Planktonic ciliate community structure and its distribution in the oxygen minimum zones in the Bay of Bengal (eastern Indian Ocean)

Chaofeng Wang [a,b,c,*], Yanchu Zhao [d], Ping Du [e], Xiao Ma [f], Suheng Li [a,b,c,g], Haibo Li [a,b,c], Wuchang Zhang [a,b,c,*], Tian Xiao [a,b,c]

[a] *CAS Key Laboratory of Marine Ecology and Environmental Sciences, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China*
[b] *Laboratory for Marine Ecology and Environmental Science, Qingdao National Laboratory for Marine Science and Technology, Qingdao 266237, China*
[c] *Center for Ocean Mega-Science, Chinese Academy of Sciences, Qingdao 266071, China*
[d] *Ecological Environment Monitoring and Scientific Research Center of Haihe River Basin and Beihai Sea Area, Ministry of Ecological Environment, Tianjin 300170, China*
[e] *Key Laboratory of Marine Ecosystem Dynamics, Second Institute of Oceanography, Ministry of Natural Resources, Hangzhou 310012, China*
[f] *State Key Laboratory of Satellite Ocean Environment Dynamics, Second Institute of Oceanography, Ministry of Natural Resources, Hangzhou 310012, China*
[g] *University of Chinese Academy of Sciences, Beijing 100049, China*

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ABSTRACT

Oxygen minimum zones (OMZs) are geographically widespread phenomena among world seas, while knowledge regarding planktonic ciliate (microzooplankton) community structure in the OMZ is lacking. In this study, we analyzed community structure of planktonic ciliates in the OMZ waters of the Bay of Bengal, eastern Indian Ocean. Both hydrological characteristics (temperature, salinity, chlorophyll *a* in vivo fluorescence (Chl *a*) and dissolved oxygen (DO)) and planktonic ciliate community showed obvious variations in vertical profile. An obvious higher ciliate abundance and biomass occurred in the thermocline zones (surface to 100 m) than in the OMZs (150–800 m). For aloricate ciliates, abundance proportions of small (10–20 μm) and large (> 30 μm) size-fractions showed increase and decrease characteristics from thermocline zones to OMZs, respectively. With regard to loricate ciliates (tintinnids), more species richness and higher abundance occurred in the thermocline zones than in the OMZs. Four vertical distribution patterns were classified for tintinnids. Three species only occurred in the OMZs. Three-dimensional representation of tintinnid lorica length, lorica oral diameter and abundance proportion revealed that small-sized species in thermocline zones decreased more sharply to OMZs compared to large-sized species. Relationship between environmental variables and ciliate abundance showed that temperature, DO and Chl *a* were main factors determining ciliate abundance. Our results provide fundamental data for better understanding on the ecological role of planktonic ciliates in the thermocline zones and OMZs of the Indian Ocean.

1. Introduction

Planktonic ciliates taxonomically belong to phylum Ciliophora, class Spirotrichea, subclass Oligotrichia and Choreotrichia (Lynn, 2008), and they morphologically consist of tintinnids and aloricate ciliates. Planktonic ciliates are important component of microzooplankton, which serve as primary consumers of pico- (0.2–2 μm) and nano-(2–20 μm) sized plankton, and are important food items of metazoans and fish larvae (Stoecker et al., 1987; Dolan et al., 1999; Gómez, 2007). Therefore, they play an important role in material circulation and energy flow

from the microbial food web to the classical food chain (Azam et al., 1983; Pierce and Turner, 1992; Calbet and Saiz, 2005). With short life cycle and delicate pellicles, planktonic ciliate can response more quickly to environmental variations than any metazoa (Coppellotti and Matarazzo, 2000; Ismael and Dorgham, 2003; Jiang et al., 2011). Tintinnids, by virtue of their high occurrence frequencies and identifiable morphology, were usually regarded as effective indicators of oceanographic conditions (e.g. Kato and Taniguchi, 1993; Kim et al., 2012; Rakshit et al., 2017; Wang et al., 2021a, 2022a).

There have been few studies on community structure of planktonic

ciliates in oceanic waters of the Indian Ocean, and most of them were about tintinnids (Sorokin et al., 1985; Jyothibabu et al., 2008; Liu et al., 2012; Jónasdóttir et al., 2013; Zhang et al., 2017). For microzooplankton (20–200 μm), heterotrophic dinoflagellates and ciliates were top two dominant groups in water columns from surface to 150 m in the western Bay of Bengal close to the Indian subcontinent (Jyothibabu et al., 2008). Yet in the middle Bay of Bengal, there were no studies about ciliate community vertical profile.

The oxygen minimum zones (OMZs) are waters at intermediate depths with low oxygen concentration in the Bay of Bengal and Arabian Sea, northern Indian Ocean (e.g. Jr et al., 2013; Roullier et al., 2014; Menezes et al., 2020). In oceanic areas of these regions, concentrations of dissolved oxygen decreased sharply in the subsurface layers due to the high decomposition of organic matter and lack of ventilation, which eventually formed OMZs (e.g., Naqvi, 1987; Madhupratap et al., 2001; Vidhya et al., 2022). The expansion of OMZs have profound effects on marine ecosystem structure and function, such as plankton vertical distribution, predation, carbon flux, physiology (Saltzman and Wishner, 1997; Pozzato et al., 2013; Roullier et al., 2014; Wishner et al., 1990, 2008, 2013, 2020). With respect to mesozooplankton copepods (aerobic organisms), there were obvious lower abundance and biomass occurred in OMZs compared to thermocline zones in the Arabian Sea and Bay of Bengal (Saltzman and Wishner., 1997; Wishner et al., 1998; Vidhya et al., 2022). Planktonic ciliates (microzooplankton) are important food sources of mesozooplankton copepods. However, there have been no studies about their community structure variations between thermocline zones and OMZs in the world oceans including the Bay of Bengal.

In this study, we hypothesized that planktonic ciliate community structure differed between thermocline zones and OMZs. By examining ciliate abundance, size and species composition between thermocline zones and OMZs in the Bay of Bengal, eastern Indian Ocean, we aimed to find out variations in (1) ciliate vertical distribution; (2) composition of different aloricate ciliate size-fractions; (3) tintinnid composition and abundance proportion of different body size (including lorica length and lorica oral diameter); and (4) relationship between ciliate and environmental variables. The output of this study is expected to be of great help in monitoring microzooplankton ecological function in the OMZs located at tropical oceans.

2. Materials and methods

2.1. Study area and sample collection

Samples were collected between 21 March and 4 April 2021 aboard *R.V.* "Xiangyanghong 10". Four stations (St. IO1 to St. IO4) in the Bay of Bengal and equator of eastern Indian Ocean were occupied. Water depth at all stations were deeper than 2000 m (Fig. 1; Table 1). At each station, vertical profiles of temperature, salinity, chlorophyll *a* in vivo fluorescence (Chl *a*) and dissolved oxygen (DO) were obtained from the surface to 1500 m (except St. IO4 with sampling depth of 100 m) using a conductivity-temperature-pressure sensor (Sea-Bird Electronics, Bellevue, WA, USA). The detection limits of temperature, salinity, Chl *a* and dissolved oxygen concentrations were 0.01 °C, 0.01, 0.01 μg L^{-1} and 0.01 mg L^{-1}, respectively. Water samples were collected by using 12 L Niskin bottles attached to a rosette. The depths sampled in Sts. IO1 to IO3 were surface (3 m and 10 m), 30, 50, 75, 100, 150, 170, 200, 250, 300, 400, 500, 600, 800, 1000 and 1500 m. Around the DCM (deep Chl *a* maximum layer), the sampling depths were changed to sample the DCM if it was within 10 m of any sampling depth. Water samples (1 L) from each depth were fixed with 1% acid Lugol's iodine and stored at <4 °C in the dark.

2.2. Sample analysis and species identification

In the laboratory, water samples were concentrated to approximately 200 mL by siphoning off the supernatant after the sample had settled for
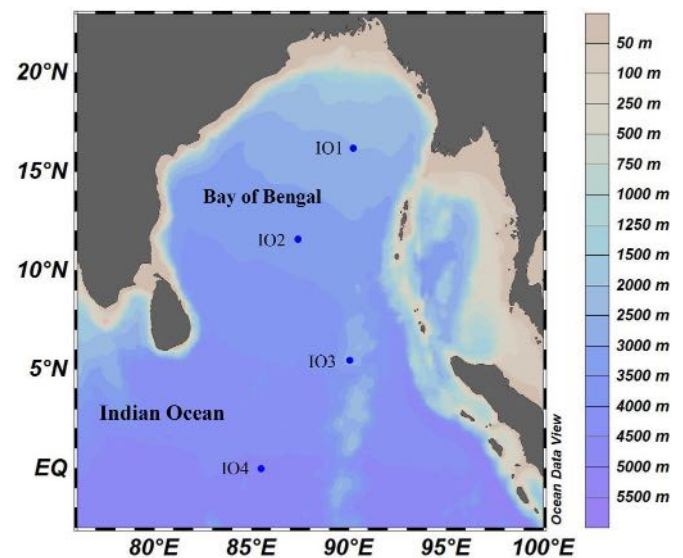

Fig. 1. Survey stations in the eastern Indian Ocean.

60 h. This settling and siphoning process was repeated until a final concentrated volume of 25 mL was achieved, which was then settled in Utermöhl counting chambers (25 mL per chamber) (Utermöhl, 1958) for at least 24 h. Planktonic ciliates were counted using an Olympus IX 73 inverted microscope (100 × or 400 ×) according to the process of Utermöhl (1958) and Lund et al. (1958). The detection limit of ciliate abundance was 1 ind. L^{-1}.

