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Preliminary studies of the tardigrada communities from a polymetallic nodule area of the deep South China Sea

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Knowledge about marine tardigrades from the South China Sea is very scarce, with only four species from shallow waters recorded to date. The present study investigated the structure and diversity of tardigrade communities from the deep sea (1517-1725 m) at 8 stations in a polymetallic nodule area of the northern South China Sea. A total of 151 arthrotardigrades were collected belonging to 11 genera (*Angursa, Batillipes, Coronarctus, Euclavarctus, Exoclavarctus, Halechiniscus, Moebjergarctus, Raiarctus, Rhomboarctus, Tanarctus* and *Tholoarctus*), representing 17 species. Two *Angursa* species (*Angursa* sp. 4 and *Angursa* sp. 3) were the most abundant (25.2% and 14.6%, respectively), followed by *Moebjergarctus* sp. (13.9%). Specimens were mostly (90.7%) distributed in the upper layer of the sandy-mud sediment (0-1 cm). The SIMPROF test showed that the composition of tardigrade communities at all stations was not significantly different. At different stations, the number of species, Shannon-Wiener diversity index and Pielou's evenness index ranged from 4 to 10, 1.94 to 2.87, and 0.75 to 1.00, respectively. The average taxonomic distinctness ($\Delta+$) ranged from 72.50 to 90.00, and the variation in taxonomic distinctness ($\Lambda+$) ranged from 316.67 to 1181.25. This study provides some basic information about the biodiversity of the marine tardigrade community in the South China Sea.

KEYWORDS

marine tardigrades, heterotardigrada, meiofauna, diversity indexes, deep sea, South China Sea

1 Introduction

Meiofaunal organisms are very important in energy conversion processes and as indicators of environmental health, as they provide links in the marine benthic food web (Higgins and Thiel, 1988; Montagna, 1995; Zeppilli et al., 2015). However, studies carried out to date all over the world have mainly focused on nematodes, as they are the most abundant meiofaunal group (Grove et al., 2006; Giere, 2009). Tardigrades are usually less numerous, although occasionally they can reach more than 2500 specimens per 50 cm^3 (Martinez, 1975), and are poorly understood. Hansen and Kristensen (2020) reported 223 known marine species, including all arthrotardigrades and all species of the three genera of the order Echiniscoidea, as well as six eutardigrade species of the order Parachela. Marine tardigrades can be found from intertidal to abyssal depths, inhabiting a great variety of sediments and living associated with algae, barnacles, holothurians and bryozoans (Nelson et al., 2018). Marine tardigrades have been recorded from all seas; they may live interstitially in the intertidal zone and subtidal coarse coralline sand, tend to be epibenthic in finer sands and mud because of decreased oxygen availability (Giere, 2009), may drift or swim weakly above the substrate thus being considered semibenthic (Kristensen and Renaud-Mornant, 1983), and may live in crevices on polymetallic nodules, abyssal mud and deep-sea ooze (Bussau, 1992; Giere, 2009; Nelson et al., 2018; Bai et al., 2020). Deep-sea tardigrades were reported for the first time by Thiel (1966) from 2600 to 4690 m depth in the Indian Ocean. The populations of marine tardigrades tend to be small and patchy (Nelson, 2002). Basic knowledge of trophic interactions in marine tardigrades is very scarce. Most marine tardigrades are likely to feed on algal cells, including macroalgae and diatoms, while others may be detritivores, bacteriovores, or ectoparasites (Kristensen and Sørensen, 2004).

Studies on marine tardigrades are mainly focused on the discovery of new species. The few tardigrade ecological approaches are focused on intertidal or shallow subtidal tardigrades and are related to the environmental factors influencing their distribution, in particular the type of substrate and characteristics of the sediment and seasonal distribution (Renaud-Debyser, 1956; Renaud-Debyser, 1959a; Renaud-Debyser, 1959b; Renaud-Debyser, 1963; Renaud-Debyser and Salvat, 1963; de Zio and Grimaldi, 1966; Pollock, 1975; Renaud-Mornant, 1979; D'Addabbo Gallo et al., 1987; Gallo D'Addabbo et al., 1999). More recently, Accogli et al. (2011) studied the structure and diversity of tardigrade communities along a Mediterranean coastline, trying to understand the effect of particular environmental factors such as sulfur springs, mussel farms and seasonal tourism; Rubal et al. (2016a) studied the diversity of tardigrades along the northern Portuguese coast, and Tilbert et al. (2019) studied the spatial and seasonal variation in tardigrade densities in a Brazilian estuary. On the other hand, Bartels et al. (2020) found some signals that, at least in the Northern Hemisphere, tardigrade body size was related to latitudinal gradients, which have an effect on minimum body size, with smaller species disappearing at higher latitudes, but not with net primary productivity. The only known biodiversity study focused on deep-sea tardigrades was carried out in the Gulf of Mexico (NW Atlantic) by Romano III et al. (2011). In that study, 54 tardigrades from 43 stations at depths of 625-3159 m were collected in total, and the authors found a slight positive correlation between the number of species and depth and a slight negative correlation between the number of species and longitude. Higgins (1972) mentioned that in aquatic environments, tardigrades were most commonly found in the interstitial habitats (coarse to medium-fine sand) of beaches and submerged sediments. Mu et al. (2020) reported that marine tardigrade abundance had a significant positive correlation with interstitial seawater temperature and median grain size in tidal zones.

