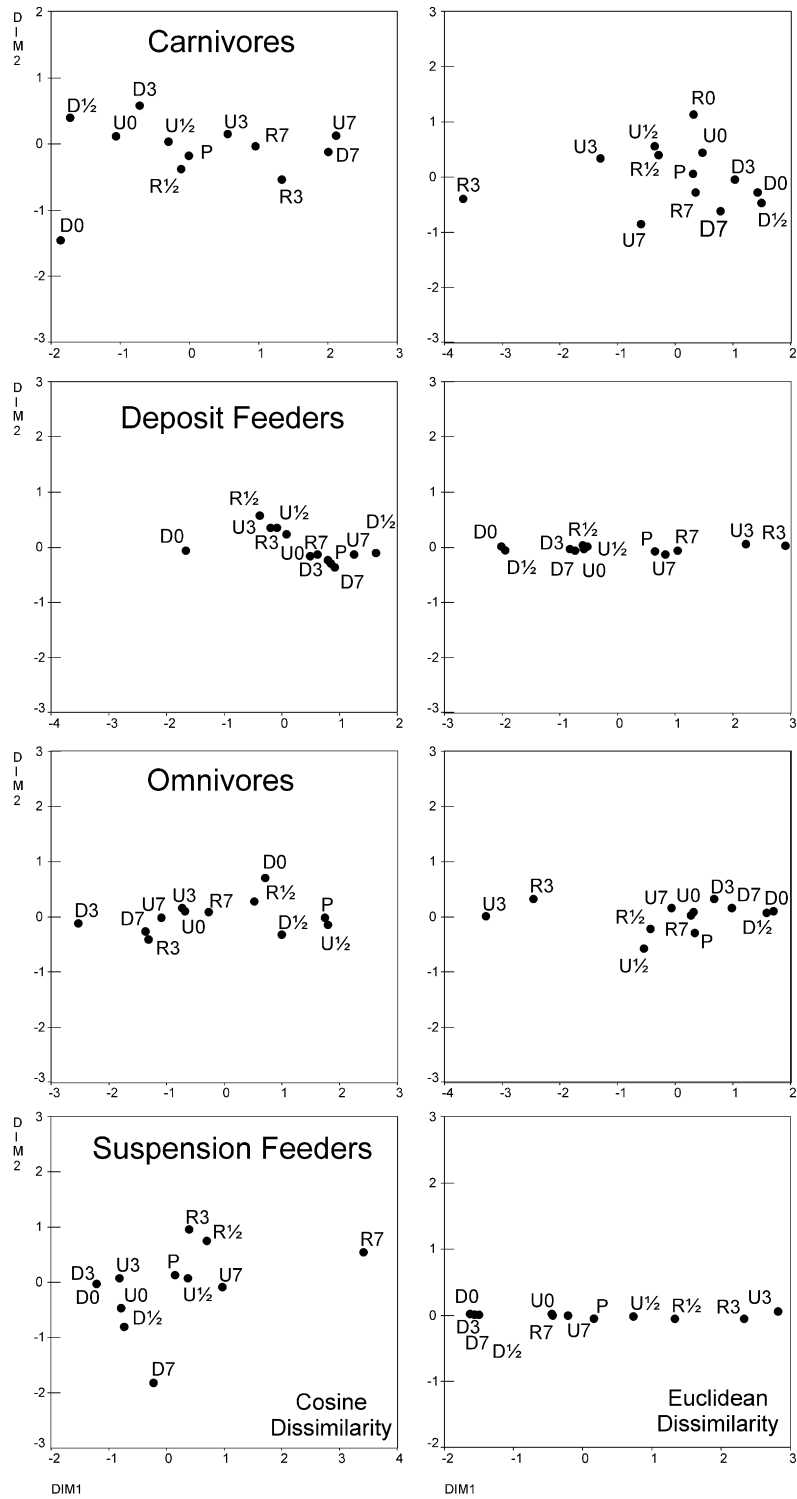
Fig. 5. Nonmetric MDS plot (left, Cosine; right, Euclidean distance) for all feeding guilds: carnivores, deposit feeder, omnivores, and suspension feeders. Sampling area codes are as for Fig. 3.

areas are comparable to the reference stations. The undisturbed and reference stations of the third post-impact study (U3 and R3) have a characteristic abundance distribution.

