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Nematode assemblages from submarine caves in Hong Kong

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Nematode assemblages from sediments of two submarine caves in subtropical Hong Kong waters were investigated, and compared with those from other local sublittoral sediments. A total of 48 putative nematode species from 44 genera and 18 families were identified from the caves. Species richness of the cave nematode assemblages lay between those of adjacent sandy control sites and muddy control sites. Species diversity of the cave assemblages was much lower than those of the sandy control sites but was comparable with those of local muddy sediment. Nematodes at Conic Island Cave were dominated by non-selective deposit feeders, while at Steep Island Cave most nematodes were omnivores/predators. This is in contrast with the more even composition of trophic guilds at the nearby non-cave sites. Multivariate analyses revealed no clear demarcation of community structure among the cave, non-cave and wreck nematode assemblages, indicating no nematode species association endemic to the cave sediment. Sediment characteristics and water depth are suggested as fundamental in determining nematode community structure and trophic composition in the area investigated. Submarine cave sediment provided a sheltered habitat with limited food resources favourable for non-selective deposit feeders and omnivores/predators.

Keywords: nematodes; species diversity; feeding groups; community structure; submarine cave Hong Kong

Introduction

Ecological studies on marine caves have been geographically restricted to the Mediterranean Sea. These studies either concerned planktonic gradients and fluxes of particulate material within a submarine cave (Garrabou and Flos 1995; Airoldi and Cinelli 1996) or suspension-feeder-dominated epifaunal communities (Harmelin 1997; Corriero et al. 2000; Martí et al. 2004a, b). Macro- and meiobenthic infauna in submarine cave sediments were largely ignored over recent decades. Two recent works on submarine cave meiofauna in the Mediterranean Sea (Gallo D'Addabbo et al. 2001) and Australia (Boesgaard and Kristensen 2001) were both taxonomic studies on tardigrades.

Free-living marine nematodes have been intensively investigated in shallow sublittoral soft-bottom habitats. Previous studies suggested that sediment composition was one of the key determinants of nematode community structure (Heip et al. 1985; Boucher 1990; Coull 1999). None of these studies, however, described the nematode assemblages occurring in submarine cave sediments. Marine caves may provide a more sheltered habitat with lower energy than the nearby non-cave sublittoral because, inside the cave, waves and currents may be greatly reduced resulting in a different sediment structure inside the caves compared with that outside. On the other hand, food composition for cave meiofauna may be different

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to that of the non-cave shallow water sublittoral due to light limitation and consequently inhibition of the growth of benthic microalgae; and food availability is supposed to be largely dependant on phytoplankton deposition from the water exchange with the outside (Olafsson & Elmgren 1997). This study aims to (1) characterize the nematode assemblages from two submarine caves in terms of species diversity, community structure and trophic composition, by comparing with assemblages from control sediments from the non-cave sublittoral, and identif nematode species endemic to marine caves, if any, (2) detect any spatial trends along the longitudinal axis of the cave from the entrance to the back, (3) understand environmental factors which may cause endemism or a spatial gradient.

Materials and methods

From 19 to 26 October 2002, sediment samples were taken by SCUBA divers from five pre-determined shallow sublittoral localities in south-eastern Hong Kong waters $(22^{\circ}12'20''-28'47''N, 114^{\circ}15'10''-23'22''E)$ at Conic Island Cave (CI), Steep Island Cave (SI), Telegraph Bay (TB), Long Kei Wan (Z) and Hoi Ha Wan Wreck (W) and non-wreck (Q) sites (Table 1). The two caves are both roughly wedge-shaped but differ in length (31 m for CI and 6 m for SI) from the entrance to the back of cave (Figure 1). They are completely submerged with openings between -11.8 m C.D. and -18.2 m Chart Datum for CI and between -9.3 m Chart Datum and -12.4 m Chart Datum for SI, respectively. The other sites with varied sediment characteristics served as sandy control (Z), mixed sediment control (TB), wreck control (W) and muddy control (Q) respectively in accordance with their granulometric compositions (Table 1). At Conic Island Cave, four stations (CI-A, CI-B, CI-C and CI-D, from the mouth to the back of the cave respectively) were sampled while at Steep Island Cave, sampling was only carried out at station B (Figure 1).

