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Holothuroidea (Echinodermata) of the Peru Basin – Ecological and Taxonomic Remarks Based on Underwater Images

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With 11 figures and 4 tables

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Abstract. The megabenthos plays an important role in the abyssal ecosystem. The holothuroids have been proposed as indicators of physical disturbance of the seabed caused, for example, by commercial deep-sea mining of manganese nodules. Environmental studies at seabed mining claims have resulted in numerous still photographs that provide an overview of the megabenthos in manganese nodule fields. Data from these investigations and from the large-scale disturbance and recolonization experiment DISCOL have been used to summarize knowledge of the taxonomy and ecology of holothurians at manganese nodule sites.

Problem

Knowledge of the taxonomy of deep-sea animals is still patchy, especially for the megabenthos, which is too sparse, too fragile and/or too mobile to be sampled adequately in any other way than by imagery (Grassle *et al.*, 1975). The megafauna plays an important role in deep-sea ecosystems and has been used in monitoring the reaction of benthic communities to physical disturbance (Bluhm *et al.*, 1995; and references therein).

The Holothuroidea comprises one of the main soft bottom taxa of abyssal communities in manganese nodule areas (Bluhm, 1994). Sea cucumbers are recognizable and determinable from images and therefore were proposed as indicator organisms for recolonization studies (Thiel *et al.*, 1992; Bluhm *et al.*, 1995). However, problems with identification of species from images still remain. The appearance of deep-sea holothurians *in situ* often differs dramatically from what scientists are accustomed to from preserved material. Soft characteristic append-

ages and the external gelatinous skin layer are easily lost while sampling. Therefore, it is essential to improve techniques for species identification from images.

The image material analysed in this paper derived from the first long-term, large-scale, DISTurbance and reCOLonization experiment (acronym DISCOL; Thiel & Schrieffer, 1989, 1990; Schrieffer, 1990; Foell *et al.*, 1990, 1992; Schrieffer & Thiel, 1992), which began in 1989 in the Peru Basin (tropical south-eastern Pacific Ocean) as part of the German deep-sea environmental protection activities (Thiel & Forschungsverbund Tiefseeweltenschutz, 1995). The aim of DISCOL was to investigate recolonization by abyssal fauna after an experimentally created physical disturbance of the abyssal sea floor. Dominant taxa of meio-, macro- and megafauna were investigated taxonomically to find indicator taxa that were representative of the recolonization process. The megafauna was monitored with a photo/videosystem. Trawl samples from the DISCOL experiment were analysed taxonomically, and identification of trawled species compared with the names given to species that had been photographed.

Although several specimens remain taxonomically uncertain, the data provide an excellent overview of the distribution of holothurians at this potential manganese nodule mining site. These data are comparable with data from investigations in the Clarion-Clipperton Fracture Zone (CCFZ), North Pacific Ocean (overview in Bluhm, 1994; Bluhm *et al.*, 1995).

The aim of this paper is to summarize our knowledge of the diversity, abundance and distribution of holothurians in areas of abyssal manganese nodules. Although taxonomic determination of preserved material is always necessary, characteristic photographs of holothurians should help scientists to identify the holothurians remotely.

Material and Methods

The DISCOL Experimental Area (DEA) is a circular area of 10.8 km² centred at 7°4.4' S and 88°27.6' W. The water depth is 4140–4160 m (Thiel & Schrieffer, 1989). A photo/videosystem (OFOS, Ocean Floor Observation System), towed by the German research vessel 'Sonne' approx. 3 m above the sea floor, was used to monitor the megabenthos (Thiel & Schrieffer, 1989; Bluhm, 1993; Bluhm *et al.*, 1995). During the DISCOL experiment OFOS was deployed 33 times (Thiel & Schrieffer, 1989; Schrieffer, 1990; Schrieffer & Thiel, 1992), and all photographs were analysed for the present study.

Seven deployments showed the natural (predisturbance) situation and were used for density calculations (Table 1); During the baseline study of the DISCOL experiment four OFOS transects were

Table 1. Locations of OFOS-deployments.

deployment	latitude	longitude	depth
SWD2	7°8.6' S	88°39.0' W	4175–4188 m
DEA3	7°2.3' S	88°25.5' W	4148–4174 m
DEA4	7°4.1' S	88°27.1' W	4152–4147 m
DEA5	7°4.8' S	88°27.1' W	4158–4146 m
DEA6	7°3.9' S	88°27.6' W	4146–4166 m
Hill 18	7°0.9' S	88°27.3' W	3852–4156 m ⁽¹⁾
Hill 25	7°3.0' S	88°22.0' W	4189–4117 m ⁽²⁾

⁽¹⁾ summit at 3847 m and ⁽²⁾ at 3911 m.

laid within the DEA (DEA3, DEA4, DEA5, DEA6). Two hill sites to the north and east of the DEA were monitored by transects. They include Hill 18 (located approximately 4 nautical miles north of DEA, water depth: 3800 m) and Hill 25 (12 nautical miles east of the DEA, water depth: 3900 m). Transect SWD2 was located south-west of the DEA at a water depth similar to the DEA.

The stations showed variable coverages of manganese nodules. High densities were found at DEA3 and site Hill 18. DEA4 was characterized by a manganese nodule coverage of less than 15%. The other stations exhibited intermediate coverages. The mean diameter of the cauliflower-like manganese nodules was 15 cm. This was especially true for low and intermediate nodule coverages. At sites with high nodule densities the manganese nodules were much smaller, *i.e.*, 2 to 5 cm in diameter. During the DISCOL study approximately 200 000 m² of the sea floor were mapped and in total 3209 still photographs taken (Table 2).

Animal density calculations were based on the video recordings. The resolution of the TV system is lower than that of the photo camera. Therefore, the preliminary density calculations required correction to obtain more realistic values. The comparison of average animal density and species richness in a single photograph and in a TV frame at the same instant of time provided an estimate of how many organisms an observer can recognize on a photograph compared with a video frame. This estimation was carried out with all useful photographs available. Swimming specimens were skipped during data processing owing to the unknown reaction of the animals to the photo/videosystem used. A more detailed description of the image analysis method is given in Bluhm *et al.* (1995).

To test the reliability of the image data the methods described in Bluhm (1994) were chosen, so that the results could be compared. For these calculations the total observation areas were used, including intervals of unusable video sequences, when the OFOS was too high above the sea floor, or when a sediment cloud was created by the OFOS touching the sea floor. The minimal area (Weinberg, 1978) was calculated by using the software package MINAREA (version July 1997; Pfeifer *et al.*, 1996).

Multi-variate statistics using the SPSS 5.1 software package (Norusis, 1990) were carried out to detect clustering of stations. Euclidian distance and cosine measure served as similarity indices. The value of the former was influenced mainly by dominant values, the latter by the relative abundances of the different species.

Results

1. Taxonomic characteristics

The following species were found on image material from the DISCOL project. Relevant species from other manganese nodule sites have been added. Charac-

Table 2. OFOS deployments of the DISCOL experiment. The correction factor was calculated by comparing the faunal distribution acquired from the photographs and video frames at each instant of time and was used to correct the density values calculated from the video data to true values.

	SWD2	DEA3	DEA4	DEA5	DEA6	Hill 18	Hill 25
location	SW of DEA	DEA	DEA	DEA	DEA	hill site north of DEA	hill site east of DEA
cruise/expedition	SO 61	SO 61	SO 61	SO 61	SO 61	SO 61	SO 64
number of photographs usable	518	551	243	717	561	277	342
length of video recording usable [h]	3.94	3.93	2.27	6.06	3.96	2.76	1.15
tow speed [nautical miles · h ⁻¹]	1.04	1.21	1.29	1.12	0.79	0.83	1.25
total area observed [m ²]	32 000	37 125	22 881	53 027	24 418	17 919	11 252
correction factor	1.03	1.03	1.03	1.08	1.09	1.03	1.11

teristic images can be found in Figures 1–6. Two other papers containing photographs of megafauna and holothurians should be mentioned as additional references: Pawson & Foell (1983; unpublished) and Tilot (1992). We address here only those morphological features that can be seen on photographs.

Order Aspidochirotida Grube 1840

In the deep sea, the Aspidochirotida are represented primarily by the family Synallactidae, which remains one of the least studied major deep-sea holothurian groups. At present this family comprises about 20 genera (Hansen, 1975; Billett, 1991), some of which can be easily confused without details of the spicules and the calcareous rings. This is one of the most difficult deep-sea holothurian groups to identify from photographs and video records.

Fam. Synallactidae Ludwig 1894

Gen. *Synallactes* Ludwig 1893

Synallactes type 1 (Fig. 1A)

Diagnostic features. Body elongated, cylindrical, reaching approximately 20 cm in length. Colour whitish. Numerous dorsal papillae, of varying length (but not exceeding the body width), are arranged in at least two rows.

Remarks. In the Clarion Clipperton Fracture Zone (CCFZ) this genus is believed to be represented by the species *Synallactes profundus* (Koehler & Vaney 1905).

Synallactes type 2 (Fig. 1B)

Diagnostic features. Body elongated, cylindrical, reaching approximately 20 cm in length. Colour from orange to brownish. At least two rows of short dorsal papillae, some of them rudimentary; some seem to be placed irregularly.

Remarks. This species resembles *Synallactes aenigma* (Ludwig 1894) and *Synallactes reticulatus* (Sluiter 1901).

Gen. *Paelopatides* Théel 1886

Paelopatides sp. (Fig. 1C)

Diagnostic features. Large form, probably exceeding 30 cm in length. Ventral side flattened with well-developed brim, dorsally arched. Colour orange-brown. Two rows of small dorsal papillae.

