Journal of the Marine Biological Association of the United Kingdom, 2013, 93(1), 13–26.
doi:10.1017/S0025315412001324

Temporal distributions of microplankton populations and relationships to environmental conditions in Jiaozhou Bay, northern China

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To analyse temporal distributions of microplankton populations and relationships to environmental conditions in marine ecosystems, a dataset of microplankton communities was investigated using a range of statistical methods. A total of 164 microplankton species comprising 100 microalgae and 64 ciliates were identified from 120 samples, respectively. Both planktonic microalga and ciliate assemblages showed temporal patterns and were significantly correlated between their temporal variations in abundance. The microplankton communities were characterized by 14 ciliates (e.g. Strombidium sulcatum, Tintinnopsis tubulosoides *and* Strombidium cheshiri*) and 18 microalgae (e.g.* Skeletonema costatum *and* Alexandrium tamarense*). Multiple regression analyses showed that the interspecies correlations among these dominant species represented a complex network with a clear seasonal shift. Temporal pattern of microplankton communities was significantly correlated with the environmental variables such as temperature, salinity and nitrate nitrogen. The results suggest the clear species distribution and temporal dynamics of microplankton communities in response to environmental changes, and multivariate statistical approaches were a useful tool to reveal the species distribution patterns and complex microplanktonic interspecies correlations in marine ecosystems.*

Keywords: microplankton, seasonal variation, microbial food web, marine ecosystem

Submitted 29 June 2012; accepted 7 August 2012; first published online 21 September 2012

INTRODUCTION

Microplankton organisms are the most important component of the plankton and play a significant role in the functioning of the microbial food loop, especially in terms of energy flow and element cycling in many aquatic ecosystems (Montagnes *et al.*, 1996; Dolan & Simek, 1997; Jiang *et al.*, 2011a, b, 2012a, b; Xu *et al.*, 2011a, b). The microalgae are responsible for the primary production in most aquatic habitats; microzooplanktons transfer these productions to higher trophic levels in the food chain (Tillmann, 1998, 2004; Gomez & Gorsky, 2003). Furthermore, some bloom-forming species are harmful to the other microorganisms and often result in red-tide events in the marine ecosystems (Tillmann, 2004; Xu *et al.*, 2008, 2010).

The planktonic ciliated protozoa as an important component of microzooplankton, with short generation time, can react rapidly to short-term variation in food conditions in case of rapid phytoplankton growth (Admiraal & Venekamp, 1986; Montagnes *et al.*, 1996; Jeong *et al.*, 1999). Many investigations have reported high numbers of ciliate species during bloom events, suggesting that planktonic ciliates play crucial roles in suppressing or shortening blooming events of microalgae (Admiraal & Venekamp, 1986; Bochstahler & Coats, 1993; Agatha & Riedel-Lorjé, 1998; Montagnes & Lessard, 1999; Tillmann, 2004). This assumption is supported by laboratory studies showing the capability of different ciliate species to feed and grow on bloom-forming algal species (Verity, 1985; Bernard & Rassoulzadegan, 1990; Stoecker & McDowell Cappuzzo, 1990; Stoecker & Michaels, 1991; Montagnes *et al.*, 1996; Dolan & Simek, 1997; Strom & Morello, 1998; Jeong *et al.*, 1999; Kamiyama & Arima, 2001; Tang *et al.*, 2001; Pedersen & Hansen, 2003). As regards the interspecies interactions between the microplanktonic grazers and the microalgae, however, further investigations on temporal distribution patterns of microplankton communities using multivariate-statistical approaches are still needed although a few relevant researches have been reported (Tillmann, 2004).

In the present study, the temporal pattern of microplankton communities and interspecies correlations between ciliates and microalgae were analysed, using a range of multivariate statistical methods, based on a dataset of microplankton communities, which was collected biweekly at five sampling sites in Jiaozhou Bay near Qingdao, northern China, during a 1-year cycle (June 2007–May 2008). Our study asks the following questions: (1) how do the distribution patterns of microplankton communities change in an annual cycle?; (2) what are their relationships with environmental changes?; and (3) what are the interactions between planktonic ciliates and microalgae in marine ecosystems?

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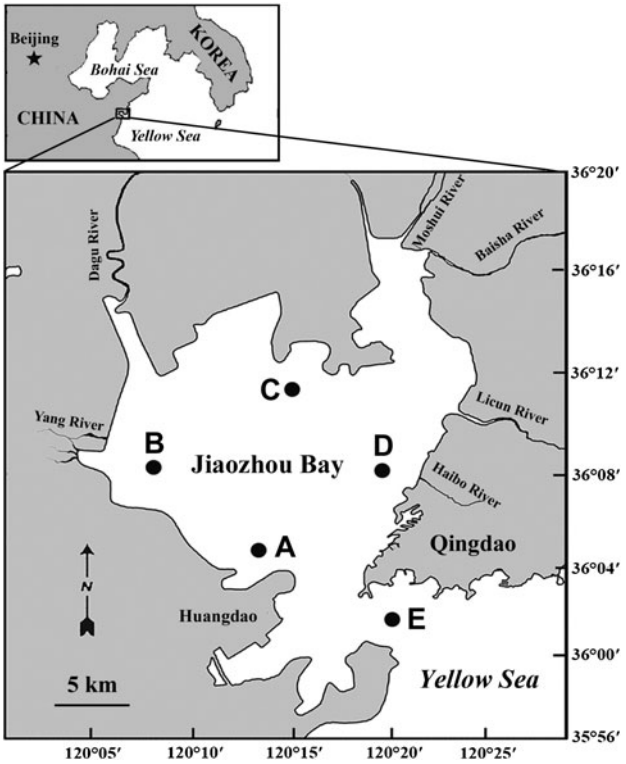