The non-metric MDS plot (cosine distances) of the suspension feeders show three clusters. The two clusters of the reference and the disturbed areas are positioned at different sides of a cluster. They contain the undisturbed stations and the pre-impact record. The temporal development of the taxa composition is comparable in all three clusters. The distance to the pre-impact station (P) is highest at the reference area seven years after ploughing (R7), indicating a changed taxonomic composition at this time.

The Euclidean distance produced a one-dimensional plot. The disturbed areas group as a distinct cluster at the edge of the plot. There is little temporal variability compared to the other areas. The undisturbed and reference records of the single expeditions are grouped together indicating high similarities in their abundance distributions. Following the schedule of the experiment the distances between the undisturbed areas and the pre-impact station (P) increase from zero years until three years after ploughing (U0–U3). Seven years later the undisturbed and reference records (U7, R7) plot back in positions next to the pre-impact record (P).

Mobility: Taxa consisting mainly of species capable of changing locations rapidly by swimming or crawling were put into the group called 'mobile taxa', and sessile and hemi-sessile animals into 'sessile taxa', respectively.

Within the plot of the non-metric MDS for the mobile taxa using the cosine distances (Fig. 6), no clustering of stations from one particular type of area could be found. However, groupings of stations from particular expeditions could be seen. This is an indication that the distribution of mobile taxa was the same in all areas.

The plot of the non-metric MDS for these same data, using the Euclidean distances, shows another spatial distribution. Despite the different data sets used to perform these calculations, the MDS plot looks similar to that of the omnivores guild (Fig. 5).

The MDS analysis (cosine distance) of the sessile association results in a cluster consisting mainly of undisturbed and reference stations, but the disturbed area sampled directly after impact also was added. There is large spatial variability in the disturbed areas and the distance to the pre-impact record (P) is greatest during the ECOBENT (D7) expedition. This is an indication that during the experiment the taxonomic composition of the fauna became increasingly different from the pre-impact situation.

A one-dimensional plot can be found when calculating the MDS with Euclidean distances. It looks similar to that of the suspension feeders (Fig. 5) despite the fact that other data sets were used.

Substrata preferences: Two definitions were used to characterise the habitats of single taxa. Taxa consisting mainly of species typical for hard-bottom communities were classified as 'hard-bottom taxa'. 'Soft-bottom taxa' were similarly defined. Taxa which contained species not characteristic of any community were ignored in this analysis.

Within the plot of the non-metric MDS (cosine distance) of the hard-bottom taxa (Fig. 7), the disturbed areas are grouped due to their comparable taxa compositions. They form a cluster located in the outlying area of the plot. Between the pre-impact station and this grouping, the undisturbed areas can be found. Seven years after ploughing, all stations (R7, U7, and D7) are located on one side of the pre-impact station (P). The reference areas have a high spatial
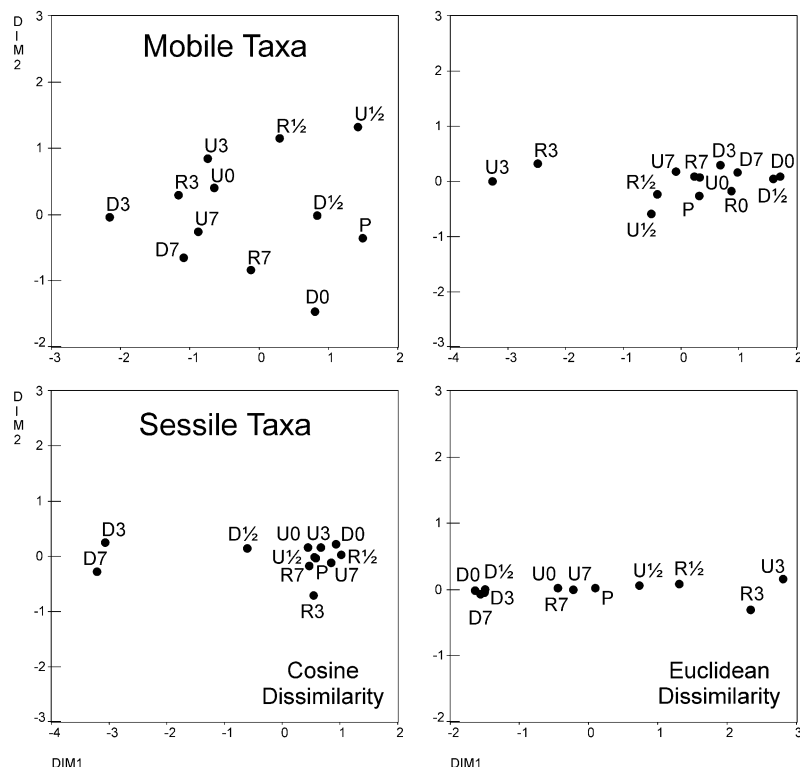
Fig. 6. Nonmetric MDS plots (left, Cosine; right, Euclidean distance) for mobile and sessile taxa. Sampling area codes are as for Fig. 3.

