

Tanaidacea
Abundance
Deep-sea benthos
Benthic storms

Tanaïdacés
Abondance
Benthos profond
Tempêtes benthiques
Atlantique Nord

The tanaid fauna from a region of the deep North Atlantic where near-bottom current velocities are high

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ABSTRACT

Data from 16 box cores taken at the Hebble site in the deep (4.8 km) North Atlantic (40°27' N, 62°20' W) were used to test Thistle *et al.*'s (1985) contention that the Tanaidacea (Crustacea, Peracarida) of this high-energy region are atypical of the deep sea as it is usually characterized. The tanaid abundance was high, and the fauna was dominated by the tube- or burrow-dwelling Leptognathiidae. The epifaunal Neotanaidomorpha were absent. An additional set of 4 box cores taken during a later cruise were used in a temporal comparison. Collectively, the results suggest that as Thistle *et al.* (1985) contend the tanaid fauna of this region is atypical. It is also relatively stable over time despite the "benthic storms" that disrupt the sediment in this region.

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RÉSUMÉ

Les tanaïdacés d'une région abyssale à circulation intense de l'Océan Atlantique Nord.

A partir des données de 16 prélèvements effectués à l'aide du carottier de type USNEL sur la station Hebble dans le domaine abyssal de l'Océan Atlantique Nord (40°27' N - 62°20' W et 4820 m de profondeur), nous avons pu tester l'hypothèse de Thistle *et al.* (1985). Ces auteurs ont considéré que les tanaïdacés de cette région à circulation profonde intense, constituent une faune atypique des bassins profonds par rapport aux caractéristiques habituelles. Les tanaïdacés y sont abondants, et dominés par les Leptognathiidae, animaux fouisseurs ou tubicoles. Les Neotanaidomorpha, qui vivent à la surface des sédiments, sont absents. Une comparaison temporelle a pu être faite à partir d'une série de 4 échantillons prélevés lors d'une autre campagne.

La synthèse des résultats confirme les hypothèses de Thistle *et al.*, en démontrant que la faune des tanaïdacés de cette région est relativement stable du point de vue temporel et qu'elle est adaptée à résister aux tempêtes benthiques qui perturbent les sédiments de cette région.

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INTRODUCTION

Thistle *et al.* (1985) have published an overview of the benthic fauna from a site at 4626 m depth in the North Atlantic. They report that, in many aspects, the fauna is different from that usually found in the deep sea. In particular, the abundance of macrofauna is much higher than expected for the depth, and the taxonomic and morphologic composition of the fauna suggests that an unusually high proportion of the fauna lives in

or can retreat into the sediment. In this region, frequent "benthic storms" occur, during which near-bottom current velocities reach values an order of magnitude greater than those typically found in the abyss (Weatherly, Kelley, 1982; 1985). These storms suspend surficial sediments. As a result, the benthos is subjected to erosion during a storm and burial as the storm passes (Hollister, McCave, 1984). Thistle *et al.* (1985) report

that the isopod and tanaid fauna consists of species that live in or can shelter in the sediment and suggest that the isopod and tanaid faunas inhabiting this region are adapted to mitigate the effects of the storms.

These data and the explanation advanced contrast with the bulk of the information on deep-sea faunas. Therefore, it is important to test the robustness of Thistle *et al.*'s (1985) conclusions. In this paper, we present data from two additional sampling trips to this region. We concentrate on the Tanaidacea (Crustacea, Peracarida), a taxon that figures importantly in Thistle *et al.* (1985) and usually ranks second in numbers of individuals and species in deep-sea macrobenthic assemblages (*see, e.g.,* Jumars, Gallagher, 1982).

LOCALITY

This study is part of the High Energy Benthic Boundary Layer Experiment (Hebble) (Nowell *et al.*, 1982). The Hebble site is at 4820 m depth on the lower continental rise south of Nova Scotia (40°27' N, 62°20' W) about 68.6 km away from the location of Thistle *et al.*'s (1985) samples (Fig. 1). The site is subjected to periodic "benthic storms" (Kerr, 1980) during which daily-averaged near-bottom velocities exceed 15 cm/s (a velocity that causes appreciable sediment erosion at the site) for 2 or more days (Weatherly, Kelley, 1985). These storms occur at irregular intervals, but 14 occurred during 20 months of measurements during 1982-1983 (Weatherly, Kelley, 1985). Storms last from a few days to 2 weeks. During storms, suspended-sediment concentrations can reach 12 mg/l, 250 times that of typical abyssal waters (Hollister *et al.*, 1984), leaving the seabed with a scoured appearance (Hollister, McCave, 1984). Between storms, large amounts of sediment are deposited. In particular, using radioisotope profiles and granulometric markers, Hollister and McCave (1984) argue that the surficial layer of sediment (*see below*) was eroded away and replaced between July, 1982, and June, 1983.