Fig. 1. Sampling stations of microplankton in Jiaozhou Bay.

MATERIALS AND METHODS

Study sites

Jiaozhou Bay is a semi-enclosed basin near Qingdao, northern China. It covers an area of about 390 km² with an average depth of 7 m and is connected to the Yellow Sea via a narrow opening about 2.5 km wide. Five sampling sites (A–E) were selected in this Bay (Figure 1).

Sampling, fixation, measurements, identification and enumeration

The study was conducted during June 2007 to May 2008 in Jiaozhou Bay, northern China (Jiang *et al.*, 2011a, b). The sampling strategy followed that described by Jiang *et al.* (2011a, b).

Salinity (Sal), pH, and dissolved oxygen concentration (DO) were measured *in situ*, using a multi-parameter sensor (MS5, HACH). Samples for nutrient analyses were preserved immediately upon collection by placing them at −20°C in the dark. Concentrations of soluble reactive phosphorus (SRP), ammonium nitrogen (NH_3-N), nitrate nitrogen (NO_3-N) and nitrite nitrogen (NO_2-N) were determined using a UV-visible spectrophotometer (DR-5000, HACH) according to the *Standard Methods for the Examination of Water and Wastewater* (APHA, 1992). For enumeration of ciliates, diatoms and dinoflagellates, a 0.1 ml aliquot of each concentrated sample was placed in a Perspex chamber and counted under a light microscope at ×400-magnification. A total of 0.5 ml concentrated samples were counted and yielded a standard error of <8% of the mean values of counts. The protargol staining method for ciliates was performed according to the

Table 1. List of the species of planktonic ciliates (Cili, ciliates) and microalgae (Dino, dinoflagellates; Dia, diatoms) from Jiaozhou Bay recorded in 120 samples including taxon type, annual average abundance and occurrence.

Species	Taxon type	Abundances (ind. l^{-1})[1]	Occurrence (%)
Codonella amphorella	Cili	++	8
Dysteria cristata	Cili	+	4
Halteria grandinella	Cili	+	4
Lacrymaria marina	Cili	+	13
Leegaardiella sol	Cili	+	8
**Leprotintinnus bottnicus*	Cili	+++	63
Leprotintinnus nerititicus	Cili	+	17
Mesodinium pupula	Cili	+++	100
Mesodinium velox	Cili	+	13
Metastrombidium sonnifer	Cili	+	17
Omegastrombidium elegans	Cili	+	13
**Omegastrombidium foissneri*	Cili	++	71
Omegastrombidium jankowski	Cili	+	25
**Parastrombidium faurei*	Cili	++	58
Placus salinus	Cili	++	4
**Pseudotontonia cornuta*	Cili	+++	83
Pseudotontonia simplicidens	Cili	++	38
Rimostrombidium caudatum	Cili	+	13
Rimostrombidium conicum	Cili	+	21
Rimostrombidium glacicolum	Cili	+++	75
Rimostrombidium orientale	Cili	+++	92
Rimostrombidium sphaericum	Cili	+++	71
Rimostrombidium undinum	Cili	+++	50
Rimostrombidium veniliae	Cili	+++	79
Spirostrombidium schizostomum	Cili	+	8
Spirotontonia turbinata	Cili	+++	75
**Stenosemella nivalis*	Cili	++	25
Stenosemella pacifica	Cili	++	25
Stenosemella steini	Cili	+	13
Strombidinopsis acuminatum	Cili	++	67
**Strombidium acutum*	Cili	+++	88
Strombidium apolatum	Cili	++	38
Strombidium capitatum	Cili	+++	100
**Strombidinopsis cheshiri*	Cili	+	17
**Strombidium compressum*	Cili	++	67
Strombidium conicum	Cili	+++	75
Strombidinopsis elegans	Cili	+	17
Strombidinopsis elongata	Cili	+	13
**Strombidium globosaneum*	Cili	+++	88
**Strombidium montagnesi*	Cili	++	46
**Strombidium styliferum*	Cili	++	71
**Strombidium sulcatum*	Cili	+++	67
Strombidium paracalkinsi	Cili	++	67
Strombidium rapulum	Cili	+	8
Strombidium tintinnodes	Cili	++	29
**Tintinnopsis tubulosoides*	Cili	++	25
**Tontonia antarctica*	Cili	++	58
Tintinnopsis acuminata	Cili	+	25
Tintinnopsis baltica	Cili	++	46
Tintinnopsis beroidea	Cili	+	21
Tintinnopsis brasiliensis	Cili	++	25
Tintinnopsis bütschlii	Cili	+	4
Tintinnopsis chinglanensis	Cili	+	8
Tintinnopsis lobiancoi	Cili	+	4
Tintinnopsis loricata	Cili	+	8
Tintinnopsis mucicola	Cili	+	17
Tintinnopsis nana	Cili	+	4
Tintinnopsis orientalis	Cili	++	25
Tintinnopsis parvula	Cili	+++	63