Three sediment samples from each station were obtained for benthic copepods and nematodes studies. Each meiofauna sample was about 200 cm³ and subsampling was conducted at the laboratory when necessary using a 50 cm³ plastic corer. Nematodes were sorted, identified under a compound microscope to putative species and enumerated (Platt and Warwick 1983, 1988; Warwick et al. 1998).

Classification of nematodes into four feeding groups was based on the buccal morphology as first described by Wieser (1953). Groups 1A and 1B represent selective and non-selective deposit feeders that consume bacteria and detritus, respectively. Group 2A comprises epigrowth feeders that scrape algae off the surface of sand grains or pierce single algal cells. Group 2B is omnivores/predators. This scheme has been criticized for over-simplification (Jensen 1987; Moens and Vincx 1997) but has been widely used and adopted.

The Primer statistical package (Clarke and Gorley 2001) was used for both multivariate analyses and species diversity estimation. Nematode species data (ind/ 50 cm^3) were used to calculate the diversity as the number of species per sample (S), the Shannon-Wiener index *H'* (calculated using Naperian logarithms), Pielou's evenness *J'* and rarefaction index ES₍₅₀₎ which allow for a comparison of the number of species in samples that have been standardized for abundance (Hurlbert 1971; Simberloff 1972). Diversity patterns were visualized by *k*-dominance curves (Lambshead et al. 1983). The nematode community structure was analyzed by CLUSTER and non-metric MDS based on the log(x+1) transformed abundance



Figure 1. Lateral sections of the submarine caves surveyed, showing the layout of meiofaunal sampling stations at Steep Island Cave (SI-B) and Conic Island Cave (CI-A, CI-B, CI-C and CI-D) (after Hodgson, PP).

data using Bray-Curtis similarities (Clarke and Warwick 1994). The species contributing most to dissimilarity between assemblages and to similarities within a cave assemblage were investigated by a similarity-percentages procedure (SIMPER). The BIOENV procedure was used to define suites of abiotic variables that best explain the nematode community structures.

Results

Species composition, density and diversity

A total of 48 putative nematode species from 44 genera and 18 families was identified from the two caves during this survey (Table 2). Considerable differences, in terms of species composition, were observed between the two caves and between the outermost and the inner assemblages at Conic Island Cave. Linhomoeidae (29.0%), Xyalidae (19.7%) and Chromadoridae (17.0%) shared the dominance in density at Conic Island Cave whereas, at Steep Island Cave, Oncholaimidae (64.7%) and Desmodoridae (10.9%) ranked as the top two. SIMPER analyses identified those species to be contributing most to the average similarity within a group of samples

| | Ĕ | | | | | | | | |
|---------------------------|-------------------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| | | ТВ | SI-B | CI-A | CI-B | CI-C | CI-D | W | Q |
| Latitude | 22°2 [*] 203"N | 22°12′20″N | 22°16′24″N | 22°21′54″N | 22°21′54″N | 22°21′54″N | 22°21′54″N | 22°28′47″N | 22°23′47″N |
| Longitude | 114°⊉⁄208″E | 114°15′10″E | 114°18′49″E | 114°23′22″E | 114°23′22″E | 114°23′22″E | 114°23′22″E | 114°20'08"E | 114°20'08"E |
| Distance into cave (m) | Nontecave | Non-cave | 3 | 0 | 8.5 | 20 | 28 | Wreck | Non-cave |
| Water depth (m) | 13.7 | 9 | 10 | 19.1 | 17 | 15 | 12.3 | 12 | 16 |
| Water temp (°C) | 26 | 26 | 26 | 25 | 24 | 22 | 22 | 25 | 25 |
| Salinity (‰) | 35 | N/A | N/A | 34 | 34 | 33.5 | 33.5 | 32 | 33 |
| pН | 8.11 | N/A | N/A | 7.88 | 7.96 | 8.00 | 7.96 | 7.77 | 8.16 |
| DO (mg. 1^{-1}) | 10.22 | N/A | N/A | N/A | N/A | 9.57 | 8.62 | 7.32 | 8.74 |
| %gravel | 0.709 | 5.640 | 14.219 | 22.577 | 17.799 | 33.718 | 15.965 | N/A | 6.998 |
| %sand | 95.971 | 63.571 | 79.844 | 38.152 | 25.255 | 28.992 | 52.690 | N/A | 18.634 |
| %silt/clay | 3.320 | 30.789 | 5.937 | 39.270 | 56.946 | 37.290 | 31.344 | N/A | 74.368 |
| %organic | 1.908 | N/A | N/A | N/A | N/A | 6.769 | 5.826 | N/A | 10.557 |

Table 1. Environmental wariables measured at the study sites.