The site was chosen because it lacked large-scale bedforms (Nowell *et al.*, 1982) and had little slope (1: 100). The largest topographic features evident in bottom photographs are more-or-less elliptical mounds typic-

ally less than 10 cm high and 20 cm long (Nowell *et al.*, 1982) that appear to have a biological origin (personal observation). During our first cruise, the site was covered with a soft, brown mud layer 0.5 to 11.3 cm thick with a 6% sand content and a water content of approximately 50% (wet weight) (Hollister, McCave, 1984). In this region, the salinity of the bottom water is 34.8, and the temperature is 2.2°C (Weatherly, Kelley, 1982).

MATERIALS AND METHODS

Our first set of samples was taken from the Hebble site (=the Hebble box) during July, 1982 (*R/V Knorr* cruise 96, Hollister, Chandler, 1982). The site was defined as a 2-km by 4-km rectangle. For the purposes of Hebble, we wished to be able to detect inhomogeneities in the distribution of the fauna within it. *A priori* at this depth in these waters, the smallest sampling quadrats feasible using a navigated box corer were thought to be 0.5 km by 1 km. Given that 16 box cores were to be taken, four 1-km by 2-km quadrats were laid out, each containing four 0.5-km by 1-km areas (Fig. 2). We sampled in the following manner to separate possible temporal changes during the several weeks of sampling from spatial variability among quadrats. The four quadrats were randomly ordered into a sequence. An area was randomly selected for sampling from the first quadrat. The procedure was repeated for each of the quadrats in turn until all 16 areas had been sampled. The order of sampling is given in Figure 2.

During coring, the ship attempted to keep station over the center of the target area during the descent of the box corer (~ 100 min.). Inefficiencies in keeping station plus the actions of very strong surface currents in the Gulf Stream and currents at depth on the descending box corer determined the location that was sampled. On the bottom, this position was located to ± 1 -m precision within an acoustic transponder navigation net. We assumed that this procedure would result in approximately equal probability of sampling for all points in the area. After 12 areas had been sampled, it was clear that the calm weather and increasing skill of

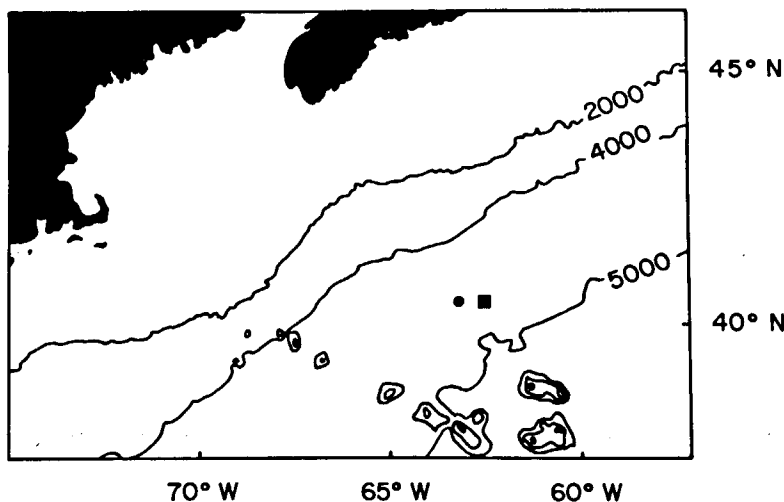
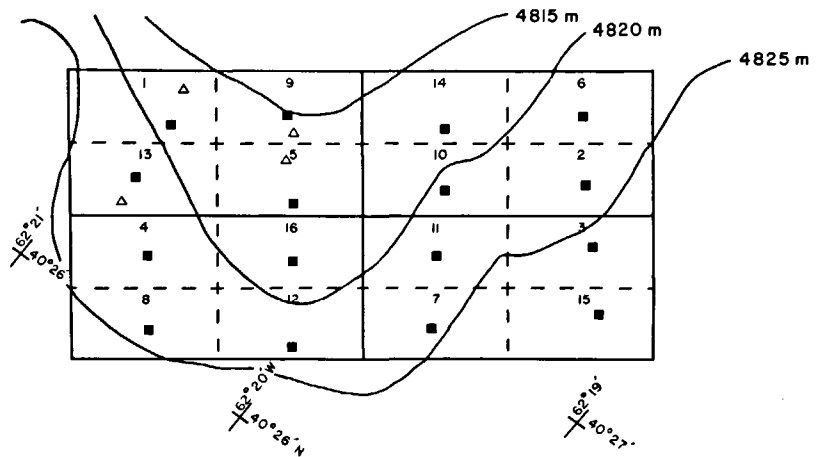


Figure 1
Chart of the northwestern Atlantic showing the Hebble site (square) and the site of the preliminary samples studied by Thistle *et al.* (1985; circle).

