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First insights into the community structure of the deep-sea benthic metazoan meiofauna off southwest Java (eastern Indian Ocean)

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Abstract. Meiofauna, an integral part of the benthic ecosystem, is poorly studied in deeper Indonesian waters. As deep-sea meiofaunal data in the waters off southwest Java is currently deficient, this study aims to provide baseline information by reporting the abundance and diversity of the metazoan meiobenthos (40–1,000 µm) for the first time. Samples were collected with a mega multiple corer at three stations at depths of 1,231 m, 1,239 m and 2,086 m during the South Java Deep-Sea Biodiversity Expedition 2018 (SJADES 2018). A total of 70,168 individuals from 19 taxa were identified. Nematoda was consistently the most dominant taxon, followed by Nauplii and Harpacticoida. Compared to other areas of similar depths which have been studied in the Indian Ocean, we found the highest meiofaunal abundance at our sites. Food availability might be high at our sites due to annual rainfall over Indonesia and the close proximity of our sampling stations to land, leading to greater nutrient run-off benefiting phytoplankton growth which eventually increased the amount of organic matter to the sea floor. Interestingly, we found high numbers of Kinorhyncha and Tardigrada, making them the fourth or fifth most abundant taxon at our sites. The high abundances of Kinorhyncha at Stations MC29 (15.7 ± 2.5 ind/10cm^2) and MC54 (22.8 ± 6.6 ind/10cm^2) could be attributed to the finer sediments at these stations, which might be more suited to the kinorhynch mode of locomotion. Coarser sediment at MC41 might favour Tardigrada (7.9 ± 4.3 ind/10cm^2) in terms of providing more microhabitats and accumulating food particles.

Key words. meiobenthos, Indonesia, abundance, diversity, SJADES 2018

INTRODUCTION

Meiofauna, size-classified as being smaller than 500–1,000 µm but larger than 44–63 µm (Giere, 2009), plays important roles in maintaining a healthy benthic ecosystem (Schratzberger & Ingels, 2018). Through a range of biological activities such as ingestion and excretion, bioturbation, burrow construction, and extracellular polymeric substances (EPS) production, meiofauna influences a variety of ecosystem processes (Schratzberger & Ingels, 2018). They affect biogeochemical cycles by enhancing mineralisation of organic matter for nutrient recycling (Findlay & Tenore, 1982; Alkemade et al., 1992; Coull, 1999; Rysgaard et al., 2000; Nascimento et al., 2012; Bonaglia et al., 2014), microbial breakdown of waste compounds and the removal of contaminants (Monserrat et al., 2003; Schratzberger & Ingels, 2018). Meiofauna is also able to alter sediment properties such as increasing oxygen and solute transport in sediment (Aller & Aller, 1992; Löhr & Kennedy, 2015) and contribute towards sediment stabilisation (de Deckere et al., 2001; Hubas et al., 2010). By feeding on organic matter, grazing on microbiota, as well as being food sources themselves, meiofauna sustains energy flow between trophic levels and maintains stable food web dynamics (Alheit & Scheibel, 1982; Nelson & Coull, 1989; Coull, 1990; Coull et al., 1995; Montagna, 1995; De Troch et al., 2005). Additionally, the meiobenthos have the potential to be excellent biological indicators to monitor and assess disturbances in the marine environment (Moore & Bett, 1989; Monserrat et al., 2003; Nipper & Carr, 2003; Mirto & Danovaro, 2004; Gyedu-Ababio & Baird, 2006; Moreno et al., 2008, 2011; Semprucci et al., 2015; Zeppilli et al., 2015).

Meiofauna can be found at all depths, but there are fewer meiofaunal studies in the deep sea because it is far more labour-intensive and expensive to sample them compared to those inhabiting shallow waters (Danovaro et al., 2010; Ramirez-Llodra et al., 2010; Rosli et al., 2018). Indeed, our knowledge of the deep-sea meiobenthos in Indonesian waters is still rudimentary. Most studies have focused on the coastal, shallow waters (Uneputty & Frid, 1998; Susetiono, 1999; Noortiningsih et al., 2008; Zeppilli & Danovaro, 2009; Neusser et al., 2011; Yusal, 2011; Jörger et al., 2012; Ostmann et al., 2012; Mahatma, 2013; Long et al., 2014; Pusceddu et al., 2014b; Suryani et al., 2014; Akbar et al., 2015; Sofani & Muzaki, 2015; Leasi et al., 2016; Swasta, 2018; Yusal et al., 2019a, b), including investigating meiofaunal

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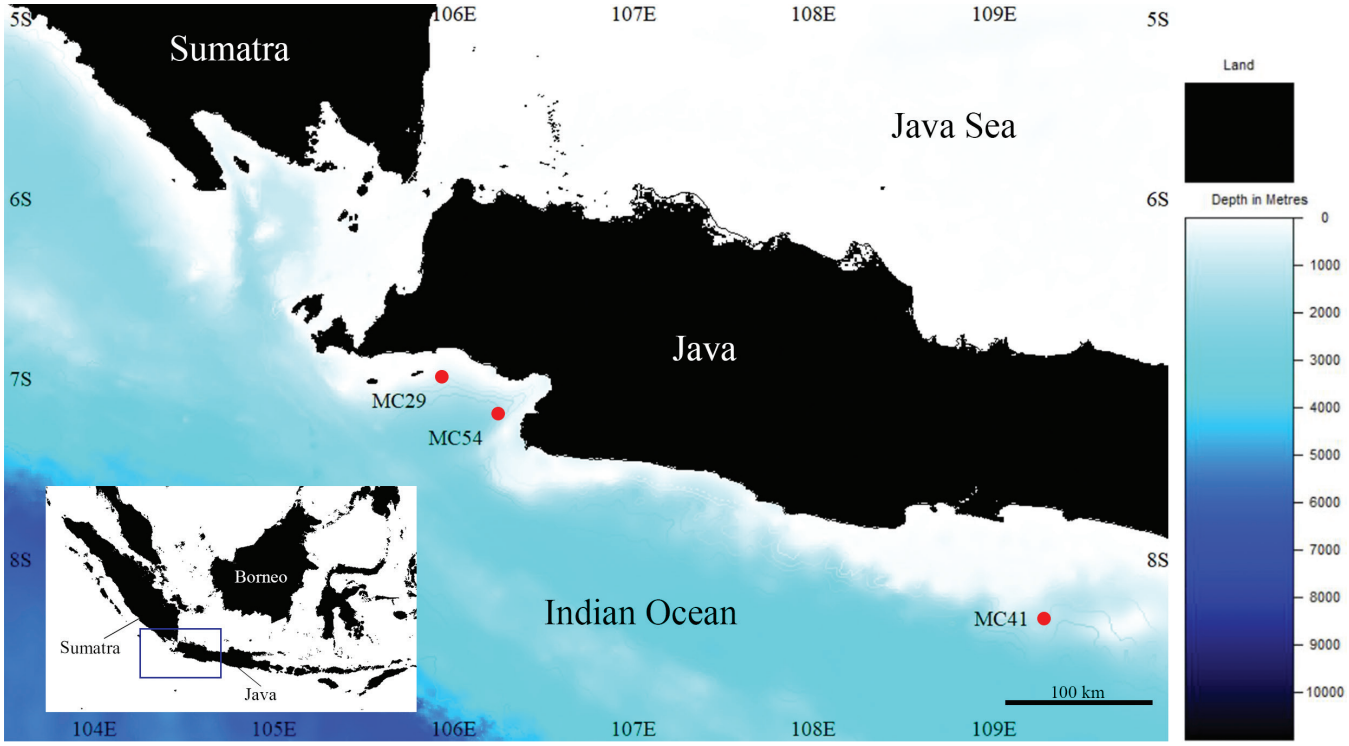