For each species, size (length, width, according to shape) of the cell (aloricate ciliate) or lorica (tintinnid, especially body length and oral diameter) were measured for at least 10 individuals if possible. Aloricate ciliates were categorized into small (10–20 μm), medium (20–30 μm) and large (> 30 μm) size-fractions according to maximum body length of each aloricate species following Wang et al. (2020). Tintinnid taxa were identified according to the size and shape of loricae following Kofoid and Campbell (1929, 1939), Lynn (2008), Zhang et al. (2012) and Wang et al. (2019, 2021a, 2021b). Tintinnid species richness in each station indicated the number of tintinnid species that appeared in that station. Because mechanical and chemical disturbance during collection and fixation can detach the tintinnid protoplasm from the loricae (Paranjape and Gold, 1982; Alder, 1999), we included empty tintinnid loricae in cell counts. Because there were no uniform criterion for oxygen minimum depth, we defined ≤2 mg L^{-1} as classification criterion in our results.

According to temperature and DO concentrations vertical distribution, we classified sampling depths into four zones: stable zone (3–50 m, high temperature and DO concentrations), rapid variation zone (60–100 m, relative high temperature and DO concentrations), oxygen minimum zone (OMZ, 150–800 m, relative low temperature and DO concentrations) and deep zone (1000–1500 m, relative low temperature but higher DO concentrations than OMZ) (Fig. 2; Fig. A1). Among them, the stable and rapid variation zones belonged to thermocline zones.

2.3. Data processing

Ciliate volumes were estimated using appropriate geometric shapes (cone, ball, and cylinder). Tintinnid carbon biomass (*C*, μg C L^{-1}) was estimated using the equation (Verity and Langdon, 1984):

$$C = V_i \times 0.053 + 444.5$$

Where V_i (μm^3) was the lorica volume of species *i*. We used a conversion factor of carbon biomass for aloricate ciliates of 0.19 pg/μm^3 (Putt and Stoecker, 1989). Calculation of ciliate water column average abundance and biomass was following Yu et al. (2014) and Wang et al.

Table 1
Sampling stations location, sampling time, water depth, total ciliate average abundance (AA) and average biomass (AB) in waters ranged from 100 m to surface at each station in the eastern Indian Ocean.

Stations	Latitude (°N)	Longitude (°E)	Date	Time	Depth (m)	AA (ind. L^{-1})	AB (μg C L^{-1})
IO1	16.1944	90.2331	2021.03.21	11:06	2480	111.06	0.26
IO2	11.5903	87.3815	2021.03.29	11:46	3267	139.28	0.36
IO3	5.4795	90.0335	2021.04.04	11:31	2872	292.63	0.64
IO4	0.0434	85.4948	2021.03.31	14:17	4491	173.87	0.40

(2022b). We used the Margalef index (d_{Ma}) (Margalef, 1958) and Shannon index (H') (Shannon, 1948) to test tintinnid diversity indices in each station. Biogeographically, classification of tintinnid genera (Cosmopolitan, species distributed widespread in the world ocean; Warm Water, species observed in open waters throughout the world ocean, but absent from sub-polar and polar waters) was based on Pierce and Turner (1993) and Dolan and Pierce (2013). The vertical distribution group of individual tintinnid species was defined according to Kršinić (1982) and Wang et al. (2019).

The dominance index (Y) of tintinnid species in one assemblage was calculated using formula (Xu and Chen, 1989):

$$Y = \frac{N_i}{(N \times f_i)}$$

Where N_i is the number of individuals of species i in all samples, f_i is the occurrence frequency of species i in all samples and N is the total number of all species. Species with $Y \geq 0.02$ represented the dominant species in an assemblage.

Distributional data of sampling stations, ciliates and environmental parameters (Depth, temperature, salinity, and Chl a) were visualized by ODV (Ocean Data View, Version 5.0, Reiner Schlitzer, Alfred Wegener Institute, Bremerhaven, Germany), Surfer (Version 13.0, Golden Software Inc., Golden, CO, USA), OriginPro 2021 (Version 9.6, OriginLab Corp., USA), and Grapher (Version 12.0, Golden Software Inc., Golden, CO, USA). Correlation analysis between environmental and biological variables was performed using Canoco (Version 5.0, NY, USA) (PCA analysis).

3. Results

3.1. Hydrography and ciliate vertical distribution

Hydrographic features (temperature, salinity, Chl a and DO) showed significant variations in four stations (Fig. 2). Horizontally, surface temperature, salinity and Chl a were lowest in St. IO1 and highest in St. IO3, while DO had highest and lowest value in St. IO1 and IO3, respectively (Fig. 2). With regard to hydrographic feature variations in different zones, salinity, Chl a, and DO showed obvious variations in thermocline zones, but almost no differences in OMZs and deep zones (Fig. 2). Vertically, temperature decreased from surface to 100 m or 1500 m in all stations. Salinity increased from surface to 100 m or 500 m approximately in all stations, then decreased to 1500 m in Sts. IO1, IO2 and IO3. Chl a showed similar characteristics in four stations, but St. IO4 and St. IO3 had deepest (100 m) and shallowest (50 m) deep Chl a maximum (DCM) layers, respectively. DO first decreased to 100 m (Sts. IO1 and IO4) or 150 m (Sts. IO2 and IO3), then keep steady to 600 m, and eventually increased to 1500 m. The OMZ mainly occurred in waters from 150 m to 800 m layers (Fig. 2; Fig. A1). In all stations, aloricate ciliate, tintinnid and total ciliate abundance fell in ranges of 8–308, 0–108 and 8–416 ind. L^{-1}, respectively. Their biomass were 0.00–0.70, 0.00–0.29 and 0.00–0.99 μg C L^{-1}, respectively. Ciliate abundance and biomass were high ($\geq$ 100 ind. L^{-1} and $\geq$ 0.2 μg C L^{-1}, respectively) in thermocline zones in all stations, and then decreased to 1500 m depth (Fig. 2). The vertical profiles of ciliate abundance and biomass showed bimodal (peaks in the surface and around DCM layers) patterns in all

stations.

Aloricate ciliates were dominant group in all stations with higher abundance and biomass proportions ($\geq$ 60% in most depths) (Fig. 2) than tintinnids. At 3 m layers, ciliate abundance was highest in St. IO4 (214 ind. L^{-1}), but highest biomass occurred in St. IO3 (0.63 μg C L^{-1}). Both lowest abundance (115 ind. L^{-1}) and biomass (0.24 μg C L^{-1}) occurred in St. IO1 (Fig. 2). Ciliate abundance and biomass showed similar decrease characteristic in OMZs in Sts. IO1–IO3 (Fig. 2). As for total ciliate average abundance and average biomass in thermocline zones, St. IO3 had highest values (292.63 ind. L^{-1}, 0.64 μg C L^{-1}), followed by St. IO4, IO2 and IO1 (Table 1).

3.2. Aloricate ciliate size-fractions

Abundance and abundance proportion of each aloricate ciliate size-fraction were different in each station (Fig. 3). Generally, abundance of aloricate ciliate small (10–20 μm), medium (20–30 μm), and large (> 30 μm) size-fractions at thermocline zone in St. IO3 were higher than that in other stations. There were almost no differences in OMZs and deep zones in Sts. IO1-IO3 (Fig. 3).

Vertically, small size-fraction were dominant group in most sampling depths, especially in OMZs (Fig. 3). With regard to variations in abundance proportion, small and large size-fractions showed increase and decrease characteristics from surface to 800 m depths, respectively. The OMZs had relative higher small size-fraction and lower large size-fraction abundance proportion compared to thermocline and deep zones in Sts. IO1-IO3. As for medium size-fraction, they mainly occupied around 30% from surface to 1500 m (Fig. 3).

3.3. Tintinnid assemblage

3.3.1. Tintinnid abundance, composition, and diversity index

Totally, 62 tintinnid species from 25 genera were found in all stations (Fig. 4; Table 2). Among them, 28 tintinnid species from 17 genera, 34 tintinnid species from 18 genera, 48 tintinnid species from 23 genera, and 25 tintinnid species from 15 genera were recorded in Sts. IO1, IO2, IO3, and IO4, respectively (Table 2). Vertically, tintinnid species richness, Margalef (d_{Ma}) and Shannon (H') indices were higher in depths from 50 m to 100 m in Sts. IO1–IO3. Compared to the thermocline zones, the OMZs had relative lower species richness and values of both d_{Ma} and H' indices (Fig. A2). In latitudinal direction, tintinnid species richness increased from St. IO1 to St. IO3, then decreased to St. IO4 at most sampling depths of the thermocline zones. But in OMZs (except 150 m depth), species richness almost had no difference (Fig. A2).