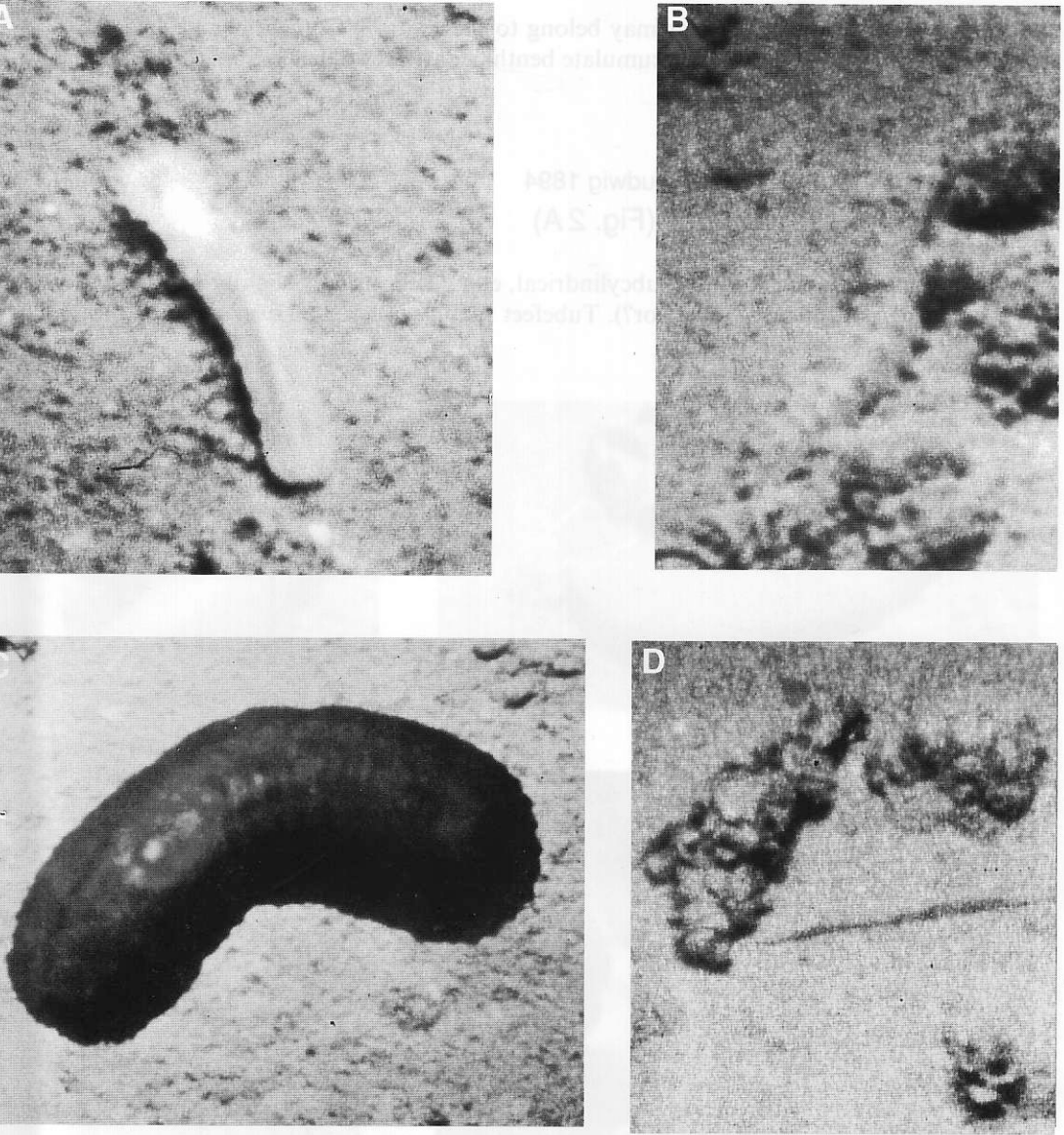


Fig. 1. A. *Synallactes* type 1 (Aspidochirotida, Synallactidae); B. *Synallactes* type 2 (Aspidochirotida, Synallactidae); C. *Paelopatides* sp. (Aspidochirotida, Synallactidae); D. *Meseres* sp. (Aspidochirotida, Synallactidae).

Gen. *Meseres* Ludwig 1894

Meseres sp. (Fig. 1D)

Diagnostic features. Body subcylindrical or slightly flattened, elongated. Colour greyish-brown. Dorsal tubefeet small, placed irregularly. Dorsal surface usually covered with fragments of benthic material, *e.g.*, manganese nodule fragments.

Remarks. These specimens may belong to the genus *Mesothuria*, some species of which are also known to accumulate benthic material on the dorsum (Deichmann, 1930).

Gen. *Mesothuria* Ludwig 1894

Mesothuria sp. (Fig. 2 A)

Diagnostic features. Body subcylindrical, elongated, usually slightly narrowing to one end of the body (anterior?). Tubefeet small, scattered all over the body; rows

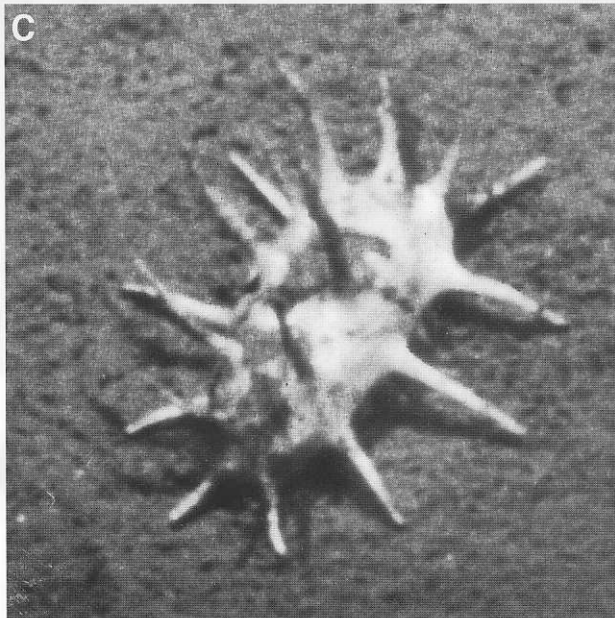
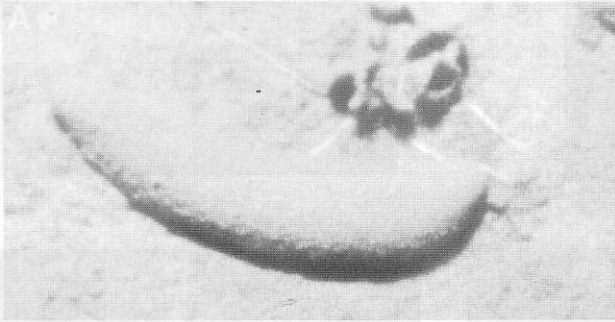


Fig. 2. A. *Mesothuria* sp. (Aspidochirotida, Synallactidae); B. Synallactidae Gen. sp. (Aspidochirotida, Synallactidae); C. *Deima validum* (Elasipodida, Deimatidae). The back of the specimen is covered with sediment resettled from the sediment cloud created during the experiment; D. *Oneirophanta mutabilis* (Elasipodida, Deimatidae).

of small ventro-lateral tubefeet (one row to each side) can be distinguished on some photographs. Colour dirty whitish-brown.

Remarks. This genus is represented by *Mesothuria murrayi* (Théel 1886) in the CCFZ (Tilot, 1992).

Gen. *Pseudostichopus* Théel 1882

Pseudostichopus sp.

Diagnostic features. Body cylindrical, with rounded ends. Dorsal surface smooth, tubefeet invisible on photographs. Colour whitish. Body may be partly covered with sediment.

Remarks. The species *Pseudostichopus mollis*, recognized by a distinct vertical anal groove, is known to occur in the CCFZ (Tilot, 1992).

Gen. sp. (Fig. 2B)

Diagnostic features. Body flattened, slightly more arched at one end; small brim seems to be present. Colour orange. Tubefeet minute on the dorsum, partly arranged in two rows, but some placed irregularly.

Remarks. The genus could not be identified with certainty, but the specimens are referred to the family Synallactidae owing to irregular placement of small dorsal tubefeet and the orange colour.

Ord. Elasipodida Théel 1882

Fam. Deimatidae *sensu* Ekman 1921

Gen. *Deima* Théel 1879

Deima validum Théel 1879 (Fig. 2C)

Diagnostic features. Body ovoid. Colour white. Dorsal papillae rigid, in two rows, five to 16 pairs. Ventrolateral papillae also rigid, in two rows, three to seven pairs.

Gen. *Oneirophanta* Théel 1879

Oneirophanta mutabilis Théel 1879 (Fig. 2D)

Diagnostic features. Body cylindrical, elongated, reaching approximately 20 cm in length. Colour white. Dorsal papillae rigid, numerous, arranged in several rows: upper rows with four to 35 pairs and side rows with four to 17 pairs of papillae.

Fam. Psychropotidae Théel 1882

Gen. *Psychropotes* Théel 1882

Psychropotes longicauda Théel 1882 (Fig. 3A)

Diagnostic features. Large form, up to 35 cm in length. Colour blue-dark violet. Dorsal side flattened, ventral side arched. Anterior brim usually conspicuous, forming a lobe. Unpaired dorsal appendage placed close to posterior end of the body; it varies in length from one-fifth to the same length as the body; the base of this appendage almost as broad as the body. Free large ventro-lateral tubefeet, seven to 25 pairs. Dorsal papillae minute, usually not distinguishable on photographs.

Remarks. This species is easily recognized owing to the very large 'sail' located close to the posterior end.

Psychropotes verrucosa Ludwig 1894 (Fig. 3B)

Diagnostic features. Large, up to 25 cm in length. Colour light-dark violet. Ventral side flattened, with well developed brim, dorsal side arched. Dorsal appendage short, located approximately one-quarter to one-third of body length from posterior end.

Gen. *Benthodytes* Théel 1882

Benthodytes incerta Ludwig 1894

Diagnostic features. Elongated, ventral side flattened, with a very narrow brim, dorsal side arched. May exceed 20 cm in length. Colour light-dark violet. Anterior brim well developed, posterior end round. Dorsal papillae conspicuous, six to nine pairs in two rows.