Fig. 1. Location of sampling stations (MC29, MC41 and MC54) in the waters off southwest Java, eastern Indian Ocean. This map was generated from GEBCO (General Bathymetric Chart of the Oceans), Sheet G.08 compiled by R.L. Fisher of the Scripps Institution of Oceanography and extracted from the GEBCO Digital Atlas published by the British Oceanographic Data Centre on behalf of the IOC and IHO, 2003.

interactions with plastic debris (Uneputty & Evans, 1997) and metal pollution (Gwyther et al., 2009). However, it is crucial to also turn a spotlight on benthic biodiversity and health of deep-sea environments (>200 m depth), since human activities (e.g., resource exploitation, oil spills and pollution) can negatively affect the deep sea (Pusceddu et al., 2014a; Baguley et al., 2015). Furthermore, the deep-sea environment supports high benthic diversity (Snelgrove, 1999; Brandt et al., 2007) and the loss of benthic animals could result in an exponential decline in deep-sea ecosystem functioning, affecting overall biogeochemical processes of the ocean (Danovaro et al., 2008). Thus, it is very essential to study and improve our current knowledge of the ocean's benthic biodiversity, but less than 0.01% of the deep sea has been studied in-depth (reviewed in Ramirez-Llodra et al., 2010). To date, there are only two published papers on meiofauna from deeper Indonesian waters. De Wilde et al. (1989) sampled a range of depths from 17 m to 1,430 m around the islands of Madura and Bali, in the Java Sea, Bali Sea and eastern Indian Ocean; and Susetiono et al. (2020) sampled from depths of 200 m to 4,500 m at the Senunu Canyon, Sumbawa, eastern Indian Ocean.

In an attempt to explore the deep-sea biodiversity in Indonesia's deep waters, the South Java Deep-Sea (SJADES) Biodiversity Expedition set off in March 2018 to survey the waters off southwest Java, eastern Indian Ocean. Aligning with the interests of various taxonomist participants, SJADES 2018 aimed to collect a variety of animal groups using trawls, dredges, and sediment corers within the short two-week expedition. Previously, there had been just one other deep-sea survey (200–1,000 m) in the same sampling area (Shimada & Soesilo, 2006), but their trawls collected only the larger animals. Since meiofaunal biodiversity data remain deficient, stations were set aside for meiofaunal sampling this time. In this study, we enumerate the abundance and diversity of the metazoan meiobenthos (40–1,000 µm) off southwest Java for the first time. This will serve as a good baseline to further improve our knowledge of deep-sea biodiversity in the eastern Indian Ocean.

MATERIAL AND METHODS

Study area. SJADES 2018 was conducted in the eastern Indian Ocean, within 100 km off the coast of southwest Java (Fig. 1). The seafloor at our sampling sites, being closer to land masses, is categorised by terrigenous sediment (Kolla & Kidd, 1982). Water temperatures at about 1,000 m depth are about 5°C, with a minimum temperature recorded at 4.87°C (Shimada & Soesilo, 2006). Salinity ranged from 34.67–34.88 ‰ (550–950 m) around Stations MC29 and MC54, which decreased slightly eastwards to 34.64–34.74 ‰ (850–1050 m) in the area around Station MC41 (Rochford, 1961).

Sample collection and processing. Seabed sampling was carried out onboard the research vessel BARUNA JAYA VIII from 23 March 2018 to 5 April 2018. A Mega Multiple Corer (OSIL) was deployed once at each of the three selected stations (Fig. 1). These stations were MC29, MC41 and MC54, at depths of 1,231 m, 1,239 m, and 2,086 m, respectively (Table 1). Each multiple corer deployment can collect up to 12 sediment cores (diameter = 10 cm), of which three cores were used for quantifying the meiofauna.

Table 1. Station details indicating the date of sampling, location, depth, and substratum type.

Station number	Sampling date	Sampling location	GPS coordinates	Depth (m)	Type of substratum
MC29	28 March 2018	Indian Ocean (East of Tinjil Island)	6°59.000′S, 105°55.977′E	1231	Loose, fine mud
MC41	30 March 2018	Indian Ocean (South of Cilacap)	8°19.850′S, 109°16.743′E	1239	Mud with fine sand
MC54	2 April 2018	Indian Ocean (Pelabuhanratu Bay)	7°11.487′S, 106°14.967′E	2086	Loose, fine mud

Unfortunately, apart from visual observations on the type of substratum, no abiotic data were collected during SJADES 2018 (Table 1).

Each sediment core was processed individually immediately upon the retrieval of the multiple corer. The top water was first carefully poured through a 40 µm sieve and the material retained on the sieve was processed together with the 0–2 cm sediment layer. Thereafter, the core was sectioned into the top 0–2 cm and 2–5 cm layers, which were preserved separately in 10% borax-buffered formalin onboard the vessel. In the laboratory, the sediment was first sieved through 1 mm (upper limit) and 40 µm (lower limit) sieves using fresh water. To extract the animals from the sediment, centrifugation with Ludox method, modified from de Jonge & Bouwman (1997) and Burgess (2001), was utilised. Each sample was centrifuged three times with Ludox HS-40 Colloidal silica (Sigma-Aldrich) diluted with distilled water to a density of 1.18 g/cm^3. The extracted meiofauna was then stained with Rose Bengal and preserved in 10% borax-buffered formalin. Sorting of the meiofauna to their major taxa was done under stereomicroscopes Leica MZ6 and Olympus SZX16 and, depending on the taxon, preserved in either 70–80% ethanol or 10% borax-buffered formalin.

