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Diel variations in planktonic ciliate community structure in the northern South China Sea and tropical Western Pacific

Chaofeng Wang^{1,2,3}, Yi Dong^{1,2,3}, Michel Denis⁴, Yuanyuan Wei⁵, Haibo Li^{1,2,3}, Shan Zheng^{1,6}, Wuchang Zhang^{1,2,3}✉ & Tian Xiao^{1,2,3}

Though diel variations are geographically widespread phenomena among phytoplankton and zooplankton, knowledge is limited regarding diel variations in planktonic ciliate (microzooplankton) community structure. In this study, we analyzed diel variations in community structure of planktonic ciliates in the northern South China Sea (nSCS) and tropical Western Pacific (tWP). Hydrological characteristics during day and night were slightly different over both the nSCS and tWP, while ciliate average abundance at night was clearly higher than in the day in the upper 200 m. In both the nSCS and tWP, abundance proportions of large size-fraction (> 30 μm) aloricate ciliates at night were higher than in the day. While for tintinnids, abundance proportion of large lorica oral diameter at night were lower than in the day. The relationship between environmental factors and ciliate abundance pointed out that depth and temperature were main factors influencing aloricate ciliate and tintinnid in both day and night. For some dominant tintinnid species, chlorophyll *a* was another important factor influencing their diel vertical distribution. Our results provide fundamental data for better understanding the mechanisms of planktonic ciliate community diel variation in the tropical Western Pacific Ocean.

Planktonic ciliates taxonomically belong to phylum Ciliophora, class Spirotrichea, subclass Oligotrichia and Choreotrichia¹, and they morphologically consist of tintinnids and aloricate ciliates. Marine planktonic ciliates are important components of microzooplankton as primary consumers of pico- (0.2–2 μm) and nano- (2–20 μm) sized plankton, and important food items of metazoans and fish larvae^{2–4}. Therefore, they play an important role in material circulation and energy flow from the microbial food web into the classical food chain^{5–7}. Owing to their rapid growth rates and sensitivity to environmental changes, ciliates, especially tintinnids, have been considered as effective bioindicators in different water masses because of distinctive species composition^{8–10}.

Diel variations, which are common phenomenon in marine plankton, include variations in abundance, behavior, physiology, feeding and cell-division^{11–15}. The diel behavior of phytoplankton was found to be affected by light-dependence of cell growth and continuous losses to grazing in the tropical and subtropical seas^{12,16–18}, which eventually led to community diel variations. For example, in the northern South China Sea (nSCS) at night, the abundance and cell size of picophytoplankton (*Prochlorococcus*, *Synechococcus*, and picoeukaryotes) were respectively higher and smaller than during the day¹⁸. With respect to marine planktonic zooplankton, most studies dedicated to meso-/macro-zooplankton, which have higher abundance at night than in the day owing to their diel vertical migration (descending at dawn and ascending in late afternoon and evening)^{19–26}.

In contrast, studies related to planktonic ciliate (microzooplankton) diel variations remain limited, even though several investigations on planktonic-ciliate diel variations were conducted in different habitats^{27–35}. In oceanic waters, the mixotrophic ciliate *Mesodinium rubrum* was shown higher abundance at surface waters at

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daytime than at night in the Baltic Sea^{30,32}. Some micro-sized heterotrophic ciliates at night were more abundant at surface water than in the day in the northwestern Mediterranean Sea³³. Those above two phenomenon about diel variations owing to their different diel vertical migration behaviors. But in the shelf and slope waters of the Georges Bank (northwest Atlantic)²⁹, and the Toyama Bay (Japan Sea)³¹, abundance of planktonic ciliates varied little during the day and night. In the eutrophic shallow waters of a Germany gravel pit lake characterised by stable water stratification, Rossberg and Wickham³⁴ found that the abundances of several dominant ciliate species were significantly higher in the day than at night. Despite their important role in marine microbial food webs, our knowledge of ciliate assemblage diel variations in tropical oceanic waters are limited due to their inaccessibility for oceanographic surveys.

The South China Sea is the largest semi-enclosed basin in the western Pacific Ocean³⁶, and the tropical Western Pacific (tWP) holds the largest warm pool area with sea-surface temperature > 28 °C throughout the year³⁷. Many studies were conducted on ciliate communities in the northern slope of the South China Sea^{9,38–41} and the tWP^{4,8,42–44}. However, none of these studies addressed ciliate community diel variations, nor provided any comparison between the nSCS (marginal oceanic sea) and tWP (tropical oceanic sea).

In the present study, we hypothesized that planktonic ciliate community structure might differ between day and night. By examining time-series data of ciliate community structure in the nSCS and tWP, we aimed to determine diel variations in: (1) ciliate abundance and biomass at each sampled depth; (2) overall abundance and abundance proportions of different size-fractions of aloricate ciliates; (3) tintinnid composition and the abundance proportions of different lorica oral diameter (LOD) size-classes. The output of this study is expected to be of great help in monitoring microzooplankton ecological influence in the marginal and tropical oceanic seas.

Results

Hydrology and ciliate vertical distribution diel variations. Hydrological characteristics throughout day and night were slightly different in the nSCS and tWP (Fig. 1). Temperature decreased with depth from surface (3 m) to 500 m. However from surface to 100 m depth at nSCS, its average values at each depth at daytime were slightly higher by 0.20 ± 0.16 °C than at night. In contrast, in the tWP, even temperature values at 30, 150 and 200 m were higher at daytime than at night, the average temperature values at each depth at daytime were slightly lower by 0.24 ± 0.26 °C than at night (Fig. 1). Salinity first increased from surface to approximately 150 m, then decreased to 500 m in both the nSCS and the tWP. Salinity average values at depths from surface to 100 m at daytime at both the nSCS and the tWP, were slightly higher by 0.01 ± 0.01 and 0.01 ± 0.03 , respectively, than at night. At each depth, salinity in the nSCS was higher than in tWP (Fig. 1). Chlorophyll *a* in vivo fluorescence (Chl *a*) showed similar characteristics in both day and night, while average deep Chl *a* maximum (DCM) layers in the day of the nSCS (82.5 ± 6.5 m) and the tWP (101.5 ± 12.0 m) were deeper than at night (nSCS: 77.0 ± 4.5 m; tWP: 98.7 ± 5.1 m), respectively (Fig. 1).