Figure 2

The 2-by 4-km Hebble sampling box. Quadrats are delineated by solid lines; areas within quadrats are shown by dashed lines. The 1982 sample locations are shown as filled squares; the numbers shown in each area give the order in which the samples were taken. The 1983 sample locations are shown as open triangles.



the navigators were causing a bias toward the centers of the areas. To minimize this effect, for the four remaining areas (one in each quadrat), we defined a central rectangle (0.13 km by 0.63 km) within which coordinates for the sample location were selected at random. The dimensions of this rectangle were chosen such that, for any point within it, anticipated navigation error would not cause the sample to be taken outside of the target area.

The Hebble box was reoccupied during June, 1983 (R/V *Knorr* cruise 103; Chandler, Hollister, 1983). Four box-core samples were taken from the west quadrat (Fig. 2). They were taken in random order and used the original scheme for positioning the box corer in an area.

Clearly, despite our efforts, the samples were not taken in a strictly random manner. However, they were not positioned because of any information about the location that was about to be sampled. We treat them as if they had been mechanically randomized.

We used a 0.25-m² USNEL box corer (Hessler, Jumars, 1974) modified to reduce bow-wave effects according to designs of R.R. Hessler, P.A. Jumars, and J. Finger (see Thiel, 1983). The box contained removable subsamplers (Fig. 3). The nine 10-cm by 10-cm subcores contained 5-cm by 5-cm subsubcores for use by other investigators. The bottom edges of the subsubcores were beveled such that the subcore sampled a 77-cm² surface. When a core was brought on deck, it was inspected for quality (e.g., clarity of top water, evidence of disturbance during coring); inferior box cores were discarded.

On deck, the water overlying each subcore was immediately aspirated off, sieved on a 0.044-mm aperture sieve, and added to the appropriate 0-1 cm layer sample. Each subcore was then extruded, sliced into layers (0-1, 1-2, 2-3, 3-5, 5-7, 7-10 cm), and preserved in a 1:5 solution of formaldehyde in 0.044-mm-filtered seawater that was buffered with sodium borate. In the laboratory, the layers were separated into fractions on sieves of 1.00-, 0.500-, 0.420-, 0.297- and 0.062-mm aperture. The tanaid data reported and used in comparisons come from the ≥ 0.297 -mm fraction of the 0-5 cm layers of the 9 subcores from each box core.

The identification of the tanaids required recognition of the developmental stage and sex of each individual. There are many schemes for recognizing and naming

developmental stages (e.g., Buckle-Ramirez, 1965; Lang, 1953; Sieg, 1972; 1978). We followed Sieg (1978) for the tanaidomorphans but included points from Gardiner (1975) and Messing (1983; Tab. 1). Also, we encountered some large females that lacked rudimentary oostegites and could not be accommodated in this structure. Gardiner (1975) noted the same situation in the Neotanaidomorpha and suggested that these individuals had passed through a copulatory stage and had molted, shedding the marsupium (a similar phenomenon has been encountered in deep-sea isopods and viewed in this way, Thistle, personal observation).

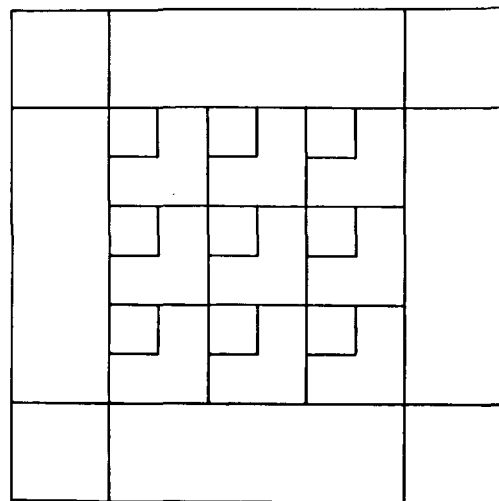


Figure 3

A schematic representation of a box core showing the subsample arrangement. The scale line equals 10 cm.

