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Spatial and seasonal variations of large tintinnid ciliates in Shenhu Bay of China

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Key words: tintinnid, community structure, dominant species, environmental factor

Abstract

In this study, the spatial distribution and seasonal variation of large tintinnids (>76 μm) were investigated in Shenhu Bay during three seasons of 2012. Of the 36 species identified, 9 were dominant (i.e. *Tintinnopsis radix*, *Leprotintinnus simplex*, *Tintinnopsis japonica*, *Tintinnopsis tubulosoides*, *Leprotintinnus nordqvisti*, *Tintinnopsis beroidea*, *Stenosemella parvicollis*, *Tintinnidium primitivum*, *Tintinnopsis nana*). A clear seasonal shift of the taxonomic composition as well as the lorica size of the dominant species was observed. The highest numbers of tintinnid species occurred in spring, while the highest abundance and biomass occurred in summer. Clustering indicated that the seasonal variations of the community structure were more obvious than spatial variations. Spearman correlation analysis revealed that density of phytoplankton prey had a significant impact on the tintinnid abundance. Redundancy analysis (RDA) illustrated that temperature, salinity and the nutrient level were the most important abiotic factors affecting the spatial and seasonal pattern of tintinnid communities in Shenhu Bay.

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INTRODUCTION

Tintinnid ciliates are common components of the planktonic microprotozoan community and important trophic intermediates from the microbial loop to higher trophic levels in the ocean (Stoecker & Capuzzo 1990, Kamiyama & Tsujino 1996, Godhantaraman 2001). Tintinnids prey on pico- and nanoplankton, ranging in size from about 2 μm to particles about half the diameter of their lorica oral openings (Dolan 2000). They can exert a strong grazing impact on nanophytoplankton assemblages and remove large portions of the daily primary production. Whereas tintinnids serve as prey for a variety of metazoan zooplankton such as copepods (Dolan 2010). Tintinnid ciliates have long been considered as ideal organisms for the study of change in the structure or composition of microzooplankton communities due to their characteristic loricae (Dolan 2000, 2010). In contrast to other microorganisms, most tintinnid taxa are not cosmopolitan (Pierce & Turner 1993, Abou Zaid & Hellal 2012). The abundance, biomass and composition of tintinnid communities in coastal waters should be much more variable than those in the open sea, due to the greater variability of influencing factors (Vaqué et al. 1997).

Shenhu Bay is a shallow natural harbor located along the eastern region of Jinjiang, Fujian, southeast China. It covers an area of about 68 km² with a 30.8 km long intertidal zone, and is connected to the Taiwan Strait via an open mouth. Shenhu Bay is geomorphologically a typical 'ria' with depth contours roughly parallel to the shoreline. The reduced impact by anthropogenic activities means the original natural environmental landscape of the bay remains undisturbed. The remains of an ancient submerged forest with a 7,500-year history have been found here. In the 1990s, the Shenhu Bay National

Natural Reserve was established, which has exerted a significant impact on the possibilities to study palaeoclimatological, paleogeographic and paleobiological changes on the coast of the Taiwan Strait. Although there are several ecological reports from Shenhu Bay, only a few studies have been carried out so far on the ecology of microzooplankton community and quantitative data on tintinnid community have not been reported from this area.

To fill gaps in our knowledge about the ecology of tintinnids in Shenhu Bay, we investigated the spatial and seasonal variation in abundance, biomass, composition and diversity of tintinnids. In addition, the present study concerns the determinants of the pattern in tintinnid communities, since tintinnid communities are sensitive to changes in multiple environmental factors (Sanders 1995, Kamiyama & Tsujino 1996, Godhantaraman 2001). The aim of this study is to clarify the spatial and seasonal pattern of the tintinnid communities on a local scale, and to determine what factors are most strongly affecting the spatial and seasonal pattern.

MATERIALS AND METHOD

Study sites

Seven sites were designed (24°38'01" - 24°39'47" N, 118°39'34" - 118°41'36" E) in Shenhu Bay, Fujian, China (Fig. 1). Sites 1-3 were located at the top of the bay, sites 4 and 5 − in the middle, sites 6 and 7 − at the bay mouth.

Sampling and treatments

Tintinnid samples were collected by vertical tows of 76-μm-mesh plankton nets from Shenhu Bay in May, August and November, 2012, representing the temporal tintinnid communities in spring, summer and autumn, respectively. Volumes of water filtered per sample varied between 0.54 and 1.40 m^3. Samples were obtained and fixed with 5% formaldehyde in plastic bottles. A total of 21 tintinnid samples were analyzed.