High ciliate total abundance (≥ 200 ind. L⁻¹) and biomass (≥ 0.5 µg C L⁻¹) values were mainly observed in the upper 100 m of nSCS and the upper 150 m of tWP, and the values decreased down to 500 m depth (Fig. 1). Aloricate ciliates were dominant groups in both the nSCS and tWP (Supplementary Fig. S1). The vertical profiles of ciliate average abundance showed bimodal (in the surface and DCM layers) patterns throughout day and night in both the nSCS and tWP. But average biomass showed surface-peak in the nSCS and DCM-peak in the tWP, respectively (Fig. 1). PERMANOVA tests indicated no significant differences between day and night of total ciliate abundance data in both the nSCS (pseudo- $F=0.074$, $P=0.944$) and tWP (pseudo- $F=0.609$, $P=0.494$) (Supplementary Table S1). From surface to 200 m depth, average abundance and biomass of ciliates at night were higher than in the day in the nSCS. While in the tWP, only average abundance of ciliates at night were higher than in the day.

Highest average total abundance and biomass values of ciliates in the nSCS occurred in surface layers, whereas in the tWP, they occurred in the DCM layers (Fig. 1). At surface layers of the nSCS, average abundance (517.0 ± 132.6 ind. L⁻¹) and biomass (2.8 ± 2.0 µg C L⁻¹) at night were 1.3 and 2.0 folds higher than in the day (413.3 ± 77.6 ind. L⁻¹ and 1.4 ± 0.7 µg C L⁻¹), respectively. At DCM layers of the tWP, average abundance (476.7 ± 21.4 ind. L⁻¹) and biomass (1.3 ± 0.2 µg C L⁻¹) at night were 1.4 and 1.1 folds higher than in the day (347.0 ± 103.2 ind. L⁻¹ and 1.2 ± 0.9 µg C L⁻¹), respectively (Fig. 1). There were almost no differences between day and night in waters deeper than 200 m in the nSCS and tWP, respectively (Fig. 1; Supplementary Fig. S1).

Water column average abundance and biomass of ciliates. Average abundance and biomass of ciliate showed different characteristics during day and night in both the nSCS and tWP (Fig. 2). In the nSCS, the average water-column abundance of total ciliates (136.3 ± 7.7 ind. L⁻¹) (Independent t -test, $P < 0.01$) and aloricate ciliates (126.2 ± 8.2 ind. L⁻¹) (Independent t -test, $P < 0.01$) at night were significant higher than that in the day (116.1 ± 8.1 ind. L⁻¹, and 106.3 ± 7.3 ind. L⁻¹), respectively. As for tintinnids, the average water-column abundance at night (10.1 ± 2.0 ind. L⁻¹) were slight higher than that in the day (9.8 ± 1.2 ind. L⁻¹) (Independent t -test, $P \geq 0.05$), but the average water-column biomass of tintinnids was lower at night (0.017 ± 0.003 µg C L⁻¹) than in the day (0.020 ± 0.004 µg C L⁻¹).

In the tWP, the average water-column abundance and biomass of total ciliates, aloricate ciliates and tintinnids at night were higher than in the day (Fig. 2). As to variations between two seas, the average water-column abundance and biomass of total ciliates and aloricate ciliates at night and day were higher in the tWP than that in the nSCS (Fig. 2), but not significant (Independent t -test, $P \geq 0.05$). Although average water-column abundance of tintinnids in both the night and day in the tWP were higher than that in the nSCS, their average water-column biomass were lower in the tWP than in the nSCS (Fig. 2).

