

Taxonomic and functional biodiversity variations of meiobenthic and nematode assemblages across an extreme environment: a study case in a Blue Hole cave

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Abstract

In this paper we have explored for the first time the biodiversity pattern of the meiobenthic assemblage in a Blue Hole of the Maldivian Archipelago. The cave is characterised by a marked change of the chemical water parameters below 50 m of depth, with a relevant increase in hydrogen sulfide, carbon dioxide, and sulfates (H₂S, CO₂ and SO₄²⁻). Thus, three stations were selected above and two below the chemo-thermocline in order to test the possible effects of the chemical variations on the meiobenthos. The difficulty of adaptation to these environmental conditions is clearly suggested by the presence of only a few dominant meiobenthic taxa in the bottom of the cave. However, meiobenthic organisms seemed more resistant than macrobenthos, which disappeared completely below this depth. The nematode assemblage was mainly represented by Xyalidae, Desmodoridae, Comesomatidae and Linhomoeidae. A high level of confinement of nematode genera at the different depths has been documented. In the upper part, their structure and biodiversity were comparable to those of the Maldivian subtidal habitats characterised by fine coralline sediments, while a notable dominance was detected in the bottom. The Blue Hole features also influenced the functional traits of the nematode assemblage with a documented increasing number of general opportunists and decrease of Maturity Index. The dominance of non-selective deposit feeders supports the hypothesis of a high amount of organic matter accumulated on the sea bottom of the cave.

Keywords: *Meiobenthos, free-living nematodes, extreme habitats, Blue Hole, Maldives*

Introduction

Nematodes are among the most abundant and diverse benthic metazoan groups (Balsamo et al. 2010, 2012; Appeltans et al. 2012). They are present in all geographical regions from shallow-water habitats to the deep sea and from soft bottoms to hard substrates (Heip et al. 1985). Many species have revealed remarkable abilities to withstand stress and adverse conditions including anoxic and sulphidic sediments (see for review Giere 2009).

Despite their importance, still little is known about their biodiversity and ecology in extreme habitats (Vanreusel et al. 2010a), and especially in tropical regions (Semprucci & Balsamo 2012).

The Maldivian archipelago shows some of the most characteristic and sizeable worldwide atoll systems (Risk & Sluka 2000), with numerous coral-reef

islands made up exclusively of carbonate sediments. Despite the great variety of habitats in Maldives and the increasing level of their exploration and conservation strategies, data on meiobenthic assemblages are largely focused on shallow subtidal waters (Semprucci et al. 2010b, 2011, 2013, 2014).

Among the most distinctive environments in Maldives, there is the Blue Hole of Faanu Madugau (Ari Atoll) (Colantoni et al. 2003). Blue holes are karst structures that were initially described from the Atlantic Ocean (Bahamian islands and banks), while they are poorly documented in the Indian Ocean in which only a cave is reported (Colantoni et al. 2003). They are water-filled vertical openings in the carbonate rock that may exhibit several morphologies and origins (Myroie et al. 1995). Furthermore, they generally show clear gradients of seawater chemistry establishing

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high levels of toxic sulphide and anoxic conditions at the bottom (Bottrell et al. 1991). In the Maldivian Blue Hole, an evident chemo-thermocline was revealed at about -50 m. Below this depth, the well-represented and abundant macrofaunal assemblage covering the walls in the upper part of the cave disappeared, showing only evidence of chemo-litho-autotrophic assemblages (Colantoni et al. 2003). However, meiobenthos and, in particular, nematodes, due to their ability to survive during environmental perturbations, may persist even in conditions that normally reduce or eliminate the macrofaunal organisms (Hendelberg & Jensen 1993). Therefore, Blue Hole sediments could be a model for testing the effects of extreme conditions on the meiobenthic assemblages. In particular, the strong biochemical gradients (e.g. high hydrogen sulfide (H_2S) and carbon dioxide (CO_2) concentrations and food limitations) may lead to a change in the assemblage abundance and to the success of nematode genera characterised by specific trophic or lifestyle modes (Vanreusel et al. 2010a).