Phytoplankton and planktonic copepods were sampled in May and August from the same sites at which tintinnids were collected. Phytoplankton samples were collected by the same method as tintinnids. Copepods samples were collected by vertical tows of the plankton net with 160 μm pore

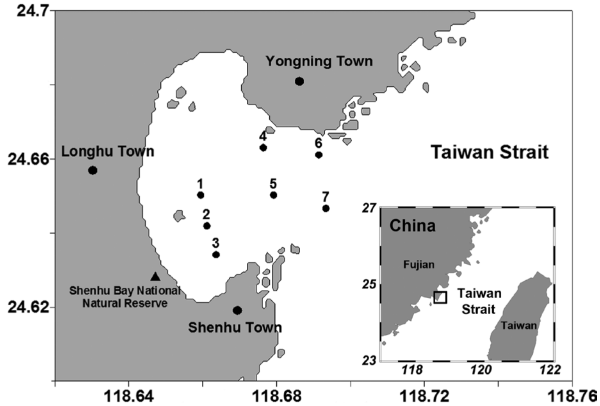

Fig. 1. Location of the study area and sampling sites of tintinnids in Shenhu Bay

size and fixed with 5% formaldehyde in plastic bottles.

At each sampling site, salinity and temperature (T) were measured in situ. Suspended particles (SP, >0.45 μm), pH, dissolved oxygen (DO), chemical oxygen demand (COD), active phosphorus (PO_4-P), active silicon (SiO_3-Si), nitrite nitrogen (NO_2-N), nitrate nitrogen (NO_3-N), ammonium nitrogen (NH_4-N) and petroleum pollutant (PP), were determined according to the standard methods presented in the Offshore Marine Chemical Survey Technical Regulations (908 Office of the State Oceanic Administration 2006).

Identification and enumeration

Formaldehyde fixed samples were settled for 48 hours and then concentrated to 50-300 ml (Utermöhl 1958). For the identification and enumeration of tintinnids, 0.1 ml of a well-mixed concentrated sample was taken and mounted on a microscope slide and examined under a light microscope at a magnification 200×. A total volume of 1 ml concentrated sample was scanned. Tintinnids were identified by lorica morphology and species description according to Kofoid & Campbell (1929, 1939), Hada (1932, 1937, 1938), Nie (1934) and Lynn (2008). The classification system was mainly referred to Lynn (2008). All ciliates were finally identified to the lowest possible taxa. Lorica dimensions were measured using an ocular micrometer. Tintinnid biomass was estimated from measurements of the lorica and subsequent conversion to biovolume by assigning approximate geometrical shapes. The volume equation from biovolume to organic carbon:

$$pg\ C = \mu m^3(lorica\ volume) \times 0.553 + 444.5$$

was applied to the data (Verity & Lagdon 1984, Thompson et al. 1999).

Copepods were observed and counted under a dissecting microscope from a subsample taken with a wide bore pipette. The subsample volume is selected to ensure counting of at least 200 organisms. Copepodite stages of copepods were taken into account, but not copepod nauplii.

Data analyses

The number of species, abundance and biomass of tintinnids were calculated, and Shannon-Wiener diversity index (H') for each sample was calculated applying the following equation:

$$H' = -\sum_{i=1}^{S}\left(\frac{n_i}{N}\right)\log_2\left(\frac{n_i}{N}\right)$$

where n_i = abundance of the i^{th} species; N = total number of specimens. The distribution pattern of tintinnid communities was displayed using software surfer 8. The abundance of phytoplankton and copepods was calculated for each sample collected in spring and summer.

Cluster analysis was used to investigate the ciliate community structure using the PRIMER v5.0 (Plymouth Routines In Multivariate Ecological Research) package according to species composition and abundance (Clarke & Gorley 2001). The Bray-Curtis similarity matrix was computed on square root-transformed biotic data and Euclidean distance matrix on ln(x+1)-transformed abiotic data. The group-average clustering was used to divide the ciliate communities into several assemblages, each comprising samples with similar species and abundance. Variances between groups were tested using the submodule ANOSIM (analysis of similarities) in PRIMER v5 (global R values range from 0 to 1, and a higher global R value demonstrates more significant variance). Species with a cumulative contribution of 90% to the average Bray-Curtis similarity within each group was analyzed using the submodule SIMPER (Similarity Percentage Analysis). The significance of the biota-environment correlation was checked using the RELATE. Detrended correspondence analysis (DCA) for the biological data was employed to decide whether linear or unimodal ordination methods should be applied. After that, the detailed relationships between tintinnid communities and environmental factors were revealed by redundancy analysis (RDA) using Canoco for Windows 4.5 package (ter Braak & Smilauer 2002). RDA analysis was conducted based on the square root-transformed species-abundance data and ln(x+1)-transformed environmental data. To eliminate collinearity among variables, explanatory variables with a high variance inflation factor (VIF) were sequentially removed until all VIFs were below 20. Subsequently, forward selection was conducted to select the minimum set of environmental variables that could explain a significant amount ($P < 0.05$) of variation. With the forward selection, the significance of correlation with environmental variables was determined by Monte Carlo permutation test (999 permutations). Spearman correlation analysis between tintinnid communities and biotic factors was conducted using statistical program SPSS v17.0.

RESULTS

Physical and chemical variables

Thirteen physical and chemical environmental variables are summarized in Table 1. The depth of the estuary ranged between 4.5 and 14 m. Most of the variables showed clear seasonal differences. Water temperature and salinity peaked in summer.