The South China Sea is a marginal sea of the western Pacific Ocean. It extends across the tropical and subtropical zones. The Kuroshio Current intrudes from the Philippine Sea through the Luzon Strait to the northern South China Sea year-round (Nan et al., 2015). The fauna of the southern South China Sea possesses typical tropical elements paralleled with the typical tropical faunal center of the Philippine-New Guinea-Indonesia Coral triangle. The shelf of the northern South China Sea holds abundant distributions of decapod crustaceans and bivalve mollusks (Zhong, 1986; Song et al., 2003; Liu, 2013). Generally, most studies have focused on micro- and megaplankton, as well as macrofauna and nekton. For example, Miao and Thunell (1993) investigated benthic foraminiferal distributions in the South China and the Sulu Sea. Li et al. (2022) studied the geographical meroplankton distribution pattern among the South China Sea and Philippine Sea. Meiofauna studies carried out in the South China Sea have mainly focused on nematodes with studies on spatial distribution (Du et al., 2010), seasonal distribution (Tang et al., 2012a; Tang et al., 2012b; Jia et al., 2020), effects of environmental factors (Wang et al., 2009; Cai et al., 2012) and abundance and biomass (Liu et al., 2014; Liu et al., 2015; Qiao et al., 2021). The structure of communities of free-living nematodes was reported in the northeastern part of the South China Sea by Jia et al. (2020) and in both deep-sea (313-1600 m) and shallow waters (87 m) by Liu et al. (2014); Liu et al. (2015). However, the marine tardigrades in the South China Sea are deeply understudied, with only four shallow-water (from 0–4 m) species reported until now: *Batillipes mirus* Richters, 1909 (Renaud-Mornant and Serène, 1967); *Batillipes philippinensis* Chang and Rho, 1997 (Chang and Rho, 1997); *Florarctus kwoni* Chang and Rho, 1997 and *Parastygarctus higginsi* Renaud-Debyser, 1965 (Renaud-Mornant, 1967; Renaud-Mornant and Serène, 1967). Such a scarcity of records justifies the great need for ecological information in this previously ignored area.

In this paper, we investigated for the first time the diversity of deep-sea tardigrade communities (1517-1725 m) from the South China Sea. This study provides some basic information about the biodiversity of the marine tardigrade community in the South China Sea.

2 Materials and methods

2.1 Sampling stations, procedures and sampling treatment

The South China Sea is a semienclosed body of water with complex bottom topography that has wide continental shelves in the north and south and steep slopes in the east and west (Liu, 2013). Tardigrades were obtained from eight sampling stations (20.97°N–21.19°N, 117.98°E –118.10°E): M1, M2, M8, J1, J4, S1, S2, and S3 at depths of 1517-1725 m from the northern South China Sea. Sampling stations were divided into three areas: area I (Station J4), area II (Stations S2, S3 and M2) and area III (Stations S1, M1, M8 and J1). The distances from J4 (area I) to S2 (area II) and M8 (area III) were 12 km and 25 km, respectively. It was 15 km from S2 (area II) to M8 (area III). Rod and oval nodules were collected at Stations J1 and M8. Samples from Station M8 were collected in May 2019; samples from Stations M1 and M2, J1 and J4, and S1, S2 and S3 were collected in May, July, and August of 2021, respectively (Figure 1). The sampling sediments were collected by an MCS-1-type multiple corer with an inner diameter of 9.5 cm and extruded into the following layers: 0-1, 1-2, 2-4, and 4-6 cm. Then, the sampled sediments were preserved in 7% neutralized formalin. In the laboratory, to release the meiofauna from the sediment, a number of subsamples at each station were washed through a set of sieves of 250-μm, 125-μm, 63-μm, and 32-μm mesh size and then were extracted from the sediment using the Ludox centrifugation technique (de Jonge and Bouwman, 1977; Wang et al., 2010). Prior to sorting, the meiofauna were stained with "Rose Bengal" for two hours, which binds to their cuticle, making specimens easier to find. The trapped tardigrades were sorted under a stereomicroscope (Leica M205 A).