Only preliminary information on the meiobenthos of the Maldivian Blue Hole was reported in Sandulli et al. (2006). In this study, we explore for the first time the structure, biodiversity and functional traits of the meiobenthic and nematode assemblages inhabiting the bottom of the Maldivian Blue Hole (-77 m) and three stations at different depths (from -17 to -37 m) of the walls facing the cave. In particular, the following question is addressed: are there changes of structure, biodiversity and functional traits of the meiobenthic and nematode assemblages in response to the chemo-thermocline variations?

Material and methods

Study area

The Maldives are a large N–S elongated isolated carbonate platform southwest of the southern tip of

India. It consists of a double row of atolls extending from the Kolumadulu Atoll in the South to the Miladummadulu Atoll in the North (Figure 1a, b). It comprises 21 atolls composed of more than 1200 reef islands originating from the mid- to late Holocene and arising steeply from abyssal and bathyal depths of 2000 m.

The Blue Hole investigated in this study is located at Faanu Madugau (Ari Atoll) (Figure 1c). It opens at the bottom of a large depression at a depth of about 30 m. The opening has a diameter of about 70 m and shows vertical or steep sloping walls, while the bottom is covered by fine, loose carbonate sediments at a depth of 70–85 m (Colantoni et al. 2003).

Sample collection and processing

Sampling operations were carried out in April 2004. Sediment samples were collected through 2.8-cm-diameter hand corers (6.2 cm^2) by scuba diving at four different depths in the Blue Hole cave (Figure 1c). In detail, three stations (St. 1, 2, 3; depths: -17 , -32 , -37 m) were located above the level of the chemo-thermocline detected by Colantoni et al. (2003), while two stations were located below, at the bottom of the cave (St. A and B; depth: -77).

Three samples for quantitative analysis of the meiobenthos and one for sediment analysis were collected at each station during this survey. Concerning the water column data of the Blue Hole, those collected by Colantoni et al. (2003) were used.

Sediment samples for grain size analysis were washed with distilled water and dried in an oven at 80°C for 24–36 h, and successively sieved for 20 min through a series of sieves from 841 to $74 \mu\text{m}$ mesh size. The sediment fractions were then weighed using an analytical balance, and weights were converted to percentages. Sediment fractions were

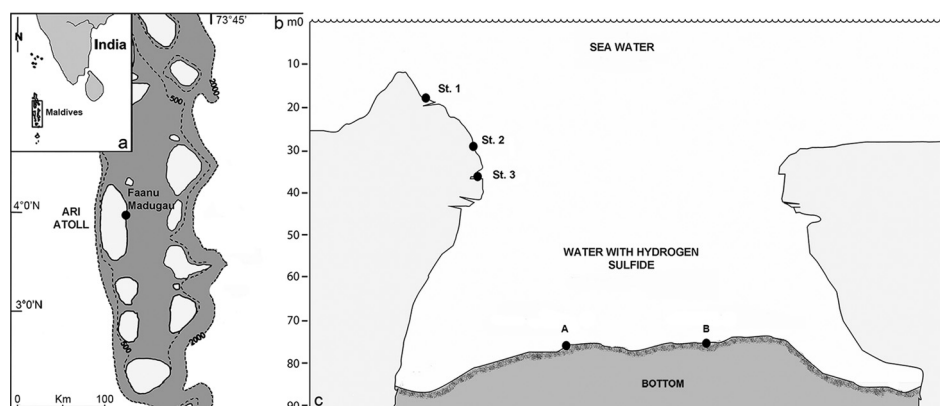


Figure 1. a, Geographic position of study area; b, location of the Blue Hole of Faanu Madugau (Ari Atoll, Maldives); c, schematic section of the Blue Hole of Faanu Madugau (modified from Colantoni et al. 2003).

defined according to Wentworth size classes (Buchanan 1984).