Continued

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Table 1. Continued

Species	Taxon type	Abundances (ind. l^{-1})[1]	Occurrence (%)
Tintinnopsis radix	Cili	+	8
Tintinnopsis tocantinensis	Cili	+	13
Tintinnopsis turgida	Cili	+	8
Tintinnopsis urnula	Cili	+	8
Uronychia setigera	Cili	+	4
Actinocyclus octonarius	Dia	+	8
**Actinoptychus senarius*	Dia	+	42
Amphora sp.	Dia	+	8
**Bacillaria paxillifera*	Dia	+	8
Bacteriastrum hyalinum	Dia	+	17
Ceratulina pelagica	Dia	+	17
Chaetoceros compressus	Dia	++	8
Chaetoceros curvisetus	Dia	+	17
Chaetoceros debilis	Dia	+	8
Chaetoceros lorenzianus	Dia	+	8
Chaetoceros paradoxus	Dia	++ +	8
Chaetoceros teres	Dia	+	8
**Coscinodiscus asteromphalus*	Dia	++ +	42
Coscinodiscus apiculatus	Dia	++	25
Coscinodiscus centralis	Dia	++	17
Coscinodiscus excentricus	Dia	+	25
Coscinodiscus gigas	Dia	++	58
Coscinodiscus granii	Dia	+	17
Coscinodiscus jonesianus	Dia	++	33
**Coscinodiscus oculus-iridis*	Dia	++	17
Coscinodiscus radiatus	Dia	+	8
Coscinodiscus sp.	Dia	+	8
**Coscinodiscus subtilis*	Dia	++ +	75
Coscinodiscus wailesii	Dia	+	8
Cyclotella striata	Dia	+	17
Detonula pumila	Dia	++	17
Diploneis bombus	Dia	++	75
**Ditylum brightwellii*	Dia	++	58
**Ditylum sol*	Dia	++	8
Eucampia cornuta	Dia	+	8
Eucampia zodiacus	Dia	++ + +	92
Eunotogramma debile	Dia	++	8
Fragilaria sp.	Dia	+	17
**Guinardia delicatula*	Dia	++ + +	50
Guinardia sp.	Dia	+	8
Guinardia striata	Dia	++	17
Hemiaulus hauckii	Dia	+	8
Hyalodiscus subtilis	Dia	+	8
Lauderia borealis	Dia	++	8
Leptocylindrus danicus	Dia	+	17
Licmophora abbreviata	Dia	++	33
Lithodesmium undulatum	Dia	++	17
Meuniera membranacea	Dia	++	33
Navicula salinarum	Dia	+	25
**Navicula* sp.	Dia	++ + +	92
Nitzschia closterium	Dia	++ +	42
Nitzschia longissima	Dia	+	8
Nitzschia lorenziana	Dia	++	42
Nitzschia sp.	Dia	++	58
Odontella regia	Dia	++	17
Odontella sinensis	Dia	++	58
Paralia sulcata	Dia	++ +	75
Pinnularia sp.	Dia	++ +	100
Planktoniella blanda	Dia	+	8
Planktoniella formosa	Dia	+	8
Planktoniella sol	Dia	+	8
Pleurosigma acutum	Dia	+	8
Pleurosigma pelagicum	Dia	+	17
Pleurosigma sp.	Dia	++	92
Pseudo-nitzschia pungens	Dia	++ +	58
Rhizosolenia alata	Dia	+	8
Rhizosolenia hyalina	Dia	+	8
Rhizosolenia robusta	Dia	+	8
**Rhizosolenia setigera*	Dia	+	33
Rhizosolenia styliformis	Dia	+	8
Schroderella delicatula	Dia	++ +	42
**Skeletonema costatum*	Dia	++ + +	67
Stephanopyxis palmeriana	Dia	++	17
Surirella sp.	Dia	+	17
Synedra sp.	Dia	+	25
Thalassionema frauenfeldii	Dia	+	8
Thalassiosira rotula	Dia	++	8
Thalassiosira sp.	Dia	++ +	83
Thalassiothrix longissima	Dia	+	17
Triceratium favus	Dia	+	25
Akashiwo sanguinea	Dino	++ +	17
**Alexandrium tamarense*	Dino	++ +	100
**Ceratium furca*	Dino	++	33
**Ceratium tripos*	Dino	++	50
**Dictyocha fibula*	Dino	++ +	75
Dinophysis acuminata	Dino	++	100
Dinophysis fortii	Dino	+	17
Gonyaulax polygramma	Dino	++	17
Gonyaulax verior	Dino	++ +	75
Gymnodinium catenatum	Dino	++	25
Gyrodimium spirale	Dino	+	25
Gyrodinium instriatum	Dino	+	17
Heterosigma akashiwo	Dino	++ + ++	67
Karenia mikimotoi	Dino	+	8
Lingulodinium polyedrum	Dino	+	17
Parahistioneis reticulata	Dino	+	8
Polykrikos schwarzii	Dino	++	17
Prorocentrum dentatum	Dino	++	8
**Prorocentrum lima*	Dino	++	42
**Prorocentrum micans*	Dino	++ +	75
**Prorocentrum minimum*	Dino	++	67
Protoperidinium conicum	Dino	++	25
Protoperidinium oceanicum	Dino	++	8
Protoperidinium pellucidum	Dino	++ +	42
Scrippsiella trochoidea	Dino	++ +	50