3.3.2. Four vertical distribution patterns of tintinnid

There were two, three, three and eight dominant species ($Y \geq 0.02$) in Sts. IO1, IO2, IO3, and IO4, respectively. Among them, only *Acanthostomella minutissima* and *Ascampbelliella armilla* appeared in at least two stations (Fig. 4; Table 2). Dominant species in all stations (Fig. 4) could be classified into two groups: *A. armilla*, *Canthariella brevis*, *Eutintinnus apertus*, *Metacylis sanyahensis*, *Protorhabdonella curta*, *Rhabdonellopsis apophysata* and *Steenstrupiella gracilis* belonged to Group I, which only occurred in waters shallower than 100 m; *A. minutissima*, *Dadayiella ganymedes*, *P. simplex*, *Salpingella acuminata*, *S. decurtata* and
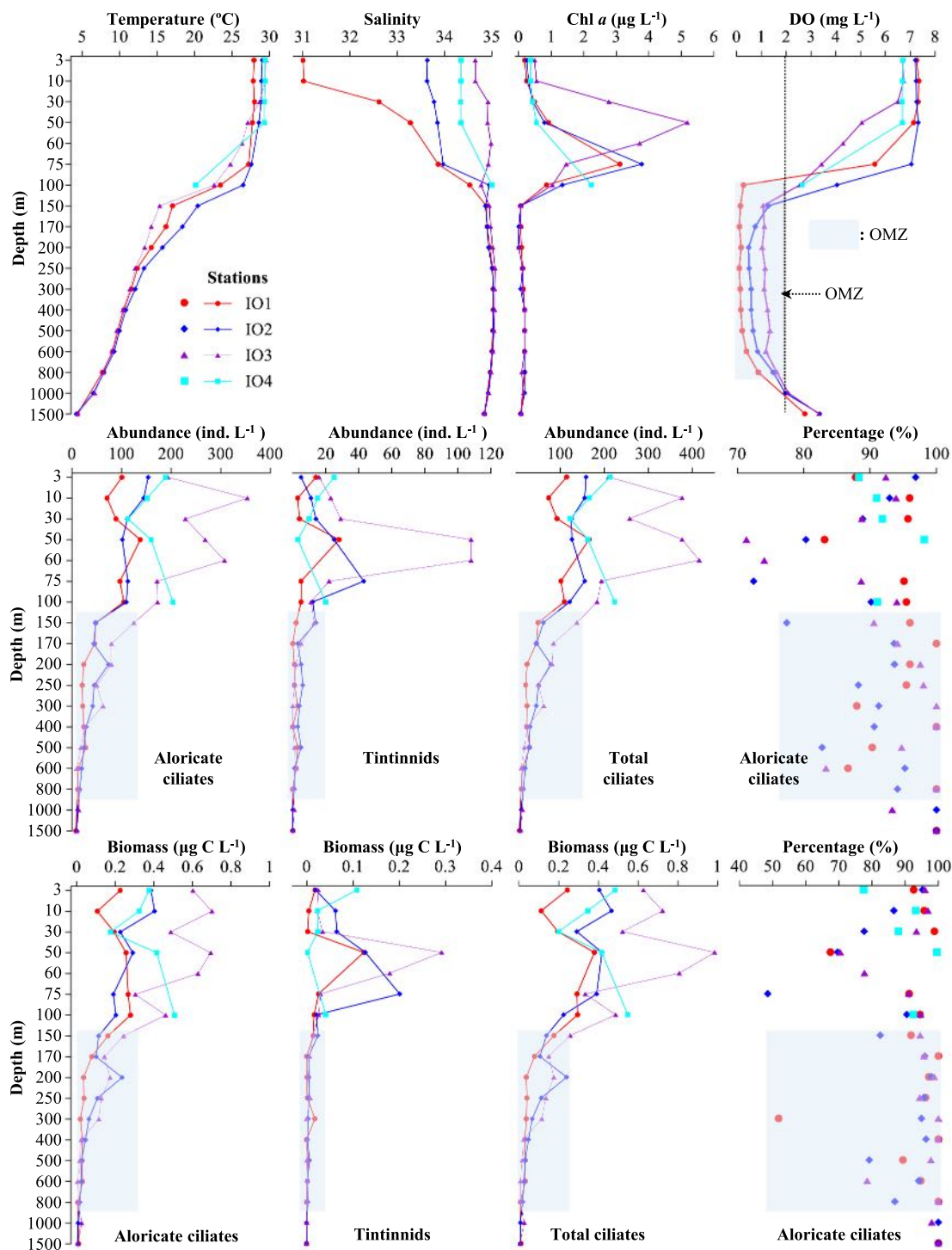
Fig. 2. Vertical distribution of environmental factors (Temperature, salinity, Chlorophyll *a* (Chl *a*) and dissolved oxygen (DO)), planktonic ciliate (aloricate ciliates, tintinnids and total ciliates) abundance and biomass, and aloricate ciliate percentage in total ciliates abundance or biomass.

S. faurei belonged to Group II, which occurred in all depths but with higher abundance at around DCM layers (Fig. 5).

With respect to other vertical distribution patterns, three species (*Amphorides laackmanni*, *Ormosella apsteini* and *Proplectella urna*) belonged to Group III which just occurred in OMZs (> 100 m) with low abundance (1 ind. L^{-1}). Four species (*S. curta*, *S. minutissima*, *Salpingella* sp.1 and *P. caudata*) belonged to Group IV which mainly occurred in waters ranged from 50 to 200 m (Fig. 5). We did not define vertical distribution patterns of other 40 species because of their low abundance

and occurrence frequency (Table 2).

3.3.3. Abundance and abundance proportion of each tintinnid in lorica length and lorica oral diameter size-classes

In stable zone (0–50 m), rapid variation zone (60–100 m) and OMZ (150–800 m) of each station, body size (lorica length, LL; lorica oral diameter, LOD) composition of tintinnid with high average abundance were different (Fig. 6). Because only 1 species with low abundance (1 ind. L^{-1}) occurred in 1000 m, we did not list species in deep water zone.

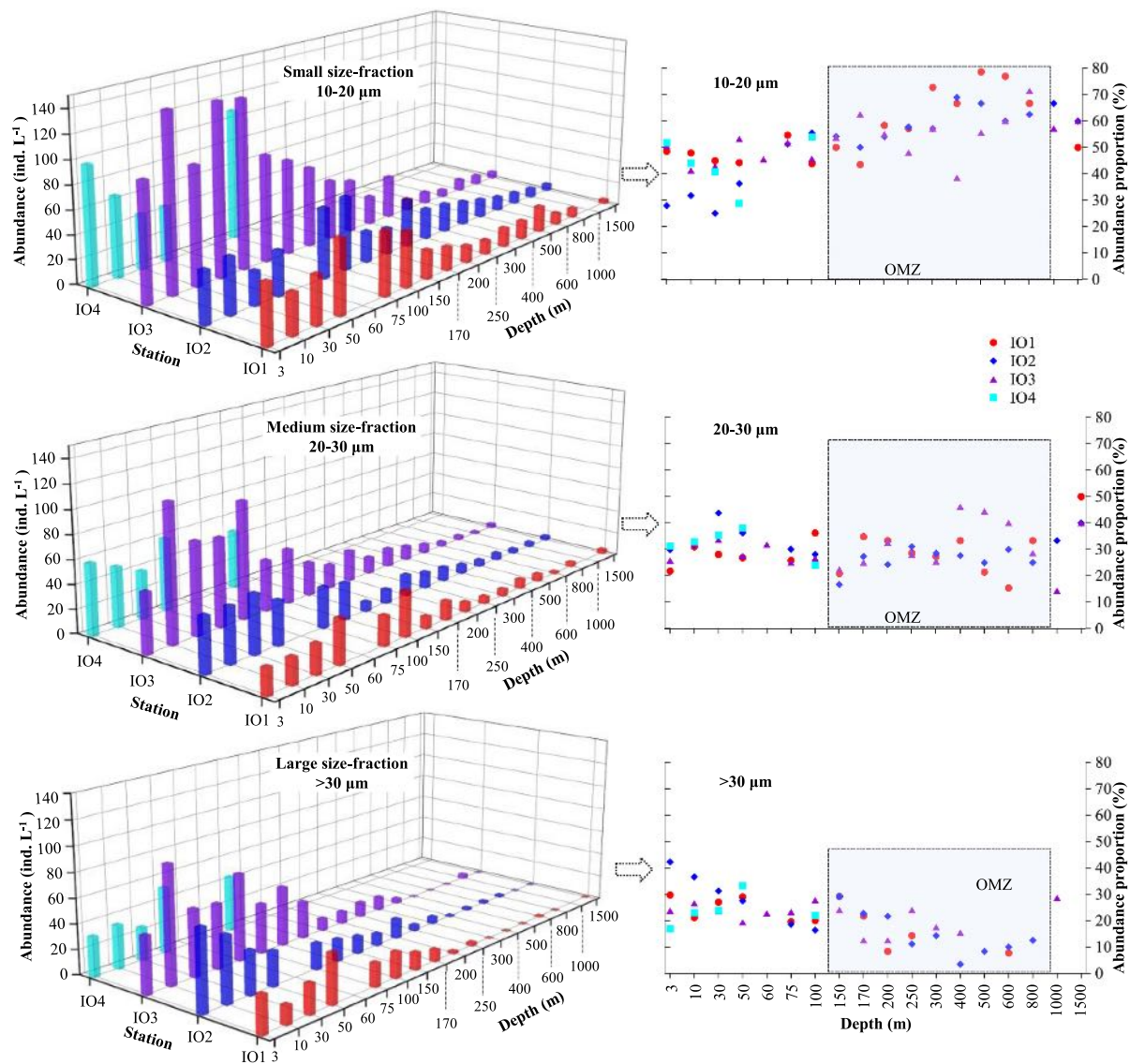**Fig. 3.** Three-dimensional vertical distribution of aloricate ciliate different size-fractions (10–20 μm, 20–30 μm, and > 30 μm) abundance and abundance proportion in different stations.

Three-dimensional representation of tintinnid lorica length, lorica oral diameter and abundance proportion revealed that small-sized (LL, 20–100 μm; LOD, 12–32 μm) species in thermocline zones decreased more sharply to OMZs compared to large-sized (LL, 100–400 μm; LOD, 32–100 μm) species (Fig. 6). Most of species in each zone owned in LL and LOD from 20 to 300 μm and 10–50 μm, respectively. Species with high average abundance (≥ 2.0 ind. L^{-1}) in rapid variation zone had wider LL (ranged from 20 to 300 μm) and LOD (ranged from 16 to 50 μm) than in stable zone (LL, 20–100 μm; LOD, 12–32 μm) (Fig. 6).