Data analysis. All metazoan animals from 40–1,000 µm were included in our analyses. The Shannon-Wiener diversity index, calculated based on raw abundance, was used to compare diversity among the three stations. To detect significant differences in the abundances and diversity among the stations, Analysis of Variance (ANOVA) and Levene's test for homogeneity of variance were used. If significant, pair-wise differences were investigated using Tukey's HSD post hoc tests. Shapiro-Wilk test was first utilised to determine whether the abundance data and Shannon-Wiener diversity indices were normally distributed. Raw abundance data were also calculated as individuals/10cm^2 (ind/10cm^2) for comparisons across other meiofaunal studies.

To investigate the community structure at our sampled stations, cluster analysis with Type 1 Similarity Profile (SIMPROF) on fourth-root transformed, Bray-Curtis dissimilarity data was used to test for compositional dissimilarity between sites. Non-metrical dimensional scaling (nMDS) on fourth-root transformed, Bray-Curtis dissimilarity data was performed to visualise any possible groupings among the three sites based on the taxon groups and their abundances. To test for any significant variabilities among the groups, one-way Analysis of Similarities (ANOSIM) was utilised. Similarity Percentages (SIMPER) was used to determine the taxa and their respective percentage contributions toward the similarities and dissimilarities among the sites.

Calculation of Shannon-Wiener diversity indices, Shapiro-Wilk test, Levene's test, ANOVA, and Tukey's HSD post hoc tests was conducted using statistical software R version 3.6.1 (R Core Team, 2019). Cluster analyses with SIMPROF, nMDS, ANOSIM, and SIMPER were conducted in PRIMER v7 (Clarke & Gorley, 2015). All analyses were carried out at 5% significance level.

RESULTS

Abundance, diversity and community structure of metazoan meiofauna. A total of 70,168 individuals from 19 taxa was identified (Table 2; Appendix). The Nematoda was the most dominant taxon at all three stations (MC29, 77.43%; MC41, 77.26%; MC54, 76.36%), followed by Nauplii (MC29, 12.11%; MC41, 9.61%; MC54, 10.69%) and Harpacticoida (MC29, 6.63%; MC41, 8.70%; MC54, 8.30%) (Table 2). Gastropoda, as well as the typically larger animals such as Cumacea and Ophiuriodea, were found in very low numbers. Only one individual of Ophiuriodea was found in MC54, a combined total of five Cumacea in MC29 and MC41, and one Gastropoda in MC41. Every other taxon was found in all three stations.

Station MC41 had the lowest mean abundance of 563.0 ± 154.3 ind/10cm^2 (n = 3) across the three stations (Table 2). Stations MC29 and MC54 had similar mean abundances at 1249.1 ± 80.5 ind/10cm^2 and 1165.5 ± 306.1 ind/10cm^2 respectively (Table 2). Univariate analyses of ANOVA on the normally distributed data indicated no statistically significant differences among the three stations in terms of abundance (p-value = 0.10) and diversity (p-value = 0.92). From Levene's test, the variance among the three stations for abundance (p-value = 0.39) and diversity (p-value = 0.64) were also not significantly different.

Based on the taxa composition and abundance, multivariate cluster analysis showed only two clusters supported by SIMPROF, with all cores from Station MC41 and one core MC54-2 in one cluster, and all the remaining cores forming

Table 2. Average density in individuals/10cm^2 (ind/10cm^2) of benthos and the percentage (%) of each taxon collected at stations MC29, MC41, and MC54, s.e. = standard error.

Station	MC29				MC41				MC54			
	ind/10cm^2	± s.e.	%	± s.e.	ind/10cm^2	± s.e.	%	± s.e.	ind/10cm^2	± s.e.	%	± s.e.
Nematoda	969.15	75.98	77.43	1.64	436.89	121.49	77.26	1.11	907.65	263.14	76.36	2.90
Nauplii	150.54	11.05	12.11	0.95	57.08	20.15	9.61	1.03	122.57	28.87	10.69	0.60
Harpacticoida	82.29	3.48	6.63	0.43	43.80	4.97	8.70	1.88	83.95	6.14	8.30	2.20
Annelida	16.89	1.92	1.38	0.24	10.02	1.36	1.97	0.42	18.33	2.82	1.87	0.67
Kinorhyncha	15.66	2.46	1.24	0.12	2.93	1.43	0.46	0.11	22.79	6.60	1.91	0.18
Tardigrada	0.17	0.17	0.01	0.01	7.85	4.32	1.22	0.37	0.04	0.04	0.01	0.01
Ostracoda	6.66	0.68	0.54	0.08	1.36	0.42	0.24	0.01	3.57	0.83	0.31	0.03
Bivalvia	1.78	0.19	0.15	0.02	0.17	0.04	0.03	0.01	3.27	1.00	0.27	0.03
Loricifera	1.74	0.47	0.15	0.05	0.98	0.47	0.16	0.04	0.13	0.13	0.01	0.01
Gastrotricha	0.64	0.15	0.05	0.01	0.08	0.08	0.01	0.01	1.19	0.47	0.09	0.02
Amphipoda	1.36	0.68	0.11	0.06	0.13	0.13	0.02	0.02	0.17	0.08	0.01	0.01
Tantulocarida	0.93	0.11	0.08	0.01	0.42	0.22	0.06	0.03	0.04	0.04	0.01	0.01
Tanaidacea	0.55	0.30	0.05	0.02	0.13	0.07	0.03	0.01	0.76	0.34	0.06	0.02
Isopoda	0.98	0.40	0.08	0.04	0.13	0.07	0.03	0.03	0.17	0.11	0.01	0.01
Acari	0.04	0.04	0.00	0.00	0.25	0.15	0.04	0.03	0.13	0.07	0.01	0.01
Gastropoda	0.00	0.00	0.00	0.00	0.04	0.04	0.01	0.01	0.00	0.00	0.00	0.00
Cumacea	0.04	0.04	0.00	0.00	0.17	0.17	0.02	0.02	0.00	0.00	0.00	0.00
Ophiuroidea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.04	0.00	0.00
Unknown	0.08	0.08	0.01	0.01	0.59	0.08	0.12	0.03	0.68	0.40	0.07	0.04
Total	1249.51	80.46			563.03	154.25			1165.48	306.09		

the second cluster. The nMDS (Fig. 2) displayed that the three stations differed in terms of meiofaunal structure, and meiofaunal variability was high at Stations MC41 and MC54. ANOSIM tests were not statistically significant, indicating that there was no difference in species composition among the three stations. SIMPER analysis showed that meiofaunal assemblages at MC29 and MC54 were more similar to each other, when compared to MC41. At all three stations, Nematoda, Nauplii, Harpacticoida, and Annelida were the top four taxa contributing to the similarity at the site. The fifth contributing taxon for MC29 and MC54 was the Kinorhyncha, whilst at MC41, the Tardigrada. SIMPER results (at 70% cut-off) showed that Stations MC29 and MC54 had an average similarity of 85.7%, compared to MC29 with MC41 (average similarity = 77.3%), and MC41 with MC54 (average similarity = 76.7%).