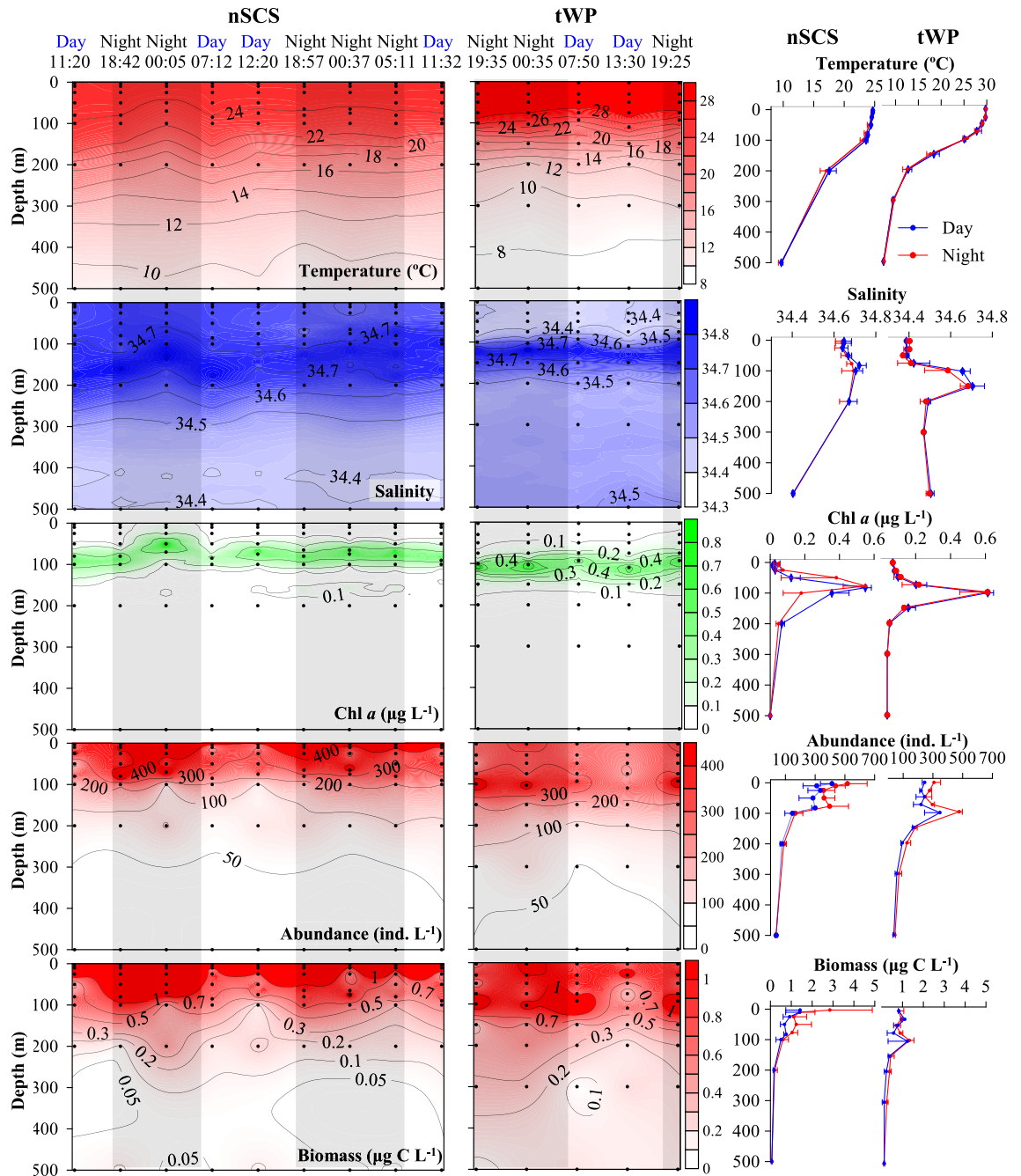


Figure 1. Temperature (T), salinity (S), Chlorophyll *a* (Chl *a*), total ciliate abundance and biomass profiles from the surface to 500 m in the northern South China Sea (nSCS) and tropical Western Pacific (tWP). Black dots: sampling depths; black shadows: night.

Aloricate ciliate size-fractions. In the nSCS and tWP, day and night average abundance and abundance proportion of each aloricate ciliate size-fraction, were different (Fig. 3). Generally, in the upper 150 m of both the nSCS and tWP, average abundance of small (10–20 µm), medium (20–30 µm) and large (> 30 µm) size-fractions of aloricate ciliate were higher at night than that in the day. In contrast, in the nSCS upper 150 m and tWP upper 75 m, abundance proportions of the small size-fraction were lower at night than that in the day. As to day and night variations in approximately the upper 80 m of nSCS and tWP, the average abundance and abundance proportion of the large size-fraction of aloricate ciliates were higher in the nSCS than that in the tWP. However, the opposite was observed at 100 m (Fig. 3). There was almost no difference between day and night abundance and abundance proportion in waters deeper than 200 m in both the nSCS and tWP (Fig. 3).

Tintinnid abundance, composition, and diversity index. In total, 69 tintinnid species from 27 genera were identified through the study (Supplementary Table S2). Among them, 57 species from 23 genera and

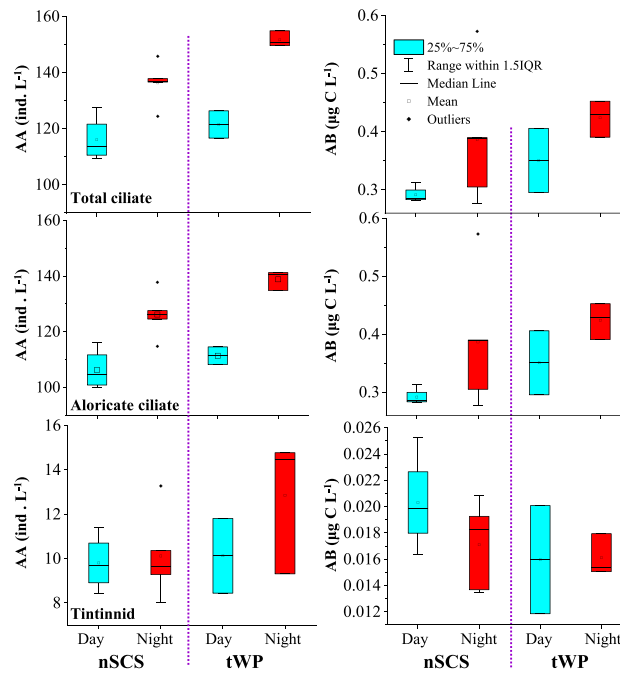


Figure 2. Diel variations of ciliate (total, aloricate ciliate and tintinnid) water column average abundance (AA) and average biomass (AB) in the nSCS and tWP.

51 species from 25 genera were observed at the nSCS and tWP, respectively. Species richness at night over the nSCS (49 species) and tWP (45 species) were slightly higher than in the day (nSCS: 44 species, tWP: 44 species), respectively (Supplementary Table S2). Tintinnid abundance ranged from 0 to 87 ind. L⁻¹ and 0–73 ind. L⁻¹ in the nSCS and tWP, respectively. Both high abundance (≥ 10 ind. L⁻¹) and species richness (≥ 5) occurred in the upper 200 m. In the nSCS, Margalef (d_{Ma}) and Shannon (H') indices were higher at night than in the day. However, in the tWP, these diversity indices hardly varied from day to night (Supplementary Fig. 2). As for tintinnid biogeography type, cosmopolitan and warm water genera were the dominant groups at both sites. Regarding diel variations in both the nSCS and tWP, more cosmopolitan and warm water species were found at night than that in the day (Supplementary Table S3).

Five and eight dominant species ($Y \geq 0.02$) occurred in the nSCS and tWP, respectively. Among them, only *Salpingella faurei* and *Proplectella perpusilla* appeared in both sites (Supplementary Table S2). As for dominant species in the nSCS, *S. faurei* and *Epiplocyclus acuminata* prefer 50 m and DCM layers and their high abundance occurred at night more frequently. In contrast, in the surface layer, *Dadayiella ganymedes* and *Steenstrupiella steenstrupii* were present in higher abundance in the day than at night. The *P. perpusilla* prefer 25 m and 50 m layers at night. But at DCM and 100 m layers, its high abundance occurred in the day more frequently (Fig. 4; Supplementary Figs. S3 and S4). In the tWP, *S. faurei*, *P. perpusilla*, *Ascampbelliella armilla*, *Acanthostomella minutissima* and *Metacyclis sanyahensis* prefer DCM layers and their high abundance occurred at night more frequently. While for *Canthariella brevis* and *Protorhabdonella curta*, their abundance were higher in the day than at night in surface layers. With regard to *Eutintinnus hasleae*, its abundance was higher at night than in the day in waters ranged from 50 to 200 m (except DCM) (Fig. 4; Supplementary Figs. S3 and S4).

Body size composition and abundance proportion of tintinnid species. Average abundance in tintinnid LOD (lorica oral diameter) size-classes had some differences throughout the day and night in both the nSCS and tWP (Fig. 5). Highest species richness and average abundance were in the 28–32 μm LOD size-class during the day and night in both the nSCS and tWP. For both day and night, the second highest species richness in the nSCS and tWP were 32–36 μm and 24–28 μm LOD size-class, respectively, while the second highest average abundance were 12–16 μm and 20–24 μm LOD size-class in the nSCS and tWP, respectively. Generally, average abundance of most tintinnid LOD size-classes were higher at night than in the day. However, these night and day values were similar in the tWP (Fig. 5).