Note: N/A, not available.

| | Relative abu | No. of | No. of | | |
|------------------|--------------|--------|--------|---------|--|
| Family | CI | SI | genera | species | |
| Linhomoeidae | 29.0 | 10.3 | 5 | 5 | |
| Xyalidae | 19.7 | 3.3 | 3 | 4 | |
| Chromadoridae | 17.0 | 3.7 | 7 | 10 | |
| Comesomatidae | 13.1 | 3.8 | 3 | 3 | |
| Monhysteridae | 7.1 | 0.0 | 5 | 5 | |
| Oncholaimidae | 4.5 | 64.7 | 5 | 5 | |
| Axonolaimidae | 4.0 | 2.1 | 2 | 2 | |
| Cyatholaimidae | 1.9 | 0.0 | 1 | 1 | |
| Trefusiidae | 1.4 | 0.0 | 3 | 3 | |
| Oxystominidae | 0.7 | 0.0 | 1 | 1 | |
| Diplopeltidae | 0.4 | 0.0 | 1 | 1 | |
| Desmodoridae | 0.3 | 10.9 | 1 | 1 | |
| Sphaerolaimidae | 0.3 | 0.0 | 1 | 1 | |
| Enchelidiidae | 0.2 | 0.0 | 1 | 1 | |
| Aegialoalaimidae | 0.1 | 0.3 | 2 | 2 | |
| Selachinematidae | 0.0 | 0.5 | 1 | 1 | |
| Anticomidae | 0.0 | 0.3 | 1 | 1 | |
| Leptolaimidae | 0.0 | 0.1 | 1 | 1 | |
| TOTAL | 100.0 | 100.0 | 44 | 48 | |

Table 2. Relative abundance of the nematode families collected at Conic Island Cave (CI) and Steep Island Cave (SI) during the survey, listed in descending order of importance at CI.

obtained from each cave station and thus the species association typical of their respective assemblage (Table 3). At Conic Island Cave, species typifying internal cave assemblages (CI-B, CI-C and CI-D) belonged to the genera *Terschellingia*, *Sabatieria*, *Daptonema*, *Paramonohystera* and *Parodontophora*, all non-selective deposit feeders (feeding group 1B). This is in contrast with the cave entrance assemblage CI-A where an epigrowth feeder (2A) *Chromadorita* sp. gained the highest density (30 ind/50 cm³). At Steep Island Cave, the nematode assemblage was dominated by the omnivore/predator (2B) *Metoncholaimus* sp. with a particularly high density (231 ind/50 cm³), followed by the selective-deposit feeder (1A) *Spirinia* sp.1 (35 ind/50 cm³).

Nematode density was also inconsistent between the two caves (Table 4). Conic Island Cave had a low density ranging from 9 to 33 ind/50 cm³ which was comparable to the density at the wreck site W (15 ind/50 cm³), but was an order of magnitude lower than those of the sandy control Z (120 ind/50 cm³) and mixed control TB (247 ind/50 cm³). Ironically nematode density in Steep Island Cave was the highest among the investigated locations (364 ind/50 cm³). Nematode fauna was sparse (6 ind/50 cm³) at Hoi Ha Wan Q station, plausibly because of oxygen depletion as a result of the extremely high organic content in the sediment (% organic=10.557).

Nematode assemblages from both caves have in common low species diversity (Table 4). Numbers of species per station (5–25 species) were much lower than the adjacent control assemblages Z and TB (49–56 species) but higher than the muddy W and Q (3–7 species) at Hoi Ha Wan. α -diversity of the cave nematodes calculated on