Species with highest average abundance and abundance proportion were different in stable, rapid variation and OMZs of each station. In St. IO1, *A. armilla* (LL: 28.9 μm; LOD: 21.6 μm) had highest average abundance (2.0 ± 1.6 ind. L^{-1}) in stable zone. While in rapid variation and OMZs, species with highest average abundance changed to *A. minutissima* (LL: 27.5 μm; LOD: 19.6 μm; 1.5 ± 0.7 ind. L^{-1}) and *D. ganymedes* (LL: 96.9 μm; LOD: 29.3 μm; 0.3 ± 0.7 ind. L^{-1}), respectively. In St. IO2, *Amphorides quadrilineata* (LL: 106.4 μm; LOD: 45.8 μm), *S. acuminata* (LL: 267.4 μm; LOD: 31.2 μm) and *A. armilla* (LL: 28.9 μm; LOD: 21.6 μm) had highest average abundance (1.5 ind. L^{-1}) in stable zone, while *D. ganymedes* (LL: 96.9 μm; LOD: 29.3 μm) was most abundant in both rapid variation and OMZs. In St. IO3, *A. minutissima*

(LL: 27.5 μm; LOD: 19.6 μm) had highest average abundance in both stable and rapid variation zones, but *S. curta* (LL: 93.5 μm; LOD: 14.4 μm) had highest value in OMZ. *Protorhabdonella curta* (LL: 39.5 μm; LOD: 27.4 μm) had highest average abundance (3.3 ± 1.5 ind. L^{-1}) in stable zone of St. IO4. But in rapid variation zone, species with highest average abundance (4.0 ind. L^{-1}) changed to *D. pachytoecus* (LL: 91.9 μm; LOD: 30.5 μm) and *Salpingella* sp.1 (LL: 49.2 μm; LOD: 14.0 μm), respectively.

Species richness and LOD size-classes in stable, rapid variation and OMZs of each station were different (Fig. A3). In St. IO1, the 24–28 μm LOD size-class had highest species richness and average abundance proportion in stable zone, while it changed to 16–20 μm LOD size-class in both rapid variation and OMZs. In St. IO2, the 28–32 μm had highest species richness and average abundance proportion in both stable and rapid variation zones. While in OMZ, the 32–36 μm and 28–32 μm LOD size-classes had highest species richness and average abundance proportion, respectively. In St. IO3, 28–32 μm LOD size-classes had highest species richness and average abundance proportion in both stable and OMZs. But in rapid zone, the 28–32 μm and 16–20 μm LOD size-classes had highest values, respectively. In St. IO4, the 24–28 μm LOD size-class had highest species richness and average abundance proportion in stable zone, but it changed to 28–32 μm LOD size-class in rapid variation zone
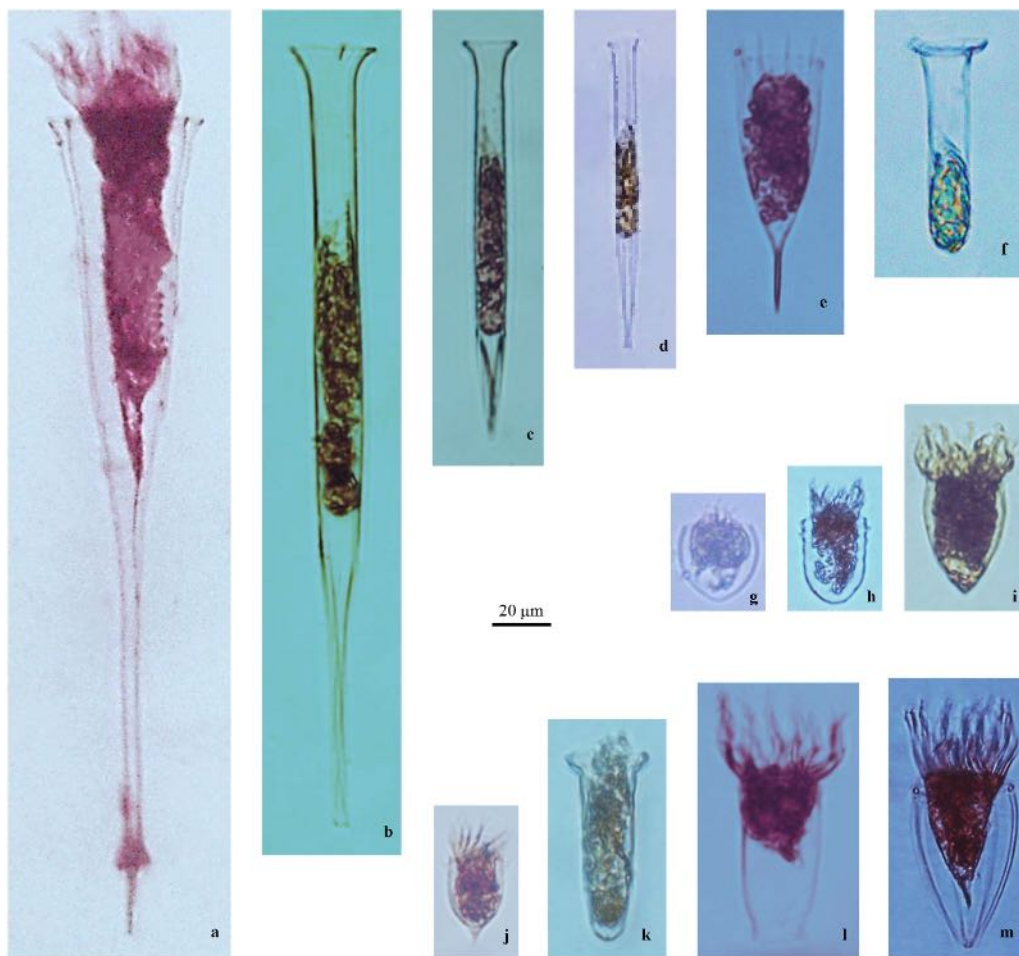
Fig. 4. Photomicrographs of tintinnid dominant species in this cruise. a, *Rhabdonellopsis apophysata*; b, *Salpingella acuminata*; c, *S. decurtata*; d, *S. faurei*; e, *Dadayiella ganymedes*; f, *Steenstrupiella gracilis*; g, *Metacylis sanyahensis*; h, *Ascampbelliella armilla*; i, *Protorhabdonella curta*; j, *Acanthostomella minutissima*; k, *Canthariella brevis*; l, *Eutintinnus apertus*; m, *P. simplex*.

(Fig. A3).

3.4. Relationship between ciliate abundance and environmental variables

Relationship between ciliate abundance (aloricate ciliate small, medium, and large size-fractions; tintinnid dominant species) and environmental variables (temperature, salinity, Chl *a* and DO) were different in OMZ and other zones at all stations (Fig. 7). For aloricate ciliates, higher abundance of small, medium, and large size-fractions occurred in sable and rapid variation zones than in OMZ. Regarding differences among the three zones at each station, aloricate ciliate of three size-fractions mainly distributed in relative high temperature, salinity, Chl *a* and DO ranges (Fig. 7; Fig. A4).

As for tintinnids, species belonged to Group I (*A. armilla*, *C. brevis*, *E. apertus*, *M. sanyahensis*, *P. curta*, *R. apophysata* and *S. gracilis*) mainly distributed in waters with temperature from 25 °C to 30 °C, salinity from 33 to 35 and DO from 4 to 8 mg L^{-1}. Species belonged to Group II (*A. minutissima*, *D. ganymedes*, *P. simplex*, *S. acuminata*, *S. decurtata* and *S. faurei*) had similar salinity and Chl *a* range to Group I, but they had wider temperature and DO range (Fig. 7; Fig. A5). Although Group II can distribute in OMZ, their abundance were much lower than in stable and rapid variation zones (Fig. 7).

Principal component analysis of the 57 samples and 3 aloricate ciliate size-fractions, 13 tintinnid dominant species was conducted to examine the contribution of the environmental variables to planktonic ciliate occurrence in each station (Fig. 8; Fig. A6). Two principal components discriminated the environmental conditions in different zones

of each station. These components explained large proportions of the variance in Sts. IO1 (78.3%), IO2 (86.5%), IO3 (92.8%) and IO4 (90.3%), respectively. In Sts. IO1-IO3, the first principal component was closely related to seawater depth, temperature, DO, tintinnid, aloricate ciliate, total ciliate. Ciliate had strong positive correlation with temperature and DO but strong negative correlation with depth. Three size-fractions of aloricate ciliate mainly had positive correlation with temperature and DO, while most of tintinnid dominant species had strong positive correlation with Chl *a* (Fig. A6).

In thermocline zones of each station, these components explained large proportions of the variance in Sts. IO1 (86.6%), IO2 (81.7%) and IO3 (88.7%), respectively. While in OMZs, these components explained relative lower proportions of the variance in Sts. IO1 (85.8%), IO2 (77.2%) and IO3 (81.6%) compared to thermocline zones, respectively.

In St. IO1, only *A. armilla*, 20–30 μm and > 30 μm size-fractions had positive correlation with temperature and DO in thermocline zone. However, both aloricate ciliate and tintinnid had positive correlation with temperature and Chl *a* (Fig. 8). In thermocline zones of Sts. IO2 and IO3, aloricate ciliate and total ciliate had positive correlation with temperature and DO. Tintinnid had positive correlation with Chl *a*. While in OMZs, both aloricate ciliate and tintinnid had positive correlation with temperature (Fig. 8). In St. IO4, the first principal component was closely related to Chl *a*, salinity, DO, temperature, depth, total ciliate, aloricate ciliate and tintinnid. Ciliate had positive correlation with Chl *a*, salinity and depth but negative correlation with DO and temperature (Fig. 8).