*, typical species determined by routine BEST within 120 microplankton samples; [1], + = 10; ++ = 10–100; ++ + = 100–1000; ++ + + = 1000–10000; ++ + ++ = over 10000.

protocol of Montagnes & Humphrey (1998). Scanning electron microscopy was used to identify the microalgal species hard to distinguish by light microscope. The cells were identified to the lowest taxonomic level possible based on the published references to keys and guides such as Hasle & Syvertsen (1997), Steidinger & Tangen (1997) and Song *et al.* (2003).

Data analyses

Multivariate analyses were carried out using the PRIMER v6.1 statistical package (Clarke & Gorley, 2006), the PERMANOVA+ for PRIMER (Anderson *et al.*, 2008) and the statistical program SPSS (version 16.0). Bray–Curtis similarity matrices were computed on species-abundance data

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while the temporal patterns of communities were summarized using the submodule CAP (canonical analysis of principal coordinates) of PERMANOVA+ on Bray–Curtis similarities. Differences between groups of samples were tested by the submodule ANOSIM (analysis of similarity) (Clarke & Gorley, 2006). The significance of ciliate–microalgae correlations was tested using the routine RELATE (Clarke & Gorley, 2006). The routine BEST was used to determine the typical species for both the ciliate and the microalgal assemblages (Clarke & Warwick, 1994). The multidimensional scaling (MDS) ordination was used to summarize species distribution on Bray–Curtis similarity (Clarke & Gorley, 2006). RELATE/BIOENV analyses were used to reveal the correlations between temporal patterns of microplankton communities and environmental conditions (Clarke & Gorley, 2006).

The best possible regression models were explored using the stepwise selection mode and the optimal model was estimated based on the statistical significance (high R^2, $P < 0.05$), using the SPSS software. Biotic data were fourth root-transformed, while abiotic data were log-transformed before analyses.

RESULTS

Taxonomic composition

The taxonomic composition, average abundance and occurrence of microplankton (planktonic ciliates and microalgae) assemblages observed during the study period are summarized in Table 1. A total of 64 ciliate species and 100 microalgae species (basically dinoflagellates and diatoms) were identified from 120 samples during the 1-year survey in Jiaozhou Bay, northern China. The BEST analysis showed that the microplankton communities were characterized by 14 ciliates and 18 microalgae respectively (Table 1).

Temporal variations of community structures

The temporal patterns of planktonic ciliate and microalgae assemblages in 1-year cycle were discriminated by using the submodule CAP (Figure 2). The first canonical axis separated the ciliate assemblages sampled in summer (on the right) from those in autumn and winter (on the left), while the second canonical axis discriminated the samples in spring (lower) from summer and winter (upper) (Figure 2A). The two canonical axes clearly separated the microalgae assemblages sampled in four seasons (Figure 2B). The ANOSIM test demonstrated significant differences between each pair of temporal groups in ciliates ($R = 0.305$, $P = 0.001$) and microalgae ($R = 0.158$, $P = 0.001$).

Temporal ordinations of species distribution

The temporal patterns of species distribution within ciliated and microalgal assemblages are summarized in Figures 3, 4, 5 and 6, using the MDS ordination on Bray–Curtis similarity from the log-transformed species-abundance data.

In spring, the species distribution represented only three groups (group Sp I–III) (Figure 3). Group Sp I was the primary contributor in communities and consisted of 10 ciliated species (e.g. *Strombidium globosaneum* and *Strombidium sulcatum*) and 3 microalgae (e.g. *Alexandrium tamarense* and *Navicula* sp.) while group Sp II included two microalgal species (*Ditylum brightwellii* and *Guinardia delicatula*) with two ciliates (*Strombidinopsis cheshiri* and *Leprotintinnus bottnicus*) and group Sp III involved four microalgal species (e.g. *Skeletonema costatum* and *Coscinodiscus subtilis*) (Figure 3B). In this season, group Sp I dominated almost all samples except in early March during which group Sp II became the primary contributor with microalgae blooming but quickly suppressed in late March by ciliates. Finally, in April, group Sp I dominated