The meiobenthic samples were preserved with 5% formalin-seawater and stained with Rose Bengal. Meiobenthos was extracted from sediment by centrifugation with LUDOX AM solution (McIntyre & Warwick 1984), retained on a 43- μ m sieve and, finally, the organisms were sorted and counted under a stereomicroscope. One hundred nematodes were randomly extracted from each replicate and mounted on permanent slides (Seinhorst 1959). The nematode specimens were identified (at the genus level) under a 100 \times oil immersion objective using a Leica DM 2500 microscope and the NeMys online identification key (Steyaert et al. 2005).

In general, species functional groups share morphological traits that are thought or known to be related to important ecological roles (Chalcraft & Reserats 2003). Among the several functional features used for nematodes, the buccal cavity structures and life history strategies are the most widely applied in the ecological surveys (see for review Semprucci & Balsamo 2012). In particular, the nematode specimens were assigned to trophic guilds according to Wieser's scheme (1953): selective (1A) and non-selective (1B) deposit feeders; epistrate feeders (2A); predators/omnivores (2B). The Maturity Index (MI, Bongers 1990; Bongers et al. 1991) was calculated as the weighted average of the individual coloniser-persistent (c-p) values. The contribution of each life-strategy group (c-p 1 to 5) to the total nematode assemblage was then calculated. MI has been proposed as detection tool for possible natural or anthropogenic stressful conditions (Bongers 1990).

Data analysis

Cluster analysis derived from Bray-Curtis similarity matrices was used to view differences in the structures of meiobenthic and nematode assemblages between the stations located at the different depths (on square-root transformed data), and analysis of similarities (ANOSIM) was performed to check the significance of the differences. Similarity Percentages (SIMPER) test (cut-off of 50%) was used to define the contribution of each taxon to the total dissimilarity. Shannon-Wiener's diversity (H') and evenness (J) indices (\log_2) were calculated to give an estimation of the biodiversity in the nematode assemblage. Multivariate analyses as well as the calculation of the Shannon-Wiener (H') and Pielou (J) indices were performed using the software package Plymouth Routines In Multivariate Ecological Research (PRIMER v. 5, Clarke & Gorley 2001; Clarke & Warwick 2001). Possible variations of the univariate faunal parameters were checked using

analysis of variance (ANOVA). Tukey's multiple-comparison tests were applied when significant differences ($p < 0.05$) were detected (SPSS v. 17 program).

Results

Data on environmental variables showed clear depth-related variations (Table I). The greater difference of redox potential (Eh), pH and temperature were detected between the surface water and the water below a depth of 40–50 m. In detail, the Eh decreased along the water column with ranges between –250 mV (at the bottom of the cave) and 175 mV (at 0 m). The same trend was followed by the pH (range: 7.1–8.2) and temperature (25–31°C, Table I). In Figure 2, the concentrations of the main ions of the seawater are reported. Their vertical profile revealed lower variations of cations than anions, especially within the upper 50 m. In particular, chlorine, almost constant within the first 50 m, progressively decreased downward, reaching the minimum level at –78 m. Sulphate showed a strong change at a depth of 60 m with the highest values detected at the bottom (4000 mg/L). Bicarbonate ion, fluctuating more along the vertical profile, ranged from 127 to 154 mg/L (Figure 2b). As reported in Figure 2, a similar pattern was exhibited by CO₂ and H₂S. The sediment grain size extended from fine sands (St. 1, 2, 3) to muddy sediments (St. A and B).

Twelve major meiobenthic taxa were identified: Ciliophora, Platyhelminthes, Nematoda, Gastrotricha, Kinorhyncha, Annelida, Ostracoda, Copepoda (adults and larvae), Tanaidacea, Amphipoda, Halacaroida and Tardigrada. Total meiobenthic abundance ranged between 71 ± 42 ind. 10 cm⁻² (St. B bottom) and 6776 ± 1986 ind. 10 cm⁻² (St. 1) (Figure 3). The dominant taxon was Nematoda, with an average percentage of 85% (range: 77–91%). The next most abundant taxa

Table I. Variations of the temperature, pH and Eh parameters in depth gradient of the cave.