Table 2
Tintinnid species dimensions (LL: lorica length; LOD: lorica oral diameter), biogeography type (BT), maximum abundance (A_{max}, ind. L^{-1}), occurrence frequency (OF, %) and its dominance index (Y) at all stations in the Bay of Bengal, eastern Indian Ocean.

Species	LL (μm)	LOD (μm)	BT	St. IO1			St. IO2			St. IO3			St. IO4		
				OF	Y	A_{max}	OF	Y	A_{max}	OF	Y	A_{max}	OF	Y	A_{max}
*Acanthostomella conicoides**	42.2	22.0	C										20.0	<0.01	1
A. minutissima	27.5 ± 3.3	19.6 ± 1.9	C	31.3	**0.04**	4	41.2	**0.03**	4	44.4	**0.07**	20	20.0	<0.01	2
*Amphorellopsis acantharus**	60.1 ± 2.6	24.4 ± 1.9	C							5.6	<0.01	2			
*Amphorides brandti**	136.9	30.6	C	6.3	<0.01	2									
*A. laackmanni**	79.0 ± 1.9	24.7 ± 0.8	C	6.3	<0.01	1				5.6	<0.01	1			
*A. minor**	76.2 ± 9.4	35.5 ± 0.3	C				5.9	<0.01	1	16.7	<0.01	1			
A. quadrilineata	106.4 ± 7.7	45.8 ± 3.8	C	6.3	<0.01	4	23.5	0.01	3	16.7	<0.01	3			
Ascampbelliella armilla	28.9 ± 1.4	21.6 ± 1.0	W	18.8	**0.02**	4	23.5	0.01	3	27.8	<0.02	8	40.0	**0.02**	3
*A. retusa**	33.1 ± 2.8	31.8 ± 2.6	W				5.9	<0.01	1	22.2	<0.01	6			
Brandtiella palliata	139.8 ± 7.3	43.7 ± 3.0	W	6.25	<0.01	4	11.8	<0.01	1	11.1	<0.01	8	20.0	<0.01	1
Canthariella brevis	62.8 ± 6.1	27.7 ± 2.7	W	6.25	<0.01	3				22.2	<0.01	2	60.0	**0.03**	2
*C. pyramidata**	47.3	23.0	W										20.0	<0.01	1
*Climacocylis scalaria**	196.5 ± 63.7	48.5 ± 12.0	W				5.9	<0.01	2	22.2	<0.01	2			
*Codonella cuspidata**	86.4 ± 7.0	58.2 ± 1.8	C	6.3	<0.01	1	17.6	<0.01	1	5.6	<0.01	1			
*Codonellopsis meridionalis**	193.8 ± 33.0	55.9 ± 4.4	C				11. 8	<0.01	3	5.6	<0.01	1			
C. morchella	80.6 ± 11.9	30.9 ± 1.8	C				17.6	<0.01	2	22.2	<0.01	2			
*Cyttarocylis eucecryphalus**	104.9	105.7	W	6.3	<0.01	1									
Dadayiella ganymedes	96.9 ± 12.2	29.3 ± 1.9	C	18.8	0.01	2	52.9	**0.08**	9	44.4	<0.02	4	20.0	<0.01	1
*D. pachytoecus**	91.9 ± 5.7	30.5 ± 3.1	C							5.6	<0.01	1	20.0	0.01	4
*Dictyocysta reticulata**	58.8	33.4	C				5.9	<0.01	1						
*D. spinosa**	49.8 ± 3.9	33.7 ± 2.5	C	6.3	<0.01	1	29.4	<0.02	3	5.6	<0.01	1	20.0	<0.01	2
*Epiplocylis constricta**	102.6 ± 1.7	59.3 ± 0.9	W				5.9	<0.01	1	5.6	<0.01	2	20.0	<0.01	1
*Epiplocyloides reticulata**	60.2	44.5	W							5.6	<0.01	1			
Eutintinnus apertus	65.5 ± 13.7	26.7 ± 1.9	C							22.2	<0.01	4	80.0	**0.05**	2
E. fraknoii	248.4 ± 27.9	46.5 ± 1.9	C				11.8	<0.01	5				20.0	<0.01	2
*E. hasleae**	37.1 ± 6.6	25.7 ± 1.9	C	6.3	<0.01	2				5.6	<0.01	1			
E. lusus-undae	174.4 ± 15.3	40.5 ± 4.1	C	12.5	<0.01	2	11.8	<0.01	4	16.7	<0.01	6	40.0	0.01	1
*E. pacificus**	58.3	25.7	C							5.6	<0.01	1			
*E. stramentus**	173.2	25.9	C							5.6	<0.01	1			
*E. tubulosus**	122	30.5	C							5.6	<0.01	1			
*Metacylis conica**	42.1	12.1	C	6.3	<0.01	1				16.7	<0.01	1			
M. sanyahensis	23.3 ± 2.0	23.0 ± 1.0	C							16.7	<0.01	5	60.0	**0.02**	1
*Ormosella apsteini**	125	41.2	–				5.9	<0.01	1						
*O. bresslaui**	65.2 ± 3.6	31.1 ± 0.7	–				5.9	<0.01	1	5.6	<0.01	1			
*O. schweyeri**	68.8	19.8	–							5.6	<0.01	1			
*Parundella aculeata**	156.2 ± 9.7	27.8 ± 0.6	C	12.5	<0.01	1	11.8	<0.01	2	5.6	<0.01	1			
*P. caudata**	154.1 ± 6.4	27.6 ± 0.4	C				11.8	<0.01	2	5.6	<0.01	1			
*P. inflata**	107.8 ± 3.6	30.2 ± 0.5	C	6.3	<0.01	1	5.9	<0.01	1						
Proplectella perpusilla	47.6 ± 3.7	29.1 ± 1.3	W				17.6	<0.01	1	33.3	<0.01	2	40.0	0.01	1
*P. urna**	34.3	10.6	W				5.9	<0.01	1						
Protorhabdonella curta	39.5 ± 1.9	27.4 ± 1.5	C	18.8	0.01	2	11.8	<0.01	3	27.8	0.01	5	80.0	**0.14**	5
P. simplex	54.6 ± 3.7	33.6 ± 1.4	C	12.5	<0.01	1	11.8	<0.01	2	16.7	<0.01	2	60.0	**0.03**	2
*Rhabdonella amor**	80.6 ± 8.4	46.1 ± 1.8	W				5.9	<0.01	1				40.0	<0.02	2
*R. elegans**	172.8 ± 10.3	47.8 ± 2.5	W				17.6	<0.01	3						
*R. exilis**	61.6 ± 8.2	27.6 ± 1.7	W	6.3	<0.01	1				22.2	<0.01	3	20.0	<0.01	1
*R. indica**	59.4 ± 2.5	33.3 ± 0.2	W							5.6	<0.01	1	20.0	<0.01	1
*R. sanyahensis**	138	39.8	W	6.3	<0.01	1									
Rhabdonellopsis apophysata	308.9 ± 33.6	56.2 ± 1.7	W										60.0	**0.04**	3
Salpingella acuminata	267.4 ± 31.0	31.2 ± 4.2	C	6.3	<0.01	1	29.4	**0.03**	5	27.8	0.01	8	200.	<0.01	2
*S. attenuata**	363.8 ± 34.7	33.0 ± 1.4	C				5.9	<0.01	1	16.7	<0.01	1	0	0	0
S. curta	93.5 ± 8.3	14.4 ± 1.0	C				23.5	0.01	3	44.4	<0.02	5	20.0	<0.01	1

Table 2 (*continued*)

Species	LL (µm)	LOD (µm)	BT	St. IO1 OF	Y	A_{max}	St. IO2 OF	Y	A_{max}	St. IO3 OF	Y	A_{max}	St. IO4 OF	Y	A_{max}
S. decurtata*	140.3 ± 15.9	17.5 ± 1.4	C	18.8	0.01	3	29.4	<0.02	2	27.8	**0.02**	15	20.0	0.01	4
S. faurei	103.5 ± 18.2	12.3 ± 1.5	C	6.3	<0.01	1				38.9	**0.04**	12	60.0	**0.03**	2
S. minutissima*	74.3 ± 9.0	13.9 ± 1.2	C							16.7	<0.01	4			
S. rotundata*	82.1	15.9	C							5.6	<0.01	1			
Salpingella sp. 1 *	49.2 ± 6.2	14.0 ± 1.8	C	6.3	<0.01	1	5.9	<0.01	2	11.1	<0.01	2			
Steenstrupiella gracilis	75.6 ± 3.2	31.3 ± 2.0	C	12.5	<0.01	2	11.8	<0.01	1	16.7	<0.01	2			
S. intumescens*	203.6 ± 10.6	35.1 ± 1.2	C	6.3	<0.01	1	11.8	<0.01	1	11.1	<0.01	4			
S. robusta*	107.4 ± 14.0	32.3 ± 0.8	C	6.3	<0.01	1				11.1	<0.01	3			
S. steenstrupii*	136.8 ± 6.2	33.5 ± 3.3	C	18.8	<0.01	1				16.7	<0.01	2			
Xystonella treforti*	216.8 ± 4.0	49.4 ± 1.4	W												
Xystonellopsis cyclas*	198.4	50.3	W							5.6	<0.01	2			

Note: The biogeography of tintinnid genera were derived according to Dolan and Pierce. (2013). C: Cosmopolitan; W: Warm Water; –: not classified; *: species with counting number < 10; Species in bold black were dominant species with Y > 0.02; LL and LOD were presented as mean values ± standard deviation.