Benthodytes typica Théel 1882 (Fig. 3C)

Diagnostic features. Body flattened, with well-developed brim. The length may exceed 20 cm. Colour blue-violet, with brim usually darker than the body; sometimes transparent. Dorsal papillae minute and few, not distinguishable on photographs.

Benthodytes sanguinolenta Théel 1882 (Fig. 3D)

Diagnostic features. Body elongated and flattened, dorsum slightly arched, posterior end narrower than anterior. Up to 30 cm in length. Brim well developed at anterior and posterior ends, narrower in the middle part of the body. Colour blue-violet, with brim (especially the anterior lobe) darker than the body. Dorsal papillae minute, not distinguished on photographs.

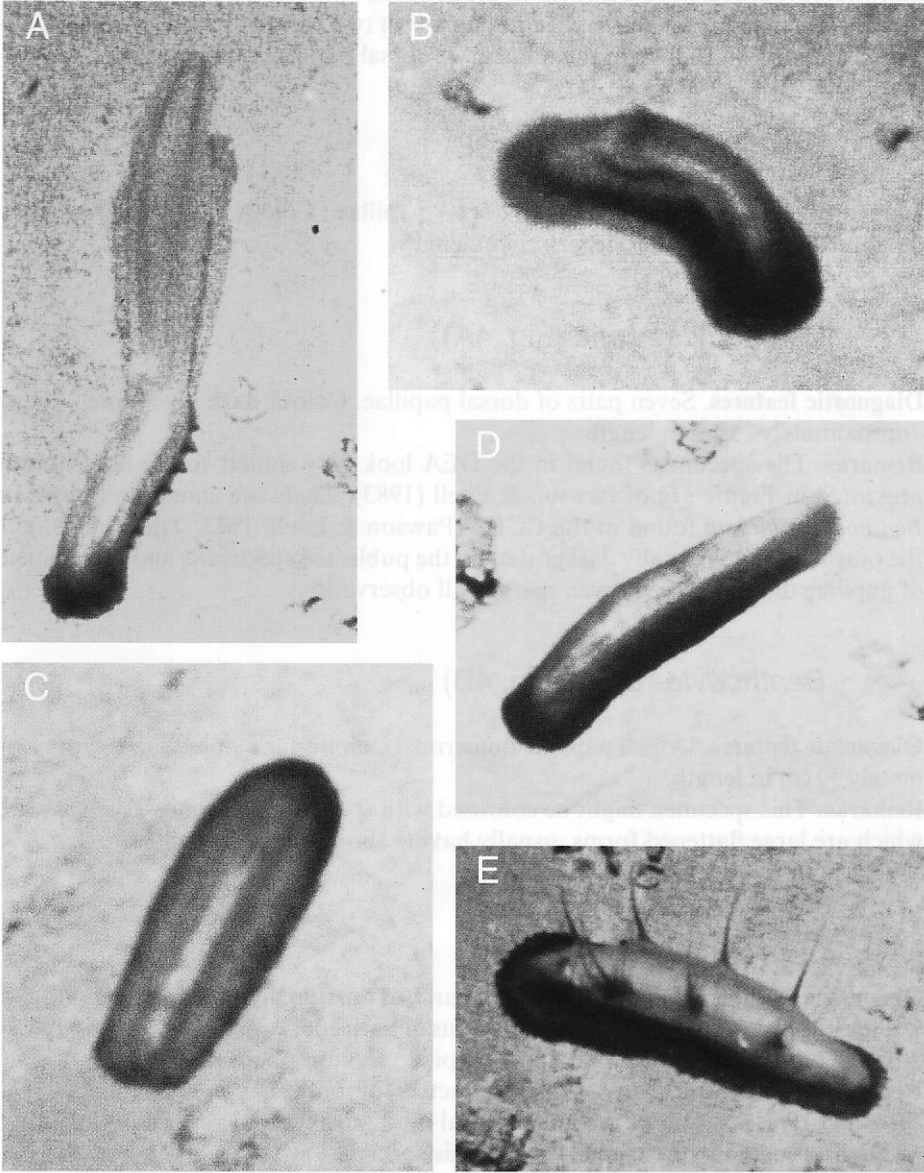


Fig. 3. A. *Psychropotes longicauda* (Elasipodida, Psychropotidae); B. *Psychropotes verrucosa* (Elasipodida, Psychropotidae); C. *Benthodytes typica* (Elasipodida, Psychropotidae); D. *Benthodytes sanguinolenta* (Elasipodida, Psychropotidae); E. *Benthodytes* sp. 1 (Elasipodida, Psychropotidae).

Remarks. This species is often seen swimming, making S-like horizontal movements.

The following three species, which are rather similar in their external

morphology, are referred herewith to the genus *Benthodytes*, owing to the presence of well-developed brim and arched dorsum with two rows of relatively long papillae. The main variation is in the number of dorsal papillae and colour.

Benthodytes sp. 1 (Fig. 3E)

Diagnostic features. Four pairs of dorsal papillae. Colour green-brown. Anus dorsal. Reaches approximately 20 cm in length.

Benthodytes sp. 2 (Fig. 4A)

Diagnostic features. Seven pairs of dorsal papillae. Colour dark blue-violet. Up to approximately 25 cm in length.

Remarks. The specimens found in the DEA look very similar to the holothurian presented in Figure 37g of Pawson & Foell (1983). There are some similarities to *Benthodytes incerta* found in the CCFZ (Pawson & Foell, 1983; Tilot, 1992), but the purple colour is usually darker than in the published specimens and the number of papillae did not exceed seven pairs in all observations.

Benthodytes sp. 3 (Fig. 4B)

Diagnostic features. Dorsal papillae numerous. Colour dark violet. Up to approximately 30 cm in length.

Remarks. This specimen might be confused with species of the genus *Paelopatides*, which are large flattened forms, usually having shorter dorsal papillae.

Gen. sp. 1 (Fig. 4C)

Diagnostic features. Body elongated, with arched dorsum, flattened ventral side and well-developed brim, especially conspicuous at both ends. Up to approximately 15–20 cm. Colour light orange. No dorsal papillae seen on photographs.

Remarks. This form shares some characters of both *Benthodytes* and *Psych-eotrephes*. The position of the anus, dorsal in the former and ventral in the latter, could clarify the taxonomic position of this species.

Gen. sp. 2 (Fig. 4D)

Diagnostic features. Large forms, up to 30 cm and more. Body flattened, broad. Colour dark grey-violet. Dorsal papillae not distinguishable on photographs. Anus seems to be dorsal.

Remarks. The external appearance is very similar to *Benthodytes*. In body form this holothurian also resembles *Paelopatides*, which, however, usually has two rows of distinct dorsal papillae.

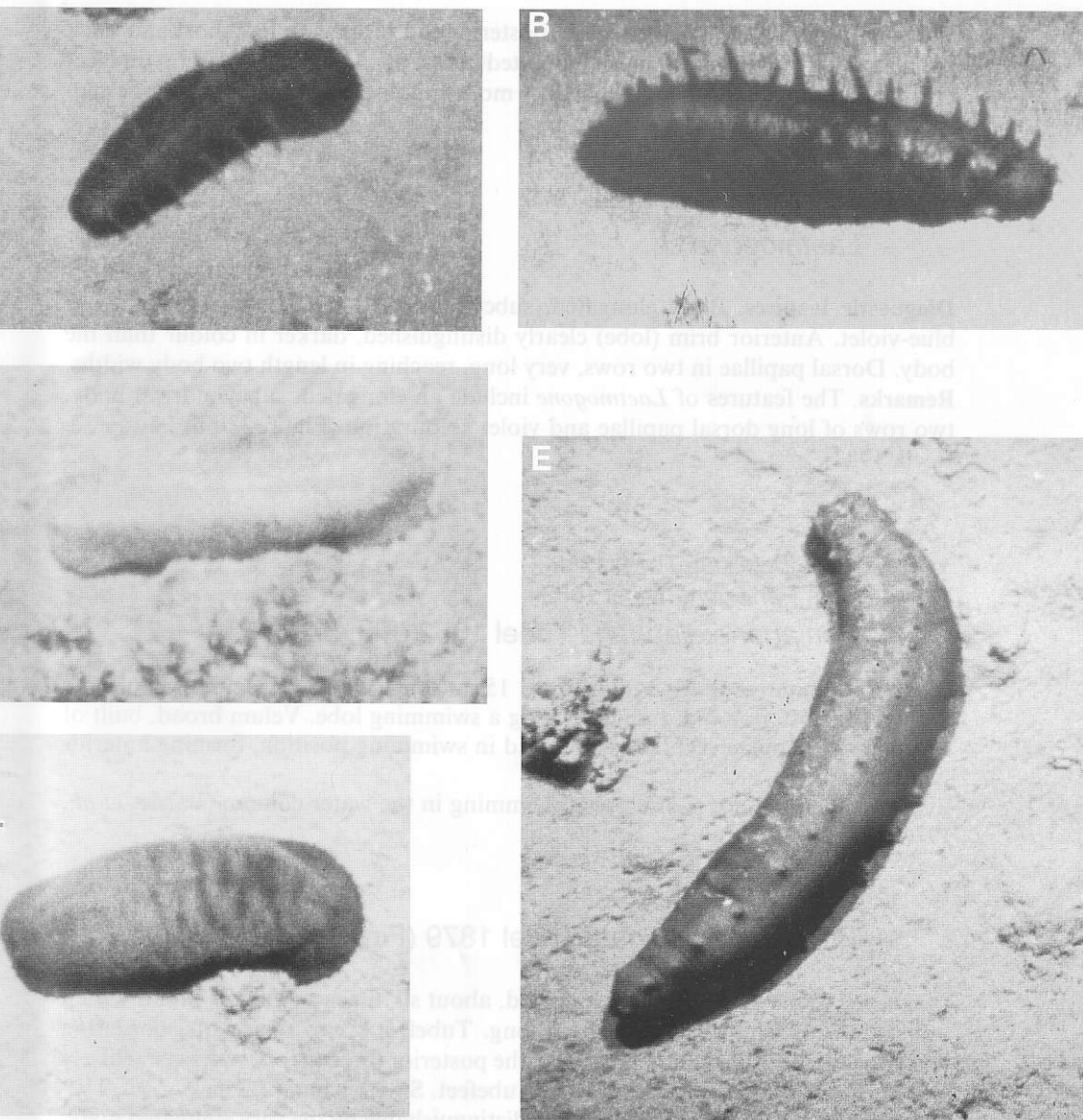


Fig. 4. A. *Benthodytes* sp. 2 (Elasipodida, Psychropotidae); B. *Benthodytes* sp. 3 (Elasipodida, Psychropotidae); C. Psychropotidae Gen. sp. 1 (Elasipodida, Psychropotidae); D. Psychropotidae Gen. sp. 2 (Elasipodida, Psychropotidae); E. *Psychronaetes hansenii* (Elasipodida, Laetmogonidae).