variability, but the one from the ECOBENT expedition is positioned next to the pre-impact record.

The Euclidean distances resulted in a one-dimensional distribution of the areas and the plot looks similar to Figs. 5 and 6 (suspension feeders and sessile organisms) despite the fact that different data sets were used.

Plotting the results of the non-metric MDS (cosine distance) of the soft-bottom taxa results in a one-dimensional distribution. The undisturbed and reference areas show similar temporal changes. Their similarity was greatest seven years after impact, but the taxonomic composition at that time was different from the pre-impact situation.

The Euclidean distance applied to soft-bottom taxa data resulted in two clusters, one consisting of disturbed areas with small spatial variability and the other consisting of reference and undisturbed records with large differences between abundances at each station. In the latter, the temporal variability is high. The undisturbed and reference areas showed the same temporal development and the plot distances to the pre-impact were at a minimum seven years after ploughing.

Fig. 8 represents the mean abundance of the two different categories found within the disturbed area. A decline of the abundance directly after impact was observed in all cases. While the
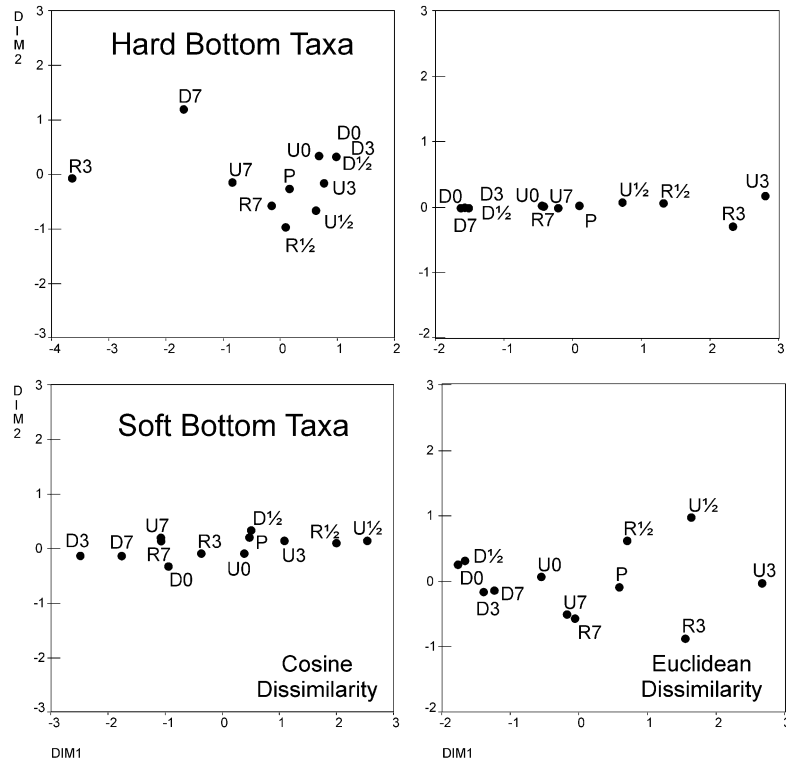
Fig. 7. Nonmetric MDS plots (left, Cosine; right, Euclidean distance) for different substrata preferences. Sampling area codes are as for Fig. 3.