4. Discussion

4.1. Vertical distribution of planktonic ciliate

Planktonic ciliates are indispensable component in the marine planktonic food web, and vertical distribution information is the key to understanding their function. With respect to vertical distribution patterns of planktonic ciliates, bimodal type (abundance peak at surface and DCM layers, respectively) were common feature in oceanic waters of the Pacific Ocean (Yang et al., 2004; Sohrin et al., 2010; Wang et al., 2019, 2020, 2021a, 2021b) and the equatorial central Indian Ocean (Sorokin et al., 1985). Our results were similar to those studies.

Abundance proportions of aloricate ciliate were higher than 80% in the tropical western Pacific Ocean (Yang et al., 2004; Gómez, 2007; Sohrin et al., 2010; Wang et al., 2019). Our result of >70% in the eastern Indian Ocean at each sampling point is comparable to that of previous studies. The more active grazing or excretion activities of aloricate ciliate than tintinnids probably be the reason (Dolan, 2000).

Compared to waters shallower than 100 m layers, planktonic ciliate abundance and biomass were much lower in OMZs (Fig. 2). There might be two possible reasons: 1, extremely low abundance of food items (such as phytoplankton, picoplankton) in marine oxygen minimum zone for planktonic ciliate to prey (Not et al., 2008; Xiang et al., 2019; Zhao et al., 2020; Ma et al., 2021a, 2021b); and 2, most planktonic ciliate belonging to heterotrophic organisms (aerobic organisms) in waters deep than 100 m (Dolan and Marrasé, 1995; Wang et al., 2019), thus their tolerance to dissolved oxygen concentrations at OMZs (≤ 2 mg L^{-1}) might be lower than that in thermocline zones (Saltzman and Wishner, 1997).

Previous study showed that microzooplankton abundance in oceanic seas with high salinity was higher than that in inshore area with low salinity in the western Bay of Bengal (Jyothibabu et al., 2008). Consistent with Jyothibabu et al. (2008), our results showed that ciliate abundance and salinity in surface waters in latitudinal direction first increased form equator (St. IO4) to St. IO3, then decreased northward to St. IO1, which had low salinity due to fresh water discharge from the land.

Through comparing total ciliate average abundance at OMZs of this study with previous studies in the Pacific Ocean at similar depths and latitude (Wang et al., 2019, 2021a, 2021b), we found lower values occurred at almost each depth in our study (Fig. A7). Previous studies showed that dissolved oxygen concentrations at each similar sampling depth in the tropical Pacific Ocean were about 1 mg L^{-1} higher than that in OMZs of our study (Ma et al., 2021b; Wang et al., 2021b), thus the low dissolved oxygen concentrations may be responsible for low ciliate abundance.

4.2. Variations in aloricate ciliate size-fractions and small size-fraction dominant in OMZ

Abundance proportions of different aloricate ciliate size-fractions were studied in the Red Sea (Claessens et al., 2008), Arctic Ocean (Wang et al., 2020, 2022b), Pacific Ocean (Yang et al., 2004; Wang et al., 2020, 2021a, 2021b, 2022b) and Antarctic (Liang et al., 2018). However, they were not studied in the eastern Indian Ocean. In the tropical Pacific Ocean, average abundance proportions of small size-fraction (10–20 µm) to total aloricate ciliates ranged from 38 to 50% (from surface to 200 m depth), suggesting that small size-fraction aloricate ciliate being dominant group at each depth in most stations (Yang et al., 2004; Wang et al., 2020, 2021a, 2021b). Our results for small size-fraction aloricate ciliate in the eastern Indian Ocean were consistent with those of previous studies in the tropical Pacific Ocean at upper 200 m depths with relatively high temperature.

In waters deeper than 200 m, our study showed that small size-fraction aloricate ciliate became more dominant with abundance proportion higher than 50% at most sampling points where temperature was relatively low. This phenomenon did not support Bergmann's rule
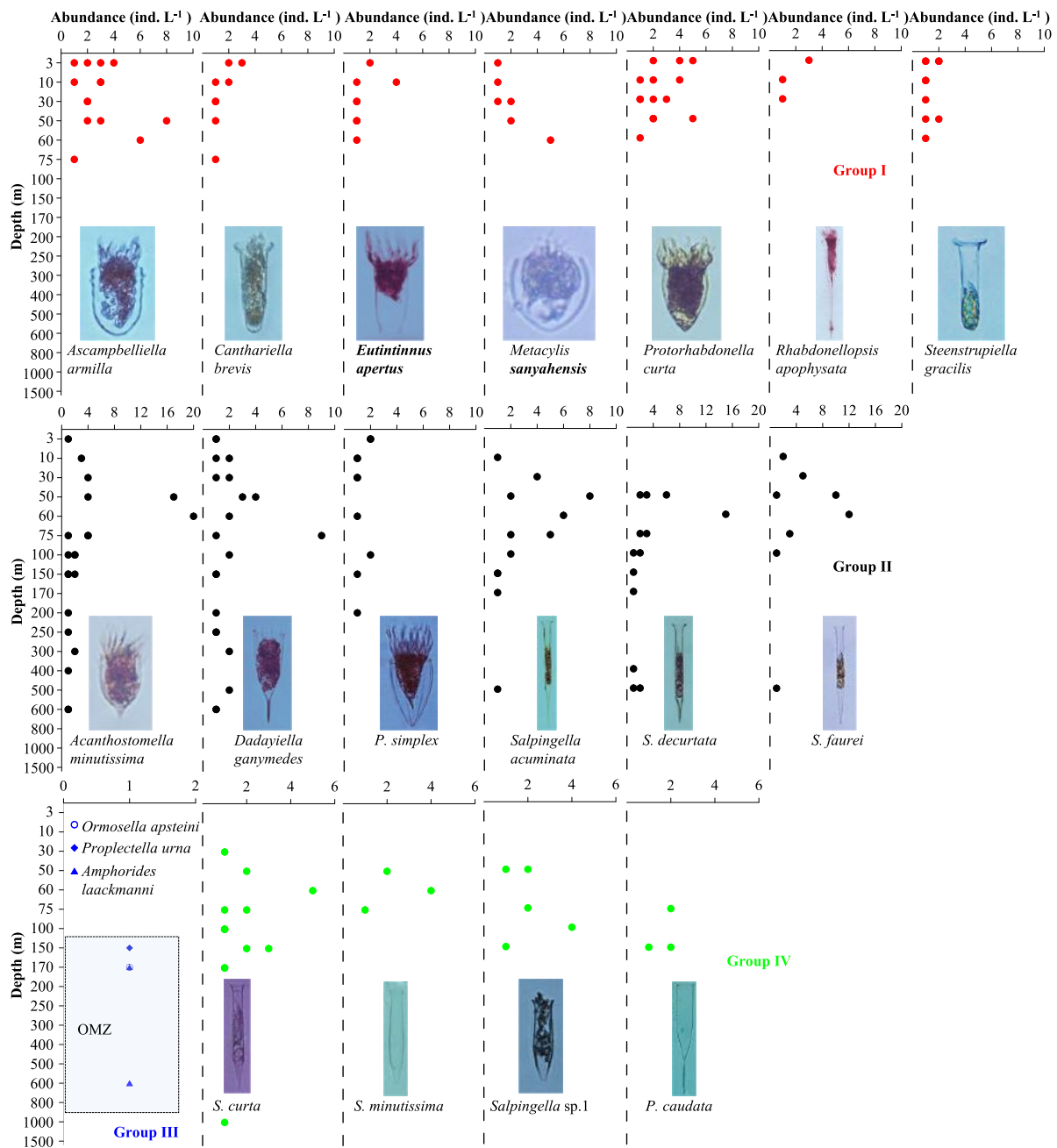
Fig. 5. Four vertical distribution groups of tintinnid species in 3–1500 m in all stations. Red dots, tintinnids belonging to group I (0–100 m); black dots, tintinnids belonging to group II (distributed through the water column); Blue dots, tintinnids belonging to group III (>100 m); Green dots, tintinnids belonging to group IV (50–200 m). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

that, in general, larger-sized animals tend to live in cold environment than their smaller-sized relatives (Bergmann, 1847). We speculated two possible reasons for this phenomenon: 1, small-bodied aloricate ciliate may had selective advantage in avoiding predators; and 2, large-bodied aloricate ciliate had stronger metabolic rate than those with small-body (Brown et al., 2004), thus they might consume more oxygen and can not survive in OMZ. If OMZs become thicker or more extensive in the Bay of Bengal in the future (Wishner et al., 2020; Vidhya et al., 2022), the aloricate ciliate small size-fraction may gain a more pronounced advantage.