Fam. Laetmogonidae Ekman 1926

Gen. *Psychronaetes* Pawson 1983

Psychronaetes hansenii Pawson 1983 (Fig. 4E)

Diagnostic features. Large, up to 30 cm long. Body cylindrical to fusiform, greatest width approximately 25% of body length. Colour dark purple-brown. Anterior

end usually with a 'head'-like region, posterior end often with few short and thick papillae. Two rows of short blunt to pointed dorsal papillae. Ventro-lateral tubefeet enlarged, evenly distributed, but slightly more concentrated around posterior end.

Gen. *Laetmogone* Théel 1879

Laetmogone sp.

Diagnostic features. Body elongated, subcylindrical. Up to 20 cm long. Colour blue-violet. Anterior brim (lobe) clearly distinguished, darker in colour than the body. Dorsal papillae in two rows, very long, reaching in length two body widths.

Remarks. The features of *Laetmogone* include an elongated, subcylindrical body, two rows of long dorsal papillae and violet colouration (Figure 38b in Pawson & Foell, 1983).

Fam. Elpidiidae Théel 1882

Gen. *Peniagone* Théel 1882

Peniagone diaphana Théel 1882 (Fig. 5A)

Diagnostic features. Body ovoid, up to 15 cm long. Often transparent. Tubefeet only at the posterior end, fused, forming a swimming lobe. Velum broad, built of two pairs of papillae. Tentacles stretched in swimming position, forming anterior swimming lobe.

Remarks. This species is often seen swimming in the water column (Barnes *et al.*, 1976).

Peniagone elongata Théel 1879 (Fig. 5B)

Diagnostic features. Body very elongated, about six times as long as broad. Often transparent or whitish. Up to 20 cm long. Tubefeet six to nine pairs, bordering posterior two-thirds of the ventral sole, the posterior three to four pairs very closely placed, sometimes larger than anterior tubefeet. Small velum present.

Remarks. This species is usually clearly distinguishable by the very elongated body, absence of tubefeet in the anterior one-third and large, closely placed posterior-most tubefeet.

Peniagone-Amperima group

Individuals in this group share the features of both *Peniagone* and *Amperima* (as well as *Ellipinion* in part): ovoid body, large velum built of two pairs of papillae, with middle papillae usually longer than the outside ones, tubefeet bordering posterior one-half to one-third of the body or spread equally along both sides. Species cannot be identified without the details of spicules.

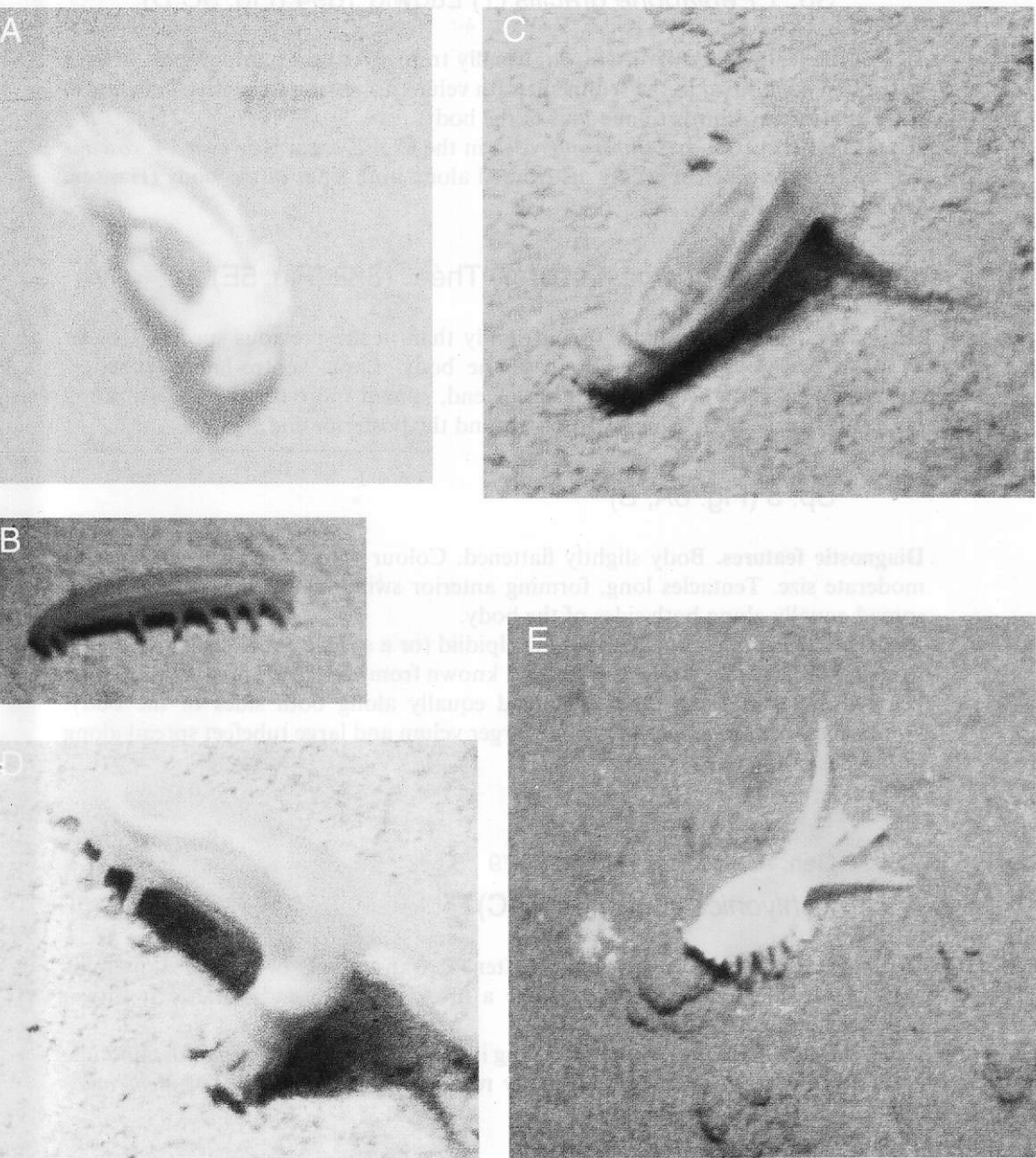


Fig. 5. A. *Peniagone diaphana* (Elasipodida, Elpidiidae), swimming; B. *Peniagone elongata* (Elasipodida, Elpidiidae); C. and D. *Peniagone gracilis*? (Elasipodida, Elpidiidae); E. *Amperima naresti*? (Elasipodida, Elpidiidae).

Sp. 1 *Peniagone gracilis* (?) Ludwig 1894 (Fig. 5C,D)

Diagnostic features. Pink or whitish, usually transparent on photographs. Mouth part often bent down to the sediment, with velum projecting frontally. Tubefeet in the posterior two-thirds to one-half of the body.

Remarks. Believed to be *Amperima rosea* in the CCFZ area. However, *A. rosea* is known to have tubefeet evenly distributed along both sides of the body (Hansen, 1975; Gebruk, 1986).

Sp. 2 *Amperima naresi* (?) Théel 1882 (Fig. 5E)

Diagnostic features. Rounder (ovoid) body than in the previous species. Colour whitish. Very long velum, as long as the body. Large ventro-lateral tubefeet, decreasing in size towards the posterior end, spread more or less equally along both sides of the body, slightly fused around the posterior end.

Sp. 3 (Fig. 6A, B)

Diagnostic features. Body slightly flattened. Colour whitish-yellowish. Velum of moderate size. Tentacles long, forming anterior swimming lobe. Tubefeet large, spread equally along both sides of the body.

Remarks. This undescribed swimming elpidiid (or a species previously not known to swim) differs from *Peniagone leander*, known from the CCFZ area, in the velum being broader and the tubefeet spread equally along both sides of the body. Differences from *P. diaphana* include larger velum and large tubefeet spread along both sides of the body.

Gen. *Achlyonice* (?) Théel 1879

Achlyonice sp. (?) (Fig. 6C)

Diagnostic features. Body strongly flattened; transparent, brownish. Skin folds along both sides of the body resemble a brim, which extends anteriorly into a broad velum.

Remarks. A brim-like structure extending into a velum is very unusual for elpidiids, although this feature has been recently reported in a new species of *Achlyonice* (Gebruk, 1997).

Fam. Pelagothuriidae Ludwig 1894

Gen. *Enypniastes* Théel 1882

Enypniastes eximia Théel 1882 (Fig. 6D)

Diagnostic features. Large form, up to 25–30 cm long. Body ovoid. Colour reddish-dark purple. Anterior and posterior fans (lobes) developed, additional fan is formed by tentacles.