Species were identified based on information from Fontoura et al. (2017); Hansen and Kristensen (2020) and original descriptions and redescriptions. For that purpose, specimens were prepared for light microscopy (LM) and scanning electron microscopy (SEM). Specimens used for light microscopy were mounted on microscope slides in glycerin with a cover slip and sealed with transparent nail polish. Images were taken and measured by a Leica DM6B microscope and a Zeiss Axio imager A2 microscope under 20×, 40× and 100× oil immersion using the bright field mode (BF) and differential interference contrast (DIC).

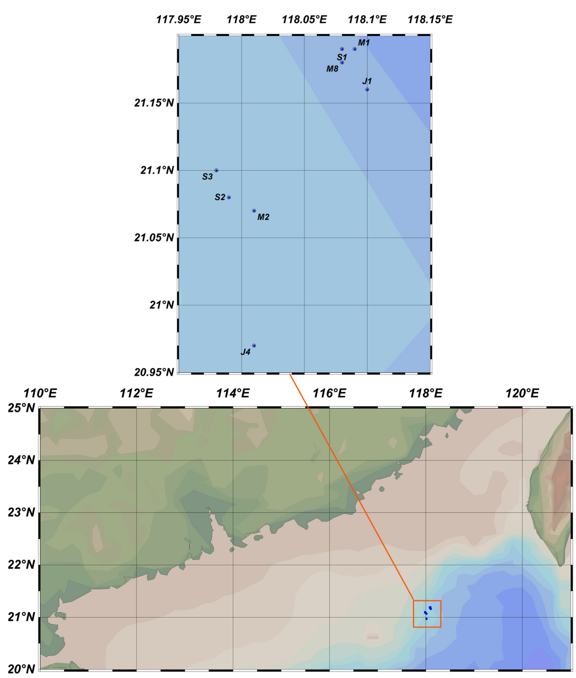

FIGURE 1
Sampling stations in the South China Sea (map made by Ocean Data View, Schlitzer, Reiner, Ocean Data View, odv.awi.de, 2021).

Specimens prepared for SEM were dehydrated in a graded series of ethanol prior to critical point drying or hexamethyldisilazane drying (Shively and Miller, 2009; Zhou et al., 2017). The dehydrated specimens were then mounted on stubs, coated with platinum and observed in a HITACHI TM-1000 scanning electron microscope.

2.2 Structural parameters of the tardigrade community

The biological information about tardigrade communities was synthesized by means of the number of species and individuals. To analyze tardigrade diversity, the Shannon–Wiener diversity index (H′), Pielou's evenness index (J′), average taxonomic distinctness (Δ+) and variation in taxonomic distinctness (Λ+) were calculated (Clarke and Gorley, 2006).

The comparison among stations was performed by means of group average CLUSTER analysis of the SIMPROF test, SIMPER analysis, calculations of diversity indices and TAXDTEST using the PRIMER version 6 software package. The SIMPROF test was carried out using the Bray–Curtis similarity measure with a significance level of 5%. The data were transformed by square root before CLUSTER and SIMPER analysis (Clarke and Gorley, 2006).

3 Results

3.1 Composition, diversity and abundance of fauna

A total of 151 specimens of Tardigrada representing 17 arthrotardigrade species from 5 families and 11 genera were collected (Table 1). The most relatively abundant families were Styraconyxidae (65.6%) and Halechiniscidae (27.8%). *Angursa* was the most relatively abundant genus, accounting for 57.0% of the total number of tardigrades, followed by *Moebjergarctus* (13.9%), *Euclavarctus* (8.6%), *Tholoarctus* (6.6%), *Coronarctus* (4.6%), *Exoclavarctus* (3.3%) and *Halechiniscus* (2.0%). Other genera were rare. *Tanarctus* and *Raiarctus* accounted for 1.3% each, and *Batillipes* and *Rhomboarctus* each accounted for 0.7% (Table 1).

Three species were clearly more abundant than all the others: *Angursa* sp. 4 (25.2%), with an average abundance of 0.67 ± 0.59 ind·10 cm^{-2}, followed by *Angursa* sp. 3 (14.6%) and *Moebjergarctus* sp. (13.9%), with average abundances of 0.39 ± 0.38 and 0.37 ± 0.37 ind·10 cm^{-2}, respectively. The relative abundances of each of the other species did not exceed 7% (Table 1).

The abundance of the marine tardigrade fauna at all stations ranged from 0.56 to 4.09, with an average abundance of 2.66 ± 1.13 ind·10 cm^{-2} (Table 2). The number of species at different stations ranged from 4 at Station J4 to 10 at Station J1. There were 7 species at Stations M1, S1 and S2. The Shannon–Wiener diversity index (H′) and Pielou's evenness index (J′) ranged from 1.94 to 2.87 and 0.75 to 1, respectively. The highest value of H' (2.87) was recorded at Station J1 with 23 specimens from 10 species, while the lowest value of the Shannon–Wiener diversity index (H′=1.94) was recorded at Station

TABLE 1 Marine tardigrades collected from the deep South China Sea.