densities of the hard-bottom fauna remained at a low level, the abundances in the soft-bottom animal categories increased during the experiment.

3.8. Densities of taxonomic groups

Abundance of the four groups of taxa in the disturbed area is depicted in Figs. 9–12. True hard-bottom taxa such as Porifera and Ascidia were absent at the disturbed site and did not show any recolonisation (Figs. 9 and 11). Others, like Cnidaria and Crinoidea (Fig. 11), were found randomly in the plough marks. Fishes (Fig. 10) were absent in the disturbed area during the first two post-impact cruises (D0 and D$\frac{1}{2}$), but had returned to the plough tracks during the two later studies. Hemichordata, mainly Lophenteropneusta (Lemche et al., 1976), occurred throughout the study but showed a wide range in abundance. They were apparently absent half a year after impact (Fig. 11: D$\frac{1}{2}$). Within the other taxa, repopulation of the plough marks was found within the four post-impact studies. In almost all cases the mean abundance of these taxa in the third post-impact records was higher compared to the fourth post-impact study (D7).

Within the fourth group (Fig. 12), consisting of taxa having low abundance and frequency, the hard-bottom taxa Pennatularia, Gorgonaria, and Antipatharia were absent during all post-impact
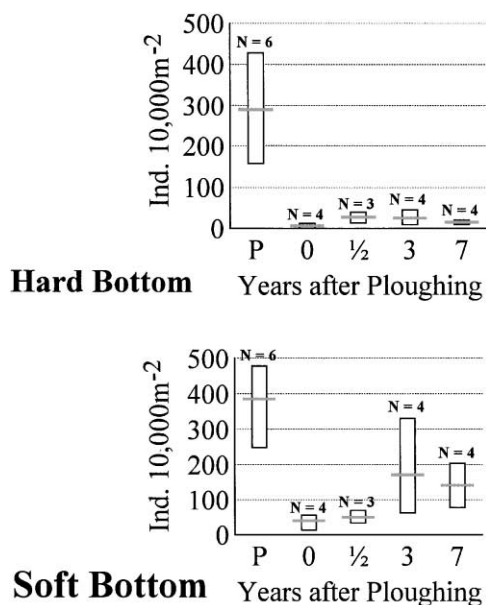
Fig. 8. Disturbed area. Densities (Ind. 10,000 m^{-2}) of hard- and soft-bottom epifauna taxa. P, the pre-impact value; N, the number of records used.
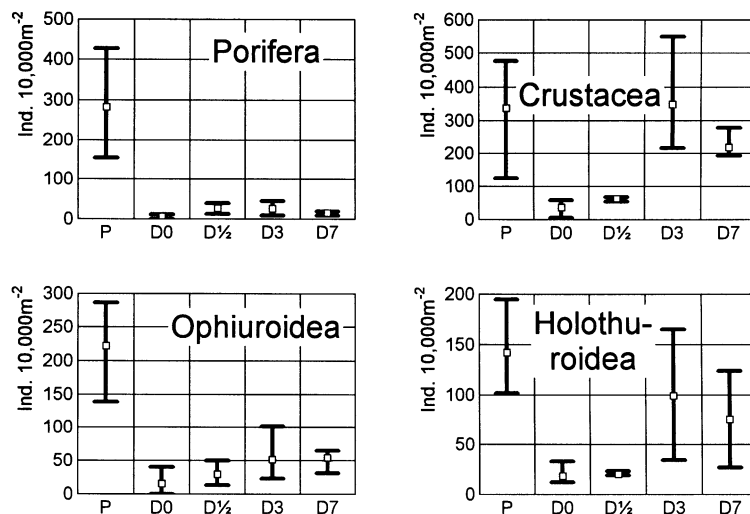