Depth (m)	Water column parameters		
	Redox Potential, Eh (mV)	pH	T (°C)
0	175.0	8.2	31.0
-10	160.0	8.3	30.0
-20	150.0	8.3	29.8
-30	145.0	8.2	29.5
-40	0.0	8.1	29.8
-50	-90.0	7.7	29.0
-60	-200.0	7.6	28.0
-70	-180.0	7.1	26.7
-80	-250.0	7.4	25.0

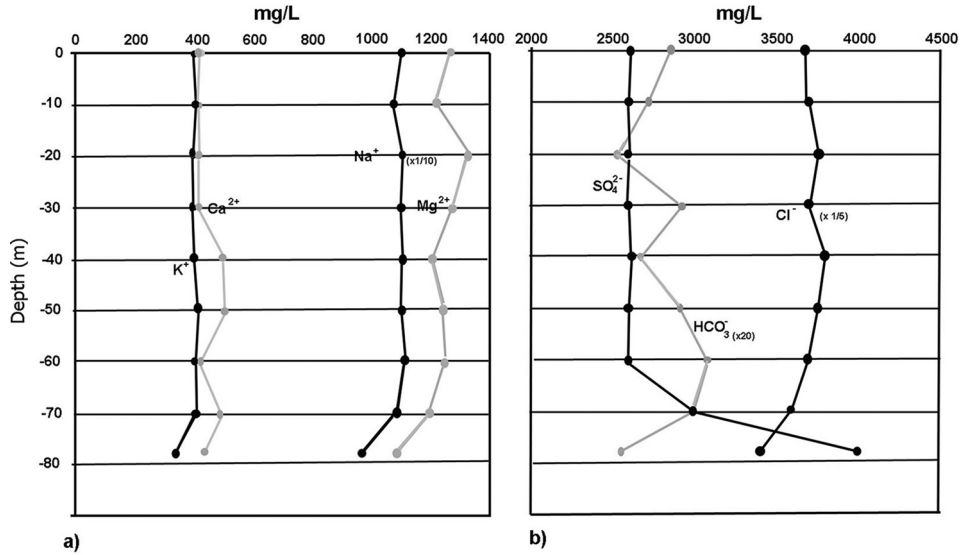


Figure 2. Trends of (a) Potassium (K^+), Calcium (Ca^{2+}), Sodium (Na^+), Magnesium (Mg^{2+}) cations and (b) Sulfate (SO_4^{2-}), Chloride (Cl^-), Bicarbonate (HCO_3^-) ions in the seawater of the cave (modified from Colantoni et al. 2003).

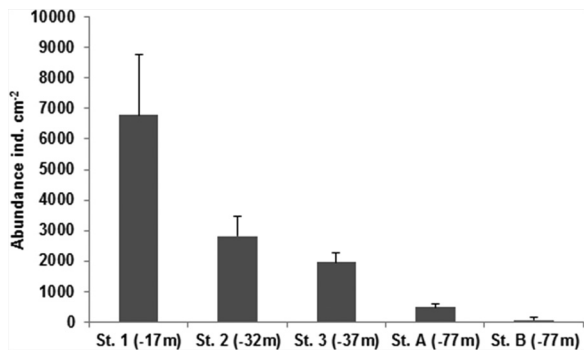


Figure 3. Meiofaunal abundance at all stations above and below the chemo-thermocline.

were Copepoda (adults and larvae) (on average: 7%; range: 7–17%), followed by Annelida (3%; 0–5%), Kinorhyncha (1%; 0–3%) and Platyhelminthes (1%; 0–1%) (Figure 4).