In the nSCS, abundance proportion of *S. faurei* (highest, 16.8%) and *D. ganymedes* (second highest, 15.7%) were lower in the day than at night (18.4% and 16.1%, respectively). Abundance proportion of *S. steenstrupii* (third highest, 9.3%) was higher in the day than at night (5.5%). In the tWP, *S. faurei* (9.2%), *C. brevis* (8.8%) and *P. curta* (7.1%) had the three highest abundance proportion in the day. At night, however, species with the three highest abundance proportion changed to *A. minutissima* (9.5%), *S. faurei* (9.0%) and *P. perpusilla* (6.2%) (Fig. 5). Additionally, tintinnid species with lorica length greater than 150 μm had higher abundance proportion in the day than at night in both the nSCS and tWP (Fig. 5).

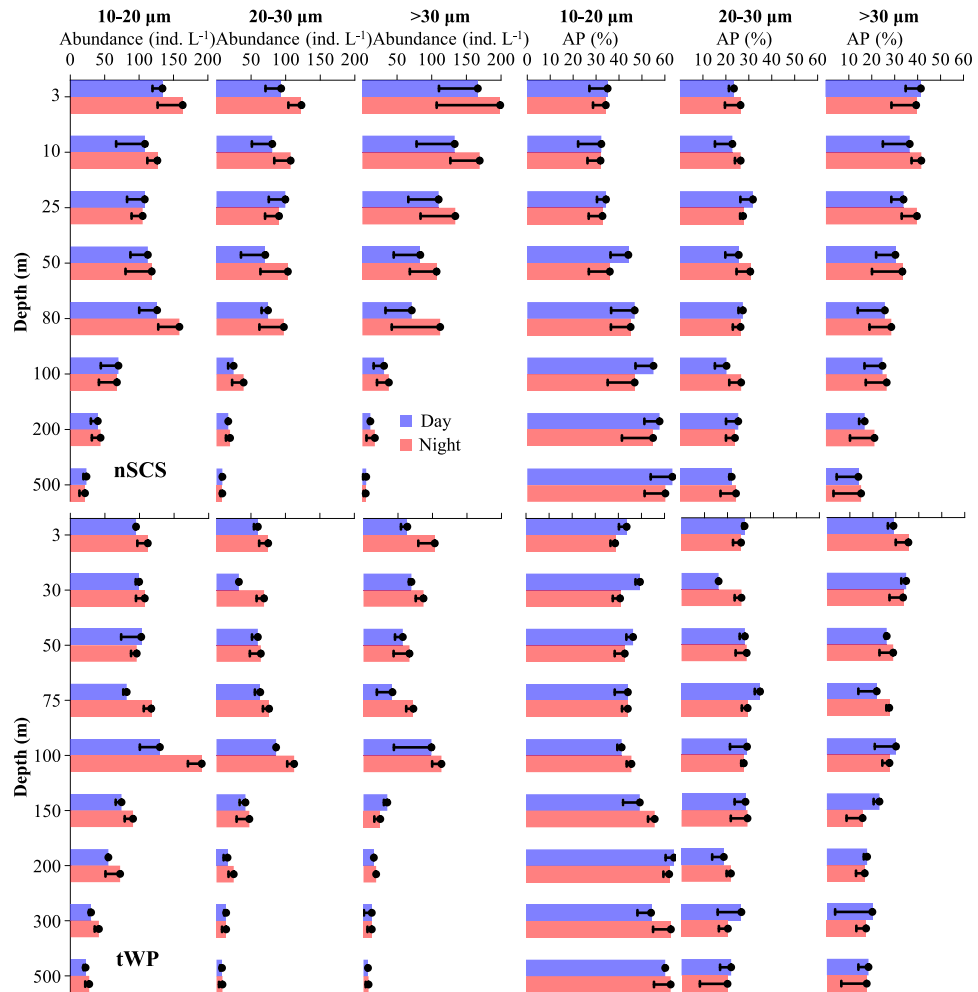


Figure 3. Diel variations of average abundance and abundance proportion (AP) of each aloricate ciliate size-fraction at each layers in the nSCS and tWP.

Relationship between ciliate abundance and environmental factors. Temperature-salinity-plankton diagrams showed that aloricate ciliate size-fractions (small, medium, and large) and tintinnid dominant species behaved within different temperature and salinity ranges that varied from day and night in the nSCS and tWP (Fig. 6). Regarding differences between the two sites, the average temperature of each aloricate ciliate size-fraction with abundance > 100 ind. L^{-1} in the nSCS ($23.1\text{--}24.8$ °C, average 24.3 ± 0.5 °C) was lower than that in the tWP ($24.8\text{--}29.8$ °C, average 27.8 ± 1.9 °C) (Supplementary Fig. S5). As for tintinnids, all dominant species (except *D. ganymedes*) in the nSCS had temperature ranges wider at night than in the day, and their higher abundance was associated with salinity higher in the day (except *E. acuminata*) than at night (Fig. 6). In the tWP, all dominant species (except *S. faurei*) corresponded to wider salinity ranges at night than in the day (Fig. 6; Supplementary Fig. S6).

Relationships between ciliate abundances and environmental factors (depth, temperature, salinity, and Chl *a*) during day and night, differed in both the nSCS and tWP (Table 1; Supplementary Table S4). In the nSCS and tWP, Aloricate ciliates and total ciliates had strong significant negative and positive correlations with depth and temperature, respectively, whether in the day or at night. As for dominant tintinnids in the nSCS, *S. faurei* had significant positive correlation with Chl *a* at night, but no correlation with Chl *a* at daytime. *P. perpusilla* had significant positive correlation with Chl *a* in the day, but no correlation with Chl *a* at night (Supplementary Table S4). In the tWP, *S. faurei*, *P. perpusilla*, *M. sanyahensis* and total tintinnids were not correlated with Chl *a* in the day, but they exhibited significant correlations at night (Supplementary Table S4).

The partial Mantel test revealed that aloricate ciliate and total ciliate had similar significant correlations with their each environmental factors between day and night in both the nSCS and tWP, respectively. But different for tintinnid. In the nSCS, except Chl *a*, tintinnid had significant correlation with depth at night ($P < 0.05$). In the tWP, tintinnid had significant correlation with temperature in the day ($P < 0.05$), but changed into had strong significant correlation with Chl *a* at night ($P < 0.01$) (Table 1).