Fig. 9. Densities (Ind. 10,000 m^{-2}) of the 'Group 1' taxa in the disturbed areas: arithmetic means and ranges. Sampling area codes are as for Fig. 3.

studies. Large epifaunal Polychaeta were found in lower abundance directly after the impact (D0), but could not be found in the other post-impact studies. An increase of animal densities during the experiment was observed for Cephalopoda and Echinoidea. The latter occurred only in the first post-impact study, while Octopods showed a high abundance seven years after the ploughing event.
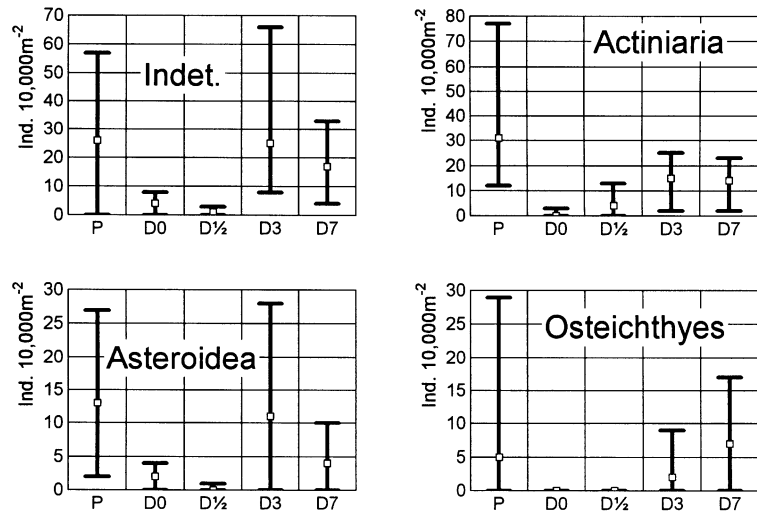
Fig. 10. Densities (Ind. 10,000 m^{-2}) of the 'Group 2' observed epifauna taxa in the disturbed areas: arithmetic means and ranges. Sampling area codes are as for Fig. 3.
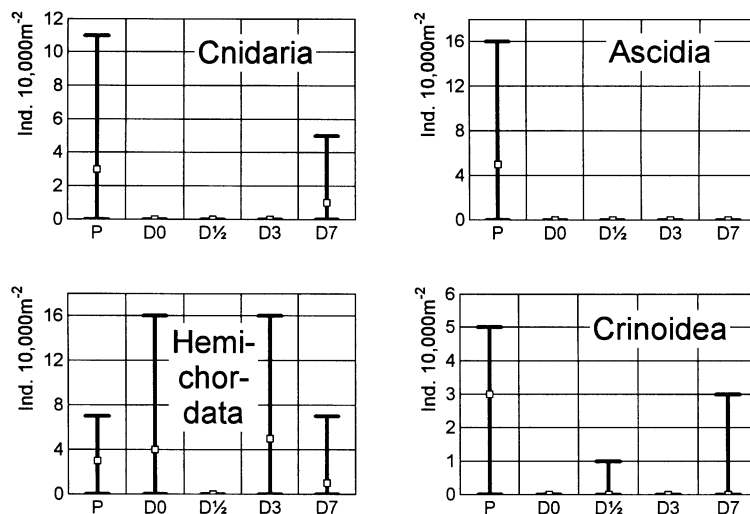

Fig. 11. Densities (Ind. 10,000 m^{-2}) of the 'Group 3' observed epifauna taxa in the disturbed areas: arithmetic means and ranges. P, the pre-impact value. Sampling area codes are as for Fig. 3.