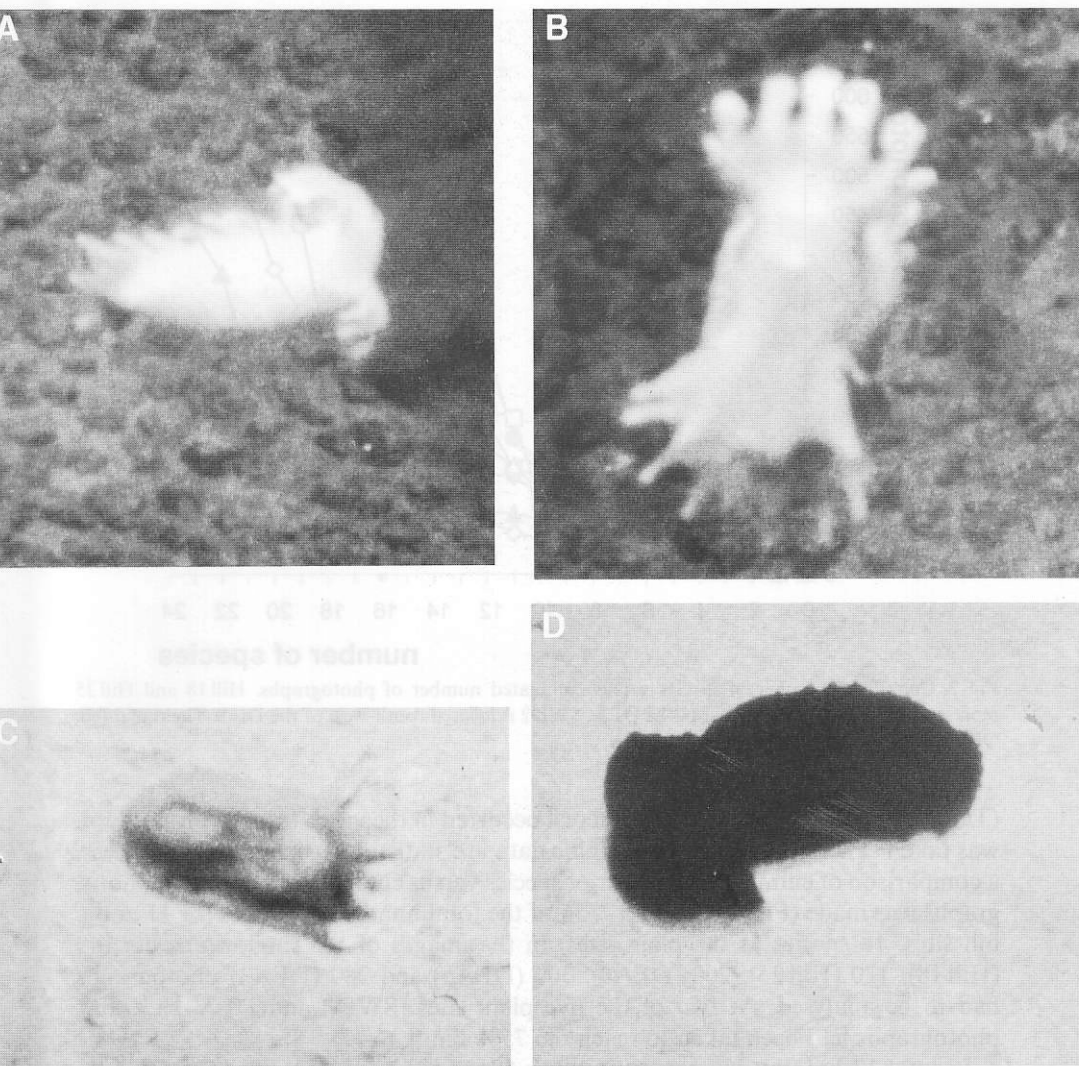


Fig. 6. A. and B. *Peniagone* sp. 3 (Elasipodida, Elpidiidae), swimming (upside down position); C. *Achlyonice* sp.? (Elasipodida, Elpidiidae); D. *Enynpiastes eximia* (Elasipodida, Pelagothuriidae).

Remarks. This species is pelagic (*e.g.*, Gebruk, 1989, 1990; Miller & Pawson, 1990), but is often observed in contact with the bottom. In some swimming positions it may not be easily recognized.

2. Image analyses

a. Reliability of the image data

The area monitored during 1 h of video observation can be calculated from the height of the image frame, which averaged 4.2 m, and the tow speed of the OFOS

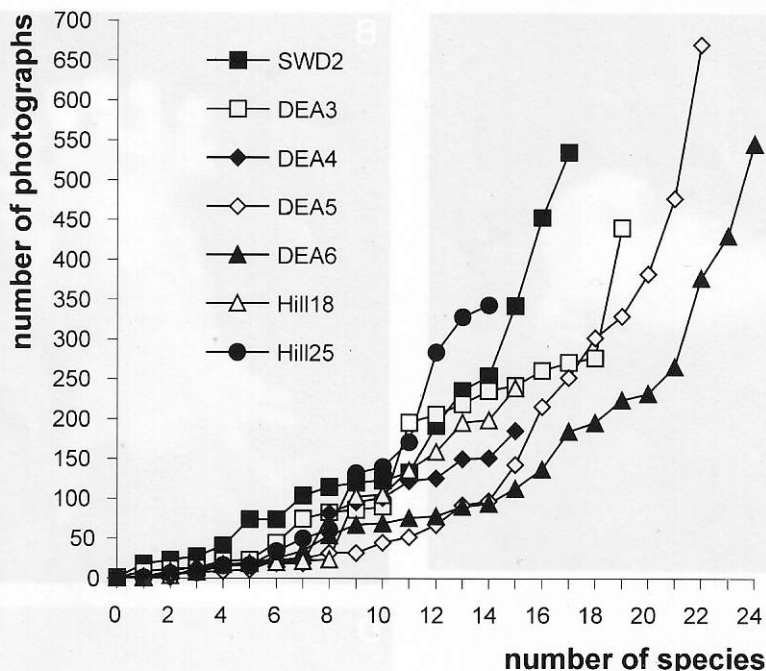


Fig. 7. Cumulated number of species versus cumulated number of photographs. Hill 18 and Hill 25 represent hill sites north and east of the DEA. SWD2 is located south-west of the DEA. The remaining OFOS transects were deployed in the DEA.

(Table 2). Each time an object of interest occurred in the video frame a photograph was taken. Therefore, the photographic data are statistically biased. Nevertheless, a comparison of cumulative number of species versus cumulative number of photographs was made (Fig. 7). To find 75% of the total number of species (or 11 at the hill sites, 18 species at the plain sites) in the images of the single transects 140 (Hill 18), 170 (Hill 25), 200 (DEA6), 300 (DEA5) and 280 (DEA3) photographs had to be analysed. At two of the five plain sites (SWD2 and DEA4) too few photographs had been taken to reach the 75% limit.

In total 13 holothurian categories were found in the video recordings (Fig. 8). Setting again an arbitrary limit of 75% (= 9.8 of the categories), the number of species at the plain sites reached this level after monitoring between 8000 m² (SWD2) and 18 000 m² (DEA5) of the sea floor. The total number of categories found at the hill sites remained at a lower level than at the plain sites. Seventy-five per cent of the total number of species (Hill 18: 6.8, Hill 25: 6 species) were reached after mapping 13 000 m² of the sea floor in Hill 18 and 8000 m² in Hill 25.

The area observed at DEA3, DEA5 and DEA6 did not reach the size of the minimal area (Table 3). It was exceeded after eliminating nine less abundant species from the database (Table 4).

b. Diversity

Photographs have higher resolution than video recordings and are more likely to distinguish different species. In the video data, 12 (SWD2) and 13 (SD = 1.9,

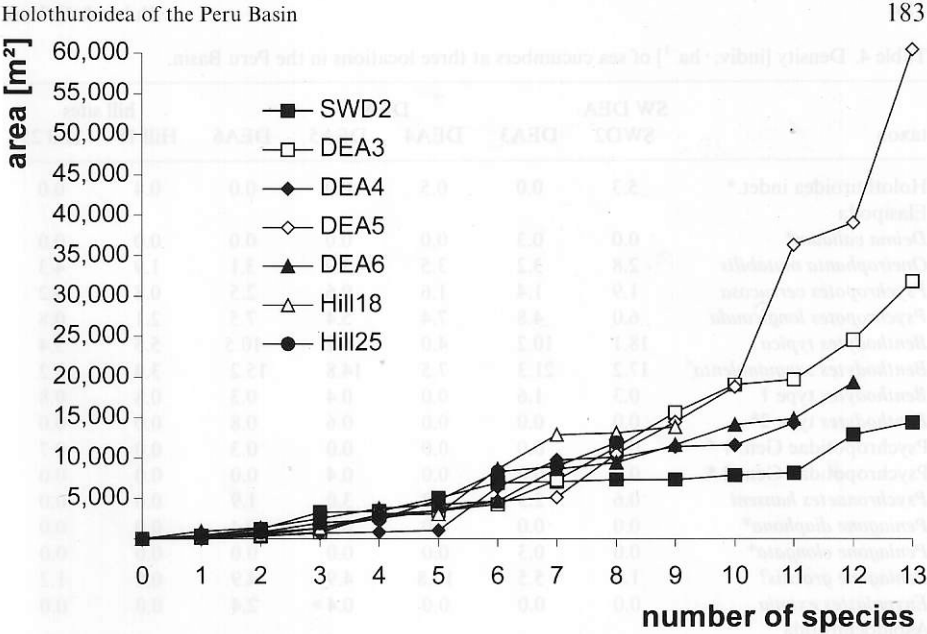


Fig. 8. Cumulated number of species versus cumulated sea floor area observed by video recordings. Hill 18 and Hill 25 represent hill sites north and east of the DEA. SWD2 is located south-west of the DEA. The remaining OFOS transects were deployed in the DEA.