Table 1

Statistical summaries of 13 environmental variables from Shenhu Bay

Environmental variables	Mean	Min	Max	SD	Median
Depth (m)	10.01	4.50	14.00	2.76	11.00
Temperature(°C)	23.49	19.60	28.90	3.63	22.40
pH	7.98	7.79	8.10	0.10	8.02
Salinity	32.41	31.00	33.60	0.95	32.80
SP (mg l^{-1})	14.15	4.30	29.00	7.06	12.10
DO (mg l^{-1})	6.92	6.03	7.48	0.36	6.99
COD (mg l^{-1})	0.48	0.15	0.93	0.20	0.45
PO_4-P (mg l^{-1})	0.01	0.00	0.03	0.01	0.01
SiO_3-Si (mg l^{-1})	0.54	0.21	2.32	0.45	0.42
NO_2-N (mg l^{-1})	0.02	0.01	0.03	0.01	0.02
NO_3-N (mg l^{-1})	0.10	0.01	0.22	0.08	0.07
NH_4-N (mg l^{-1})	0.04	0.01	0.13	0.03	0.04
PP (mg l^{-1})	0.01	0.00	0.03	0.01	0.01

DO and pH changed a little bit. COD in autumn were higher than in spring and summer, and the maximum was recorded at site 3 every season. Concentrations of PO_4-P, SiO_3-Si and NO_3-N were relatively high in autumn, and NO_2-N content was at its minimum in summer.

Taxonomic composition

A total of 36 species representing 10 genera were identified (Table 2). The taxonomic composition of tintinnids was characterized by a clear seasonality (Fig. 2A). The agglutinated genus *Tintinnopsis* was the most common and diverse, accounting for up to 68% of the total tintinnid abundance, followed by genera *Leprotintinnus* and *Stenosemella*.

In spring, a total of 21 tintinnid species, representing 6 genera (*Codonellopsis*, *Favella*, *Leprotintinnus*, *Ptychocylis*, *Stenosemella*, *Tintinnopsis*), were identified. The genus *Tintinnopsis* was most diverse and represented 12 species. *Tintinnopsis radix* and *Leprotintinnus simplex* were the most common species recorded at all sites. Whereas *Codonellopsis schabi* and *Ptychocylis minor* were observed at a single site.

In summer, 7 genera (*Codonellopsis*, *Eutintinnus*, *Favella*, *Leprotintinnus*, *Parafavella*, *Tintinnopsis*, *Undella*) and 16 species of tintinnids were identified. *Tintinnopsis* and *Leprotintinnus* were the most diverse genera, representing 5 and 4 species respectively.

Table 2

List of tintinnid species encountered in Shenhu Bay

Tintinnid species			
1	*Codonellopsis schabi*	19	*Tintinnopsis bütschlii*
2	*Eutintinnus lusus-undae*	20	*Tintinnopsis elongata*
3	*Favella campanula*	21	*Tintinnopsis gracilis*
4	*Favella ehrenbergii*	22	*Tintinnopsis japonica*
5	*Favella panamensis*	23	*Tintinnopsis lobianci*
6	*Leprotintinnus nordqvisti*	24	*Tintinnopsis minima*
7	*Leprotintinnus bottnicus*	25	*Tintinnopsis minuta*
8	*Leprotintinnus elongatus*	26	*Tintinnopsis mortensenii*
9	*Leprotintinnus simplex*	27	*Tintinnopsis nana*
10	*Parafavella inflata*	28	*Tintinnopsis nucula*
11	*Ptychocylis minor*	29	*Tintinnopsis radix*
12	*Stenosemella pacifica*	30	*Tintinnopsis rotundata*
13	*Stenosemella parvicollis*	31	*Tintinnopsis schotti*
14	*Stenosemella* sp.	32	*Tintinnopsis* sp.
15	*Stenosemella steini*	33	*Tintinnopsis tocantinensis*
16	*Tintinnidium primitivum*	34	*Tintinnopsis tubulosoides*
17	*Tintinnopsis baltica*	35	*Tintinnopsis turgida*
18	*Tintinnopsis beroidea*	36	*Undella parva*