Order	Family	Subfamily	Genus	Species	Number of specimens	Mean abundance (ind·10 cm^{-2})	Relative abundance (%)	Frequency (%)	Depth (m)
Arthrotardigrada Marcus, 1927	Batillipedidae Ramazzotti, 1962		*Batillipes* Richters, 1909	*Batillipes* sp.	1	0.02 ± 0.05	0.7%	12.5%	1517
	Coronarctidae Renaud-Mornant, 1974		*Coronarctus* Renaud-Mornant, 1974	*Coronarctus* sp.	7	0.12 ± 0.24	4.6%	37.5%	1583-1628
	Halechiniscidae Thulin, 1928	Euclavarctinae Renaud-Mornant, 1983	*Euclavarctus* Renaud-Mornant, 1975	*Euclavarctus* sp. 1	5	0.09 ± 0.13	3.3%	37.5%	1517-1586
				Euclavarctus sp. 2	8	0.14 ± 0.15	5.3%	62.5%	1517-1628
			Exoclavarctus Renaud-Mornant, 1983	*Exoclavarctus* sp.	5	0.09 ± 0.20	3.3%	25.0%	1517-1518
			Moebjergarctus Bussau, 1992	*Moebjergarctus* sp.	21	0.37 ± 0.37	13.9%	87.5%	1517-1725
		Halechiniscinae (Thulin, 1928)	*Halechiniscus* Richters, 1908	*Halechiniscus* sp.	3	0.05 ± 0.07	2.0%	37.5%	1586-1725
	Styraconyxidae Kristensen & Renaud-Mornant, 1983		*Angursa* Pollock, 1979	*Angursa* sp. 1	8	0.14 ± 0.26	5.3%	25.0%	1583-1586
				Angursa sp. 2	6	0.11 ± 0.15	4.0%	50.0%	1541-1586
				Angursa sp. 3	22	0.39 ± 0.38	14.6%	75.0%	1517-1725
				Angursa sp. 4	38	0.67 ± 0.59	25.2%	87.5%	1517-1725
				Angursa sp. 5	9	0.16 ± 0.31	6.0%	25.0%	1517-1518
				Angursa sp. 6	3	0.05 ± 0.15	2.0%	12.5%	1518
			Raiarctus Renaud-Mornant, 1981	*Raiarctus* sp.	2	0.04 ± 0.10	1.3%	12.5%	1517
			Rhomboarctus Renaud-Mornant, 1984	*Rhomboarctus* sp.	1	0.02 ± 0.05	0.7%	12.5%	1570
			Tholoarctus Kristensen & Renaud-Mornant, 1983	*Tholoarctus* sp.	10	0.18 ± 0.44	6.6%	25.0%	1517-1628
	Tanarctidae Renaud-Mornant, 1980		*Tanarctus* Renaud-Debyser, 1959b	*Tanarctus* sp.	2	0.04 ± 0.07	1.3%	25.0%	1518-1570

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TABLE 2 Biodiversity and abundance of marine tardigrade fauna from different stations in the South China Sea.

Station	Abundance (ind·10 cm^{-2})	N	S	J'	H'(log_2)	Δ+	Λ+
M1	1.69	12	7	0.92	2.58	84.52	742.63
M2	2.54	18	5	0.84	1.95	72.50	1181.25
J1	3.24	23	10	0.86	2.87	80.00	766.67
J4	0.56	4	4	1.00	2.00	83.33	763.89
S1	4.09	29	7	0.92	2.59	76.19	1159.30
S2	3.24	23	7	0.81	2.28	79.76	870.18
S3	2.40	17	6	0.75	1.94	90.00	316.67
M8	3.53	25	6	0.89	2.29	81.67	955.56

S, Number of species; N, Number of marine tardigrade specimens collected; J'-Pielou's evenness index; H'- Shannon–Wiener diversity index. When species are placed within a taxonomic hierarchy, based on the Linnean classification into family, subfamily, genus and species (Table 1).

S3 with 17 specimens from 6 species (Table 2). The highest value of Pielou's evenness index (J'=1) was recorded at Station J4, with only 4 specimens from 4 species: *Angursa* sp. 3, *Angursa* sp. 4, *Moebjergarctus* sp. and *Halechiniscus* sp.

The highest value of Δ+ was recorded at Station S3 (90.00), while the lowest value was recorded at Station M2 (72.50). The Δ+ values of Stations J4, M8, M1 and S3 were above the simulated mean Δ+, while the Δ+ values of Stations M2, S1, S2 and J1 were lower than the simulated mean Δ+. The variation amplitude of Λ+ ranged from 316.67 at Station S3 to 1181.25 at Station M2, representing a large change in unevenness in the tardigrade community in terms of taxonomy. The values of Λ+ at all stations except Station S3 were higher than the simulated mean Λ+ (Table 2). Both the values of Δ+ and Λ+ at all stations fell inside the 95% probability limit.