Significant differences in the meiofaunal assemblage were detected among the depths (ANOSIM, $R = 0.95$, $P = 0.001$) as highlighted also by the cluster and SIMPER analyses (Table II; Figure 5A). In detail, SIMPER showed a marked decrease of all meiobenthic taxa between the stations above and below the chemo-thermocline, as well as of the richness that ranged between 12 taxa in the St. 1 and 3 taxa in the stations of the bottom. In particular, the taxa present at the bottom were mainly Nematoda, followed by Copepoda (adults and larvae) and Ostracoda (SIMPER 50%).

A total of 63 nematode genera, belonging to 27 families, were recorded. Desmodoridae (10 genera),

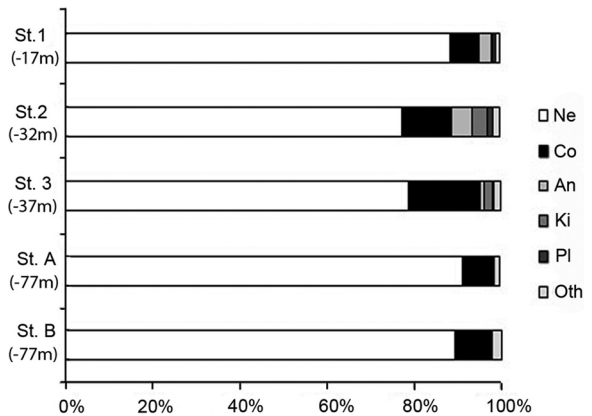


Figure 4. Composition of the meiofaunal assemblage at all stations above and below the chemo-thermocline. Nematoda (Ne), Copepoda (Co), Annelida (An), Kinorhyncha (Ki), Platyhelminthes (Pl) and others (Oth).

Chromadoridae (7), Cyatholaimidae (5) and Comesomatidae (4) represented the richest families. However, the most abundant families were Xyalidae (37.4%), Desmodoridae (13.9%), Comesomatidae (11.7%) and Linhomoeidae (5.1%), while the most abundant genera were *Daptonema* (36.7%), *Dorylaimopsis* (6.0%), *Sabateria* (5.1%), *Anoplostoma* (4.8%) and *Terschellingia* (4.2%).

The highest number of genera, 37, was found at St. 2, while only six and four genera were recorded at St. A and B, respectively. H' and J values were the lowest at St. A and B of the bottom and highest at St. 2 (ANOVA $p < 0.001$; Tukey's test $p < 0.01$) (Table III). J was significantly higher also at St. 1.

Table II. Average dissimilarities calculated on meiobenthic and nematode assemblages with SIMPER tests with 50% cut-off. Data were square-root transformed.

Groups	Average dissimilarity	
	Meiobenthos	Nematodes
St. 1 versus St. 2	21%	80%
St. 1 versus St. 3	33%	76%
St. 2 versus St. 3	19%	59%
St. 1 versus St. A	67%	84%
St. 2 versus St. A	59%	90%
St. 3 versus St. A	53%	89%
St. 1 versus St. B	86%	82%
St. 2 versus St. B	81%	100%
St. 3 versus St. B	76%	96%
St. A versus St. B	49%	42%

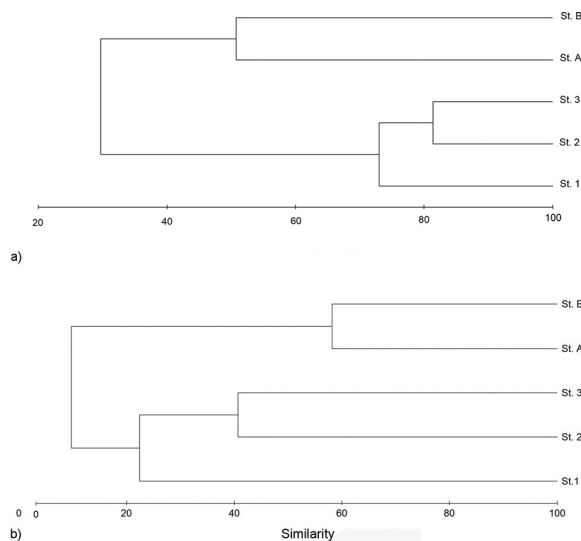


Figure 5. Cluster analyses of the (a) meiobenthic and (b) nematode assemblages (both square-root transformed). The sampling grouping was based on Bray-Curtis clustering.