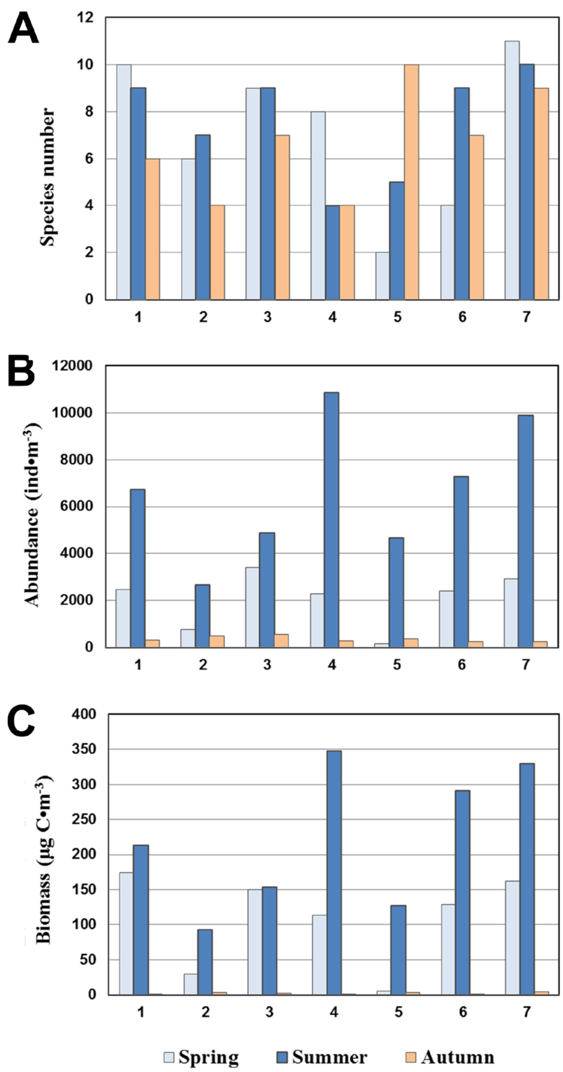

Fig. 2. Variation in the species number (A), abundance (B) and biomass (C) of tintinnids in Shenhu Bay

Tintinnopsis radix, *Leprotintinnus simplex* and *Leprotintinnus nordqvisti* were the most common species occurring at all sites. Whereas low abundance of *Codonellopsis schabi*, *Undella parva*, *Tintinnopsis schotti* and *Tintinnopsis gracilis* was recorded at only one site.

In autumn, 5 genera and 16 species were recorded. *Tintinnopsis* was still the most common and diverse genera, which included 8 species and was followed by *Leprotintinnus* and *Stenosemella*. *Tintinnopsis beroidea* and *Stenosemella parvicollis* were recorded at all sites, whereas *Favella campanula*, *Stenosemella* sp. and *Tintinnopsis minima* were recorded at only one site with lower abundance.

Distribution of tintinnid communities

Tintinnid abundance and biomass showed marked seasonal changes, with the highest values observed in summer during the temperature maximum and the lowest in autumn (Fig. 2B, C). The distributions of tintinnids were generally patchy and uneven.

In spring, tintinnid abundance ranged from 169.19 to 3411.92 ind. m^{-3}, with an average of 2063.98 ±440.56 ind. m^{-3}. Their biomass ranged from 5.62 to 174.17 μg C m^{-3}, with an average of 109.30 ±24.95 μg C m^{-3}. Abundance and biomass of tintinnids in spring were high at the top and the mouth of the bay but low in the middle. The distributions of the species number and diversity were almost identical (Fig. 3).

In summer, mean tintinnid abundance was up to 6704.70 ±1108.75 ind. m^{-3}, ranging from 2651.99 to 10856.10 ind. m^{-3}. The mean biomass was 219.28 ±38.02 μg C m^{-3}, ranging from 92.08 to 342.67 μg C m^{-3}. High values of abundance and biomass of tintinnids were recorded at the bay mouth and nearby the town of Yongning, while low values occurred at the top of the bay. The higher number and diversity of species occurred at the top and the mouth of the bay, and lower in the middle of the bay (Fig. 4).

Abundance and biomass of tintinnids were dramatically reduced in autumn. The abundance ranged from 237.80 to 539.70 ind. m^{-3}, with an average of 352.23 ±44.48 ind. m^{-3}, and the biomass ranged from 0.73 to 3.86 μg C m^{-3}, with an average of 2.38 ±0.46 μg C m^{-3}. The abundance of tintinnids was high at the top of the bay and low at the mouth, however the trend of biomass, the number and the diversity of species was exactly the opposite (Fig. 5).

Tintinnid community structure

In order to further investigate the spatial and temporal pattern of tintinnid distribution, cluster analysis was performed, which divided the tintinnid communities into four groups at a similarity level of 34.13% in terms of their temporal distribution in Shenhu Bay in the study period. The dendrogram