Vertical Distribution. The majority of the animals (77.8%) were distributed in the upper 0–2 cm layer of the sediment (Table 3). Across all taxa, more individuals were found in the upper sediment layer than the lower 2–5 cm layer. The dominant groups found in both sediment layers were Nematoda, followed by Nauplii and Harpacticoida (Fig. 3).

DISCUSSION

Few deep-sea meiofaunal studies have been conducted in Indonesian waters and the Indian Ocean, making quantitative comparisons in the Indian Ocean very difficult. Most deep-sea meiofaunal studies were carried out in the Central Indian Ocean Basin (CIOB), possibly due to the presence of manganese nodules and probable mining prospects (Parulekar et al., 1982, 1992; Sharma et al., 1997; Ingole et al., 2000; Zeng et al., 2018), and in the northern part of the Indian Ocean (Thiel, 1966, 1979; Ansari et al., 1980; Ansari & Parulekar, 1981; Thiel et al., 1987; Parulekar et al., 1992; Pfannkuche, 1993b; Duineveld et al., 1997; Sommer & Pfannkuche, 2000). In contrast, apart from this study, only two other deep-sea meiofaunal studies in the eastern Indian Ocean have been carried out (de Wilde et al., 1989; Susetiono et al., 2020). As meiofaunal abundance

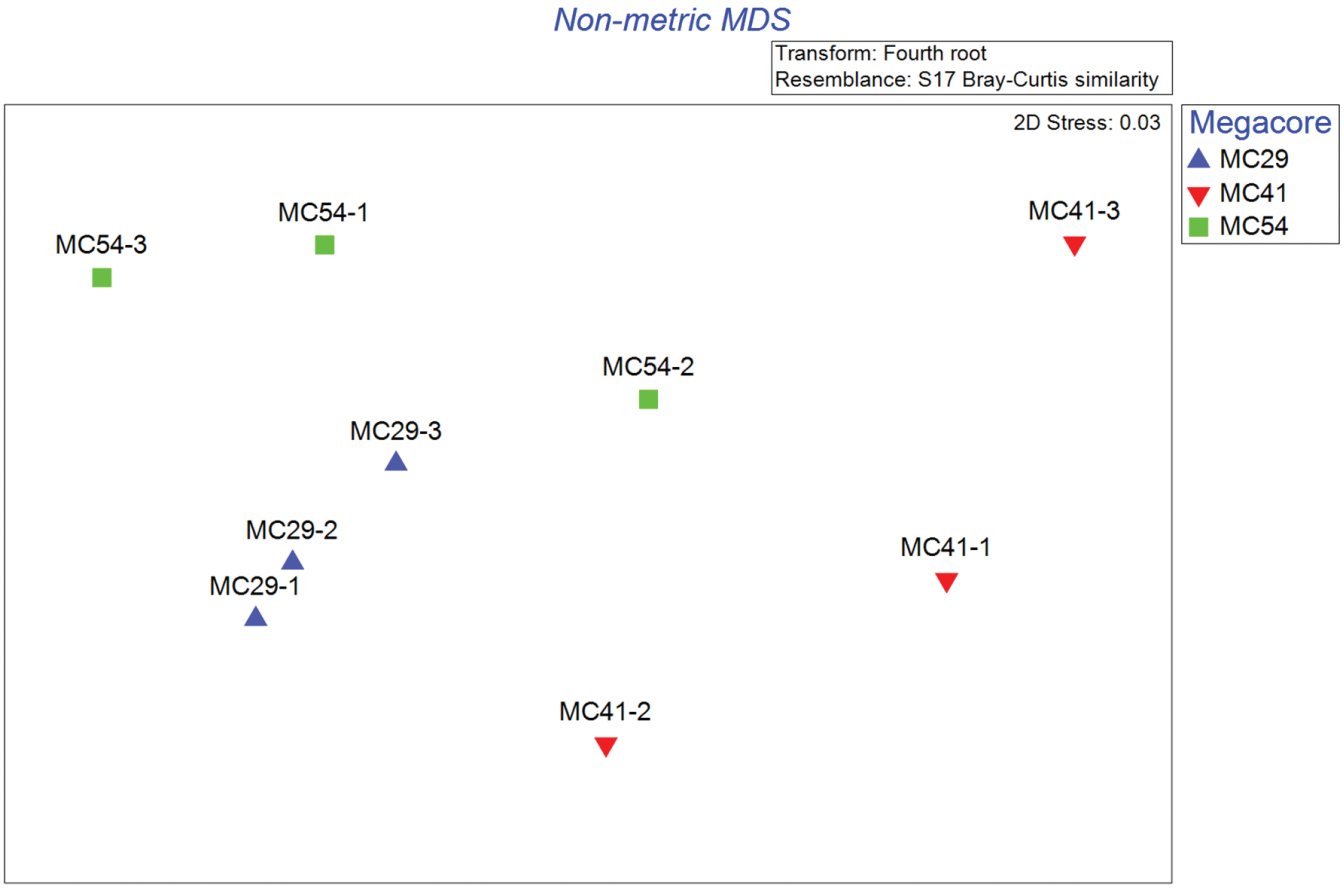

Fig. 2. Non-metric dimensional scaling (nMDS) visualisation of three cores of each station based on their major metazoan taxa groups and abundances.