The trophic group 1B was dominant, followed by 2A and 1A (Table III). In detail, 2A significantly decreased at St. 3, A and B (ANOVA $p < 0.001$; Tukey's test $p < 0.001$). The trophic groups 1A and 1B showed significant differences, decreasing and increasing at the bottom stations, respectively (ANOVA $p < 0.001$; Tukey's test $p < 0.001$). The trophic group 2B was significantly more abundant at St. 3 (ANOVA $p < 0.001$; Tukey's test $p < 0.001$).

MI ranged between 2.1 ± 0.0 at the bottom and 2.8 ± 0.1 at St. 2, revealing a significant decrease at the bottom stations (ANOVA $p < 0.001$; Tukey's test $p < 0.05$). All the c-p classes were represented. The class c-p2 was the most abundant, followed by c-p3, c-p 4, c-p 5 and c-p1 (Table III). In particular, c-p2 was significantly different in the station comparison and higher in the bottom stations (ANOVA $p < 0.001$; Tukey's test $p < 0.05$). C-p3 was significantly more abundant at St. 2 (ANOVA $p < 0.001$; Tukey's test $p < 0.05$), whereas c-p 4 was more abundant at St. 2 and 3 (ANOVA $p < 0.001$; Tukey's test $p < 0.01$) (Table III).

A significant difference in the structure of nematode assemblages between the stations above the chemothermocline was detected (ANOSIM, $R = 0.98$, $P = 0.001$) (Figure 5B; Table II). The most abundant genera at St. 1 were *Sabateria* and *Terschellingia*, while *Dorylaimopsis* and *Richtersia* were more abundant at St. 2, and *Anoplostoma* and *Metachromadora* were more abundant at St. 3 (SIMPER, 50%). The genus *Daptonema*, followed by *Halichoanolaimus*, *Eubostrichus* and *Onyx*, mainly characterised the bottom substrata (SIMPER, 50%).

Discussion

As documented by Colantoni et al. (2003), the surface waters of the Faanu Madugau cave appeared to

Table III. Faunal parameters of the nematode assemblage (Shannon-Wiener index, H' ; Pielou index, J ; Maturity index, MI; c-p and trophic guild percentages) detected in the stations of the cave.

Station	St. 1 (-17 m)	St. 2 (-32 m)	St. 3 (-37 m)	St. A (-77 m)	St. B (-77 m)
H'	3.3 ± 0.2	4.5 ± 0.3	3.8 ± 0.1	0.5 ± 0.0	0.9 ± 0.1
J'	0.9 ± 0.1	0.9 ± 0.0	0.8 ± 0.0	0.2 ± 0.0	0.5 ± 0.0
MI	2.4 ± 0.0	2.8 ± 0.1	2.4 ± 0.2	2.1 ± 0.0	2.2 ± 0.0
c-p1	0.0 ± 0.0	0.0 ± 0.0	1.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
c-p2	59.2 ± 2.5	34.9 ± 4.8	67.3 ± 17.0	95.9 ± 0.0	83.3 ± 1.3
c-p3	39.7 ± 1.4	48.9 ± 3.6	19.8 ± 13.3	3.1 ± 0.2	16.7 ± 1.7
c-p4	1.1 ± 1.1	15.1 ± 0.6	11.9 ± 3.4	1.0 ± 0.2	0.0 ± 0.0
c-p5	0.0 ± 0.0	1.1 ± 1.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
1A	15.0 ± 5.5	18.5 ± 2.9	13.8 ± 0.8	2.1 ± 0.1	5.6 ± 1.0
1B	33.4 ± 6.9	18.5 ± 3.7	36.6 ± 1.5	93.8 ± 0.2	83.3 ± 1.3
2A	42.3 ± 8.7	40.2 ± 4.7	18.8 ± 7.5	4.1 ± 0.4	0.0 ± 0.0
2B	9.5 ± 5.0	22.7 ± 0.7	30.8 ± 6.8	0.0 ± 0.0	11.1 ± 1.0