| | Feeding group | Average density (ind/50 cm ³) | Contribution (%) | Cumulative (%) |
|-----------------------|------------------|--|---------------------|-------------------|
| SI-B | | | | |
| Metoncholaimus sp. | 2 B | 230.50 | 26.18 | 26.18 |
| Spirinia sp.1 | 1A | 35.00 | 18.20 | 44.38 |
| Chromadorita sp. | 2A | 10.50 | 10.35 | 54.73 |
| Terschellingia sp.2 | 1 B | 29.50 | 9.10 | 63.83 |
| Parodontophora marina | 1 B | 6.5 | 7.43 | 71.26 |
| CI-A | | | | |
| <i>Sabatieria</i> sp. | 1 B | 3.00 | 33.33 | 33.33 |
| Chromadorita sp. | 2A | 30.33 | 33.33 | 66.67 |
| Daptonema sp.1 | 1 B | 2.67 | 33.33 | 100 |
| CI-B | | | | |
| Daptonema sp.1 | 1 B | 6.00 | 69.90 | 69.90 |
| Terschellingia sp.2 | 1 B | 2.50 | 30.10 | 100 |
| CI-C | | | | |
| <i>Sabatieria</i> sp. | 1 B | 6.83 | 27.54 | 27.54 |
| Terschellingia sp.2 | 1 B | 6.33 | 20.03 | 47.57 |
| Terschellingia sp.1 | 1 B | 1.67 | 19.18 | 66.75 |
| Parodontophora marina | 1 B | 1.83 | 18.02 | 84.77 |
| Daptonema sp.1 | 1 B | 6.67 | 8.03 | 92.80 |
| CI-D | | | | |
| Terschellingia sp.2 | 1 B | 6.17 | 22.77 | 22.77 |
| Paramonohystera sp. | 1 B | 4.33 | 18.29 | 41.06 |
| Daptonema sp.2 | 1 B | 4.17 | 12.39 | 53.45 |
| Parodontophora marina | 1 B | 3.83 | 9.06 | 62.51 |
| Sabatieria sp. | 1 B | 1.33 | 6.96 | 69.47 |

Table 3. Result from SIMPER analysis, showing the top few species which contributed the most (rank percentage) to average similarity for each species association.

Note: Analysis based on log (x+1) transformed abundance data using Bray-Curtis similarity.

Shannon-Wiener and rarefaction indices (H'=1.3-2.2; $ES_{(50)}=4-10$) are comparable to that of the wreck assemblage W (H'=1.7; $ES_{(50)}=7$) but much lower than those of the non-cave stations Z and TB (H'=3.3-3.4; $ES_{(50)}=24$). Low evenness (J'=0.5) was observed only at Steep Island Cave (SI-B) and the entrance station A at Conic Island Cave (CI-A) which could be attributed to high dominance of *Metoncholaimus* sp. and *Chromadorita* sp. in the respective assemblages (Table 3). Diversity visualized by

Table 4. Average values (n=3) of nematode density $(ind/50 \text{ cm}^3)$ and species diversity indices obtained at the study sites.

| | Z | ТВ | SI-B | CI-A | CI-B | CI-C | CI-D | W | Q |
|--------------|-----|-----|------|------|------|------|------|-----|-----|
| N | 247 | 120 | 364 | 33 | 12 | 9 | 28 | 15 | 6 |
| S | 49 | 56 | 25 | 10 | 5 | 6 | 15 | 7 | 3 |
| $H'(\log_e)$ | 3.3 | 3.4 | 1.6 | 1.3 | 1.3 | 1.7 | 2.2 | 1.7 | 1.0 |
| J' | 0.9 | 0.8 | 0.5 | 0.5 | 0.8 | 0.9 | 0.8 | 0.9 | 0.9 |
| ES (50) | 24 | 24 | 10 | 8 | 4 | 6 | 11 | 7 | 3 |



Figure 2. *K*-dominance curves to compare diversity among sampling sites. Each curve represented an average value of three replicates.

k-dominance curves revealed a similar pattern with the curve of CI falling between the lower curves of Z and TB and upper curves of muddy control W and Q (Figure 2). The curve of Steep Island Cave (SI-B) was highly elevated at the first position of species rank, interacting with the curves of muddy control assemblages, again, owing to the high dominance of *Metoncholaimus* sp.

A decreasing tendency from the entrance into the back of the cave for either density or species diversity of nematode assemblages was not clear at Conic Island Cave (Table 4). Although the greatest density did occur at the outermost station A (N=33 ind/50 cm³), lowest density was observed at station C (N=9 ind/50 cm³) rather than the innermost station D (N=28 ind/50 cm³). At the Conic Island Cave diversity was the highest at the innermost station D (S=15, H'=2.2, ES₍₅₀₎=11) among the four stations sampled.