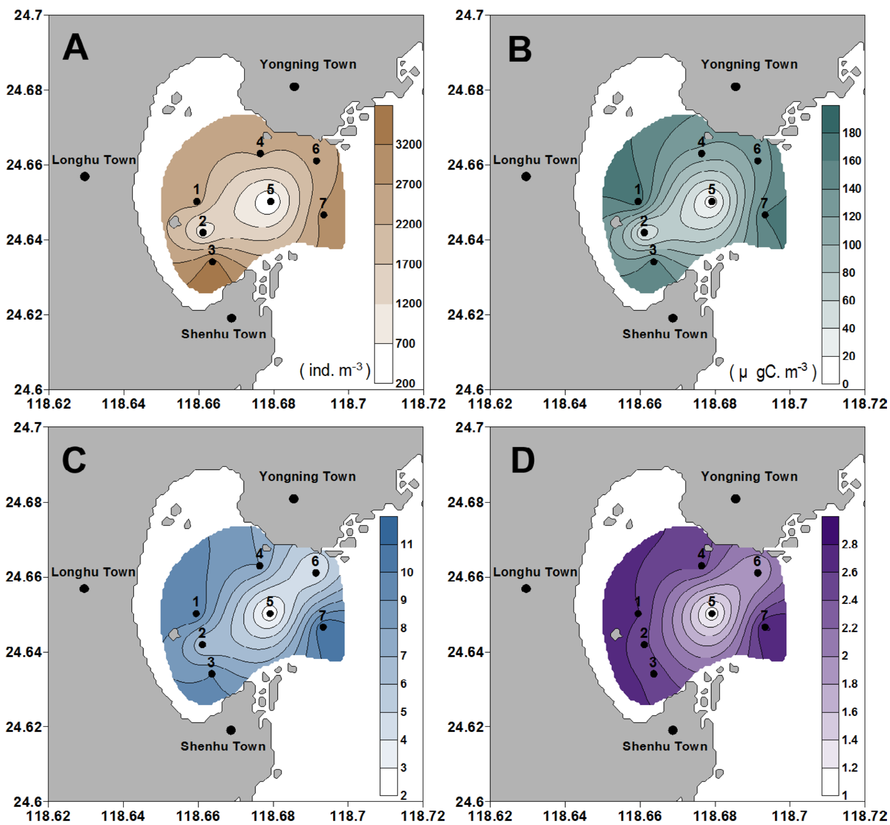

Fig. 3. Distribution of tintinnid abundance (A), biomass (B), species number (C) and Shannon-Wiener diversity (D) in spring in Shenhu Bay

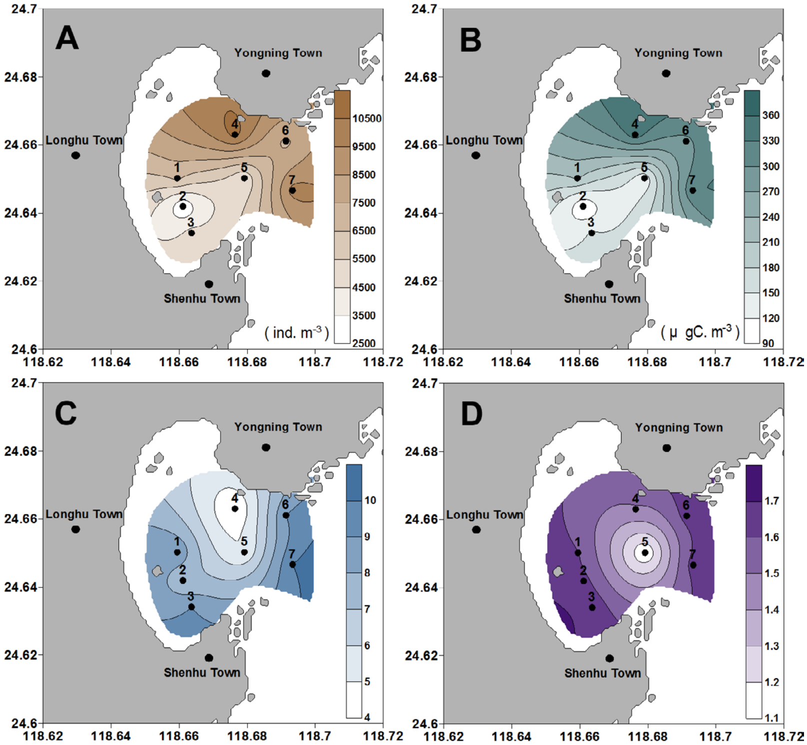

Fig. 4. Distribution of tintinnid abundance (A), biomass (B), species number (C) and Shannon-Wiener diversity (D) in summer in Shenhu Bay

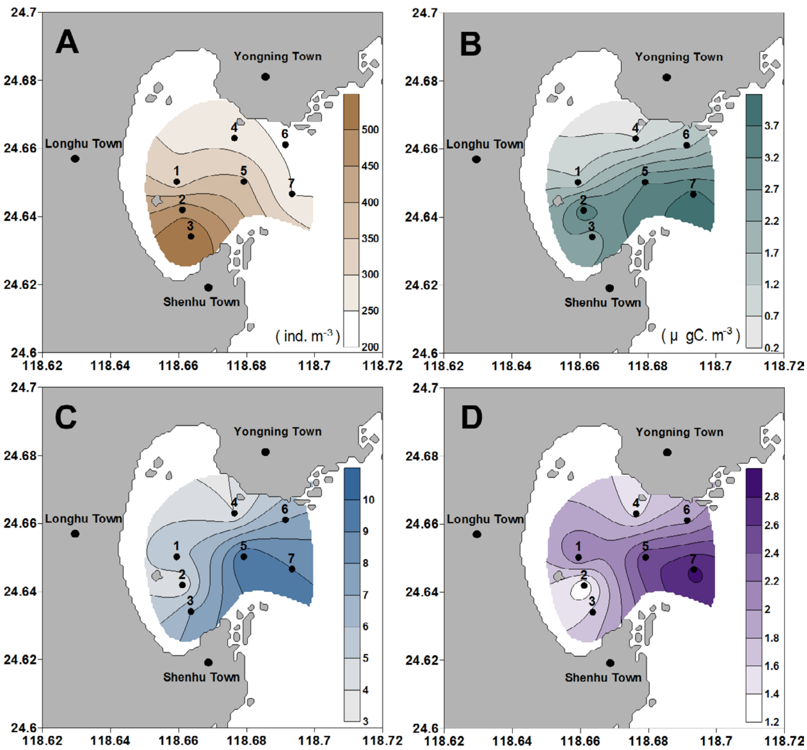

Fig. 5. Distribution of tintinnid abundance (A), biomass (B), species number (C) and Shannon-Wiener diversity (D) in autumn in Shenhu Bay

showed that the total samples were generally classified into three groups based on seasonal differences, with the exception of the sample collected from site 5 in spring (Fig. 6). ANOSIM demonstrated significant differences between the three seasonal groups (global $R = 0.938$, $P < 0.001$), implying an obvious seasonal pattern of tintinnid communities. Although the interrelationship within each group differed, the differences between groups were more obvious than within groups, that is, more significant seasonal variation in tintinnid communities was exhibited than the spatial variation.