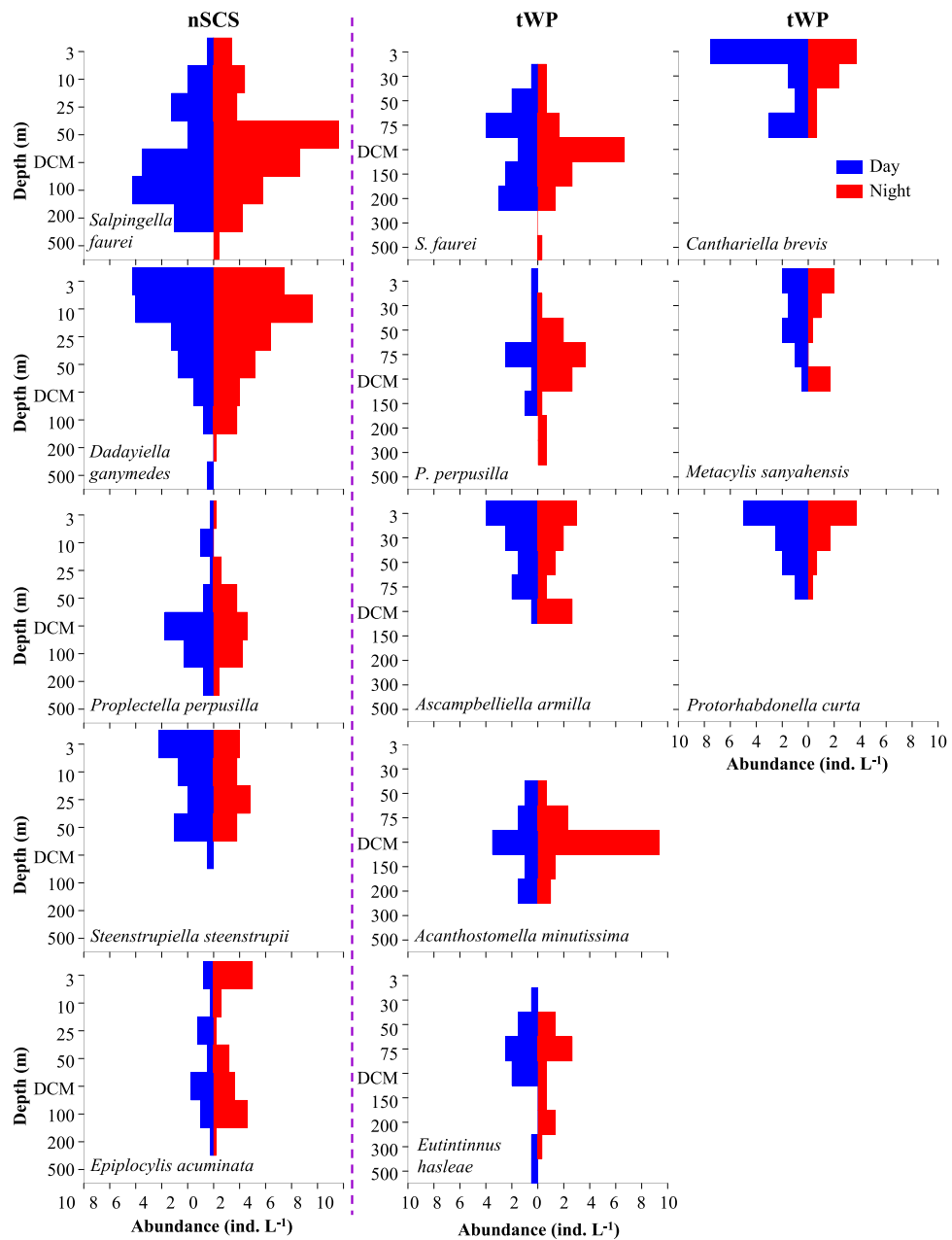


Figure 4. Diel variations of average abundance of tintinnid dominant species at each layer in the nSCS and tWP.

Discussion

Diel vertical distribution variations of ciliate community. In oceans, there were multiple factors that could influence diel variations of ciliate (diel-vertical-migration, food items concentration and quality, predator avoidance, light intensity, body metabolic rates, etc.) in various seas^{27,33,34,45–47}. Previous studies found that most planktonic ciliates do not show perceivable vertical migration^{29,31}, thus we speculate that diel-vertical-migration might not be an determining factor for ciliate diel variations. In the oligotrophic seas, the phytoplankton assemblage was dominated by *Prochlorococcus*, *Synechococcus* and picoeukaryotes, and they showed different diel variations^{12,48}. As important food items of ciliate, heterotrophic bacteria also displayed clear daily oscillations in the oligotrophic Ionian Sea (Mediterranean)⁴⁸. Thus we speculate that diel variation of food items was possibly the main reason in determining ciliate diel variation in the oligotrophic tropical seas.

The ciliate abundance was high in surface and DCM layers in both day and night of both the nSCS and tWP. These results were similar to previous ones established in the western Pacific Ocean^{40,42–45,49} and eastern Indian Ocean⁵⁰. However, the studies that previously investigated the ciliate vertical distribution, did not assess potential differences between day and night in vertical direction. Therefore, our study provides more accurate data on ciliate diel variation in the nSCS and tWP. Additionally, our results in the upper 200 m provide evidence that