4.3. Tintinnid abundance and species richness decreasing in OMZ

Tintinnid vertical distribution were studied in the Mediterranean Sea (Kršinić, 1982, 1998; Kršinić and Grbec, 2002), Bedford Basin (Nova Scotia, Canada, Paranjape, 1987), Barents Sea (Boltovskoy et al., 1991), Southwestern Atlantic Ocean (Thompson et al., 1999, 2001; Thompson and Alder, 2005), tropical Pacific Ocean (Li et al., 2018; Wang et al., 2019, 2021b) and Antarctic waters (Liang et al., 2018, 2020). However, there was no similar study in the Indian Ocean. Kršinić (1982) and Wang et al. (2019, 2021b) divided tintinnids species into several groups based on depth range of their distribution: 0–100 m, 50–200 m, > 100 m, > 600 m (not found in the Pacific Ocean) and in whole water column. Tintinnids in our results were also classified into four groups with that of
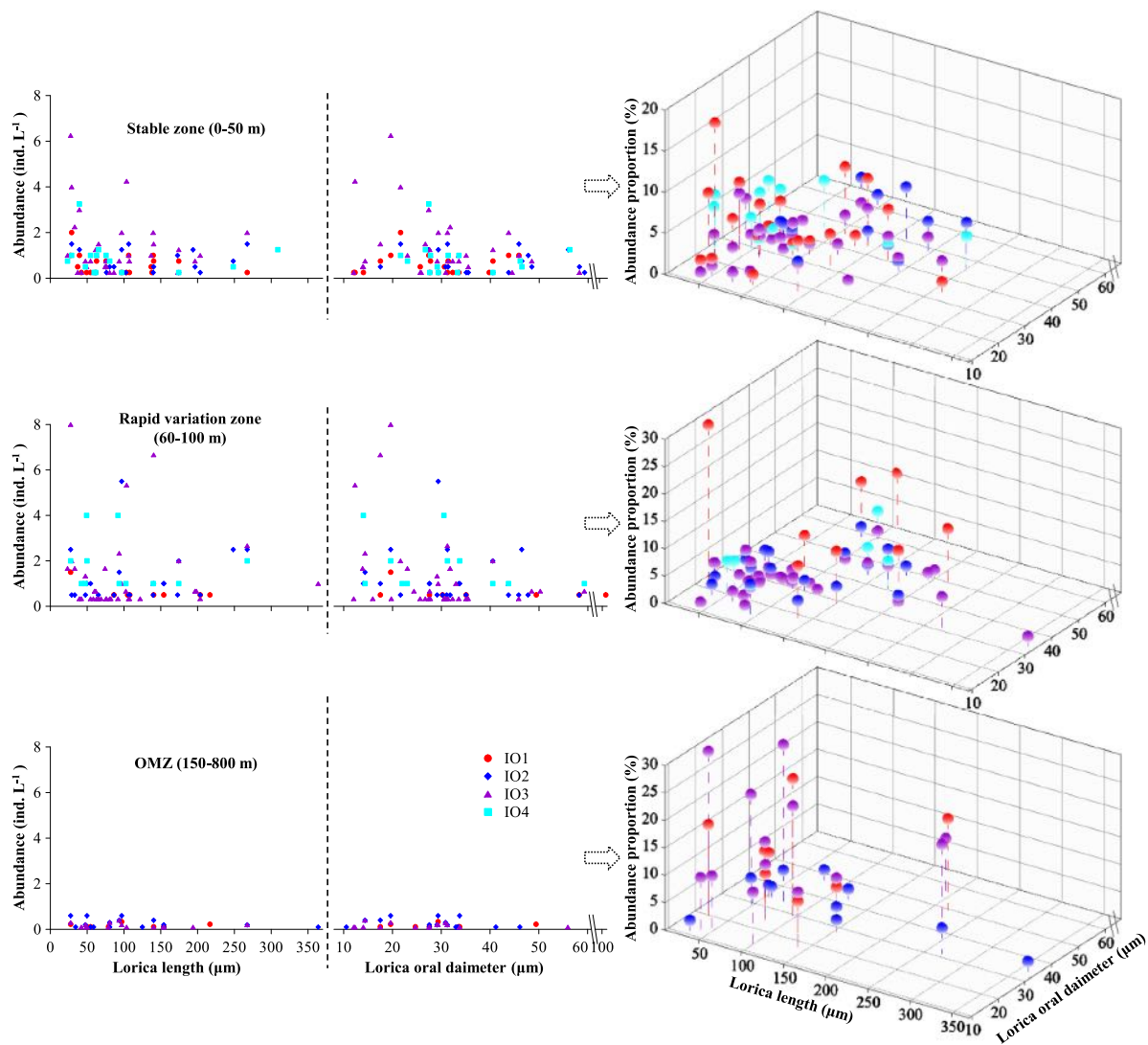
Fig. 6. Three-dimensional representation for abundance and abundance proportion of tintinnid lorica length and lorica oral diameter in stable, rapid variation zones and OMZs.

Wang et al. (2019, 2021b). Our results also showed that all dominant species in all stations belonged to 0–100 m and whole water column groups. We speculated that food items composition in surface and around DCM layers of the eastern Indian Ocean might be similar to that in the tropical Pacific Ocean (Venrick, 1988; Zhao et al., 2020), thus supporting similar two dominant groups.

Tintinnid abundance were highest at around DCM layers in the Pacific Ocean, then followed by surface layers (Li et al., 2018; Wang et al., 2019, 2021a, 2021b). Our results in the eastern Indian Ocean showed a similar vertical distribution pattern. With respect to tintinnid species richness, Zhang et al. (2017) and Jyothibabu et al. (2008) found 126 species and 75 species in the eastern Indian Ocean, respectively, which were much higher than in our results. Low number of sampling stations might be the main reason of lower species richness in present work. All tintinnid species in our study also occurred in previous researches in the Indian Ocean (Sorokin et al., 1985; Jyothibabu et al., 2008; Liu et al., 2012; Jónasdóttir et al., 2013; Zhang et al., 2017). No species belonging to neritic genera were found in the Bay of Bengal in our study compared to Jyothibabu et al. (2008). Oceanic species *D. ganymedes*, which is a warm water species in the Pacific (Li et al., 2021), occurred in St. IO1 in our study. Therefore, we speculated that sampling stations were not located at mixing areas between oceanic and neritic waters (e.g., the

Ganges River discharging area). Tintinnid species richness in thermocline zones decreased from south (St. IO3) to north (St. IO1) along with the decreasing gradient of salinity as in the Pearl River estuary, southern China (Li et al., 2019). In the OMZ, both tintinnid abundance and species richness decreased sharply comparing to 100 m layers. Coupled with positive correlation between tintinnid and DO, we speculated that low oxygen concentrations might be the vital reason for low abundance of heterotrophic tintinnids.

Body size constrains prey-predator interactions and physiology, thus plankton size spectra were used to indicate plankton community structure and ecological function (Vandromme et al., 2012). For microzooplanktonic tintinnid, the LOD is closely related to the size of its preferred food item (approximately 25% of the LOD) (Dolan, 2010). As for number of species richness in each LOD size-class, Zhang et al. (2017) found that both 28–32 μm and 58–62 μm LOD size-classes were highest in the Indian Ocean. Our study found that 28–32 μm LOD size-class had highest number of species richness in most depths, consistent with Zhang et al. (2017). But no species belonging to 58–62 μm LOD size-class were found in our study might be due to the low sampling frequency (Dolan et al., 2007, 2009). With respect to tintinnid abundance proportion, the 24–28 μm and 28–32 μm LOD size-classes had highest value at most zones in each station (Fig. A3). These results
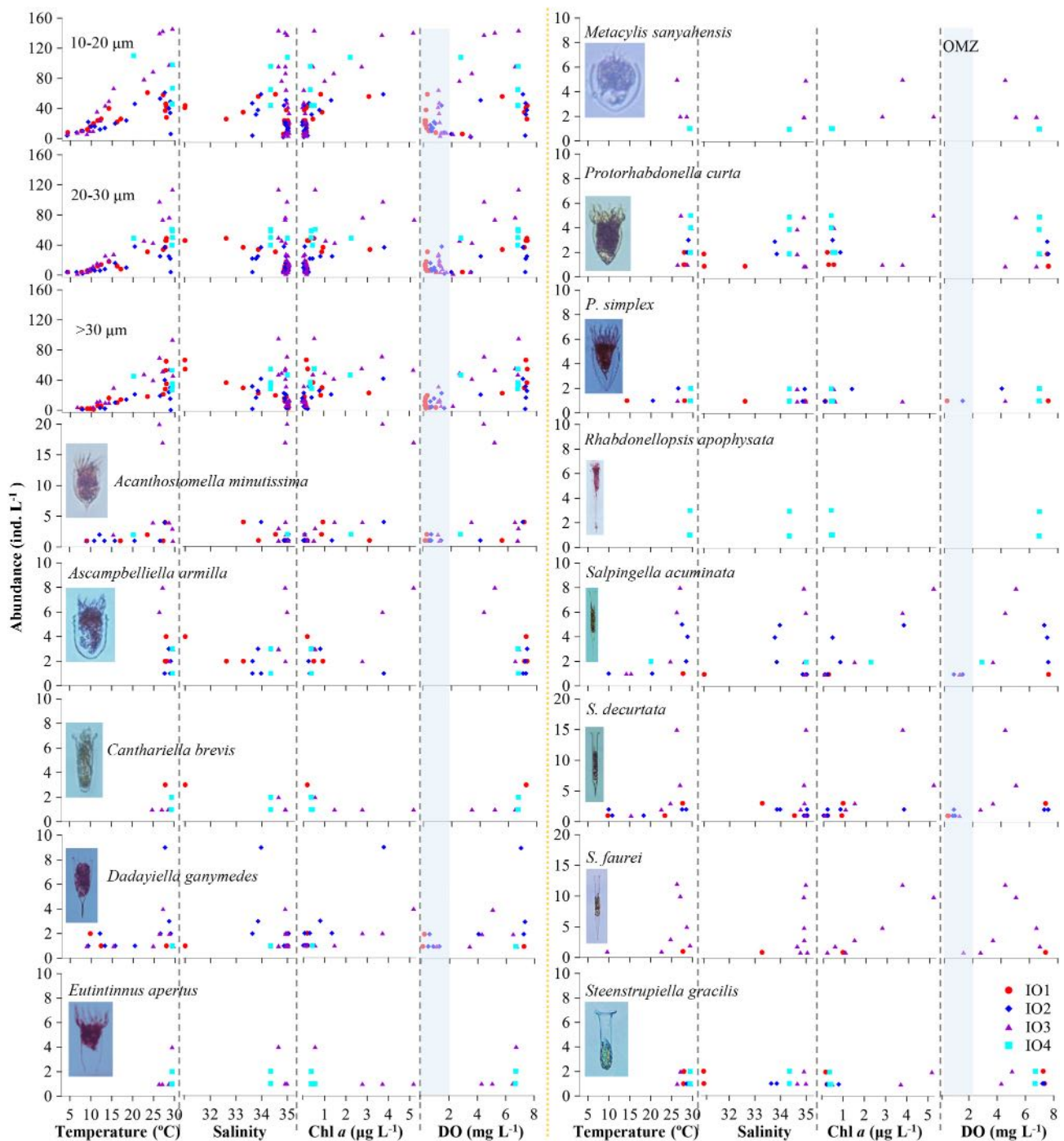
Fig. 7. Relationship between aloricate ciliate three size-fractions (10–20 µm, 20–30 µm and > 30 µm), tintinnid dominant species abundance and environmental variables (temperature, salinity, Chl *a* and dissolved oxygen (DO)).

suggested that preferred food item size of tintinnid ranged from 6 to 8 µm in our study area, which were similar to that in the tropical west Pacific Ocean (Li et al., 2018).