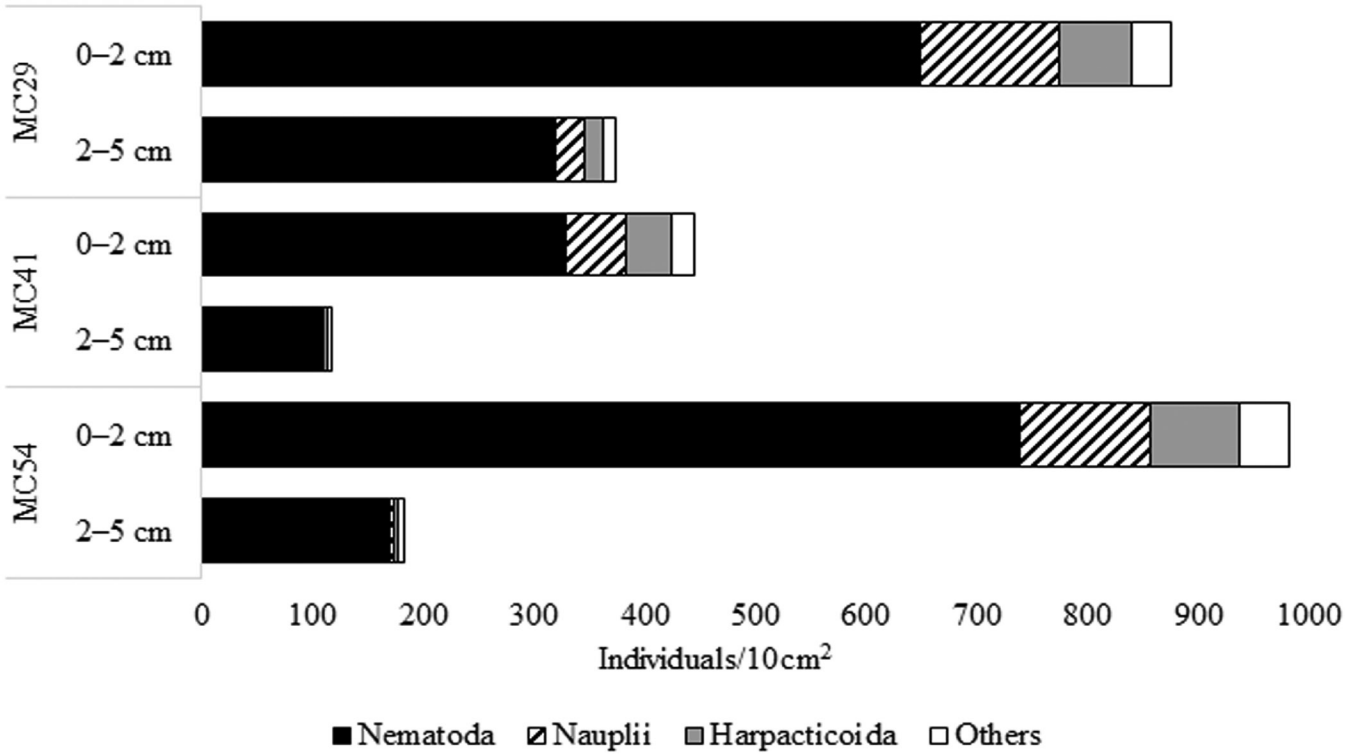

Fig. 3. Vertical distribution of major metazoan taxa groups in the 0–2 cm and 2–5 cm sediment layers of Stations MC29, MC41, and MC54 in the deep waters off southwest Java, eastern Indian Ocean.

Table 3. Percentage (%) of benthos collected in the 0–2 cm and 2–5 cm sediment depth of stations MC29, MC41, and MC54, s.e. = standard error. The percentages were calculated based on the averaged abundance at each station.

Sediment layer	0–2 cm					2–5 cm				
Station	MC29	MC41	MC54	average	± s.e.	MC29	MC41	MC54	average	± s.e.
Nematoda	51.95	58.40	63.32	57.89	3.29	25.61	19.19	14.56	19.79	3.20
Nauplii	9.95	9.65	10.13	9.91	0.14	2.10	0.49	0.38	0.99	0.56
Harpacticoida	5.34	7.32	6.93	6.53	0.61	1.25	0.46	0.27	0.66	0.30
Annelida	0.90	1.12	1.18	1.07	0.08	0.45	0.66	0.40	0.50	0.08
Kinorhyncha	1.02	0.51	1.89	1.14	0.40	0.23	0.02	0.07	0.11	0.07
Tardigrada	0.01	1.35	0.00	0.45	0.45	0.00	0.05	0.00	0.02	0.01
Ostracoda	0.47	0.21	0.29	0.32	0.07	0.07	0.03	0.01	0.04	0.02
Bivalvia	0.10	0.02	0.26	0.13	0.07	0.04	0.01	0.02	0.02	0.01
Loricifera	0.09	0.17	0.01	0.09	0.04	0.05	0.01	0.00	0.02	0.02
Gastrotricha	0.03	0.02	0.10	0.05	0.03	0.02	0.00	0.00	0.01	0.01
Amphipoda	0.05	0.02	0.01	0.03	0.01	0.05	0.00	0.00	0.02	0.02
Tantulocarida	0.04	0.07	0.00	0.04	0.02	0.03	0.01	0.00	0.01	0.01
Tanaidacea	0.04	0.02	0.05	0.04	0.01	0.01	0.00	0.01	0.01	0.00
Isopoda	0.07	0.02	0.01	0.04	0.02	0.01	0.00	0.00	0.00	0.00
Acari	0.00	0.04	0.00	0.01	0.01	0.00	0.01	0.01	0.01	0.00
Gastropoda	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cumacea	0.00	0.03	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00
Ophiuroidea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Unknown	0.00	0.10	0.05	0.05	0.03	0.01	0.01	0.01	0.01	0.00
Total	70.06	79.07	84.25	77.79	5.30	29.94	20.93	15.75	22.21	4.31

tends to decrease in deeper waters (Parulekar et al., 1992; Tietjen, 1992; Soltwedel, 2000; Shimanaga et al., 2007), only studies which sampled at similar water depths to ours were compiled for comparison (Table 4). The lack of standardisation of sampling methods in terms of sieve size limits, collection tools, sampling depth and sediment depth further exacerbated the problems of comparing data across different areas. Nevertheless, these studies still provided good estimates of meiofaunal numbers. While acknowledging these differences across the few available studies, the waters off southwest Java appear to have the highest abundance of benthic fauna in the Indian Ocean (Table 4).

Studies have shown that availability of food, in terms of organic matter, is a key factor influencing meiofaunal abundance (e.g., Soetaert et al., 1991; Danovaro et al., 1995, 2002; Fabiano & Danovaro, 1999; Gambi & Danovaro, 2016; Leduc et al., 2016). Areas with high input of food particles (e.g., beneath the ice margins in deep-sea polar regions with a rich phytodetritus supply), have high meiofaunal densities of up to 5,000 ind/10cm^2 (Pfannkuche & Thiel, 1987; Vanhove et al., 1995). Conversely, a decreased supply of organic matter due to increased water depth, sediment depth, and distance from land, generally supports a lower meiofaunal abundance in the deep sea (Pfannkuche, 1993a; Relexans et al., 1996; Soltwedel, 1997; Fabiano & Danovaro, 1999; Baguley et al., 2006). The supply of organic matter to the sea floor is mainly associated with nutrient discharge from land and sea surface primary production (Müller & Suess, 1979; Suess, 1980). At our sampling sites, sediment discharge and nutrient inputs into the ocean through river runoff might be high (Shimada & Soesilo, 2006) since Indonesia experiences rainfall throughout the year (Lavigne & Suwa, 2004; Adji & Bahtiar, 2016), coupled with the close proximity of our stations to land (within 100 km from the nearest coastline; Fig. 1). River discharges are an important source of nutrients for phytoplankton growth at the surface (Penna et al., 2004; O'Connor et al., 2016; Masotti et al., 2018), resulting in higher sea surface productivity which will increase the input of organic matter to the sea floor (Billett et al., 1993; Pfannkuche, 1993a; Sigman & Hain, 2012; O'Connor et al., 2016). Shimada & Soesilo (2006) have also reported that nutrient distribution generally showed a higher concentration shoreward than seaward in the waters south of Java. It is possible that higher levels of utilisable organic matter at our sites led to higher meiofaunal abundances than reported by