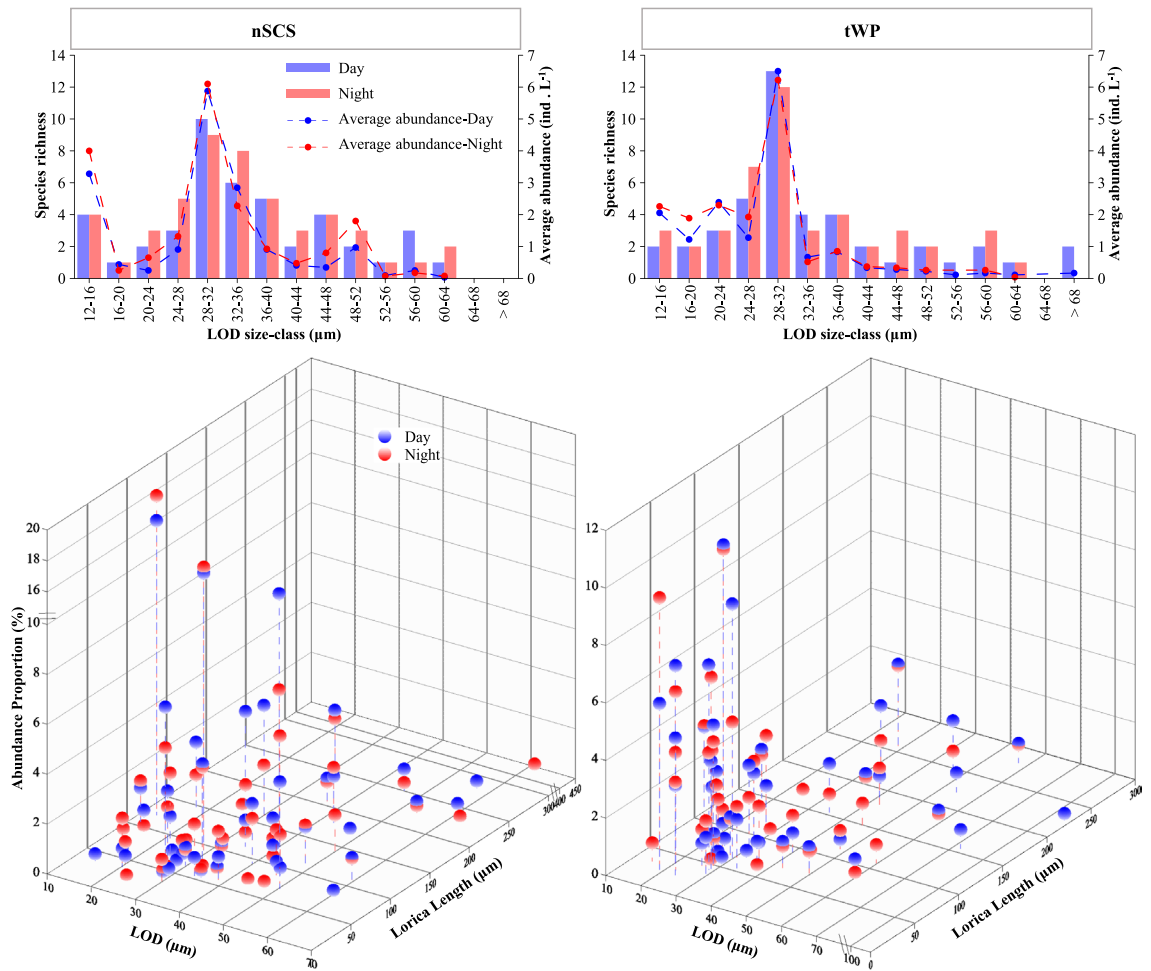


Figure 5. Day-night variations of tintinnid species richness, lorica oral diameter (LOD), lorica length, average abundance and abundance proportion in the nSCS and tWP.

ciliate abundance were higher at night than in the day in both the nSCS and tWP (Figs. 1 and 2). Zooplankton distribution in waters mainly depends on phytoplankton presence^{51,52}. Thus, it is possible that the availability of more food items (flagellates, picoeukaryotes, *Prochlorococcus*, *Synechococcus* and heterotrophic bacteria) at night than in the day explains the higher ciliate abundance at night^{18,32,48}.

Diel variations in aloricate ciliate size-fractions. Abundance proportions of different aloricate ciliate size-fractions have rarely been reported in the nSCS and tWP. In the tropical Pacific Ocean, average abundance proportions of small size-fraction (10–20 μm) of aloricate ciliates to total ciliates ranged from 38 to 50% (from surface to 200 m depth), and it belonged to the dominant group at each depth in most stations^{43,44,49}. Our results for the small size-fraction of aloricate ciliates in the tWP are consistent with those of previous studies in both day and night. In the upper 100 m of both nSCS and tWP sites, the large size-fraction (> 30 μm) of aloricate ciliates had more pronounced diel variations than those of the small size-fraction (Fig. 3). We speculated that the large size-fraction of aloricate ciliates were migrating along distances longer than those crossed by the small size-fraction. This phenomenon may be similar to that observed in meso-/macro-zooplankton in the nSCS²⁵, equatorial Pacific Ocean⁵³, subtropical and subarctic North Pacific Ocean⁵⁴, and northwest Mediterranean⁵⁵.

Potential reason for tintinnid diel variations. The LOD of a tintinnid is closely related to the size of its preferred food item (approximately 25% of the LOD)⁵⁶. Our results showed that tintinnid abundance was higher but biomass was lower at night than in the day in both the nSCS and tWP (Fig. 2). We also found that abundance and biomass proportion of the 12–16 μm LOD size-class of tintinnids was higher at night than in the day. These results suggest that both LOD size-classes of tintinnids and the size of their preferred food items were smaller at night than in the day. The night-dominant smaller cell sizes of food items (picoeukaryotes, *Prochlorococcus*, *Synechococcus*) at night than in the day¹⁸ may be coupled with the observed tintinnid diel variations.

For photosynthetic organisms, cell division generally occurs at night and/or in the late afternoon^{17,57}, which eventually leads to higher abundance at night than in the day¹⁸. As for heterotrophic microzooplankton tintinnids, photosynthetic organisms, e.g., nanoplankton (nanoflagellates), are important food items influencing their abundance and composition in the oligotrophic seas^{58,59}. Our study showed that tintinnid abundance at night