3.2 Distribution in sediment layers

Tardigrades were mainly distributed in the upper 0–1cm sediment layer (Table 3) at all sampling stations (mean > 90%). The proportion of specimens recorded in deeper layers was residual (mean values in the 2–4 cm and 4–6 cm layers were 1.0% and 1.5%, respectively).

All tardigrade specimens at Stations M2, J1 and J4 were collected from the upper 0–1 cm layers of sediments. Tardigrades were collected from both the 0–1 cm and 1–2 cm layers at Stations M1, S1, S2 and S3. However, at Station M8, specimens were collected from the upper 0–1 cm layer and then from the deeper layers (2-4 cm and 4-6 cm) (Figure 2).

3.3 Similarity analysis

According to CLUSTER analysis of the Bray–Curtis similarity matrix for the tardigrade species composition at different stations, all eight stations belonged to one group. This finding meant that the composition of tardigrade communities among all three areas and between depths of 1500-1600 m and above 1600 m was not significantly different (SIMPROF test, p >0.05) (Figures 3A, B).

SIMPER analysis showed that the average similarity among the eight stations was 39.20%. The three most dominant species that contributed strongly to the average similarities were *Angursa* sp. 4, *Moebjergarctus* sp., and *Angursa* sp. 3, which contributed 28.99%, 23.77% and 19.16%, respectively, to the average similarity. *Angursa* sp. 4, *Moebjergarctus* sp., and *Angursa* sp. 3 were present in all three areas (Tables 4, 5).

Some species were distributed widely. The most frequent species were *Angursa* sp. 4 and *Moebjergarctus* sp., which was only absent at one station with a frequency of 87.5%. However, four species were only present at a particular station with a frequency of 12.5%: *Angursa* sp. 6 only existed at Station M8, *Batillipes* sp. and *Raiarctus* sp. at Station J1, and *Rhomboarctus* sp. at Station S2 (Tables 1, 4).

At each station, the dominant species belonged to only three genera: *Angursa* sp. 4 was the most relatively abundant species at three stations, namely, S2 (47.8%), M2 (44.4%) and M8 (36.0%); *Tholoarctus* sp. (52.9%) was the most relatively abundant species at Station S3; *Angursa* sp. 1 (33.3%) was the most relatively abundant species at Station M1; *Angursa* sp. 3 was the most relatively abundant species at Station J1 (30.4%); and *Moebjergarctus* sp. was the most relatively abundant species at Station S1 (27.6%) (Table 5).

TABLE 3 Percentage and mean abundance (mean values and standard deviation - SD) of tardigrade specimens collected in each sediment layer at the eight stations in the South China Sea.

Layer	N	Mean ± SD	Average abundance (ind·10 cm^{-2})
0-1 cm	8	92.2% ± 7.4%	2.42 ± 0.98
1-2 cm	8	5.3% ± 5.9%	0.16 ± 0.21
2-4 cm	8	1.0% ± 2.8%	0.04 ± 0.10
4-6 cm	8	1.5% ± 4.2%	0.05 ± 0.15

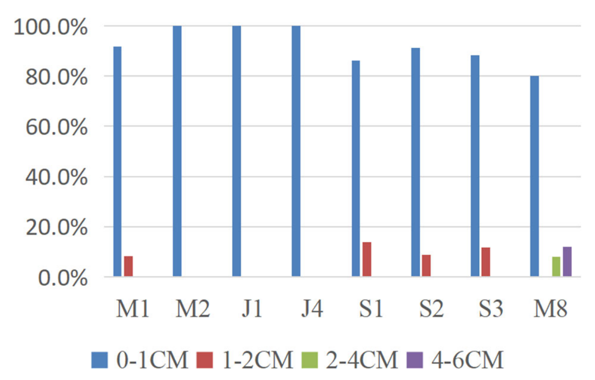

FIGURE 2
Vertical distribution of the marine tardigrade fauna. Percentage of specimens found in each sediment layer at different stations.