Table 3. Minimal area calculation for DEA stations DEA3, DEA5 and DEA6.

	total area observed [ha]	minimal area μ [ha]	number of taxa in μ	SD	μ -SD	number of taxa in μ -SD
17 taxa included	11.47	26.78	16.54	16.62	10.16	15.15
11 taxa included	11.47	2.38	10.54	1.42	0.96	9.12

DEA3 to DEA6) species were found in plain areas compared to eight (Hill 18) and 10 (Hill 25) at hill sites. The lower diversity at hill sites can also be observed in the photographic data ($12, 14 \pm 2.4, 11$ and 10 , respectively).

Rarefaction curves for all stations calculated with the diversity software ‘Bio-diversity’ (Natural History Museum, London) showed no significant differences between the stations.

c. Density

The density of indeterminate holothurians was found to be 49.9% (SD = 16.7) of the total raw video data. Within this group, consisting of the three subcategories ‘indeterminable’, ‘dark-coloured’ and ‘light-coloured’ sea cucumbers, the last dominates with 82.9% (SD = 34.6). Whereas *Synallactes* type 1, *Deima validum* and *Oneirophanta mutabilis* are the only species showing a light colouring in the video recordings, the dark sea cucumbers belong to numerous families and species. To

Table 4. Density [indiv. \cdot ha⁻¹] of sea cucumbers at three locations in the Peru Basin.

taxon	SW DEA		DEA			hill sites	
	SWD2	DEA3	DEA4	DEA5	DEA6	Hill 18	Hill 25
Holothuroidea indet.*	5.3	0.0	0.5	0.0	0.0	0.4	0.0
Elasipoda							
<i>Deima validum</i> *	0.0	0.3	0.0	0.0	0.0	0.0	0.0
<i>Oneirophanta mutabilis</i>	2.8	3.2	3.5	3.9	3.1	1.9	4.3
<i>Psychropotes verrucosa</i>	1.9	1.4	1.6	0.6	2.5	0.8	0.2
<i>Psychropotes longicauda</i>	6.0	4.8	7.4	5.4	7.5	2.1	0.8
<i>Benthodytes typica</i>	18.1	10.2	4.0	6.2	10.5	5.5	3.4
<i>Benthodytes sanguinolenta</i>	17.2	21.3	7.5	14.8	15.2	3.4	8.2
<i>Benthodytes</i> type 1	0.3	1.6	0.0	0.4	0.3	0.8	0.8
<i>Benthodytes</i> type 2*	0.0	0.0	0.0	0.6	0.8	0.0	0.0
Psychropotidae Gen. 1 *	0.0	0.0	0.0	0.0	0.3	0.0	0.7
Psychropotidae Gen. 2 *	0.8	0.0	0.0	0.4	0.0	0.0	0.0
<i>Psychronaetes hanseni</i>	0.6	2.5	3.9	3.0	1.9	0.0	0.0
<i>Peniagone diaphana</i> *	0.0	0.0	0.0	0.0	0.4	0.0	0.0
<i>Peniagone elongata</i> *	0.0	0.3	0.0	0.0	0.0	0.0	0.0
<i>Peniagone gracilis</i> ?	1.9	5.5	10.8	4.9	4.9	0.0	1.2
<i>Enypniastes eximia</i>	0.0	0.0	0.0	0.4	2.4	0.0	0.0
Aspidochirotida							
<i>Synallactes</i> type 1	7.5	2.3	2.0	1.1	0.9	1.5	0.6
<i>Synallactes</i> type 2	4.8	1.8	1.6	1.6	1.6	0.8	1.3
<i>Paelopatides</i> type 1*	0.8	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mesothuria</i> sp.*	0.0	0.0	0.5	0.0	0.0	0.0	0.0
total	68.2	55.2	43.2	43.4	52.5	17.3	21.7

* = species excluded in the minimal area analysis.

solve this problem, the data for light- and dark-coloured categories were distributed according to the distribution of potential light- and dark-coloured species found in the photographs, a procedure similar to the method of distributing white spots commonly used in image analyses (Bluhm *et al.*, 1995).

The densities of nine species are represented in Fig. 9. These species were chosen because eight of them occur at all stations. *Psychronaetes hanseni* was found at the plain sites and was represented in all samples from the DEA. The other species occurred only at a few stations with a frequency of less than 50%. All species selected represent more than 89% of the total density found in the image material (SWD2: 89%, DEA stations: $95.5 \pm 2.4\%$, Hill 18: 93%, Hill 25: 93%).

The most abundant holothurian species in the DEA and adjacent deep sea floor areas were the psychropotids *Benthodytes sanguinolenta* and *Benthodytes typica*. The former is usually the dominant species within the DEA where it reaches a density of > 21 indiv. \cdot ha⁻¹ (Table 4), whereas the latter was dominant in adjacent areas with densities of > 18 indiv. \cdot ha⁻¹ (Table 4). *Benthodytes sanguinolenta*, however, was also the most abundant species at the hill site east of DEA (Table 4). *Benthodytes sanguinolenta* and *B. typica* in total may comprise nearly 40% of holothurians identified from photographs (Table 4). Adding *Peniagone* sp., these dominant species make up 50–60% of the total individuals found (SWD2: 55%, DEA stations: 59.3 ± 6.3 , Hill 18: 51%, Hill 25: 89%).

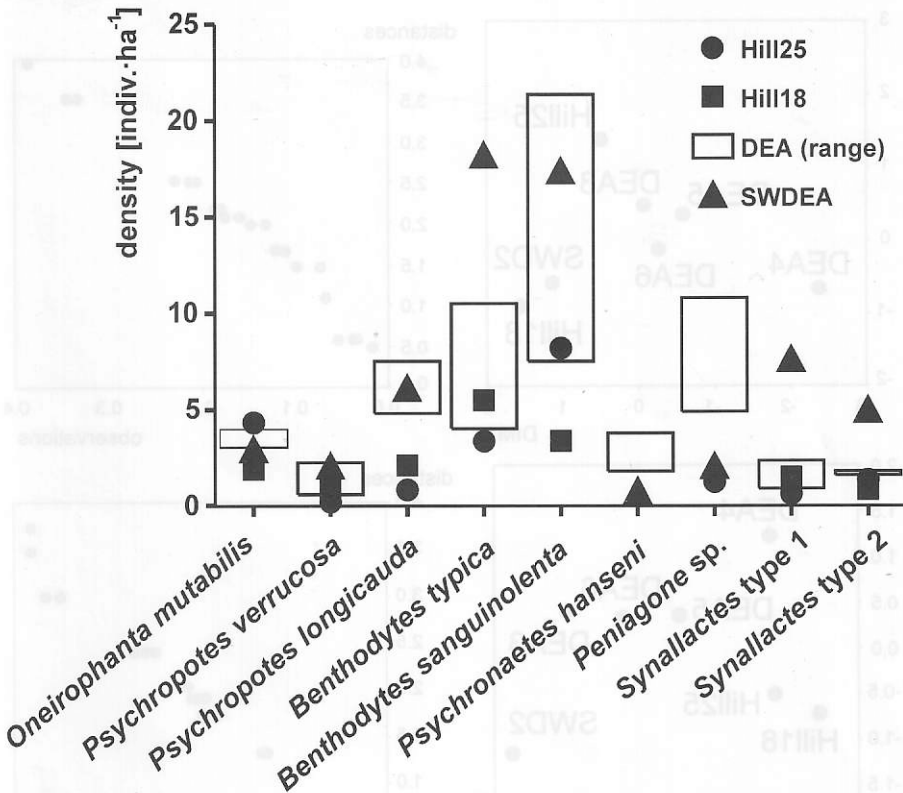


Fig. 9. Total densities of nine selected species [indiv. · ha⁻¹] at two hill sites (Hill 25 and Hill 18), the DEA (range of DEA3, DEA4, DEA5 and DEA6) and a station south-west of the DEA (SWD2), representing more than 89% of the total holothurian densities found.

Another rather common species within the DEA is *Psychropotes longicauda* (up to 7.5 indiv. · ha⁻¹). 'Relatively common' for the DEA are *O. mutabilis* and *P. hansenii* (up to 3.9 indiv. · ha⁻¹ each). Species relatively common adjacent to the DEA include two synallactids (7.5 and 4.8 indiv. · ha⁻¹) and *O. mutabilis* (4.3 indiv. · ha⁻¹; Table 4). The species found to be most abundant in the DEA and its surroundings are in general considered as common for the Central East Pacific (Maluf, 1988).

The total density of holothurians was higher at plain sites (68.2 indiv. · ha⁻¹ and 48.5 ± 6.1 indiv. · ha⁻¹ in SWD2 and the DEA sites) than at hill sites (Hill 18: 17.3 indiv. · ha⁻¹ and Hill 25: 21.7 indiv. · ha⁻¹).

The OFOS deployments were grouped (Table 4) into the plain sites DEA (DEA3 to DEA6) and south-west of DEA (SWD2), and hill sites 1 (Hill 25) and 2 (Hill 18). The ranges of the densities of the DEA samples are high in *B. typica*, *B. sanguinolenta* and *Peniagone sp.* The station south-west of the DEA (SWD2) shows some distinctiveness owing to the deviation of the densities from plain values in *B. typica*, *P. hansenii* and both *Synallactes* types. There is some indication that *Psychropotes longicauda* occurs in lower densities at hill sites compared to the plain areas.