be equilibrated with the atmospheric CO₂, the content of which decreased down to 40 m in depth. Below this level, its values significantly increased along with the concentration of H₂S. Accordingly, the most prominent vertical variation occurred at – 50 m depth with significantly high values of the above-cited dissolved volatile compounds as well as a notable reduction of the pH and temperature. Given the simultaneous enrichment of H₂S and SO₄²⁻ along the depth gradient, a deeper origin of the H₂S has been inferred by Colantoni et al. (2003) and, as suggested for the Bahamian Blue Holes, a strong bacterial activity on the organic matter accumulated on the floor of the Faanu Madugau cave has been supposed.

The change of the chemo-thermocline referred to by Colantoni et al. (2003) might have led to a decrease in abundance and diversity of the assemblages in this cave, as in other extreme habitats (Dinet et al. 1988; Flint et al. 2006; Gooday et al. 2010). The difficulty of adaptation of meiobenthos to these environments is clearly suggested by the presence of only few dominant taxa (Figure 4). A great dominance of nematodes, as observed in Faanu Madugau, was documented in other habitats under oxygen-depleted conditions (Fricke et al. 1989; Montagna et al. 1989; Shirayama & Ohta 1990; Kamenev et al. 1993; Cook et al. 2000). Giere et al. (1991) have suggested that anoxic and sulphidic chemoclines may supply meiobenthos with a good food source and a habitat with low competition and predation pressure, but only if species are able to tolerate the toxic effects of sulphide. Generally, copepods are known in the literature to be among the meiobenthic groups most sensitive to low oxygen concentrations (see review by Wetzel et al. 2001; De Troch et al. 2013); however, Grego et al. (2013) documented in a field study in the Northern Adriatic Sea that, after 9 days of anoxia, one fourth of the harpacticoid copepods survived. A longer duration of anoxia was necessary to remove almost all the individuals. These findings could explain the presence of copepods even under the extreme conditions of the Blue Hole bottom, and prove that some species of harpacticoids may be less sensitive than generally stated in the literature (Murrell & Fleeger 1989; Wetzel et al. 2001). The existence of a thermocline may greatly influence meiobenthos as well. Indeed, the different temperature and also energy availability may have a marked effect on the structure of the meiobenthic assemblage (see Giere 2009 for review and Vanreusel et al. 1995; Debenham et al. 2004).

The nematode assemblage biodiversity was higher above the chemocline level with values overall

comparable to those reported in other areas of the Maldives (Semprucci et al. 2010b, 2011, 2013, 2014). The dominant families and genera found in this study were typical of muds or fine sands worldwide (Heip et al. 1985; Soetaert & Heip 1995; De Leonardis et al. 2008; Semprucci et al. 2010a; Muthumbi et al. 2011). Indeed, the stations above the chemocline were mainly characterised by *Sabatieria*, *Terschellingia* and *Dorylaimopsis*, genera well known as abundant from shallow subtidal to silty and muddy deep-sea sediments characterised by organic enrichment and even oxygen depletion (e.g., Vitiello 1974; Muthumbi et al. 2004; Schratzberger et al. 2006; Liu et al. 2007; De Leonardis et al. 2008; Gollner et al. 2010; Sajan et al. 2010; Vanreusel et al. 2010a; Guilini et al. 2012).

Among the genera present in the upper stations is *Richtersia*, generally reported as associated with sediments with a high percentage of gravel (Vanreusel et al. 2010a). However, little detailed information is available on the biology of this genus (Vanreusel et al. 2010a), and its presence has been well documented in the subtidal sediments of Maldivian islands where the intricate physical micro-structure of the biogenic substrata seems to favour sediment-dwelling taxa like this one (Semprucci et al. 2013, 2014).