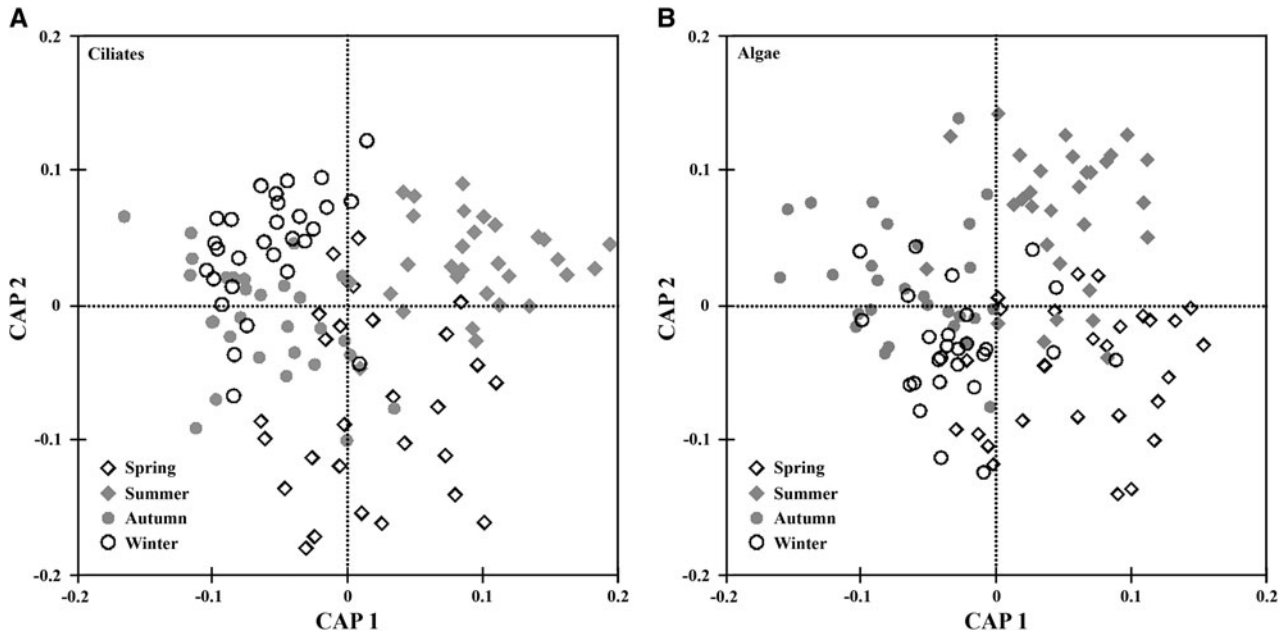

Fig. 2. Canonical analysis of principal coordinates (CAP) on Bray–Curtis similarities from species-abundance data of two assemblages (ciliates and microalgae) in 120 samples from five sampling sites in Jiaozhou Bay during the annual cycle from June 2007 to May 2008.

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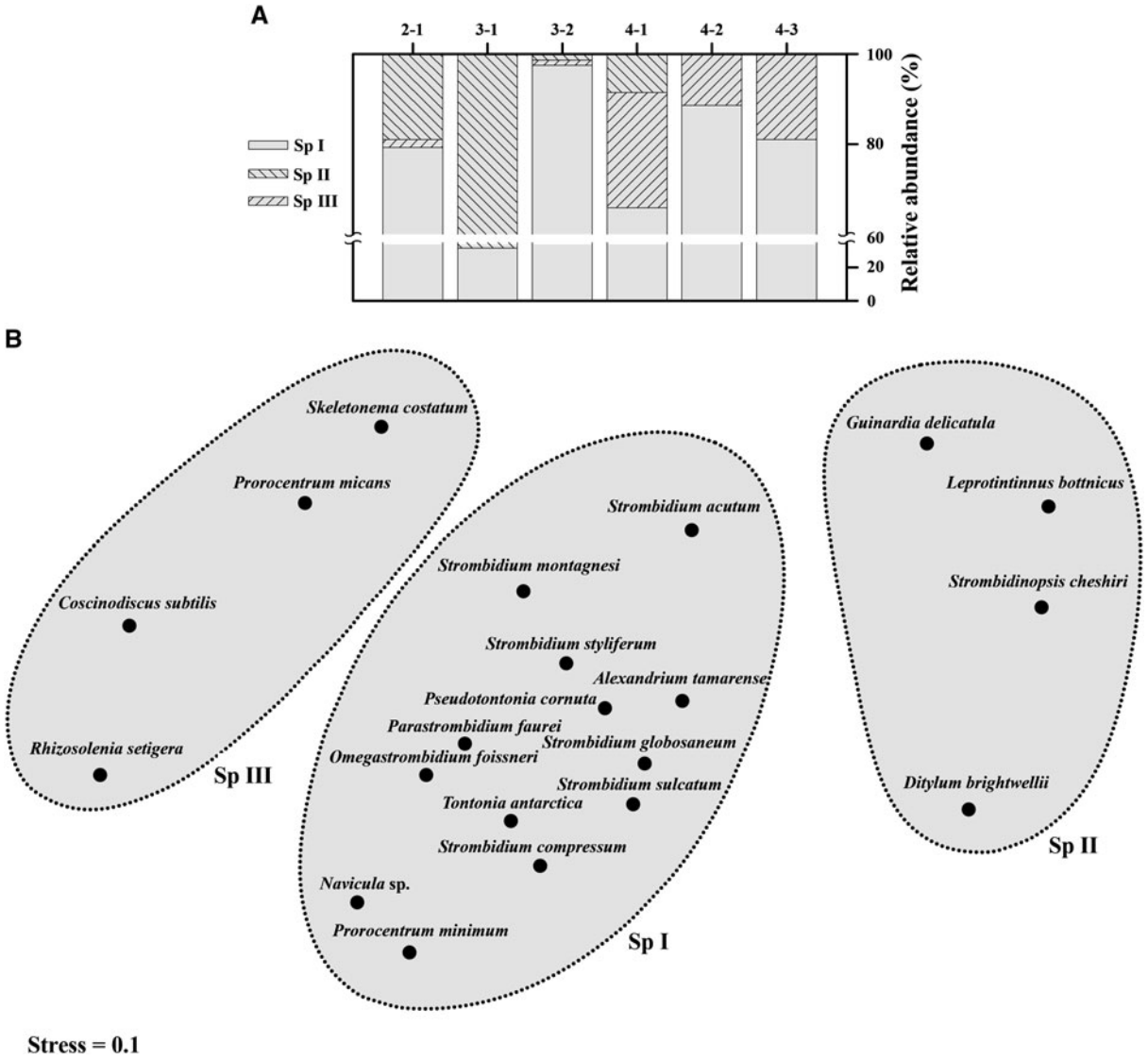