4. Discussion

4.1. Physical disturbance and resedimentation

Physical disturbance of the seafloor is not an uncommon phenomenon. For instance, the carcasses of large animals fall onto the seafloor (Stockton and DeLaca, 1982; Smith, 1985, 1986; Priede et al., 1991) and the activities of scavenging animals change the physical and chemical
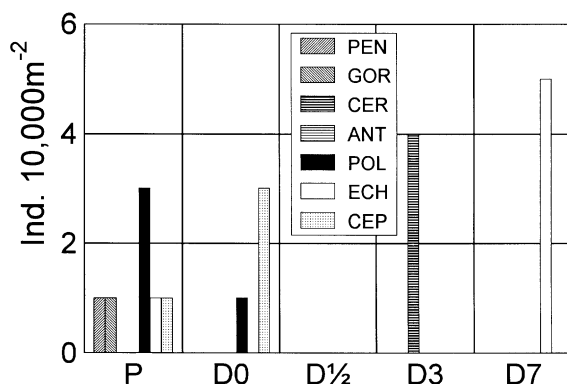
Fig. 12. Mean densities (Ind. $10,000\,m^{-2}$) of the 'Group 4' observed epifauna taxa (Pennatularia, Gorgonaria, Ceriantharia, Antipatharia, Polychaeta, Echinoidea, and Cephalopoda) in the disturbed areas. Sampling area codes are as for Fig. 3.

structure of the sediment surface. On a larger scale, turbidity currents, debris flows, and benthic storms modify benthic communities (Nardin et al., 1979; Hollister and Nowell, 1991). Commercial mining will impact the surface sediments to an even greater degree.

The DISCOL experiment successfully showed what effects commercial mining might have on the seafloor. Plough tracks were evident even seven years after the impact. The plough device changed the structure of the sediment from a flat smooth surface to a mosaic of lumps, valleys, and ridges. The sediment structures affected the composition of the meiofaunal and macrofaunal communities (Ahnert and Schriever, 2001; Borowski, 2001; Vopel and Thiel, 2001), and it is likely that this change in landscape also affected the megafauna because some of these animals feed on the meio- and macrofauna, and organic matter for deposit feeders tends to collect in hollows and around mounds.

The plough-harrow worked effectively but left patches of sediment untouched so that some manganese nodules and the associated fauna remained within the tracks. Although the plough marks created look very similar to those of the Benthic Impact Experiments (see below), the collecting gear used during future commercial mining will probably penetrate the seafloor to a much higher degree.

Sediment plumes were created during ploughing and could be observed drifting in the water column as long as several hours after the impact. Depending on speed and direction of the local bottom currents they were driven away from the point of origin. The sediment particles resettled in the surrounding areas. X-ray analyses of nine multiple corer samples showed different degrees of resedimentation and suggested that the predominant bottom currents during the experiment were oriented in a northerly direction (Schriever and Thiel, 1992). OFOS deployments were made mainly in a northwest to southeast or west to east direction because it was easier to manoeuver the photo/video system with the research vessel orientated into the surface wave field. As a result areas affected by high resedimentation rates were only partly monitored by OFOS.

Depending on the geographic locations of the undisturbed sub-areas monitored within the DEA different amounts of sediment particles had resettled to the bottom. The hypothetical model of Bluhm et al. (1995) assumed that at least filter feeding animals would be negatively affected by

this process. Therefore, the undisturbed areas should be inhabited by a mosaic of slightly different megafauna associations. This assumption was supported by the high values for the minimal areas which were found to be highest at undisturbed areas, indicating an increased spatial heterogeneity within the DEA after the impact. A small decrease in total animal densities was evident at the undisturbed locations directly after ploughing when compared to the temporal development at the reference areas, confirming the initially negative effect of the physical disturbance on the megafauna.

The sediment plume created by the collector vehicle during future marine mining also will impact undisturbed areas (Bluhm et al., 1995) to a large extent. The effects of resettled sediment on the fauna is currently being studied in detail within the US–Japanese, IOM (InterOcean Metal Consortium), and Indian Benthic Impact Experiments (Barnett and Yamauchi, 1995; Fukushima, 1995; Tkatchenko et al., 1996; Sharma et al., 1997; Trueblood and Ozturgut, 1997).