Trophic composition

The relative abundance of the four nematode feeding groups is illustrated in Figure 3. The trophic structures of the two cave nematode assemblages have a common feature of predominance by one of the feeding types and thus give rise to a low trophic diversity. This was clearly in contrast with the more even distribution of the four feeding types for non-cave assemblages Z and TB. The two caves also have a different trophic structure if both of the mid-way "B" assemblages were compared. Steep Island Cave "B" assemblage (SI-B) was dominated by the feeding-type predator/omnivore 2B (66% of all nematodes) whilst at Conic Island Cave, the "B" assemblage (CI-B) was dominated by non-selective deposit feeder 1B (79% of all nematodes). The trophic structure of the three internal cave assemblages at the Conic Island Cave (CI-B, CI-C and CI-D) all resembled the muddy Hoi Ha Wan wreck and



Figure 3. Mean relative abundance (n=3) of nematode feeding groups at the study sites.

non-wreck assemblages (W and Q) in that total abundance consisted mainly of nonselective deposit feeders (>60% of all nematodes). Nematode assemblage at the mouth of Conic Island Cave (CI-A) was dominated by epigrowth feeder 2A (76% of all nematodes), in contrast with the inner cave sites.

If the distribution of nematode feeding groups among species were taken into account (Figure 4), a common feature identified for cave nematodes, regardless of different caves or different zones within the cave, was that the species number of non-selective deposit feeders ranked first among the four feeding types. This pattern was in agreement with the muddy control assemblages at Hoi Ha Wan but rather different from the adjacent control assemblages Z and TB in which the number of epigrowth feeding species ranked first.

Community structure

Hierarchical clustering and MDS ordination (Figure 5) divided all nematode assemblages into four different groups at a similarity threshold of 25%. This



Figure 4. The distribution of nematode feeding groups among species at the study sites. Each bar represents an average of three replicates.

grouping indicated no clear demarcation between cave and non-cave nematode assemblages but rather reflected a gradient of particle size from the sandy Long Kei Wan site Z to the muddy Hoi Ha Wan sites W and Q. The two caves and the Telegraph Bay site with more or less mixed sediment characters lie in between. The four stations from Conic Island Cave were more similar to those of the wreck and non-wreck muddy controls at Hoi Ha Wan but far more separated from the adjacent sandy control site Z. The assemblage from Steep Island Cave showed greater similarity with that of the adjacent Telegraph Bay site.

Species making the major contribution to dissimilarities of nematode community structure among cave and non-cave assemblages were identified by a SIMPER analysis (Table 5). Species characterizing Long Kei Wan site Z, i.e. *Epacanthion* sp., *Setosabatieria* sp.1 and *Trichotheristus* sp. and *Pselionema* sp. were all absent from the adjacent Conic Island Cave as well as the other sites which have more or less mixed or muddy sediment compositions. These species could be considered typical of hydrodynamically exposed shallow sublittoral habitat like Long Kei Wan Z with a sandy substratum, low sediment organic content and oxygen-saturated water



Figure 5. Hierarchical clustering and MDS ordination of nematode species assemblages, using group average linkage of Bray-Curtis similarity calculated on log (x+1) transformed species abundance data (averaged across three replicates). The groups of sites separated at approximately 25% similarity threshold on the dendrogram are super-imposed on the ordination plot.

(Table 1). Notably, there were few species which were totally absent from the other non-cave sites. Nematode species which occurred in the two caves were also present at other control sites, although in different density (Table 5). The two cave nematode assemblages shared more common species with the Telegraph Bay site.