Fig. 3. Ordination of the typical species on the multi-dimensional scaling-diagram (B) and temporal variation in relative abundance (A) in spring. Sp I–III, group Sp I–III.

the community with the cooperation of group Sp III (Figure 3).

In summer, the species distribution comprised five groups (group Su I–V) of which groups Su I and Su II with most dominant species were the primary contributors to the communities in terms of abundance compared to group Su III–V with low abundance (Figure 4). Group Su I mainly comprised some ciliates coming from group Sp I in spring (e.g. *Pseudotontonia cornuta*, *Omegastrombidium foissneri* and *Strombidium conpressum*) associated with diatom *Navicula* sp. (also coming from group Sp I) and dinoflagellate *Prorocentrum micans* (from Sp III) while group Su II comprised mainly microalgal species which were bursting out, e.g. *Ceratium tripos*, *Dictyocha fibula* and *Coscinodiscus asteromphalus*, or coming from species in spring such as *Alexandrium tamarense* (group Sp I) and *Skeletonema costatum* (group Sp III) (Figure 4B). It should be noticed that the communities in summer presented a clear continuity to the pattern in spring (Figures 3 & 4): in early May, groups Su I and IV, with the species mainly from group Sp I in spring, dominated the community in cooperation with group Su II (Figures 3 & 4). After that, group Su I and II exhibited such an interspecies relationship that they alternately dominated the communities during this season until group Su II almost occupied the community in the last sample (Figure 4B).

In autumn, the species distribution consisted of six groups (group Au I–VI). Group Au I, included the 19 most dominant species (e.g. ciliates *Leprotintinnus bottnicus*, *Tintinnopsis bubulosoides* and *Strombidium styliferum*; diatom *Skeletonema costatum* and dinoflagellate *Prorocentrum lima*) mainly coming from group Su I and II in summer, and was the primary contributor to communities. While group Au II comprised four species of which, diatom *Navicula* sp. and ciliate *Strombidium sulcatum* were coming from summer group Su I and *Prorocentrum minimum* from group Su IV. As regards group Au III–VI, this was composed of several less dominant species from group Su II and III (Figures 4B &5B). Although with community continuity in summer, however, the pattern of communities was different (Figures 4 & 5): group Au I dominated the most samples afterwards being replaced by group Au II, followed by group Au IV and VI in late autumn (Figure 5A).