Bongers (1990) and Bongers et al. (1991) proposed a classification of nematodes into colonisers (comparable to r-strategists, characterised by high tolerance to disturbance) and persisters (k-strategist, with low colonisation ability and tolerance to disturbance). According to this classification, it is possible to note a higher abundance of c-p3 and c-p4 (k-strategists), along with higher MI values in the upper stations. This may show moderate or even unstressed conditions in this part of the Blue Hole cave (Moreno et al. 2011). The analysis of the MI revealed decreasing values and gradually more stressed conditions with increasing depth. This is mainly due to the marked dominance of the c-p2 genus *Daptonema* (83–94% of the total nematode fauna) that is well recognised as an opportunistic genus related to several types of disturbances (e.g., Mahmoudi et al. 2005; Boufahja et al. 2011). *Daptonema* is also well documented in subtidal muddy sediments rich in hydrogen sulphide (Shirayama & Ohta 1990; Liu et al. 2007; Guilini et al. 2012). The presence of another thiobiotic representative taxon was also recorded at the bottom of the hole, namely the genus *Eubostriachus* (Stilbonematinae). The species of this sub-family usually appear with a multi- or single-layered coat made of ectosymbiotic bacteria, which cover the

body cuticle, while some other species have filamentous ectocommensals covering their entire body surface, giving the animal a bushy appearance. Stilbonematinae species live in sheltered intertidal and subtidal marine, sulphide-rich sediments, where they aggregate around the Redox Potential Discontinuity (RPD) layer depth (Riemann et al. 2003; Ott et al. 2005; Raes et al. 2007; Semprucci et al. 2010b; Vanreusel et al. 2010b). *Eubostrichus*, even if detected also in the shallow subtidal habitats of this archipelago (Semprucci et al. 2010b, 2011), was one of the most abundant or exclusive genera of the Blue Hole seabed. However, an important level of dissimilarity was detected also between the two stations at the bottom. This might reflect the patchy distribution of the food source or predation and competition pressures, which on a small scale may have an important spatial impact (Pinckney & Sandulli 1990; Sandulli & Pinckney 1999; Raes et al. 2007).

The trophic guilds were overall equally distributed above the 50-m depth, indicating a good heterogeneity of food resources in the sediments at the stations considered. Epistrate feeders were the dominant component, especially in the upper two stations, in line with the trophic structure of the nematode assemblage in coral sediments worldwide and with the reduction of the diatoms in the deeper part of the cave (Raes & Vanreusel 2006; Raes et al. 2007; Semprucci et al. 2010b, 2011, 2013).

Non-selective deposit feeders (1B) accounted for more than 80% of the nematode assemblage at the bottom stations: their relevance is consistent with the presence of large amounts of organic detritus (Alongi 1986). The decrease of selective deposit-feeder nematodes (1A) did not seem to follow the supposed increase of the bacterial activity at the bottom (Colantoni et al. 2003). However, Semprucci et al. (2010a) also reported no significant correlations between bacteria amount and 1A nematode presence, suggesting possible limits in trophic classification, especially of this group.

Conclusions

The Blue Hole of Faanu Madugau (Ari Atoll) is among the most distinctive habitats in the Maldivian archipelago. Given its extreme conditions, this Blue Hole has been studied to evaluate the effects of strong biochemical gradients on the meiobenthic assemblages. Indeed, the meiobenthos seemed highly affected by changes of the chemocline and thermocline both in abundance and biodiversity. The structure and biodiversity of nematode assemblage in the upper part of the cave was comparable to

those of the Maldivian shallow subtidal habitats. Instead, the bottom sediments were strongly dominated by *Daptonema*, a tolerant genus. Blue Hole features also influenced the functional traits of the nematode assemblage, with a documented increasing number of general opportunists and deposit feeders. The dominance of the latter trophic guild supports the hypothesis of a high amount of organic matter accumulated on the sea bottom of the cave.

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