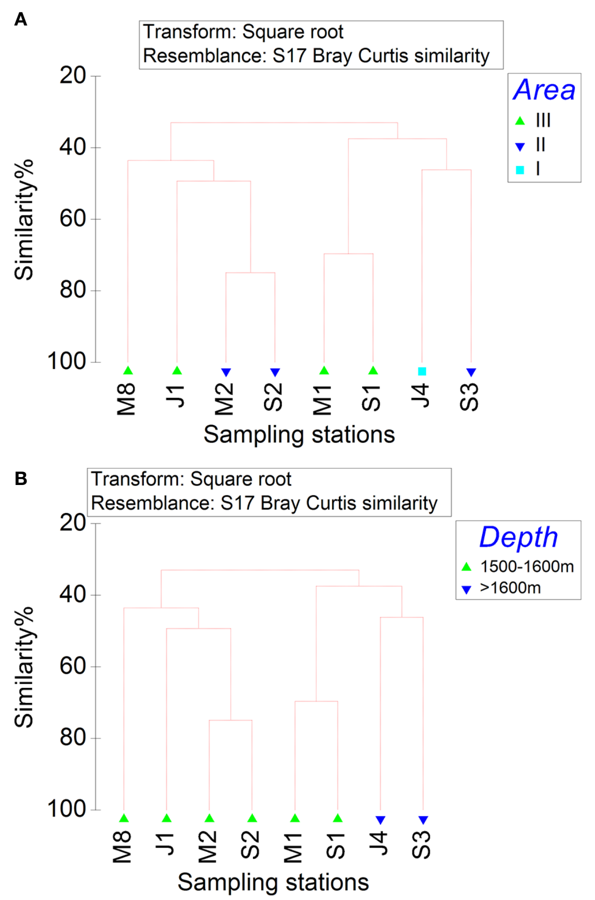

FIGURE 3
Species composition of marine tardigrade fauna at all stations in the deep South China Sea based on CLUSTER analysis. **(A)** Area factor, **(B)** Depth factor.

4 Discussion

4.1 Comparison of the abundance of marine tardigrade fauna in the South China Sea to that in other deep-sea areas

This study showed that the marine tardigrade abundance in the deep South China Sea was much higher than that in the abyssal East Pacific Ocean and the adjacent areas to the Yap Trench of the Western Pacific Ocean (Table 6) (Wang et al., 2013; Wang et al., 2019). Many studies have indicated that food availability is an important factor that affects meiofauna abundance (Danovaro et al., 2002; Gambi and Danovaro, 2016; Leduc et al., 2016). The water depth of this study ranged from 1517 to 1725 m. Although the analysis of the organic matter content of sediments in the stations of this study was not carried out, since the South China Sea is a marginal sea of the western Pacific Ocean, ocean margins are the repository for approximately 90% of the organic carbon buried in marine sediments. The Pearl River, which is the second largest river in China, discharges onto the northern shelf of the South China Sea (Hedges and Keil, 1995; Hu et al., 2006). Studies have shown that the organic matter content of sediments usually decreases with increasing water depth (Billett et al., 1993). Therefore, the organic matter in the northern South China Sea is generally higher than that in both the abyssal East Pacific Ocean and the adjacent areas to the Yap Trench. The data from Liu et al. (2015) showed that the organic matter of the northern South China Sea ranged from 1.31% to 1.55% at depths of 313-1600 m. It was much higher than that adjacent areas of the Yap trench (2896-7837 m), with just 0.02%-0.37% at 22 of 23 sites (except 0.76% at one site) (Wang et al., 2019). This likely caused the abundance of marine tardigrade fauna in the South China Sea to be much higher than that in the abyssal East Pacific Ocean and the adjacent areas to the Yap Trench of the Western Pacific Ocean.

4.2 Community of the tardigrade fauna in the South China Sea compared to other areas

In this study, deep-sea tardigrades were surveyed in the South China Sea for the first time. A total of 151 specimens from 5 families, 11 genera and 17 species were recorded. The South China Sea connects with the Pacific Ocean through the Bashi straits and connects with the Indian Ocean through the Malacca straits. The marine tardigrade fauna from the South China Sea shows the connection between the Pacific Ocean and the Indian Ocean. All the genera of the South China Sea were recorded either in the Pacific Ocean or the Indian Ocean except the genus *Exoclavarctus*, which has been recorded only in the Atlantic Ocean until now (Table 7). The genera *Exoclavarctus* and *Moebjergarctus* are likely to be present in the Indian Ocean and have not yet been collected.

Kaczmarek et al. (2015) divided the meiofauna habitat into four zones: littoral (intertidal), shallow sublittoral (below low tide to

TABLE 4 SIMPER analysis for the contributions of species to the average similarity among all stations in the deep South China Sea.

Average similarity: 39.20%				
Species	Av. Abund	Av. Sim	Contrib%	Cum.%
Angursa sp. 4	1.89	11.36	28.99	28.99
Moebjergarctus sp.	1.41	9.32	23.77	52.76
Angursa sp. 3	1.37	7.51	19.16	71.92
Euclavarctus sp. 2	0.77	3.41	8.70	80.62
Angursa sp. 2	0.59	2.02	5.16	85.78
Halechiniscus sp.	0.38	1.51	3.84	89.62
Coronarctus sp.	0.53	1.03	2.64	92.26

Av. Abund, Average abundance of each tardigrade species; Av. Sim, Average similarity of each tardigrade species; Contrib%, Contribution to total average similarity of each tardigrade species; Cum.%, Cumulative contribution.