4.2. Temporal development in the plough tracks

Manganese nodules together with the attached fauna were buried by the plough-harrow. This device worked effectively resulting in reduced megafauna densities directly after impact (Figs. 4 and 9–12). In Hemichordata and Cephalopoda (mainly Octopoda) (Figs. 11 and 12) this negative effect was not noticeable, but the abundances of these taxa are low and variable and, therefore, it is not known if the differences are significant.

The ploughing activities left undisturbed patches, so that in the disturbance records hard-bottom fauna also occurred. Therefore, the minimal area values were comparatively large and exceeded the values of the areas observed. The reverse is the case when the taxa list is reduced to only five soft-bottom taxa (Crustacea, Asteroidea, Ophiuroidea, Holothuroidea, and Hemichordata). The results of the non-metric MDS considering five or 12 taxa looked very similar.

The re-establishment of the megabenthic community was a long process (Bluhm et al., 1995) and even seven years after the impact, the megabenthos of the disturbed area showed a different abundance composition compared to the pre-impact study. The disturbed areas formed distinct clusters in the non-metric MDS plots (Euclidean distance) of all different functional groups (Figs. 5–7) because of the low numbers of individuals found. The disturbed areas are very distinct from the pre-impact record.

The greatest difference in taxa composition compared to the pre-impact situation was found directly after the impact. During the experiment the similarities between the disturbed and pre-impact records increased and were greatest after seven years for total megafauna, carnivores, deposit feeders, suspension feeders, and soft-bottom taxa, and after three years for omnivores and mobile taxa. The results are influenced by additional factors (see below), but a trend in abundance composition to the pre-impact situation is noticeable.

In the non-metric MDS plots using cosine dissimilarity the disturbance records were grouped into a cluster with a different taxa composition compared to the pre-impact situation for total megabenthos, carnivores, suspension feeders, mobile, sessile, and hard-bottom taxa, but in the others they were distributed randomly around the pre-impact record. Maximum different taxa compositions compared to the baseline were found directly after the impact for carnivores and deposit feeders. Within the other taxa these differences increased during the experiment, but

decreased again seven years after impact. At this time the taxa composition of the disturbed area was still different from that of the baseline study.

In total, the different soft-bottom taxa and abundance compositions found seven years after ploughing indicate that the recovery process is still in progress.

4.3. Natural variability

The DEA is located approximately 800 km nautical miles away from the high-production zone off the coast of Peru (Cowles et al., 1977; Zuta et al., 1978). Its surface production is classified as mesotrophic (Weikert et al., 1993). Surface currents originating in the coastal upwelling areas transport phyto- and zooplankton into oceanic waters where they die and/or pass through the food web. Eventually their remains reach the seafloor as detritus or 'marine snow' and serve as food resources for the abyssal benthos.

In the video recordings of one OFOS deployment, during the exploration phase of DISCOL prior to the pre-impact study of the experiment, patches of greenish soft-structured material were detected that were to a lesser extent and lower frequency also occasionally found in the image material of this study. Borowski and Thiel (1998) observed patches of degraded pelagic diatoms within some of the third post-impact samples. Both observations indicate that the DEA is influenced by periodic food impulses. The variability of the particle flux to the seafloor should have a large effect on the composition of the benthos.

The differences in the composition of megafauna communities at the undisturbed and reference sites were small. During the experiment animal densities in both areas showed the same temporal development, an increasing difference from the faunal composition of the pre-impact sites up to three years after ploughing and a gradual approach to the pre-impact situation again seven years after impact. In the nonmetric MDS plots using cosine distance, the undisturbed sites were distributed randomly around the pre-impact record. The same is true of the reference site. This is an indication that variation in the composition of the megafauna community during the experiment depended mainly on changes in the abundances of individual taxa.