Seasonal succession of dominant species

The dominant species in each season are listed in Table 3. Tintinnid communities were dominated by *Tintinnopsis radix*, *Leprotintinnus simplex*, *Tintinnopsis japonica* and *Tintinnopsis tubulosoides* in spring. *T. radix* and *L. simplex* were still dominant in summer, whereas *T. radix* gained importance to the similarity of the tintinnid taxonomic composition. Meanwhile a new dominant species, *Leprotintinnus nordqvisti*, emerged. In autumn, the dominant species in summer were totally replaced by new species, i.e. *Tintinnopsis beroidea*, *Stenosemella parvicollis*, *Tintinnidium primitivum* and *Tintinnopsis nana*.

The abundance and biomass of dominant species were much lower in autumn than in spring and summer. In addition to this, larger species dominated in the tintinnid communities in spring and summer, whilst smaller species became dominant in autumn. The length and the oral diameter of their loricae were significantly reduced (Table 3).

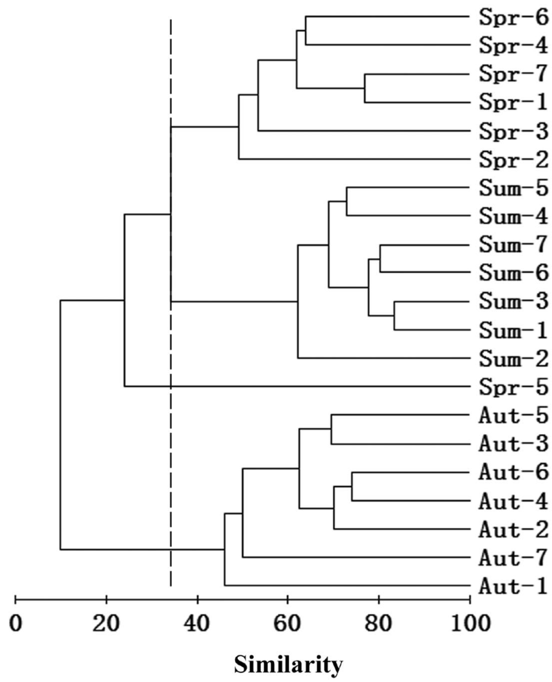

Fig. 6. Cluster analysis of tintinnid communities in Shenhu Bay based on the abundance data. Spr, Sum and Aut indicate spring, summer and autumn, respectively. The numbers indicate site numbers

Correlation between tintinnid communities and environmental factors

There was a significant and positive correlation between tintinnid abundance and phytoplankton abundance ($R = 0.714$, $P < 0.01$), whereas the relationship was weak when tintinnid abundance was

Table 3

Dominant tintinnid species in each season in Shenhu Bay

Dominant species	Dominant season	Contribution (%)	Abundance (ind. m^{-3})	Biomass (μg C m^{-3})	Lorica length (μm)	Lorica oral diameter (μm)
Tintinnopsis radix	Spring	33.54	610.73±179.54	23.48±8.01	200~460	35~60
	Summer	76.31	4511.47±667.75	158.81±24.30	130~500	30~70
Leprotintinnus simplex	Spring	29.46	381.13±72.85	13.54±2.23	130~380	40~75
	Summer	7.31	774.38±346.06	20.16±7.62	120~480	35~60
Tintinnopsis japonica	Spring	25.89	526.02±152.65	62.40±19.01	160~240	115~150
Tintinnopsis tubulosoides	Spring	4.56	115.02±48.43	1.01±0.47	100~145	30~45
Leprotintinnus nordqvisti	Summer	9.16	517.43±75.08	7.25±1.71	110~300	50~110
Tintinnopsis beroidea	Autumn	63.56	191.94±47.08	0.38±0.10	43~85	25~40
Stenosemella parvicollis	Autumn	19.80	49.48±7.93	0.31±0.05	50~60	25~30
Tintinnidium primitivum	Autumn	6.11	18.91±6.01	0.05±0.01	45~90	20~25
Tintinnopsis nana	Autumn	3.49	12.89±4.75	0.03±0.01	25~40	15~30

compared to the abundance of copepods (R = -0.437, P > 0.05).