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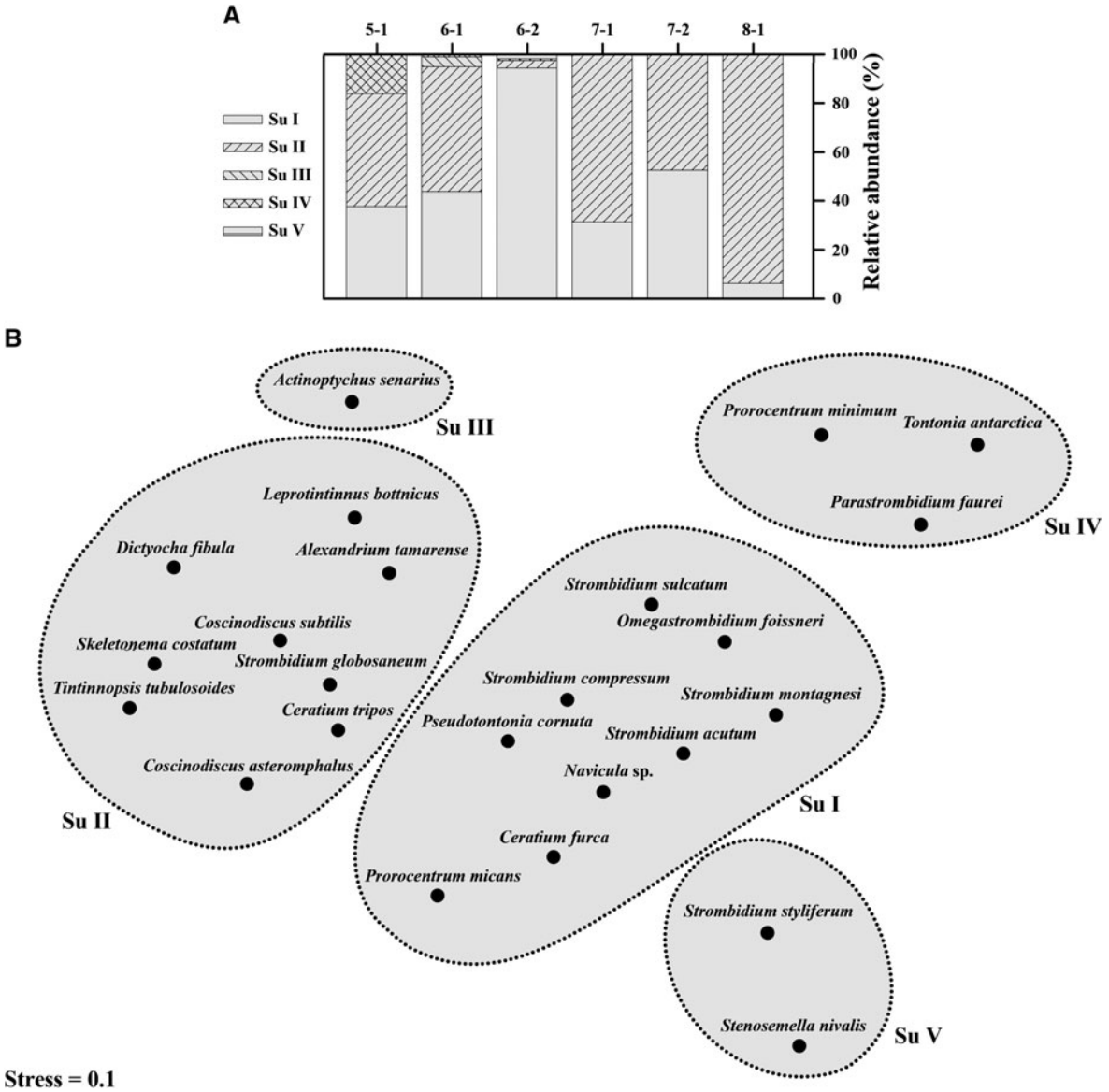

Fig. 4. Ordination of the typical species on the multi-dimensional scaling-diagram (B) and temporal variation in relative abundance (A) in summer. Su I–V, group Su I–V.

In winter, the species distribution represented six groups (group Wi I–VI) (Figure 6B). Group Wi I comprising 13 dominant species, of which mainly ciliates from autumn group Au I (e.g. ciliates *Strombidium acutum*, *Strombidium styliferum* and *Leprotintinnus bottnicus*) associated with diatom *Guinardia delicatula* of group Au III, was the main contributor to communities in all samples (Figures 5 & 6) while group Wi IV included two dinoflagellate *Prorocentrum minimum* (from group Au II) and *Prorocentrum lima* (from group Au I) in cooperation with two ciliates (from group Au I) (Figures 5B & 6B). Furthermore, group Wi V comprised ciliate *Stenosemella nivalis* (group Au I) and diatom *Coscinodiscus oculus-iridis* (group Au VI) (Figures 5B & 6B); group II–VI comprised several species from autumn groups but in low abundance (Figures 5 & 6). Although the community in late November is very consistent with that of early November, the temporal pattern had significant differences with that in autumn (Figures 5A & 6A): group Wi I was always the main component in communities in cooperation with group Wi III, IV and V and predominated in late winter (Figures 5A & 6A). After that, the species distribution in spring represented clear species relationships with that in winter (Figures 3B & 6B): primary contributor group Sp I were merged by group Wi I–IV, e.g. ciliates *Strombidium globosaneum* (from group Wi I), *Strombidium sulcatum* (group Wi II) and *Strombidium montagnesi* (group Wi II) were associated with microalgae *Alexandrium tamarense* (group Wi I), *Navicula* sp. (group Wi I) and *Prorocentrum minimum* (group Wi IV). Furthermore, some species of group Wi I forming the group Sp II and III, for instance, microalgae *Ditylum brightwellii* and *Guinardia delicatula* associated with two ciliates in group Sp II; *Coscinodiscus subtilis* associated with the other three microalgae in group Sp III.