Table 1

A list of the tanaidomorph developmental stages identified.

Manca I — Pereopods VII and pleopods absent.

Manca II — Pereopods VII unsegmented, short, straight rudiments; pleopods absent.

Juveniles — All thoracic appendages completely developed; rudimentary oostegites and male genital cones absent.

Preparatory ♀ — Rudimentary oostegites knoblike or paddle-shaped, arising from coxae of 1 or more pereopods.

Intermediate ♀ — Much larger in body size than Preparatory ♀ but without even rudimentary oostegites.

Copulatory ♀ — Complete marsupium (brood pouch) present. ♂ — Genital cones (2) present on ventrum of last thoracic somite.

Because body length was strongly correlated with developmental stage within a population, large females not fitting into the juvenile size category for their species were classified as "intermediate females" (*sensu* Gardner, 1975).

The taxonomy of deep-sea tanaids is poorly known. We used Sieg and Winn's (1978) key to the families and the following keys to the genera of the various families: Sieg, 1977 (Pseudotanaiidae); Lang, 1970 (Anarthruridae); Sieg, unpublished (Leptognathiidae). At the species level, we developed working keys to our fauna. Because the taxonomy of Leptognathiidae males is fragmentary, no attempt was made to place these individuals.

We use the 1982 data for our comparisons to Thistle *et al.*' (1985) results. Because of Hebble requirements, the 1983 data were taken from a single quadrat of the Hebble box. In our temporal comparison, we compare these data to those from the same quadrat taken in 1982.

RESULTS AND DISCUSSION

The tanaid fauna studied by Thistle *et al.* (1985) appeared to be unusual in three ways: tanaid abundance was higher than any reported for depths greater than 2000 m; individuals of the surface-dwelling, deep-sea family Neotanaiidae were absent; and those tanaids that were abundant seemed to be morphologically adapted for tube or burrow dwelling. From a knowledge of the physical regime at the study site, they argued that these data suggested that the tanaid fauna was adapted to shelter in the seabed to mitigate the effects of the erosion-deposition regime created by the episodically intense near-bottom flows. Further, they suggested that this physical regime allows enhanced standing stocks of this primarily deposit-feeding tanaid fauna (personal observation of gut contents) by stimulating the growth of sedimentary microbes. In the following, we show that the physical regime at the Hebble site is comparable to that at Thistle *et al.*'s (1985) site. We then examine the parameters they cite to test whether their results accurately represent the region and add new data in order to examine their hypotheses as to the forces acting on the tanaid fauna. Finally, we test for temporal differences at the Hebble site. Such a test is relevant in this context because a storm occurred just before the 1983 samples were taken.

The Hebble site is 68 km away from Thistle *et al.*'s (1985) site and 194 m deeper. The physical environments are similar. In particular, benthic storms create an erosion-deposition regime in both, so the Hebble data can be used to explore Thistle *et al.*'s (1985) results.

In terms of abundance, tanaid numbers in the Hebble box in 1982 did not differ significantly from those at Thistle *et al.*'s (1985) site (Mann-Whitney U test, $N_1=2$, $N_2=16$, Sokal and Rohlf, 1981). There is no evidence in the Hebble tanaid data that Thistle *et al.*'s (1985) abundances are other than representative of the

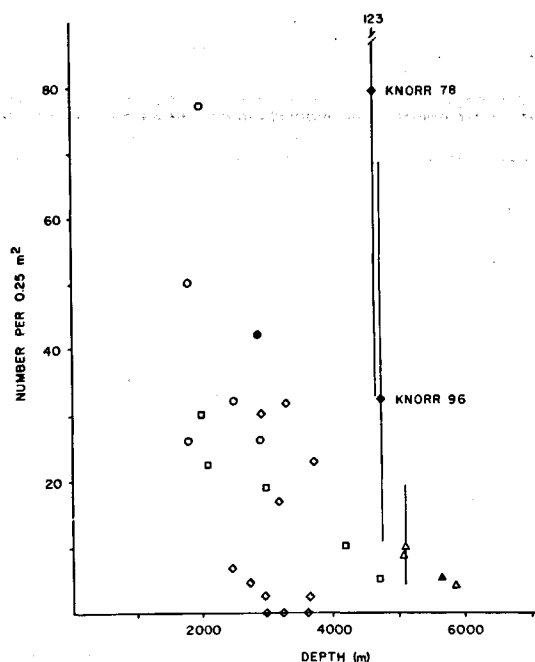


Figure 4

Median tanaid abundances versus depth. Symbols are as follows: Hessler and Jumars (1974), filled triangles; Dahl *et al.* (1976), open diamonds; Gage (1977), filled circles; Gage (1979), open circles; Laubier and Sibuet (1979), open squares; Khripounoff *et al.* (1980), open triangles. Ranges are shown for Khripounoff *et al.* (1980), Thistle *et al.* (1985) = Knorr 78, and the 1982 samples = Knorr 96.