200 m), deep sublittoral (200-2000 m) and abyssal (>2000 m). All tardigrade specimens collected in this study belong to the exclusively marine order Arthrotardigrada, and the family Echiniscoididae (order Echiniscoidea) is not found in the deep sublittoral South China Sea. Marine heterotardigrades belonging to Echiniscoididae represent the dominant tardigrade group in intertidal zones worldwide, and the evolution of this family is interesting because it holds key evidence as to how heterotardigrades colonize terrestrial and freshwater environments (Møbjerg et al., 2016). The absence of this family infers that it is probably not adapted to deep-sea environments.

Thirteen recorded species belong to seven genera (*Angursa*, *Coronarctus*, *Moebjergarctus*, *Euclavarctus*, *Exoclavarctus*, *Tanarctus*, and *Tholoarctus*) frequently found in the deep sublittoral and abyssal zones (Kaczmarek et al., 2015). Two other species, namely, *Halechiniscus* sp. and *Rhomboarctus* sp., belong to genera already found in the deep sublittoral zone but not in the abyssal zone (Kaczmarek et al., 2015). *Batillipes* sp. and *Raiarctus* sp. belong to genera found in both littoral and shallow sublittoral zones (Kaczmarek et al., 2015). All the described species of the genus *Batillipes* have been recorded in that zone (Kaczmarek et al., 2015; Rubal et al., 2016b; Menechella et al., 2017; Santos et al., 2017;

TABLE 5 Species composition of marine tardigrade fauna at different stations in the deep South China Sea.

Species	Station							
	M1	M2	J1	J4	S1	S2	S3	M8
Moebjergarctus sp.	8.3%	22.2%	4.3%	25.0%	27.6%	8.7%	23.5%	–
Angursa sp. 1	33.3%	–	–	–	13.8%	–	–	–
Angursa sp. 2	8.3%	5.6%	–	–	3.4%	13.0%	–	–
Angursa sp. 3	16.7%	22.2%	30.4%	25.0%	20.7%	8.7%	–	–
Angursa sp. 4	–	44.4%	21.7%	25.0%	10.3%	47.8%	5.9%	36.0%
Angursa sp. 5	–	–	13.0%	–	–	–	–	24.0%
Angursa sp. 6	–	–	–	–	–	–	–	12.0%
Euclavarctus sp. 1	16.7%	–	4.3%	–	6.9%	–	–	–
Euclavarctus sp. 2	–	5.6%	4.3%	–	–	13.0%	5.9%	8.0%
Exoclavarctus sp.	–	–	4.3%	–	–	–	–	16.0%
Tholoarctus sp.	–	–	4.3%	–	–	–	52.9%	–
Halechiniscus sp.	8.3%	–	–	25.0%	–	–	5.9%	–
Coronarctus sp.	8.3%	–	–	–	17.2%	–	5.9%	–
Raiarctus sp.	–	–	8.7%	–	–	–	–	–
Batillipes sp.	–	–	4.3%	–	–	–	–	–
Tanarctus sp.	–	–	–	–	–	4.3%	–	4.0%
Rhomboarctus sp.	–	–	–	–	–	4.3%	–	–

TABLE 6 Comparison of marine tardigrade studies in the South China Sea and other seas.

Locality	Depth (m)	Mean abundance (ind·10 cm^{-2})	Authors
South China Sea	1517–1725	2.66 ± 1.13	Present study
Adjacent areas to the Yap trench of the Western Pacific Ocean	2896–7837	0.05 ± 0.13	Wang et al. (2019)
East Pacific Ocean	Eastern region: 5236–5329 Western region: 5074–5159	Eastern region: 0.11 ± 0.14 Western region: 0.14 ± 0.23	Wang et al. (2013)

Santos et al., 2018; Bartels et al., 2021). However, taking into account the record from the South China Sea and the records of two new undescribed *Batillipes* species from the deep sublittoral zone (260 m) in the Faroe Bank, Atlantic Ocean (Hansen et al., 2001; Hansen, 2005), this assumption needs to be reevaluated.

Species of three genera, namely, *Exoclavarctus*, *Raiarctus* and *Rhomboarctus*, were recorded for the first time in the Pacific Ocean. *Exoclavarctus* is a monotypic deep-sea genus only known from the Atlantic Ocean at 1369 m (Renaud-Mornant, 1983). The genus *Rhomboarctus* includes 3 species: *Rhomboarctus aslaki* Hansen et al., 2003 known from the Faroe Islands in the North Atlantic Sea, between 138.5 and 260 m; *Rh. duplicicaudatus* Hansen et al., 2003, a subtidal species recorded in the Tyrrhenian Sea (Italy, Europe); and *Rh. thomassini* Renaud-Mornant, 1984, known only from the Mozambique Channel (770 m), Indian Ocean (Renaud-Mornant, 1984; Hansen et al., 2003).