During the DISCOL experiment the total megafauna abundance in undisturbed areas increased to a level three to four times higher (three years after the impact) as compared to the pre-impact situation. This temporal development was similar to that observed at the reference areas and indicated a natural oscillation of megabenthic densities in the DEA. High abundance of bacteria, meio-, and macrofauna three years after impact also were observed during the other DISCOL investigations (Foell et al., 1997). Macrofauna total density increased significantly during the experiment at the reference and undisturbed sample sites (Borowski, 2001). Maximal total abundance of Nematoda was found three years after ploughing (Schriever et al., 1997; Ahnert and Schriever, 2001). The values observed were double the pre-impact values. No drastic increase in population density could been found within the Harpacticoidea, the second most populous taxon within the meiofauna of the DEA. Seven years after impact, nematode abundance again equaled pre-impact values (Schriever et al., 1997; Ahnert and Schriever, 2001).

The reason for the strong increase of the benthos three years after the impact is still unknown. The ploughing activities may have led to imbalances of the fauna that occurred over a wide area of seabed. The natural stochastic variability in the populations also might be responsible for the phenomena observed.

The particle flux into the deep sea at the DEA seems highly variable. Seasonality has been observed several times in abyssal regions (Billett et al., 1983; Rice et al., 1986; Thiel et al., 1989) and probably also occurs in the Peru Basin. Variations in the weather system over the Pacific ('Southern Oscillation'; Wyrtki, 1982) and El Niño events (e.g. Philander, 1989) might additionally influence the flux of particles into the deep sea of the DEA. In the literature, only one reference exists with regard to the relationships between surface and abyssal benthic productions in association with upwelling systems. Ingram and Hessler (1987) related an alteration in the recruitment and standing crop of a population of *Eurythenes gryllus* in the North Pacific to an El Niño event. Further data exists on the reaction of the upper shelf benthos to El Niño (Philander, 1989) events (Rosenberg et al., 1983; Arntz, 1986; Thiel, 1982; Arntz et al., 1991; Thompson et al., 1993). Arntz et al. (1991) analysed benthic assemblages in up to 400 m depth off the coasts of Peru and Chile. Dependent on the geographic positions of the samples taken, the authors reported a positive effect of El Niño on some taxa found deeper than 40 m. An increase in mollusc numbers one and a half year after this event was also attributed to El Niño. Thompson et al. (1993) analysed the megabenthic assemblages of coastal shelves, slopes, and basins off southern California from trawl samples. The authors detected increased biodiversity at the lower slope stations (478–780 m depth) after an El Niño event and observed a time delay in the benthic effects attributable to El Niño. In the occasionally anoxic sub-sill basins (715–878 m depth), no observable effects of El Niño were found.

5. Conclusion

The results of the DISCOL and ECOBENT surveys show that photo/video image systems are useful in detecting changes of epibenthic communities resulting from physical disturbance impacts. The megafauna play an important role in the deep-sea ecosystem and, therefore, should be monitored in future environmental studies.

During the experiment, natural variations in the taxonomic and abundance compositions of the megafauna communities were observed. Clear relationships to the flux of organic matter into the deep sea could not be perceived due to a lack of long time series data, biomass data, and detailed information about life strategies of individual species, of the structure of the food web, and of transport processes into the deep sea off the South American coast.

Due to the removal of hard substrata, the re-establishment of the megafauna community in the disturbed area is limited to soft-bottom species. Seven years after experimental impact, the megafauna community still differed in the taxonomic and numerical composition of soft-bottom animals although the difference from the pre-impact situation was found to be small. Further post-impact studies should be done to clarify the time interval required for the community in the disturbed areas to become comparable to the baseline.

Due to time restrictions within the present study only higher taxa were taken into account and, therefore, information about the relationships between the different faunal size classes is limited. In the future, with the help of modern technologies and higher resolution image materials, more detailed investigations should be possible, which will enhance our currently limited knowledge of the abyssal megafauna.

Large uncertainties in the taxonomic determination still exist in deep-sea research and knowledge of the ecology of deep-sea species is limited. To obtain more precise information there is a need to identify suitable indicator taxa for this type of environmental impact. Future research should continue to test and develop the Holothuroidea as an effective indicator taxon.

Acknowledgements

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