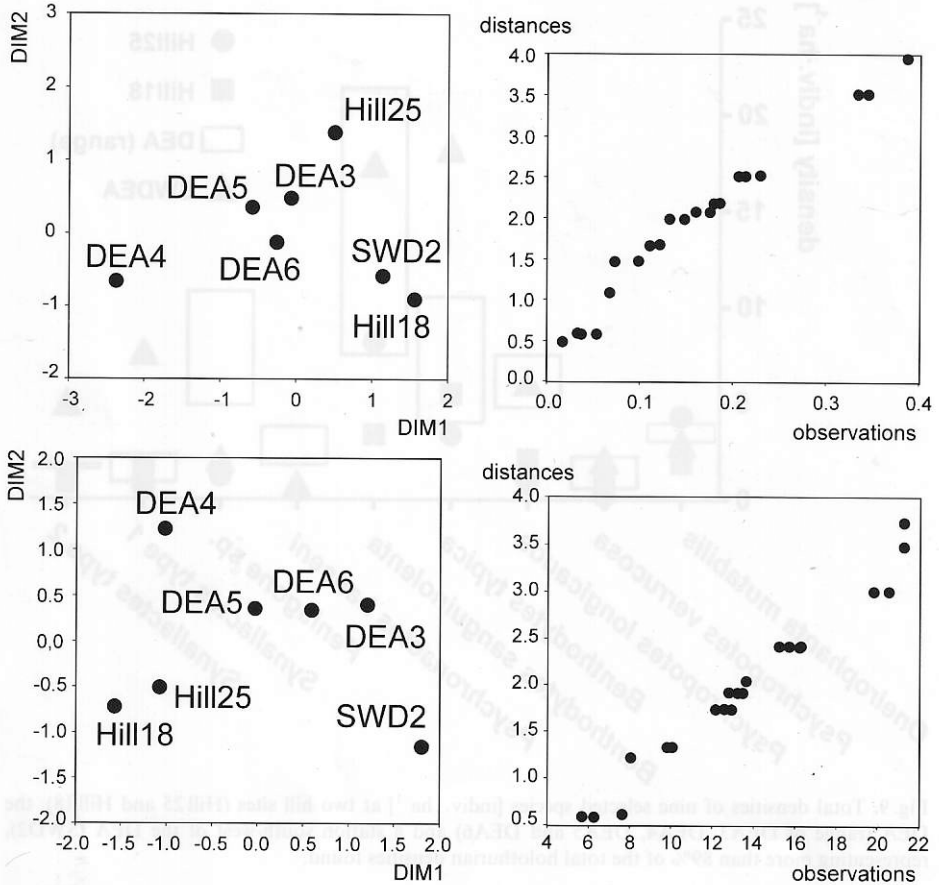


Fig. 10. Nonmetric multi-dimensional scaling (MDS, left) and Sheppard diagram (right) using Euclidian distance (top) and cosine similarity (bottom).

d. Community analysis

Nonmetric multi-dimensional scaling with Euclidian distance and cosine similarity show similar results (Fig. 10). DEA4 has a characteristic community distinguishable from the cluster of DEA stations. The station SW of the DEA incorporates dominant species other than those at the DEA stations or hill sites. The composition of the taxa is different to that found at the DEA.

Figure 11 shows results of the analysis of clustering of the species. Four clusters were found using the cosinus approximation (Fig. 11, top). Cluster 1 includes species with relatively high abundances at the station SW of DEA. Dominant species at the DEA stations and SW of DEA form cluster 2. Species with similar abundances at all stations form cluster 3. Cluster 4 comprises species with high densities at station DEA6.

Analysis using Euclidian distance created four distinct clusters (Fig. 11, bottom). Species with high abundances at station SW of DEA only form cluster 1. Cluster 2 includes dominant species at the stations SW of DEA and DEA (exclusive

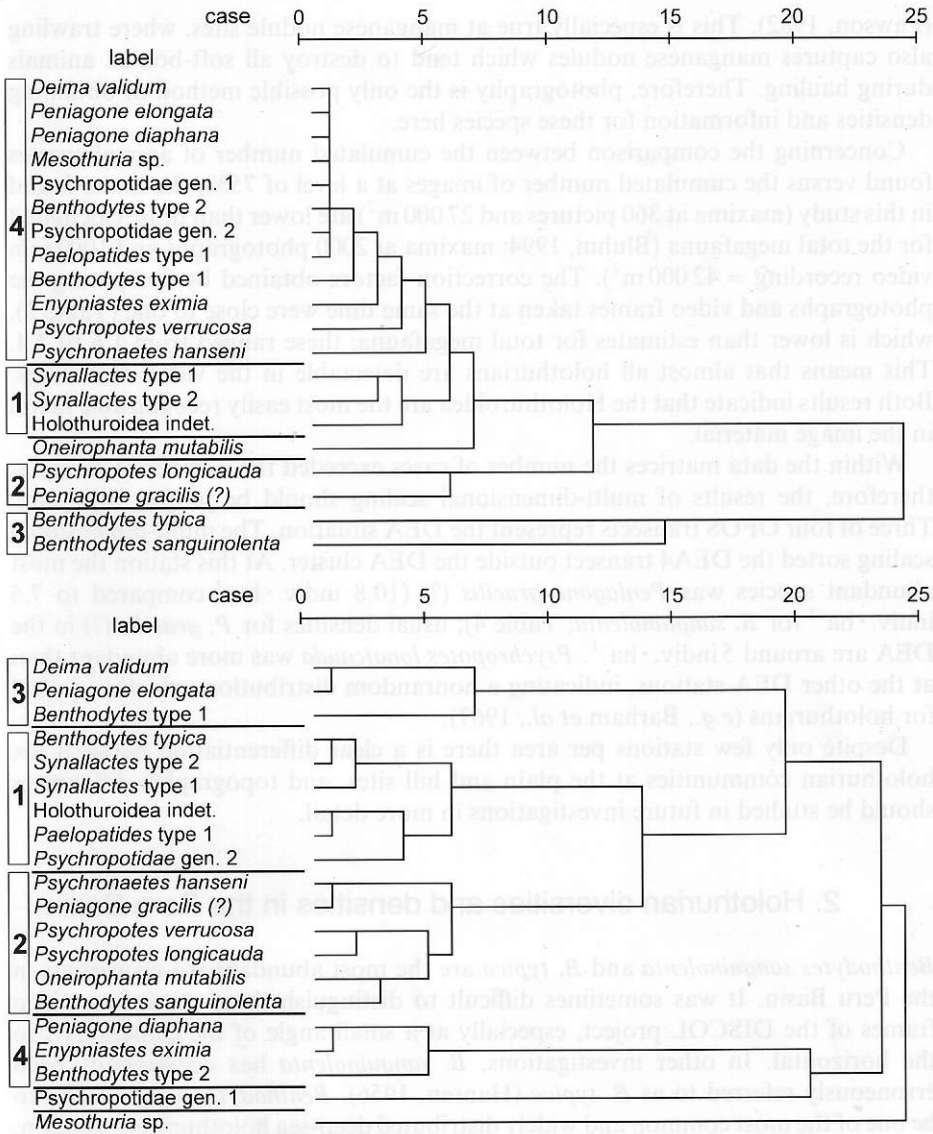


Fig. 11. Cluster analyses using cosine similarity (top) and Euclidian distance (bottom).

DEA4). Species with low abundances at hill sites and high densities at the other stations form cluster 3. Cluster 4 includes species with low densities.

Discussion

1. Reliability of the image data

Many holothurians such as *Enypniastes eximia* or specimens of the family Elpidiidae are exceedingly fragile and are reduced to gelatinous masses in trawl samples

animals should be kept in mind. Future bottom samples should provide more knowledge on the distribution of elpidiids in the manganese nodule areas.

Different holothurian assemblages were found at hill and plain sites and differed again at a location only a few nautical miles away from the DEA. Most of the sea cucumbers in the Peru Basin seem to avoid elevated sites north and east of DEA, although the density of some species, e.g., *O. mutabilis*, is slightly greater there (Table 4).

Most holothurians in the Peru Basin feed on the upper layers of the soft-bottom sediment. A high density of polymetallic nodules would be expected to decrease the area exploitable by these animals and therefore reduce their densities, but in the DISCOL data no such reduction with increasing nodule densities was observed. This contrasts with the results of other investigations (Pawson, 1988; Tilot, 1992).

Eric Foell (personal communication) noticed a remarkable shift in megabenthic community structure to increased densities of soft bottom taxa in large-scale topographically diverse areas. Different densities and diversities of megafauna, especially holothurians, were found in the manganese nodule claim areas at the same order of latitude in the CCFZ (H. Bluhm, personal observation).

Densities of most sea cucumber species show some variation, sometimes significant, between the DISCOL transects (Table 4), indicating an uneven distribution on the sea floor. Sibuet (1988) demonstrated earlier that the size of holothurian patches on the abyssal floor ranges between 150 and 2000 m in diameter. The scale of holothurian patches was also discussed by Billett (1991).

3. Comparison with other regions

Species composition and densities, based on deep-sea photographs, were previously studied in the manganese nodule-rich CCFZ (Pawson & Foell, 1983; Tilot, 1992). Pawson & Foell (1983), using a scale from 'rare' to 'very common', reported *P. leander* as the most common species there. 'Common' species included *Mesothuria murrayi* and *Psychropotes semperiana*. *Benthodytes incerta*, *Psychronaetes hansenii*, and *Paelopatides* sp. were reported as 'relatively common'.

According to Tilot (1992) the most abundant holothurian in the CCFZ was *M. murrayi* (up to 40 indiv. \cdot ha⁻¹). *B. incerta* showed up to 26 indiv. \cdot ha⁻¹ and *E. eximia* and *Synallactes profundus* up to 25 indiv. \cdot ha⁻¹ each (Table 16 in Tilot, 1992). Also abundant were *Peniagone/Amperima* sp. (up to 13 indiv. \cdot ha⁻¹), *Meseres macdonaldi* (11 indiv. \cdot ha⁻¹), *P. leander* and *P. hansenii* (10 indiv. \cdot ha⁻¹ each). Thus, data from Pawson & Foell (1983) and Tilot (1992), although with some variation, agree on high densities (= 'common occurrence') of *Mesothuria murrayi*, *P. leander*, *P. hansenii* and *B. incerta*. The variation between the two sets might reflect the different bottom topography, different nodule coverages and sizes, and/or an uneven distribution of holothurians on the sea floor. Geographic variations may also play a role. However, Tilot (1992) reported very high densities (at maximum 25 indiv. \cdot ha⁻¹) for *E. eximia*, which was not noted by Pawson & Foell (1983).