Table 4. Compilation of deep-sea metazoan meiofaunal studies of similar depths in the Indian Ocean and Indonesian waters. Results from this study were presented in 0–2 cm and 0–5 cm sediment slices for comparison with other studies. Mean meiofaunal density, Kinorhyncha and Tardigrada density in individuals/10cm^2 (ind/10cm^2) ± standard error, unless otherwise stated. '?' denotes that data was not available.

Localities	Depth (m)	Sediment type/habitat	Collection method	Sieve size limits (µm)	Sediment slice	Mean meiofaunal density (ind/10cm^2)	Kinorhyncha density (ind/10cm^2)	Tardigrada density (ind/10cm^2)	Remarks/ modifications from original study	References
Indian Ocean (East of Tinjil Island)	1231	Loose, fine mud	Multiple corer	40–1000	0–2 cm	875.44 ± 63.65, n = 3	12.73 ± 2.21, n = 3	0.13 ± 0.13, n = 3		This study
Indian Ocean (South of Cilacap)	1239	Mud with fine sand				445.17 ± 133.84, n = 3	2.84 ± 1.47, n = 3	7.60 ± 4.42, n = 3		
Indian Ocean (Pelabuhanratu Bay)	2086	Loose, fine mud				981.92 ± 272.67, n = 3	21.98 ± 6.24, n = 3	0.04 ± 0.04, n = 3		
Indian Ocean (East of Tinjil Island)	1231	Loose, fine mud	Multiple corer	40–1000	0–5 cm (combined)	1249.51 ± 80.46, n = 3	15.66 ± 2.46, n = 3	0.17 ± 0.17, n = 3		This study
Indian Ocean (South of Cilacap)	1239	Mud with fine sand				563.03 ± 154.25, n = 3	2.93 ± 1.43, n = 3	7.85 ± 4.32, n = 3		
Indian Ocean (Pelabuhanratu Bay)	2086	Loose, fine mud				1165.48 ± 306.09, n = 3	22.79 ± 6.60, n = 3	0.04 ± 0.04, n = 3		
south of Sumbawa Island	1047	Not specified	Box corer	32–1000	10 cm	95	0	0	Only data with tailings of 0% were included, to prevent the percentage of tailings being a factor influencing meiofaunal density	Susetiono et al., 2020
	2473					11	0			
	2550					38	0			
	2301					0	0			
	1517					154	1			
Northwestern Indian Ocean	1050	Not specified	Modified van Veen grab	65–?	0–1 cm	15.2	0	0	Corrected to ind/10 cm^2	Thiel, 1966
	1045					22	0	0		
	2600					116	0.8	3.6		
	2650					170.4	2	0.4		
	2650					164.4	1.6	0.4		

Localities	Depth (m)	Sediment type/habitat	Collection method	Sieve size limits (µm)	Sediment slice	Mean meiofaunal density (ind/10cm²)	Kinorhyncha density (ind/10cm²)	Tardigrada density (ind/10cm²)	Remarks/ modifications from original study	References
Western and Central Indian Ocean	1500–1999	Not specified	van Veen grab, box corer, spade corer, peterson grab	63–500	2 cm slices	232.912	0%	0	Mean meiofaunal density data included Foraminifera; corrected to ind/10cm²	Parulekar et al., 1992
	2000–2499					168.189	4.50%			
	2500–2999					105.332	3.60%			
	3000–3499					102.51	0%			
Northwestern Indian Ocean (Kenya coasts-Gazi transect)	1000	Not specified	Box corer	32–1000	5 cm	131	0	0	Only Nematoda and Copepoda were recorded	Duineveld et al., 1997
	2000					169				
Northwestern Indian Ocean (Kenya coasts-Sabaki transect)	1000					461				
	2000					273				
Northwestern Indian Ocean (Kenya coasts-Kiwayu transect)	1000					223				
	2000					446				
Andaman Sea	1001–1500	Clayey, muddy	Peterson grab	62–500	five 2 cm layers	220	0 or 34 at each station	0	Meiofaunal density data included Foraminifera. Depth for each station was not given, thus we were unable to determine the density of Kinorhyncha at the different depths.	Ansari & Parulekar, 1981
	1501–2000					134				
	>2000					68				
Arabian sea	840	Muddy (clayey silt and sandy silt)	van Veen grab	62–500	five 2 cm layers	222	28	0	Removed Foraminifera from meiofaunal density data	Ansari et al., 1980
Arabian sea	3158	Silty clay	Multiple corer	32–500	0–5 cm	162.8 ± 39.4 (s.d.)	0	0	± standard deviation	Sommer & Pfannkuche, 2000

Localities	Depth (m)	Sediment type/habitat	Collection method	Sieve size limits (µm)	Sediment slice	Mean meiofaunal density (ind/10cm²)	Kinorhyncha density (ind/10cm²)	Tardigrada density (ind/10cm²)	Remarks/ modifications from original study	References
Red Sea	831	Not specified	Box grab	40–?	1 cm slices	53	<1%	<1%		Thiel, 1979
	1549					39	<1%	<1%		
	1977					127	<1%	<1%		
Red Sea	1084	Coarse, loose sedimentary material, mainly composed of pteropod shells at about 1061 –1165 m	Box grab	42–1000	5 cm, divided into 1 cm slices	195	Occurred occasionally	0	Combined density data for 42–500 µm and 500–1000 µm; density data included Foraminifera	Thiel et al., 1987
	1945					61				
	1024					107				
	1025					153				
	1449					67				
	1070					51				
	1046					78				
	1377					75				
Red Sea	1223–1227	Not specified	Box grab	500–1000	5 cm, divided into 1 cm slices	0.725 ± 0.55, n = 3	Rare	0	Corrected to ind/10cm²	Pfannkuche, 1993b
	1484		Box grab	500–1000		0.448			Corrected to ind/10cm²	
	1420–1462		Box grab	500–1000		0.064 ± 0.048, n = 3			Corrected to ind/10cm²	
	1248–1252		Box grab	500–1000		0.698 ± 0.134, n = 3			Corrected to ind/10cm²	
	1227		Box grab	40–500		74				
	1650		Multiple corer	40–500		123				
	1492		Multiple corer	40–500		64			Meiofaunal density data included Foraminifera	
	1565		Box grab	40–500		33				
	1433		Box grab	40–500		62				
	1252		Box grab	40–500		90				

other Indian Ocean studies (Table 4). Similar to observations in other meiofaunal studies (e.g., Ansari & Parulekar, 1981; Shirayama & Horikoshi, 1982; Shirayama, 1984; Woods & Tietjen, 1985; Kaneko et al., 1997; Ansari, 2000), the majority of the meiofauna at the three stations were also concentrated in the upper sediment layer where organic matter accumulates (Shirayama, 1984), further supporting the importance of food availability in affecting abundances.