region (*i.e.*, the upper Scotian Rise). The new data do permit a second estimate of the region's median abundance. Although the Hebble abundances are lower than those of Thistle *et al.* (1985), they are still high for the depth (Fig. 4). In particular, the results of Khripounoff *et al.* (1980) (station B, 5100 m depth near the Vema Fracture Zone) are the most comparable to the Hebble results in terms of water depth; the 1982 median abundance is significantly higher than their value (Mann-Whitney U test, $N_1=8$, $N_2=16$).

Thistle *et al.* (1985) found relatively high bacterial standing stocks at their site and speculated that the disturbance caused by benthic storms could promote bacterial growth, resulting in the high bacterial values observed, and subsequently support larger numbers of deposit feeders, in particular, tanaids. Their argument is based on shallow-water studies showing that disturbing sediments promotes bacterial growth. Mechanistically, the disturbance is thought to disrupt the microenvironments surrounding bacterial colonies, thereby renewing the nutrient and electron acceptor supplies required for bacterial growth that had been reduced or exhausted (Yingst, Rhoads, 1980; Aller, 1982; Findlay, White, 1984; Findlay *et al.*, submitted).

Bacterial abundances were also high in the Hebble box. Baird, Nivens, Parker, and White (1985) measured the bacterial standing stock in the corner subcores (Fig. 3) from the box cores used for tanaids. The bacterial biomass was 6 to 10 times greater on the Hebble site than at other deep-sea locations of comparable depth and is one third the value measured in a subtropical estuary. These results lend support to Thistle *et al.*'s (1985) data and interpretation.

Thistle *et al.* (1985) used the abundance of the Neotanaidomorpha in their argument because this group of tanaids is thought to be epifaunal, with limited ability to burrow into the sediment (Gardiner, 1975). The region is within the geographic range of *Neotanaid americanus*, *N. micromorpha*, and *N. affinis*, yet no neotanaidomorphans were collected from the 16 Hebble box cores.

This result appears to support Thistle *et al.*'s (1985) contention, but the issue requires additional consideration. If neotanaids live on the sediment surface, the bow wave of the box corer could blow them out of the sample, making their apparent abundance artificially low. Williams and Grassle (personal communication) report that box corers of this type catch neotanaids in other environments although less efficiently than do *in situ* samplers (e.g., Alvin corers). It seems safe to conclude that neotanaids are rare at the Hebble site, but before this fact can be used to lend strong support to Thistle *et al.*'s (1985) ideas, the relative abundance of neotanaids at similar sites where the hydrodynamic regime is more typical of the abyss will need to be determined and quantitatively compared to that of the Hebble site.

Thistle *et al.*'s (1985) last point was that the tanaids were primarily infaunal and tube dwelling and thus may be able to escape the adverse effects of the benthic storms by sheltering in the sediment. They pointed to the dominance of the Leptognathiidae (90%) in their samples, noting reports that these are tube or burrow dwellers in shallow water and that they have morphological adaptations to tube dwelling (e.g., short, stout pereopods, Johnson, Attramadal, 1982; see also Sars, 1899; Greve, 1967).

The tanaid fauna of the Hebble box consists of three families, all previously known from the deep sea (Hansen, 1913; Lang, 1968; Sieg, 1977): Anarthruridae (2 species, 8 individuals), Pseudotanaididae (2 species, 51 individuals), and the Leptognathiidae (16 species, 102 individuals; Tab. 2). Leptognathiidae again dominate the fauna (63%), and *Leptognathia cf. uncinata* is

Table 2

A list of the tanaid species collected during 1982.