| Species | Feeding group | Ζ | TB | SI | CI | Q | W |
|------------------------|---------------|----|----|-----|----|---|---|
| Catanema sp. | 1A | 0 | 8 | 1 | 0 | 0 | 0 |
| Halalaimus sp. | 1A | 5 | 11 | 0 | 1 | 0 | 0 |
| Paranticoma sp. | 1A | 11 | 0 | 0 | 0 | 0 | 1 |
| Pselionema sp | 1A | 8 | 0 | 0 | 0 | 0 | 0 |
| Spirinia sp.1 | 1A | 0 | 1 | 35 | 0 | 0 | 0 |
| Odontophora sp. | 1B | 13 | 0 | 1 | 0 | 0 | 0 |
| Setosabatieria sp.1 | 1B | 22 | 0 | 0 | 0 | 0 | 0 |
| Terschellingia sp.1 | 1B | 0 | 8 | 2 | 1 | 0 | 0 |
| Terschellingia sp.2 | 1B | 0 | 2 | 30 | 4 | 0 | 0 |
| Terschellingia sp.3 | 1B | 0 | 2 | 0 | 0 | 0 | 3 |
| Trichotheristus sp. | 1B | 19 | 0 | 0 | 0 | 0 | 0 |
| Dorylaimopsis rabalasi | 2A | 1 | 15 | 0 | 1 | 0 | 0 |
| Dorylaimopsis sp.2 | 2A | 0 | 9 | 0 | 0 | 0 | 0 |
| Paracanthonchus sp. | 2A | 11 | 0 | 0 | 1 | 0 | 0 |
| Paracomesoma sp. | 2A | 11 | 2 | 1 | 1 | 0 | 0 |
| Epacanthion sp. | 2B | 33 | 0 | 0 | 0 | 0 | 0 |
| Metoncholaimus sp. | 2B | 0 | 1 | 231 | 0 | 0 | 0 |
| Pomponema sp. | 2B | 10 | 0 | 0 | 0 | 0 | 0 |
| Viscosia sp. | 2B | 16 | 6 | 0 | 1 | 0 | 1 |

Table 5. Result from the SIMPER analysis showing the average abundance of the species $(ind/50 \text{ cm}^3)$ contributing to a cumulative dissimilarity of 25% between sampling sites, based on log(x+1) transformed abundance data using Bray-Curtis similarity.

The two caves have rather different sediment granulometry (Table 1). At Steep Island Cave, sand was the dominant component, with an average sand content of 80%, whereas at Conic Island Cave, the fine component (<63 µm) tended to gain dominance, although internal variation along the cave was also marked. The Pearson product-moment correlation analysis did not reveal high correlation (ρ >0.95) between abiotic variables, and thus all the selected variables (except those not available for all the stations) were used in the BIOENV analysis (Table 6). Among the individual factors, sediment granulometric composition (%gravel, %silt-clay and %sand) were most important in explaining the observed pattern of community structure whereas distance from cave entrance, the only variable directly related to cave habitat gained less importance. A combination of percentage contents of gravel and sand as well as water depth best explained the nematode community structure (maximum correlation ρ =0.824).

Discussion

Comparison of species composition and community structure between the two caves and between cave and non-cave control assemblages failed to identify any species associations of nematodes endemic to the cave habitat. Most of the species typical of cave sediments are also found in the non-cave assemblages, although with different relative abundance (Tables 3 and 5). Species dominant at Steep Island Cave, *Metoncholaimus* sp., *Spirinia* sp. 1 and *Terschelligia* sp. 2, were also present at the adjacent Telegraph Bay control site; the epigrowth feeder *Chromadorita* sp., a species Table 6. Spearman correlation between environmental variables and nematode community structure using BIOENV in PRIMER, showing the coefficient ρ for individual variables as well as for a combination of several variables which yielded the best match (maximum correlation) between biotic and abiotic (Bray-Curtis) similarity matrices.

| Variables | ρ |
|--|--------------------------------------|
| %orave] | 0.665 |
| %silt/clay | 0.603 |
| %sand | 0.540 |
| Distance into cave (m) | 0.447 |
| Water depth (m) | 0.119 |
| Water temperature (°C) | -0.014 |
| Max. correlation Variable combination | 0.824 %gravel, %sand, water depth |

Note: Log(x+1) transformation was applied to both the biotic and abiotic data. Site W was not included in the analysis.

typical of both Steep Island Cave and the entrance station of Conic Island Cave was also identified from Telegraph Bay; *Parodontophora marina* Zhang, 1991 occurred at most of the cave stations, and has been documented as a widespread species occurring in different habitats both in temperate and subtropical Chinese Waters (Zhou and Zhang 2003). The multivariate analyses indicate that the differences between the cave and non-cave assemblages are not well defined and tend to overlap (Figure 5). This seems to correspond with the observation made for oligochaetes (Clitellata) from the caves survey, where all taxa are in the family Tubificidae and all have been reported from non-cave Hong Kong sediments before (C. Erséus personal communication). Lack of an endemic species association possibly reflected the topographic nature of the two caves, namely short longitudinal distance and a tapering morphology from the entrance to the back (Figure 1). This allows for more water and sediment exchange and hence more faunistic similarity with the adjacent open area.