In addition, the relationship between tintinnid communities and abiotic environmental factors (Table 1) was studied. RELATE analysis revealed a significant correlation between tintinnid communities and 13 abiotic factors (R = 0.687, P = 0.001). Results of RDA implied that there was an obvious collinearity between 13 environmental variables. As it can be seen in the RDA plot for all the three seasons (Fig. 7A), samples collected in spring gathered together and were totally located on positive Axis 2, indicating higher optima for pH, water depth, salinity, PP, but lower values for COD, PO_4-P, NO_3-N. Samples collected in summer were totally on positive Axis 1, indicating higher optima for temperature and salinity, whereas lower optima for DO, NO_3-N, NO_2-N, PO_4-P, SP and PP occurred in spring samples. Autumn samples were located on negative Axis 1, indicating higher optimum values for COD, NO_3-N, NO_2-N, PO_4-P, SiO_3-Si, SP, DO and PP, but lower values for temperature, salinity, water depth and pH. On account of complex interactions and correlations between the tested environmental factors as well as the unmeasured ones, the influence of one factor should not be analyzed separately and independently. Thus considering the marginal effects, forward selection determined that the variables significantly affecting the tintinnid communities during three seasons included temperature, NO_2-N, salinity, SP, NO_3-N, PO_4-P, DO, PP, pH and depth. In general, temperature, salinity and the nutrient level were the most important abiotic factors that affected the seasonal variation of tintinnid communities.

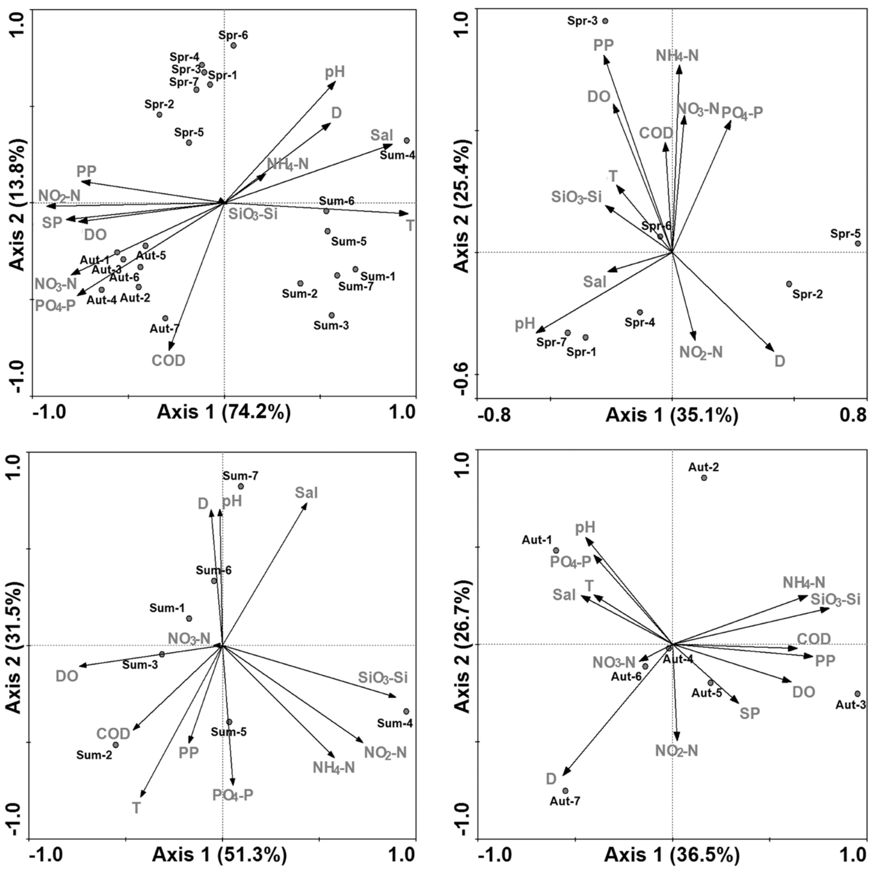

Fig. 7. RDA ordination plot showing the relationship between tintinnid communities and environmental factors during three seasons (A), in spring (B), in summer (C), and in autumn (D). The length of vectors indicates the marginal effects of environmental variables they represent. The sample points can be projected perpendicularly onto the line overlaying the arrow of a given environmental variable. The sample points are arranged in the order of a predicted increase in values of a given environmental variable and the predicted increase occurs in the direction indicated by the arrow. (A) expressed mainly seasonal variation of tintinnid communities in relation to environmental factors. (B)-(D) expressed spatial variation of tintinnid communities in each season in relation to environmental factors. D-depth, T-temperature, Sal-salinity. See Fig. 6 for other abbreviations.