Sediment grain size could be another factor affecting meiofaunal assemblages (Wieser, 1959; Boaden, 1962; Jansson, 1967; Gray, 2002; Veiga et al., 2010; Leduc et al., 2012). Terrigenous sediments (i.e., material from land brought by runoff) at our sampling sites usually consist of a range of fine and coarse sediments (Kolla & Kidd, 1982). This might provide some habitat heterogeneity by increasing microhabitats, niches, and the possibility of accumulating more food particles between sediment grains (Dean & Connell, 1987; Vladimir et al., 2005; Giere, 2009; Vanaverbeke et al., 2011; Kovalenko et al., 2012). However, granulometry did not appear to be a driving factor of overall abundance and diversity in some cases, because habitat preferences are also dependent on feeding types, body shapes and locomotion of the taxa group/genera/species (Jansson, 1967; Hockin, 1982; Bell et al., 1987; De Troch et al., 2006; Vanaverbeke et al., 2011; Fonseca et al., 2014; Landers et al., 2018, 2019). For example, some Nematoda studies have found higher densities and diversity in coarser sediment (Steyaert et al., 1999; Vanaverbeke et al., 2002, 2011; Gheskiere et al., 2005) but more Kinorhyncha was found in finer sediments (Landers et al., 2018, 2019; Grzelek & Sørensen, 2019). A number of studies conducted elsewhere in the Indian Ocean also reported clayey, muddy, and sandy silt (Ansari et al., 1980; Ansari & Parulekar, 1981; Sommer & Pfannkuche, 2000) which reflected our own observations at the three stations, but meiofaunal abundances were consistently lower than the numbers obtained in this study. We suggest that granulometry is not the driving factor for the higher meiofaunal abundance at our sites. Rather, the overall higher meiofaunal abundance found in our study is more likely attributable to higher organic matter to the sea floor as a result of higher sea surface productivity.

As in other deep-sea meiofaunal studies (e.g., Thiel, 1979; Ansari & Parulekar, 1981; Parulekar et al., 1982; Parulekar et al., 1992; Sommer & Pfannkuche, 2000; Zeng et al., 2018), Nematoda dominated the metazoan meiofauna, followed by Nauplii and Harpacticoida in the bathyal sediments of Indonesia. Interestingly, our sites found high numbers of Kinorhyncha (Stations MC29 and MC54) and Tardigrada (Station MC41). Even though Kinorhyncha abundances of up to 267 ind/10cm^2 have been reported between 300–400 m in the Arctic Ocean (Pfannkuche & Thiel, 1987), abundances at greater depths (>1,000 m) were usually much lower at only 0.5–10 ind/10cm^2 (Pfannkuche & Thiel, 1987; Soetaert et al., 1991; Vanhove et al., 1995; Table 4). Similarly for Tardigrada, abundances reported were generally low at about 0–4 ind/10cm^2 (Soetaert et al., 1991; Vanhove et al., 1995; Table 4). Some studies combined Tardigrada together with other rare taxa under the category 'Others' due to their low numbers (e.g., Pfannkuche & Thiel, 1987), while some did not even find Tardigrada in their samples at all (e.g., Ansari et al., 1980; Ansari & Parulekar, 1981; Parulekar et al., 1992; Sommer & Pfannkuche, 2000; Susetiono et al., 2020). Yet, Kinorhyncha was the fifth and fourth most abundant taxon at Stations MC29 and MC54 respectively, boasting a mean of 15.7 ± 2.5 ind/10cm^2 (n = 3) and 22.8 ± 6.6 ind/10cm^2 (n = 3); and Tardigrada was the fifth most abundant taxon at Station MC41, with 7.9 ± 4.3 ind/10cm^2 (n = 3).

The high numbers of Kinorhycha and Tardigrada contributed to the dissimilarities of meiofaunal assemblage along southwest Java, where our sampling sites in the west (Stations MC29 and MC54) were more similar to each other than to Station MC41. The only difference in the substratum we observed among the three stations was the loose, fine mud found at Stations MC29 and MC54, and coarser sediment of mud with fine sand at MC41. Kinorhyncha appeared to favour finer sediments (MC29 and MC54), which is in line with observations made by other studies (Landers et al., 2018, 2019; Grzelek & Sørensen, 2019). Ansari et al. (1980) also found comparable Kinorhyncha abundances of 28 ind/10cm^2 at one deep-sea station, 840 m, in the Arabian Sea, where a muddy deposit of clayey and sandy silt was observed. The kinorhynch mode of locomotion might offer an explanation for their higher abundance in finer sediments. Kinorhyncha drag their body forward through protrusion-eversion of their introvert (Giere, 2009), and thus fine sediment might present less movement barriers (Grzelek & Sørensen, 2019). In contrast, Tardigrada distribution did not appear to be affected by sediment granulometry (Martinez, 1975). Little is known of the ecology of Tardigrada, let alone in deep-sea habitats, but it might be possible that they prefer habitats with higher complexity which provide some form of shelter or potential habitable areas for their food source (Green, 1950; Crisp & Hobart, 1954; Morgan, 1980). Interstitial spaces present between coarse sediment particles at MC41 may provide microhabitat availability as well as accumulate food items for detritivorous and carnivorous Tardigrada species (De Troch et al., 2006; Giere, 2009). Among our stations, the difference in the type of substratum might be a factor structuring the deep-sea Kinorhyncha and Tardigrada communities off the coast of southwest Java.