A species of the genus *Moebjergarctus* was dominant in samples from the South China Sea. Three species in this genus have been described: *Moebjergarctus manganis* Bussau, 1992 and *Mo. clarionclippertonensis* Bai et al., 2020, both recorded in polymetallic nodule areas in the Eastern South Pacific (Peru Basin) and in the Northeastern Pacific (Clarion-Clipperton Fracture Zone) (Bussau, 1992; Bai et al., 2020), and *Mo. okhotensis* in the North-Western Pacific (Saulenko et al., 2022). In the sampling area of this study in the South China Sea, polymetallic nodules were also collected, suggesting that species of the genus *Moebjergarctus* can be closely associated with this kind of substrate.

Saulenko et al. (2022) reported that representatives of nine marine tardigrade genera were found only deeper than 200 m, with the exception of *Coronarctus neptunus* found at depths of 150-1300 m. Four of them, that is, *Coronarctus*, *Moebjergarctus*, *Euclavarctus*, and *Exoclavarctus*, were found in this study, while *Bathyechiniscus*, *Clavarctus*, *Ligiarctus*, *Parmursa* and *Proclavarctus* have not yet been found in the South China Sea. It is also interesting to note that the *Halechiniscus* species found in the South China Sea is new to science and has already been described (*Halechiniscus janus* Bai et al., 2022).

4.3 Biodiversity of the marine tardigrade communities

In the absence of other studies that could be used for comparison, the obtained biodiversity values should be used for future reference. The results of the present study show that 13 genera and at least 20 species, including the four previously recorded shallow-water species, are present in the South China Sea at present. This study increases the diversity estimation of both the South China Sea and the Pacific Ocean. To date, only 51 tardigrade species from 23 genera have been recorded from the deep sea (> 200 m depth), including the deep sublittoral and abyssal zones (Kaczmarek et al., 2015; Gomes-Júnior et al., 2020; Hansen and Kristensen, 2020; Degma et al., 2009-2023; Saulenko et al., 2022). Eleven genera and 17 species from the South China Sea accounted for 48% of the recorded deep-sea genera and 33% of the recorded deep-sea species. Considering the inadequate deep-sea sampling in the South China Sea (Liu, 2013) and the generally poor knowledge about marine tardigrades, it can be expected that the diversity of deep-sea tardigrades in the South China Sea, where only a minute area was surveyed coupled with the fact that a very low sampling effort was made in the present study, may be much higher. Bartels et al. (2016) suggested that with the continuing exploration of marine habitats, marine tardigrade species diversity will be similar to that of limnoterrestrial tardigrades.

The results of the SIMPROF test showed that the composition of tardigrade communities between depths of 1500-1600 m and above 1600 m was not significantly different at the stations of this study in the South China Sea. Hansen et al. (2001) reported that samples of the Faroe Bank with similar sediment at depths of 104–

TABLE 7 Comparison of the genus composition of the marine tardigrade fauna of the South China Sea to others.

Area	Genus										
	Ba.	*Co.*	*Ta.*	*Rh.*	*Ra.*	*Ha.*	*An.*	*Eu.*	*Mo.*	*Th.*	*Ex.*
South China Sea (present study)	+	+	+	+	+	+	+	+	+	+	+
Pacific Ocean	+	+	+			+	+	+	+	+	
Indian Ocean	+	+	+	+	+	+	+	+		+	
Atlantic Ocean	+	+	+	+	+	+	+	+		+	+

Ba., Batillipes; Co., Coronarctus; Eu., Euclavarctus; Ex., Exoclavarctus; Mo., Moebjergarctus; Ha., Halechiniscus; An., Angursa; Ra., Raiarctus; Rh., Rhomboarctus; Th., Tholoarctus; Ta., Tanarctus.

260 m had similar species distributions, indicating that the type of sediment was the key factor related to the species distribution and that depth was less important. The results of the present study also agreed with that conclusion. The locations of all stations in this study are quite near, with the same type of sandy mud sediment, which is probably the factor that caused the species composition of marine tardigrade communities at all stations to be very similar.

Although marine tardigrade biodiversity was investigated in this study, unnamed species are urgently in need of identification to further understand the marine tardigrade biodiversity in the South China Sea. Large-scale and large-depth studies are also urgently required to investigate the environmental factors responsible for the distribution of marine tardigrades in the South China Sea.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Ethics statement

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Author contributions

XW and CW conceived the study, and XW and LB drafted the manuscript. XW, BL, YL, QL and XH sampled the sediments. LB conducted experiments in the laboratory with instructions of PF. PF, BL and CW revised and improved the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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