In photographs, specimens of the genus *Mesothuria* closely resemble the faecal casts of holothurians and often could be distinguished only by their trails. There-

fore, these species might be underestimated in the DISCOL data. The same is true for *Meseres* sp. in the Peru Basin; it resembles a manganese nodule.

Psychropotes semperiana has been found only at North Pacific sites. In the Peru Basin *Psychropotes longicauda* is common, but it is less abundant in the CCFZ. It reaches high densities in other oceans, e.g., the Atlantic Ocean (Billett, 1991). The cause of the different distribution of these two species is currently unknown owing to our limited knowledge of their autecology. Another species of this genus, *Psychropotes hyalinus*, reported in abyssal depths north of Hawaii (Pawson, 1985), has not been found in manganese nodule areas so far.

In general, holothurian abundance in the deep sea is very variable, depending primarily on depth and distance from continents (see Billett, 1991, for a review): abundances range from less than 10 up to 100 indiv. \cdot ha⁻¹. The DISCOL data (17 to 68 indiv. \cdot ha⁻¹) confirm this observation. Elpidiid holothurians can form high densities on the deep-sea floor, especially in canyon and trench areas (Gebruk, 1986; Billett, 1991) and also in large-scale depressions in the subarctic North Atlantic (Thiel *et al.*, 1997). On the flat abyssal plain in the north-east Atlantic, Billett & Hansen (1982) observed up to 500 000 indiv. \cdot ha⁻¹ of *Kolga hyalina*. High densities of other species were reported, based on photographs from the abyssal north-east Pacific (34°N), by Lauerman *et al.* (1996). *Elpidia minutissima* exceeded 2600 indiv. \cdot ha⁻¹ and *Peniagone vitrea* and *Peniagone diaphana* reached 495 indiv. \cdot ha⁻¹ and 447 indiv. \cdot ha⁻¹, respectively.

According to Billett (1991), holothurian abundance is highest at mid to lower-slope depths and at abyssal depths close to the base of the continental slope, ranging from 100 to 1000 indiv. \cdot ha⁻¹. Carney & Carey (1982) found infaunal forms to be more abundant in slope areas than in the basins of the north-eastern Pacific Region (Cascadia Basin and Tufts Abyssal Plain) and vice-versa for epifaunal sea cucumbers.

Comparisons between the north-east Pacific, the DISCOL experimental area and the CCFZ show a significant latitudinal variation in holothurian abundance. A considerable seasonal variation in holothurian abundance has been reported in moderate and high latitudes, where the seasonality of primary production and organic flux to the deep-sea floor is pronounced (e.g., Billett, 1991, for the Atlantic Ocean; Smith *et al.*, 1994, for the Pacific Ocean). Greenish 'fluffy objects' were also found in the DEA (Bluhm, 1994), especially at station SWD2, which explains the different cluster formation to that of the DEA stations in community analyses.

4. Lifestyle

Holothurians dominant in the DEA have various lifestyles (see Gebruk, 1995, for definitions). The most abundant sea cucumber in the DEA, *B. sanguinolenta*, is a facultative swimming form. Its swimming movement is similar to that described by Pawson (1976) for *Psychropotes depressa*. The animal can leave the sea floor by flexing its body in the vertical plane: '... the flexing activity is quite slow, but it is effective in moving the animal away from the source of disturbance' (p. 286 in Pawson, 1976). In the DISCOL material, $66.1 \pm 20.7\%$ (SD) of the *B. sanguinolenta* specimens were observed swimming. In most cases the bow wave or light of the

photo/videosystem did not stimulate this species to flee, although the weight fixed 3 m between the sea floor and the OFOS sometimes touched the animals. Assuming that OFOS has no effect on this sea cucumber the proportion of swimming animals should be added to the density values measured, yielding densities three times larger than measured.

Other sea cucumbers capable of swimming and found in the Peru Basin are *P. diaphana* and *E. eximia*. Swimming *P. diaphana* occurred regularly in the video recordings. Their colour ranged from hyaline to red. Barnes *et al.* (1976) found that large specimens seem to be darker than smaller animals. The swimming behaviour observed during submersible dives is described in detail in Barnes *et al.* (1976). *Peniagone diaphana* feeds at the sea floor (*e.g.*, Billett *et al.*, 1985) but is very rarely seen in the contact with it (Barnes *et al.*, 1976). As with *B. sanguinolenta*, the densities of *P. diaphana* are up to three times higher in the Peru Basin than originally calculated. The CCFZ has a very large portion of true swimming forms: *E. eximia* (Tilot, 1992) and *P. leander* (Pawson & Foell, 1983). *Enypniastes eximia* is rare in the DEA, while no *P. leander* were found in the DISCOL material.

Psychropotes longicauda probably moves with the help of long dorsal appendages acting as a sail (Gebruk, 1995). Juveniles have been found thousands of metres above the seabed (Gebruk *et al.*, 1997; Billett *et al.*, 1985). Juvenile specimens (approx. 10 cm in length) were rarely observed in the Peru Basin; those seen were moving at the sea floor.

Most of the sea cucumbers of the *Peniagone/Amperima* type are benthic 'walking' forms; they are very often seen on the sea floor with their velum facing into the current and lifting the anterior part of the body (Gebruk, 1995). The present study also indicates that *Psychropotes* and *Peniagone/Amperima* show a pattern of nonrandom orientation on the sea floor; this is currently being studied in detail and will be published later.

Other holothurians common in the DEA – *B. typica*, Synallactidae and *O. mutabilis* – are typical benthic forms, the last known to be a very active and fast-moving species (Smith *et al.*, 1997). *Benthodytes typica* was reported to be incapable of swimming (Pawson, 1982), but Billett & Huggett (1987) found juveniles several metres above the sea floor.

The north-east Pacific appears to be the realm of minute, typically benthic *Elpidia minutissima*, forming aggregations, and swimming *P. diaphana* and *P. vitrea* (Lauerman *et al.*, 1996). Small benthic holothurians (*e.g.*, *Kolga hyalina*) are similarly abundant in the abyssal north Atlantic (Billett, 1991), where, among larger forms, the highest densities were shown by *O. mutabilis* and *P. longicauda* (Billett, 1991). A burrowing *Pseudostichopus* sp. is among the dominant holothurians in the north-east abyssal Atlantic Ocean (Roberts *et al.*, 1996).

The above-mentioned larger species are not only the most abundant in the abyssal north-east Atlantic, but they also clearly show different feeding strategies and trophic niche partitioning. *Oneirophanta mutabilis* seems to respond rapidly to episodic pulses of phytodetritus and feeds on richer food sources than *P. longicauda*, which also feeds at the sediment surface. *Pseudostichopus* sp. is partly submerged in the sediment, very slow moving and uses poorer resources in the subsurface sediment (Moore & Roberts, 1994; Moore *et al.*, 1995; Roberts *et al.*, 1996). Detailed studies in the north-east Atlantic have demonstrated that when phytodetritus arrives at the seabed, highly mobile *Oneirophanta* rake the sediment

surface first, then psychropotids carefully browse and collect their share, and *Pseudostichopus* slowly takes the rest of organics by ploughing the subsurface (*op. cit.*). Very similar niche separation has recently been demonstrated for *Pannychia moseleyi*, *Scotoplanes globosa*, *Chiridota* sp. and *Molpadia* sp. in the Santa Catalina Basin (Miller *et al.*, in press).

The arrival of food in pulses, patchiness of food and a dominance of vertical over horizontal transport of food to megafauna deposit feeders in the deep sea apparently favour highly mobile megafauna capable of rapidly processing rather labile material, such as the sea cucumber *O. mutabilis* (see also Khripounoff & Sibuet, 1980; Jumars *et al.*, 1990; Lauerman *et al.*, 1997). This may also help to explain why this feeding strategy is not known in shallow waters, where horizontal physical transport to deposit feeders prevails; as a result, some shallow-water deposit feeding holothurians (*e.g.*, *Holothuria leucospilota*) may stay for months at one spot, even though the content of organic matter in the sediment at any given time may be relatively low (Levin, 1987, 1988).

A low abundance of *O. mutabilis* or other highly mobile forms in the DEA, accompanied by high densities of swimming holothurians, most likely indicate poorer feeding conditions on the abyssal Central East Pacific sea floor compared with conditions at higher latitudes in the Pacific and the Atlantic.

Swimming in deep-sea holothurians may have evolved as an adaptation to exploit vast areas of abyssal plains that are poor in food resources (Gebruk, 1986). This capability should be useful to repopulate defaunated areas, which may occur for example during commercial marine mining. Physical disturbances created by human activities may change the sediment characteristics of the sea floor and therefore affect food availability for deposit-feeding sea cucumbers.

The holothurians of the manganese nodule areas in the Pacific Ocean are now well known, although some uncertainties remain in determination of single specimens. They will in the future be analysed in detail using the DISCOL data to test their value as an indicator group for physical disturbance. The present investigation found some indication that holothurian diversities and densities are dependent on different topographies. This must be studied in detail in the future.

Summary

Knowledge of the diversities and densities of sea cucumbers in manganese nodule claims and in the abyss in general is still poor. Image material from the DISCOL project provides detailed information on the distribution of holothurians at an abyssal site in the Peru Basin. A brief summary of the taxonomic status and the occurrence of sea cucumbers in the abyssal Pacific Ocean is given together with notes on ecology and behaviour. Photographs of relevant species should help deep-sea scientists to give names to animals seen on images; such names can be confirmed after detailed taxonomic analyses of preserved animals. The current compilation will enhance our knowledge of the taxonomy and distribution of holothurians in the world oceans and will be important in estimating human impact on this ecosystem.

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p3102

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