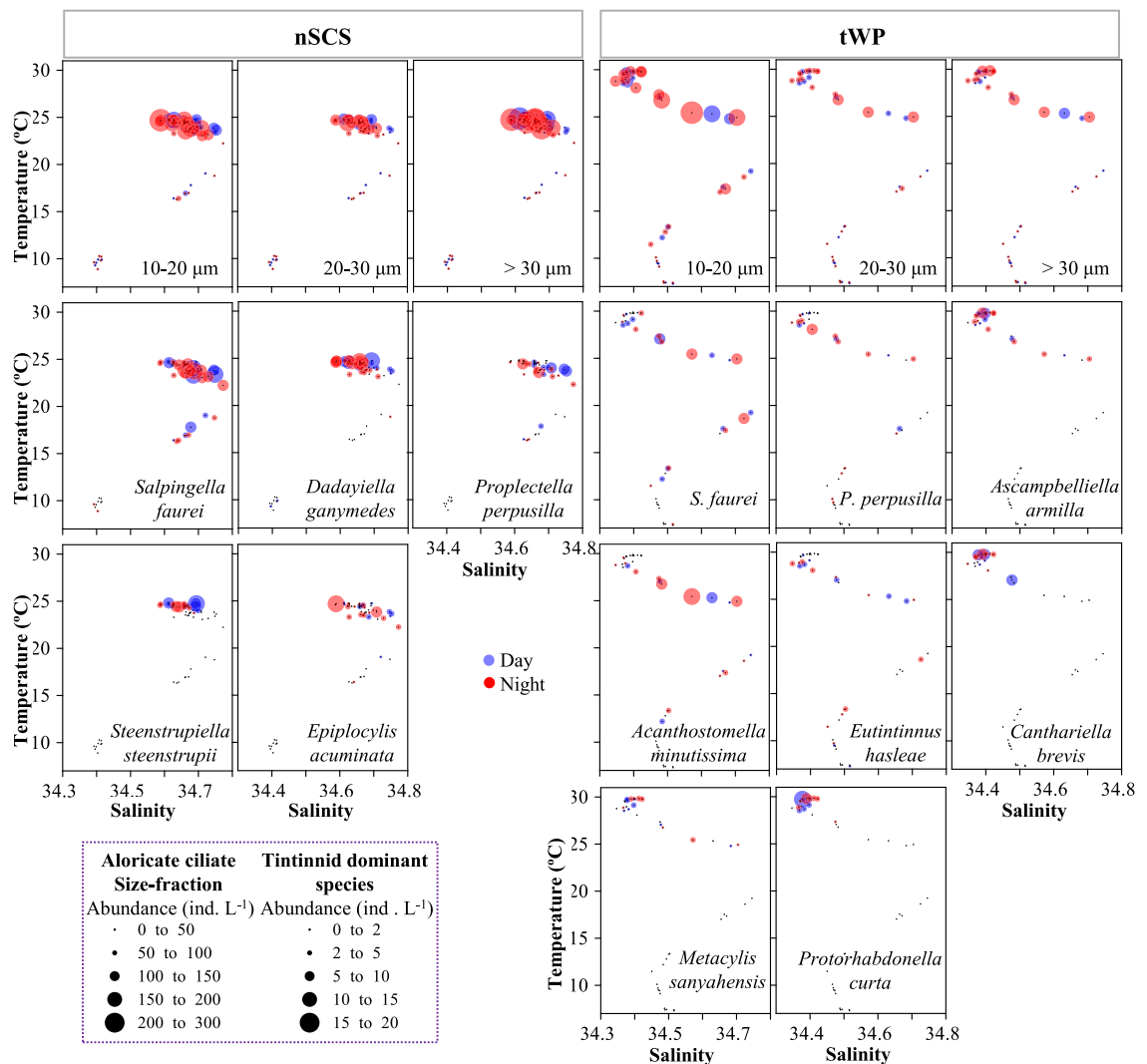


Figure 6. Temperature-salinity-plankton diagrams for day-night variations of size-fractions (10–20 μm , 20–30 μm and > 30 μm) of aloricate ciliate and tintinnid dominant species in the nSCS and tWP.

was higher than in the day for two possible reasons: (1) oceanic tintinnid species have stronger cell division in midnight than in the day in tropical Pacific waters⁶⁰; and (2) predation on picoplankton, nanoplankton and heterotrophic bacteria occurred primarily at night^{61–63}. Further studies on growth rates and cell division of tintinnid species are needed to better characterizing their diel vertical migration in the Pacific Ocean.

Differences of ciliate community between the nSCS and tWP oceanic waters. Abundance peaks of planktonic ciliates occurred in surface and DCM layers in both the nSCS and tWP, but highest abundances occurred in surface layer of the nSCS, and DCM layer of the tWP (Fig. 1). Our results are consistent with Wang et al.⁴⁰, which discovered this phenomenon and proposed a hypothesis to verify it. The nSCS is located at the convergence area of the shelf and slope waters where exchanges often occur with nutrient loaded waters originating from the Pearl River through surface current^{64–71}. For example, the nutrient values in the Pearl River ($\sim 100 \mu\text{M}$) were about 100 folds higher than in the nSCS slope ($\sim 1.2 \mu\text{M}$)^{66,70,71}. Nutrients are material basis for the growth of microphytoplankton and heterotrophic bacteria⁶⁸. High nutrient concentrations always accompanied with high abundance of microphytoplankton and heterotrophic bacteria in surface waters in the oligotrophic tropical seas, which further affected and determined microzooplankton abundance and composition^{72–76}. In contrast, the tWP is located at a tropical Pacific warm pool surrounded year-round by oligotrophic oceanic water. This may be the main reason for the surface layer ciliate abundance in the nSCS clearly higher than in the tWP.

Aloricate ciliates were dominant groups at each sampled depth of both sites (Supplementary Fig. S1), which was similar to previous observations in adjacent seas^{4,9,40,42,44,49}. As for tintinnid assemblages, we identified more species in the nSCS (57 species) than in the tWP (51 species) (Supplementary Table S2), which was not consistent with previous investigations^{40,43,77}, who found more species in adjacent seas. Low sampling frequency is often accompanied by low species richness^{78,79}. The total samples in the tWP (45 samples) and nSCS (72 samples) were much lower than in previous studies (≥ 100 samples)^{40,43,77}. Thus we speculate that low sampling frequency in our

Seas	Day/Night	Environmental factors	Aloricate ciliate		Tintinnid		Total ciliate	
			<i>P</i>	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>	<i>R</i>
nSCS	Day	Depth	0.001	0.803	0.322	0.034	0.001	0.867
	Day	Temperature	0.001	0.810	0.430	−0.002	0.001	0.877
	Day	Salinity	0.001	0.560	0.384	0.019	0.001	0.682
	Day	Chl <i>a</i>	0.969	−0.106	0.040	0.186	0.591	−0.037
	Night	Depth	0.001	0.855	0.045	0.155	0.001	0.843
	Night	Temperature	0.001	0.865	0.055	0.139	0.001	0.843
	Night	Salinity	0.001	0.634	0.201	0.069	0.001	0.670
	Night	Chl <i>a</i>	0.762	−0.069	0.047	0.151	0.498	−0.020
tWP	Day	Depth	0.001	0.822	0.140	0.151	0.001	0.859
	Day	Temperature	0.001	0.814	0.003	0.360	0.001	0.802
	Day	Salinity	0.624	−0.048	0.077	0.177	0.759	−0.081
	Day	Chl <i>a</i>	0.124	0.174	0.317	0.040	0.219	0.109
	Night	Depth	0.001	0.847	0.477	−0.014	0.001	0.832
	Night	Temperature	0.001	0.838	0.054	0.129	0.001	0.739
	Night	Salinity	0.575	−0.032	0.059	0.190	0.477	−0.015
	Night	Chl <i>a</i>	0.070	0.176	0.001	0.524	0.013	0.328

Table 1. Partial Mantel tests comparison between ciliate community (aloricate ciliate, tintinnid, and total ciliate) and environmental factors (depth, temperature, salinity, and Chl *a*). Numbers in bold indicate statistically significant results.

results could be the main reason for the disagreement. High tintinnid abundance and species richness mainly appeared at around DCM depths in both the nSCS and tWP. A high Chl *a* environment may be an important factor for influencing tintinnid distribution in oceanic waters^{80,81}.