A decrease in species richness, biomass and coverage of epibenthic organisms from the outermost to the innermost part of the cave has been reported as a common feature worldwide in submarine caves (see Martí 2004b and the references therein). This pattern seems not marked for the nematode assemblages at Conic Island Cave. Among the four assemblages compared from the mouth to the back of the cave, the density of the innermost assemblage was not the lowest and species richness and diversity were, unexpectedly, the highest (Table 4). This is likely to be related to a higher sand component (52.7%, Table 1) at this site. BIOENV analysis suggested that sediment structure was the most important factor which, together with water depth, best explained the difference in species composition and community structure of nematode assemblages from the two caves and between cave and non-cave environments (Table 6). This is in correspondence with the previous perception that granulometric composition of the substrate and water depth are often the structuring factors in governing the distribution of nematode species in sublittoral habitats (Boucher 1990; Muthumbi et al. 2004).

Differences in grain size composition driven by local hydrodynamic conditions give rise to concomitant differences in food resources and sediment chemistry. Within two Mediterranean caves, light irradiance was the only factor that clearly diminished from the entrance to the innermost zone determining the zonation of algal-dominated communities but not that of animal-dominated communities (Martí 2004b). Light availability may also be important for determining food resources and therefore feeding composition of the cave nematodes. At the entrance of Conic Island Cave, the assemblage dominated by epigrowth feeders 2A was in clear contrast to the internal assemblages dominated by non-selective deposit feeders 1B, reflecting a difference in food species composition which may be related to a decreasing gradient of light level from the entrance into the cave. In Mediterranean submarine caves, epifaunal assemblages were dominated by suspension feeders (Martí et al. 2004a, b). This, on the other hand, suggested that caves can have food input even if light is limited and phytoplankton sedimentation can be the main food resource (Olafsson & Elmgren 1997). This will give rise to a deposit-feeder dominated nematode assemblage as observed at the internal sites of the Conic Island Cave. The extent of food availability, however, can be varied by topography and hydrodynamic condition of respective cave and hitherto water exchange. Steep Island Cave differed from Conic Island Cave in topography and hydrodynamic conditions, being much shorter in length and having sediment with a larger sand component. These differences may result in differences both in species composition and trophic structure of nematode assemblages in the two caves. At Steep Island Cave, the oncholaimid nematode *Metoncholaimus* sp. was the dominant species. Its dominance gives rise to low diversity and a feeding composition predominated by omnivores/predators (2B) at this site. Oncholaimid species have been described as either scavengers (Jensen 1987) or facultative predators (Moens and Vincx 1997). Several closely related oncholaimid species were considered to ingest water with highly enriched dissolved organic matter under decaying diatom and bacterial mats (Meyers et al. 1970; Lopez et al. 1979) or take advantage of the high numbers of moribund or dead animals killed by the sulphide at the fringes of hydrothermal vents (Thiermann et al. 1997). They appear to have a high colonization capability in subtropical areas and can be considered as opportunistic dominants in a sequence of nematode colonization (Bell 1983). The high dominance of Metoncholaimus sp. at Steep Island Cave may be also related to their feeding strategy and opportunistic trait which allowed them to explore more efficiently the limited food resource in the relatively unpredictable submarine cave habitat.

Irrespective of different caves or different zones within a cave, common features perceived from the submarine cave nematode assemblages are the low species diversity (H'=1.3-2.2, $ES_{(50)}=4-11$) and uneven distribution of feeding groups as compared with the adjacent non-cave sediment. Taxonomic information available and sampling effort are, as yet insufficient to make confident assertion about endemics and spatial pattern of nematode species in these subtropical marine caves.

Acknowledgements

This work is part of the expedition on Hong Kong marine cave jointly organized by the Swire Institute of Marine Science, University of Hong Kong and the Natural History Museum of London. Thanks go to the organizers, members of the diving team and the staff at SWIMS.

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