The variables which significantly affected the spatial pattern of tintinnid communities in spring were: PP, depth, NH_4-N, pH, PO_4-P (Fig. 7B). The highest petroleum concentration was detected at site 3 where the tintinnid abundance peaked. In summer, the significant variables were SiO_3-Si, NO_2-N, temperature, DO, NH_4-N, salinity, COD, PO_4-P (Fig. 7C). High levels of Si (SiO_3-Si) and N (NO_2-N, NH_4-N), and low DO concentration were displayed at site 4 nearby the town of Yongning, where tintinnid abundance and biomass peaked. The level of SiO_3-Si was the lowest at site 2 where tintinnid abundance and biomass were also the lowest. The most significant environmental variables in autumn were depth, SiO_3-Si, COD, NH_4-N, DO, PP (Fig. 7D). The depth at site 3, where tintinnid abundance peaked, was the shallowest, but the levels of NH_4-N, PP, SiO_3-Si, SP, DO, COD were found relatively high at site 3. High values of biomass, the species number and diversity were recorded at site 7, where the water was the deepest and the levels of NH_4-N, PP, SiO_3-Si were relatively low. The dominant abiotic factors affecting the spatial pattern of tintinnid communities differed from season to season. They were PP, PO_4-P, pH in spring, Si (SiO_3-Si) and N (NO_2-N, NH_4-N) in summer, and SiO_3-Si, NH_4-N, PP in autumn. Even so, the nutrient level seemed to be crucial to the spatial pattern of tintinnid communities in this area.

In summary, among the abiotic environmental factors, temperature, salinity and the nutrient level played the most important role in forming the spatial and seasonal pattern of tintinnid communities in Shenhu Bay.

DISCUSSION

Sampling method

The net method, which is the most common method of zooplankton collection, was used for sampling of tintinnids in this study. The vertical haul is conducted to sample the water column. Combined with a flowmeter, it can be applied in ecological studies requiring assessments of zooplankton abundance (Havens 2013). The main advantage to using a net is that seawater samples of large volumes can be collected quickly. Various mesh sizes can be chosen, depending on the size of zooplankton to be collected from the water. Moreover, samples collected by a vertical haul are conducive to conducting a general survey of the water column. The plankton net used in this work was suitable for evaluating the larger individuals of tintinnid populations (>76 μm). Some small species, such as *Tintinnopsis nana*, may pass through the net during sampling. So it should be noted that our observation on small tintinnids (<76 μm) was qualitative rather than quantitative, in consideration of the underestimation of their individual numbers.

Spatial and seasonal variation of tintinnids

Tintinnids were abundant and diverse at the mouth of Shenhu Bay during three seasons. It is likely that the southward current on the west coast of the Taiwan Strait (Jan et al. 2002) carried colder China Coastal Water into the bay and brought non-native tintinnid species. Higher abundance and biomass also occurred in the area nearby the town of Yongning in summer, while the abundance was higher at the top of the bay nearby the town of Shenhu in autumn. These local high values were most likely caused by the uneven distribution of nutrients and the coastal pollution.

An obvious seasonal shift of lorica dimensions in the dominant species was observed in Shenhu Bay. Some previous studies suggested that the lorica dimensions of tintinnids, especially the oral dimensions, were directly and positively correlated with the size of phytoplankton prey (Verity 1987, Dolan et al. 2002, Dolan 2010). It was also reported that tintinnids mainly feed on nano-sized prey, preferably nanoflagellates (Dolan et al. 2002, Balkis 2004). The small-sized tintinnids were dominant in autumn in Shenhu Bay, unlike in spring or summer, probably because of the reduced prey size caused by a seasonal succession of the phytoplankton community.

Relationship between tintinnid communities and environmental factors

The tintinnid community may be affected by multiple environmental factors (Sanders 1995, Kamiyama & Tsujino 1996, Wang et al. 2013, Wang et al. 2014). The population of tintinnids are regulated not only by the abundance of prey (e.g. phytoplankton, bacteria), but also by the abundance of predators (e.g. copepods, larval fish) and competitors (e.g. aloricate ciliates, rotifers) (Miyaguchi et al. 2006, Pitt et al. 2007, Sato et al. 2010). The tintinnid community may also be affected by other abiotic factors, such as temperature, salinity, turbulence, the nutrient level (Capriulo & Carpenter 1983, Sanders 1995, Wang et al. 2013). Capriulo & Carpenter (1983) reported a weak correlation between tintinnid density and phytoplankton density in Long Island Sound. Urrutxurtu (2004) found the tintinnid abundance in the Nervio´n River estuary, Spain, was significantly and positively correlated with temperature. Data for Büyükçekmece Bay indicated that the abundance of tintinnids was negatively correlated with the abundance of phytoplankton and positively correlated with temperature (Balkis 2004). Uye et al. (1996) tested the relationship between tintinnid biomass and chlorophyll in the Inland Sea of Japan and found a significant positive correlation only in autumn, speculating that the tintinnid population was regulated by other factors besides the food supply. In this study, a significant and positive correlation was observed between the abundance of tintinnids and the abundance of phytoplankton in spring and summer, suggesting that food supply is an important factor affecting the variation of tintinnid communities during these seasons. Also, a negative correlation was observed between the tintinnid abundance and the copepod abundance. It is likely that lower abundance of copepods reduced the predation pressure on tintinnids. However, the correlation was not as significant as that between tintinnids and phytoplankton, suggesting that the bottom-up control of the tintinnid population was dominant during these seasons in Shenhu Bay. Abiotic environmental factors also played an important role in controlling the tintinnid communities, and the dominant factors were different in each season. The nutrient level played an important role in controlling both the spatial and the seasonal pattern of tintinnid communities in Shenhu Bay. The effects of the nutrient level on tintinnid communities may be indirect because it regulates the density of phytoplankton prey in this area.

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