Methods

Study area and sample collection. The variation of ciliate vertical distribution was addressed by conducting two time-series sampling in the upper 500 m at two distinct sites, Station (St.) S1 in nSCS and St. P1 in tWP, during two different cruises (Fig. 7). St. S1 was visited from 29 to 31 March 2017 aboard R.V. “Nanfeng”, and St. P1 from 2 to 3 June 2019 aboard R.V. “Kexue”. During 48 h (St. S1) or 24 h (St. P1) sampling periods, seawater samples were collected by using a CTD (Sea-Bird Electronics, Bellevue, WA, USA)—rosette carrying 12 Niskin bottles of 12 L each (Supplementary Table S5). In the nSCS, the sampling depths were 3, 10, 25, 50, DCM (deep Chl *a* maximum layer), 100, 200 and 500 m; in the tWP, the sampling depths were surface (3), 30, 50, 75,

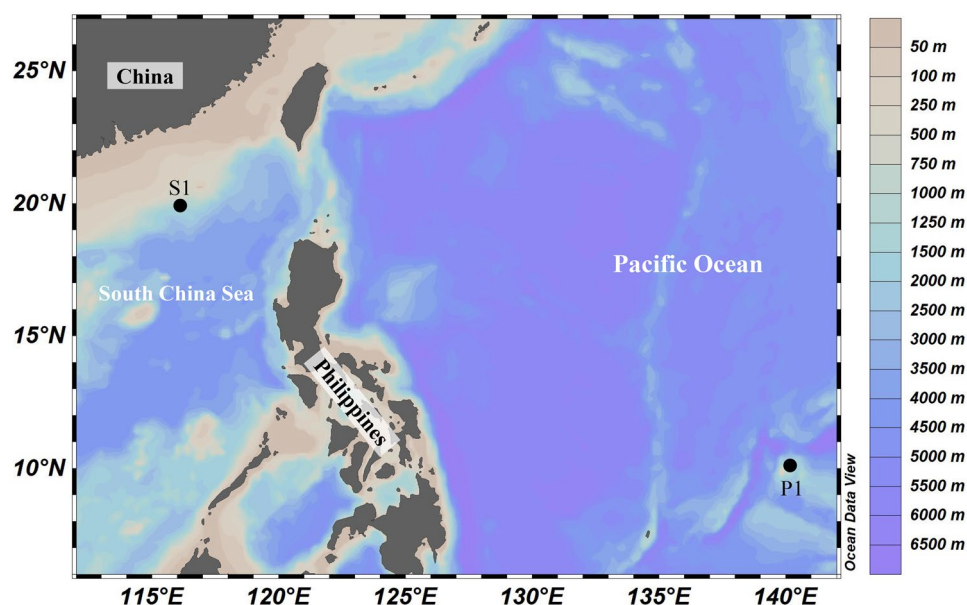


Figure 7. Survey stations in the northern South China Sea (nSCS) and tropical West Pacific (tWP).

DCM, 150, 200, 300 and 500 m. Casts were approximately launched every 6 h, the CTD determining vertical profiles of temperature, salinity and chlorophyll *a* in vivo fluorescence (Chl *a*). A total of 117 seawater samples were collected for planktonic ciliate community structure analysis. For each depth, 1 L seawater sample was fixed with acid Lugol's (1% final concentration) and stored in darkness at 4 °C during the cruise.

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 60 h. This settling and siphoning process was repeated until a final concentrated volume of 50 mL was achieved, which was then settled in two Utermöhl counting chambers (25 mL per chamber)⁸² for at least 24 h. Planktonic ciliates were counted using an Olympus IX 73 inverted microscope (100× or 400×) according to the process of Utermöhl⁸² and Lund et al.⁸³.

For each species, size (length, width, according to shape) of the cell (aloricate ciliate) or lorica (tintinnid, especially length and oral diameter) were determined 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 for maximum body length of each individual following Wang et al.⁴³. Tintinnid taxa were identified according to the size and shape of loricae following previous references^{1,9,40,44,84–86}. Tintinnid species richness in each station was highlighted by 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^{87,88}, we included empty tintinnid loricae in cell counts.

Data processing. Ciliate volumes were estimated using appropriate geometric shapes (cone, ball, and cylinder). Tintinnid carbon biomass was estimated using the equation⁸⁹:

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

where C (µg C L⁻¹) is the carbon biomass, V_i (µm³) is the lorica volume. We used a conversion factor of carbon biomass for aloricate ciliates of 0.19 pg/µm³⁹⁰. The average abundance and biomass of the water column were calculated following Yu et al.⁹¹ and Wang et al.⁹². We used the Margalef index (d_{Ma})⁹³ and Shannon index (H')⁹⁴ to test tintinnid diversity indices in the day and night variations. Biogeographically, the tintinnid genera are mainly classified into two groups in the oceanic waters based on Dolan and Pierce⁹⁵: Cosmopolitan, species distributed widespread in the world ocean; Warm Water, species observed in both coastal systems and open waters throughout the world ocean, but absent from sub-polar and polar waters.

The dominance index (Y) of tintinnid species in one assemblage was calculated using formula⁹⁶:

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

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 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), Surfer (Version 13.0), OriginPro 2021 (Version 9.6), and Grapher (Version 12.0). Correlation analysis between environmental and biological variables (nonparametric-test, Independent t -test, Spearman's rank analysis) were performed using SPSS (Version 16). The significance for grouping in the environment and ciliate community (aloricate ciliate and tintinnid) was tested by PERMANOVA analysis in PERMANOVA C of PRIMER 6^{97,98}. The partial Mantel tests were performed between ciliate community and environmental factors in R4.1.1.

Data availability

Datasets for this research are included in this paper and its supplementary information files (Supplementary Data).

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Author contributions

C.W.: field sampling, sample counting and tintinnid taxonomy, data analysis, writing-original draft and conceptualization. Y.D.: data analysis. M.D.: writing-original draft. Y.W., H.L. and S.Z.: data analysis. W.Z.: conceptualization and writing-original draft. T.X.: conceptualization.

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Competing interests

The authors declare no competing interests.

Additional information

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