The deeper waters of the Indian Ocean are generally very understudied, and available meiofaunal baseline data for meaningful comparisons is not extensive. SJADES 2018 has been very successful in contributing to our knowledge of deep-sea biodiversity, with several new species and first records of fish and crustaceans already reported (Komai et al., 2019, 2020; Ahyong et al., 2020; Chang et al., 2020; Komai & Chan, 2020; Lane & Vimono, 2020; Larson et al., 2020; Matsunuma et al., 2020; Sidabalok et al., 2020). These are certainly indications that there is still much to discover about the biodiversity of Indonesia's deep waters. With the sheer abundance of meiofauna, there is no doubt that there will be more discoveries from across the many taxa. Although this biodiversity expedition did not collect physico-chemical parameters of the seabed, we still managed to fulfil our aim in reporting the first deep-sea meiofaunal

baseline data, finding high abundances and a wide range of meiobenthic organisms off southwest Java. Together with information on the other deep-sea fauna and larger benthos, it is hoped that a more holistic understanding of Indonesia's deep-sea biological communities will emerge in time to come.

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APPENDIX

Appendix Table 1. Raw abundance data at Stations MC29, MC41, and MC54.

Megacore	MC29	MC29	MC29	MC29	MC29	MC29	MC41	MC41	MC41	MC41	MC41	MC41	MC54	MC54	MC54	MC54	MC54	MC54
Core	C03	C03	C04	C04	C07	C07	C03	C03	C04	C04	C05	C05	C04	C04	C05	C05	C06	C06
Fraction (cm)	0–2	2–5	0–2	2–5	0–2	2–5	0–2	2–5	0–2	2–5	0–2	2–5	0–2	2–5	0–2	2–5	0–2	2–5
Nematoda	5885	2635	4207	2280	5203	2625	2501	845	4009	1116	1238	585	6244	1378	2460	868	8684	1752
Nauplii	1091	232	1065	135	772	252	390	38	713	19	177	8	1087	50	495	18	1201	37
Harpacticoida	572	118	566	87	434	162	278	31	401	21	292	9	595	33	572	24	737	17
Annelida	85	39	117	45	64	48	23	45	75	25	50	18	71	32	107	43	145	34
Kinorhyncha	126	30	67	22	107	17	15	1	45		7	1	215	5	75	1	228	13
Tardigrada	3	1					29	6	129		21				1			
Ostracoda	35	7	47	8	55	5	8	1	14	3	6		33	2	15		33	1
Bivalvia	7	4	10	6	13	2	1	1	1		1		29	3	10		32	3
Loricifera	9		16	5	1	10	5		14	1	3		3					
Gastrotricha	5	2	3			5			2				11	1	2		14	
Amphipoda		16	16						3				1	1			2	
Tantulocarida	4	2	6	1	3	6	3	1	6						1			
Tanaidacea			5		6	2	2				1		6	1		1	9	1
Isopoda	6	2	12	1	2				1		2				1		3	
Acari	1						3	1	2					2				1
Gastropoda											1							
Cumacea			1						4									
Ophiuroidea																	1	
Unknown						2	6		3	1	4		10	1	3	2		
Total	7829	3088	6138	2590	6660	3136	3264	970	5422	1186	1803	621	8305	1509	3742	957	11089	1859

Appendix Table 2. Abundance in individuals/10cm^2 at Stations MC29, MC41, and MC54.

Megacore	MC29	MC29	MC29	MC29	MC29	MC29	MC41	MC41	MC41	MC41	MC41	MC41	MC54	MC54	MC54	MC54	MC54	MC54
Core	C03	C03	C04	C04	C07	C07	C03	C03	C04	C04	C05	C05	C04	C04	C05	C05	C06	C06
Fraction (cm)	0–2	2–5	0–2	2–5	0–2	2–5	0–2	2–5	0–2	2–5	0–2	2–5	0–2	2–5	0–2	2–5	0–2	2–5
Nematoda	749.30	335.50	535.65	290.30	662.46	334.22	318.44	107.59	510.44	142.09	157.63	74.48	795.01	175.45	313.22	110.52	1105.68	223.07
Nauplii	138.91	29.54	135.60	17.19	98.29	32.09	49.66	4.84	90.78	2.42	22.54	1.02	138.40	6.37	63.03	2.29	152.92	4.71
Harpacticoida	72.83	15.02	72.07	11.08	55.26	20.63	35.40	3.95	51.06	2.67	37.18	1.15	75.76	4.20	72.83	3.06	93.84	2.16
Annelida	10.82	4.97	14.90	5.73	8.15	6.11	2.93	5.73	9.55	3.18	6.37	2.29	9.04	4.07	13.62	5.47	18.46	4.33
Kinorhyncha	16.04	3.82	8.53	2.80	13.62	2.16	1.91	0.13	5.73	0.00	0.89	0.13	27.37	0.64	9.55	0.13	29.03	1.66
Tardigrada	0.38	0.13	0.00	0.00	0.00	0.00	3.69	0.76	16.42	0.00	2.67	0.00	0.00	0.00	0.13	0.00	0.00	0.00
Ostracoda	4.46	0.89	5.98	1.02	7.00	0.64	1.02	0.13	1.78	0.38	0.76	0.00	4.20	0.25	1.91	0.00	4.20	0.13
Bivalvia	0.89	0.51	1.27	0.76	1.66	0.25	0.13	0.13	0.13	0.00	0.13	0.00	3.69	0.38	1.27	0.00	4.07	0.38
Loricifera	1.15	0.00	2.04	0.64	0.13	1.27	0.64	0.00	1.78	0.13	0.38	0.00	0.38	0.00	0.00	0.00	0.00	0.00
Gastrotricha	0.64	0.25	0.38	0.00	0.00	0.64	0.00	0.00	0.25	0.00	0.00	0.00	1.40	0.13	0.25	0.00	1.78	0.00
Amphipoda	0.00	2.04	2.04	0.00	0.00	0.00	0.00	0.00	0.38	0.00	0.00	0.00	0.13	0.13	0.00	0.00	0.25	0.00
Tantulocarida	0.51	0.25	0.76	0.13	0.38	0.76	0.38	0.13	0.76	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00
Tanaidacea	0.00	0.00	0.64	0.00	0.76	0.25	0.25	0.00	0.00	0.00	0.13	0.00	0.76	0.13	0.00	0.13	1.15	0.13
Isopoda	0.76	0.25	1.53	0.13	0.25	0.00	0.00	0.00	0.13	0.00	0.25	0.00	0.00	0.00	0.13	0.00	0.38	0.00
Acari	0.13	0.00	0.00	0.00	0.00	0.00	0.38	0.13	0.25	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.13
Gastropoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cumacea	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.51	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ophiuroidea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00
Unknown	0.00	0.00	0.00	0.00	0.00	0.25	0.76	0.00	0.38	0.13	0.51	0.00	1.27	0.13	0.38	0.25	0.00	0.00
Total	996.82	393.18	781.51	329.77	847.98	399.29	415.58	123.50	690.35	151.01	229.56	79.07	1057.42	192.13	476.45	121.85	1411.89	236.69