Pseudotanaididae	
<i>Pseudotanaid</i> sp. 101	
<i>Pseudotanaid</i> sp. 102	
Leptognathiidae	
<i>Leptognathia</i> sp. 201	
<i>Leptognathia</i> sp. 202	
<i>Leptognathia</i> sp. 203	
<i>Leptognathia</i> sp. 204	
<i>Leptognathia</i> sp. 205	
<i>Leptognathia</i> sp. 206	
<i>Leptognathia</i> sp. 207	(cf. <i>uncinata</i>)
<i>Leptognathia</i> sp. 208	(? n. gen.)
<i>Leptognathia</i> sp. 209	(<i>parabrevimanu</i>)
<i>Leptognathia</i> sp. 210	
<i>Leptognathia</i> sp. 211	
<i>Leptognathia</i> sp. 212	
<i>Leptognathia</i> sp. 213	
<i>Leptognathia</i> sp. 214	
<i>Leptognathia</i> sp. 220	
<i>Leptognathia</i> sp. 221	
Anarthruridae	
<i>Paranarthrura</i> sp. 401	(cf. <i>insignis</i>)
<i>Anarthruopsis</i> sp. 402	

the dominant leptognathiid in the Hebble box as it was in Thistle *et al.*'s (1985) samples.

Thistle *et al.*'s (1985) inference that leptognathiids in this region are tube or burrow dwellers is strengthened by our discovery of individuals of two *Leptognathia* species in tubes. In addition, 10 of the 16 leptognathiid species were found deeper than 3 cm in the sediment. We also found a species of *Anarthruopsis* in a tube, suggesting that this genus may also be tube dwelling. Finally, we were able to compare the abundance and composition of the tanaid fauna of a portion of the Hebble site over time. Data from the four box cores taken in 1983 were compared to those from the four taken in 1982 (Fig. 2). The abundances and species compositions of the two faunas were nearly identical (Tab. 3 and 4, respectively). Current-meter records show that a storm occurred just before the 1983 samples were taken (the storm was active from 7 June through 9 June 1983, Weatherly, Kelley, 1985; box cores were taken on 8, 10, 11, and 13 June 1983). Further, Hollister and McCave (1984) report that several cm of surficial sediment were eroded and deposited in the interval between the 1982 and 1983 samplings. The similarities of the tanaids despite the dramatic (for the deep sea) environmental perturbations suggests that the fauna of this region is relatively stable over time and is adapted to withstand benthic storms without major change.

Table 3

1982 and 1983 tanaid abundances in box cores taken within subareas 1, 5, 9, and 13 of the Hebble box.

Subarea	# tanaids	
	1982	1983
1	3	1
5	5	5
9	11	6
13	8	11
Total	27	23
\bar{x}	6.75	5.75

Table 4

Pooled species composition of the 4 box cores from 1982 and 1983 taken within subareas 1, 5, 9, and 13 of the Hebble box.

	1982	1983
<i>Pseudotanaid</i> sp. 101	9	5
<i>Pseudotanaid</i> sp. 102	3	0
<i>Leptognathia</i> sp. 201	1	1
<i>Leptognathia</i> sp. 202	2	2
<i>Leptognathia</i> sp. 204	1	1
<i>Leptognathia</i> sp. 205	2	4
<i>Leptognathia</i> sp. 207	2	2
<i>Leptognathia</i> sp. 208	2	1
<i>Leptognathia</i> sp. 209	0	1
<i>Leptognathia</i> sp. 211	2	0
<i>Leptognathia</i> sp. 218	0	1
<i>Leptognathia</i> sp. 219	0	1
<i>Leptognathia</i> sp. 220	1	0
<i>Leptognathia</i> sp. 221	0	1
<i>Leptognathia</i> damaged manca	1	0
<i>Leptognathia</i> damaged adult	1	0
<i>Paranarthrura</i> sp. 401	0	3
	27	23

CONCLUSIONS

The abundance of tanaids in the Hebble box is conspicuously higher than that of other locations in hydrodynamically tranquil regions at similar depths. Bacterial standing stocks are also elevated, so the tanaid abundances may be explicable, at least in part, by increased food available to this primarily deposit-feeding fauna. A plausible explanation for the bacterial densities is the increased growth rates that bacteria are likely to achieve when the seabed is disturbed by benthic storms. The composition of the tanaid fauna is atypical for the deep sea. Surface-living neotanaids are rare or absent. The bulk of the tanaid fauna (Leptognathiidae, Anarthruridae) appears to be infaunal tube or burrow dwellers. This shift in composition appears to be a consequence of the latter's ability to shelter from the effects of storms.

An unresolved question is whether this fauna is a typical deep-sea fauna that has had its surface-living members swept away by the benthic storms leaving a

group of species that were preadapted by their use of the seabed to be successful in these circumstances or whether it is one that has evolved from typical deep-sea species in response to conditions in this region. The answer to this question appears to require comparative biogeographic studies at the species level.

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