4.4. Relationship between ciliate and environmental variables and potential bottom-up control in OMZs

The relationship between ciliate abundance and environmental variables has been studied almost all around the world oceans (e.g., Dolan and Marrasé, 1995; Suzuki and Taniguchi, 1998; Jiang et al., 2011; Li et al., 2018; Liang et al., 2018) without uniform conclusions. For example, ciliate abundance showed significant correlations with Chl

a concentration in the Mediterranean Sea (Dolan and Marrasé, 1995). While in the Arctic Ocean, temperature was the main influence factor for ciliate (Wang et al., 2022b). In our results, aloricate ciliates and tintinnids had positive correlation with Chl *a*, temperature, and DO (Fig. A7). The metabolic theory of ecology (MTE) revealed that high temperature accompanied with high metabolic and grazing rate of heterotrophic zooplankton, which eventually contributed to their higher abundance (e.g., Brown et al., 2004; Lara et al., 2013). Our results about high abundance of ciliate occurred at high temperature environment also supported this theory. A high Chl *a* usually accompanied by sufficient food items, and may be important factor influencing tintinnid distribution in oceanic waters (Dolan and Marrasé, 1995; Suzuki and Taniguchi,
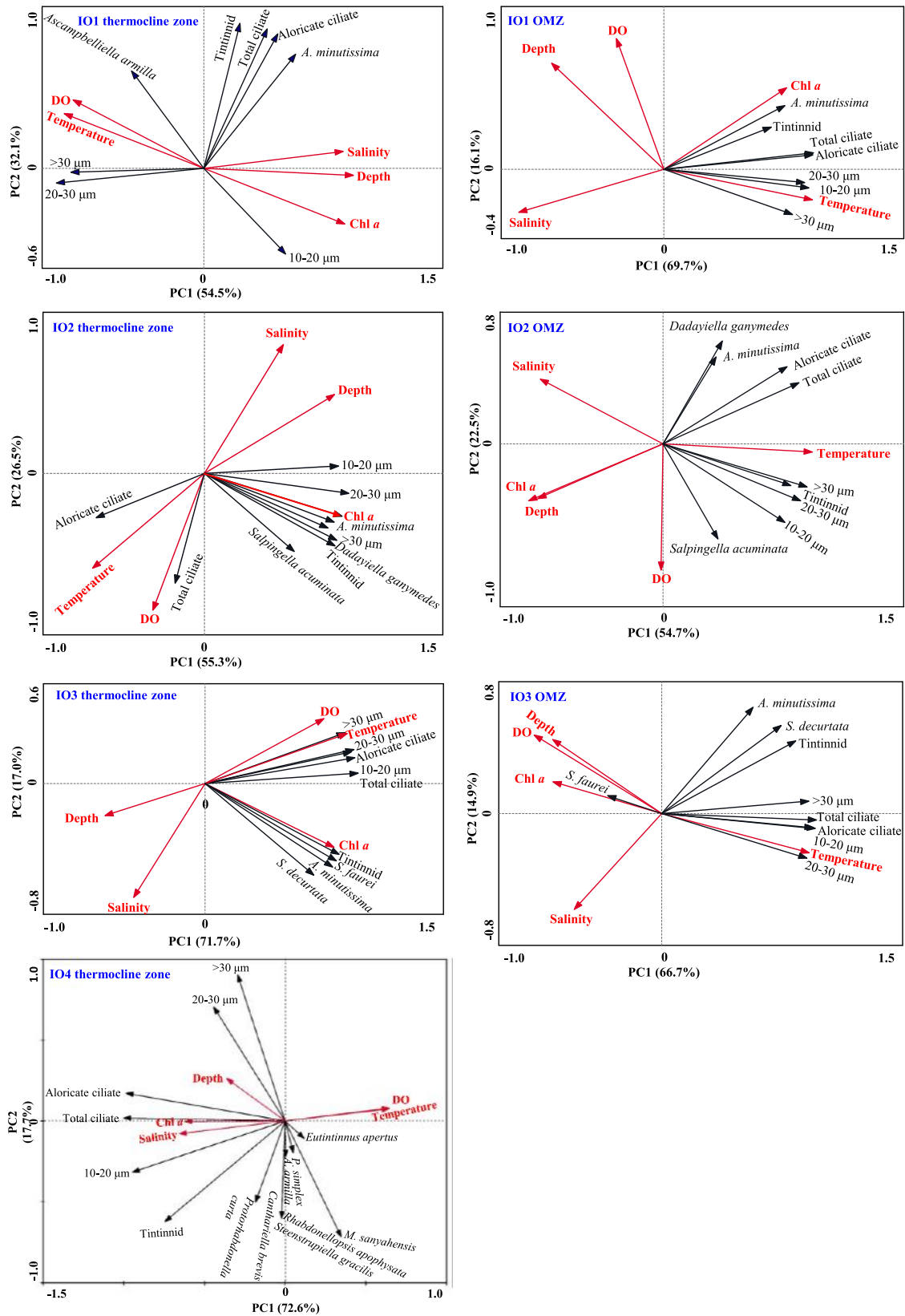
Fig. 8. Principal component analysis (PCA) of aloricate ciliate (10–20 μm, 20–30 μm and > 30 μm), tintinnid (dominant species), total ciliate abundance and environmental variables (depth, temperature, salinity, Chl *a* and dissolved oxygen (DO)) between thermocline zone and OMZ in each station. The *x*-axis is the first PCA axis, and the *y*-axis is the second PCA axis. Environmental variables and ciliate are indicated by red arrows and black arrows, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

1998). Most ciliate species were heterotrophic in tropical seas (Stoecker et al., 1996; Yang et al., 2004; Wang et al., 2019), thus high DO concentrations may be another essential driving factor for maintaining their population.

Planktonic ciliate is top grazer in the microbial food web and a connection to classical food chain (Azam et al., 1983; Pierce and Turner, 1992; Calbet and Saiz, 2005). Thus, their abundance and composition in marine ecosystem were influenced by both bottom-up control (abundance and community structure of organisms were determined by environmental resources) and top-down control (organisms at the top of food chains had strong effect on abundances of organisms at lower trophic levels) (Power, 1992; Granéli and Turner, 2002; Worm and Myers, 2003). For oxygen-consuming heterotrophic planktonic ciliates, their abundance and composition were affected by oxygen concentrations. Therefore, we speculated that the bottom-up control play a key role in determining ciliate community structure at the OMZs of the Indian Ocean. Low oxygen concentrations resulted in low abundance of ciliate and higher trophic levels (Saltzman and Wishner, 1997; Wishner et al., 1998, 2000, 2008, 2020).

5. Conclusions

The present study presented the first data on planktonic ciliate community structure variations between thermocline zones (surface to 100 m) and OMZs (150–800 m) in the eastern Indian Ocean. Planktonic ciliates showed a bimodal distribution pattern in each station with high abundance ($\geq$ 100 ind. L^{-1}) and biomass ($\geq$ 0.5 μg C L^{-1}) mainly occurred in upper 100 m, which is similar to the tropical oceanic Pacific Ocean. Aloricate ciliate small size-fraction (10–20 μm) showed increase characteristic from surface to 800 m depth. Tintinnid abundance decreased from surface or subsurface to 1500 m. Total ciliate abundance and tintinnid species richness decreased from south (St. IO3) to north (St. IO1) in the thermocline zones in latitudinal direction. All tintinnid belong to the oceanic species without influence from neritic species. Three-dimensional representation of tintinnids revealed that small-sized species in thermocline zones decreased more sharply to OMZs compared to large-sized species. In the OMZs, lower ciliate abundance occurred at almost each depth in our study compared to that in the Pacific Ocean at similar depths and latitude. Planktonic ciliate community structure showed obvious variations between thermocline zones and OMZs. Temperature and DO were main influence factors for aloricate ciliate, while for tintinnid, Chl *a* was another driving factor for their distribution. Our results represent a snapshot variations in ciliate community structure between thermocline zones and OMZs in the eastern Indian Ocean. It constitutes a baseline for further comparative studies on the temporal and spatial environmental influence on ciliate in the OMZ areas.

CRediT authorship contribution statement

Chaofeng Wang: Investigation, Conceptualization, Methodology, Writing – original draft, Funding acquisition. **Yanchu Zhao:** Writing – original draft. **Ping Du:** Writing – original draft. **Wuchang Zhang:** Conceptualization, Investigation, Writing – review & editing, Supervision, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.seares.2022.102311.

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