The temporal succession process of 32 microplankton species (14 ciliates and 18 microalgae) is indicated in Figure 7 and highly consistent with the MDS ordination results in Figures 3, 4, 5 and 6. In this 1-year cycle, planktonic ciliates and microalgae formed a loop together. During each

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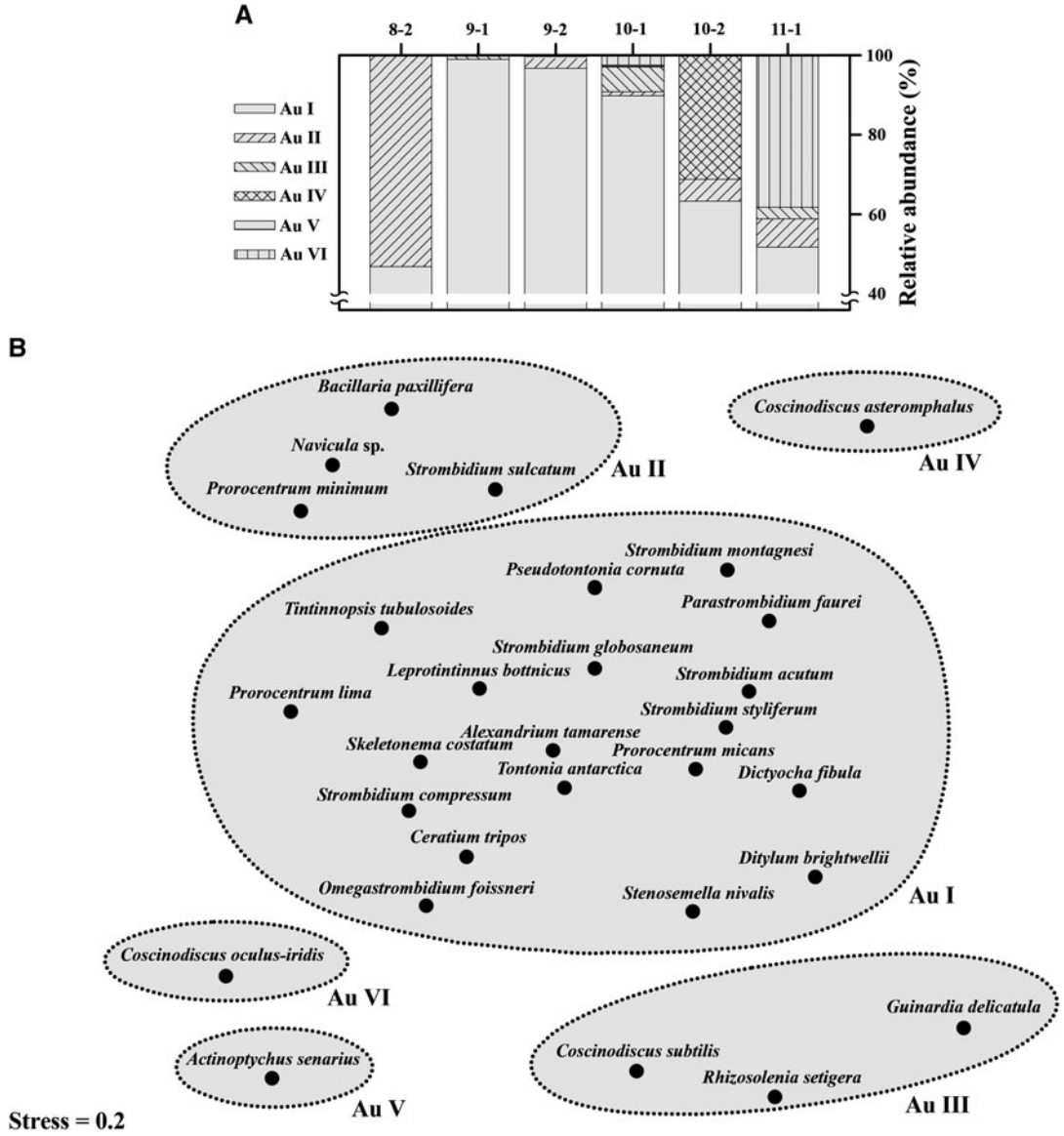

Fig. 5. Ordination of the typical species on the multi-dimensional scaling-diagram (B) and temporal variation in relative abundance (A) in autumn. Au I–VI, group Au I–VI.

season or period, the one-way arrows show succession of species and the two-way arrows show their occurrence at the same time (Figure 7).

Interspecies correlations between planktonic ciliates and microalgae

The Mantel test, by using RELATE analysis, revealed that there was a significant correlation between temporal variations in ciliated and microalgal assemblage structures ($R = 0.218$; $P = 0.001$).

In Table 2, the correlations between the abundances of 14 ciliates and 18 microalgae were obtained by linear regression and indicated that species-specific correlations existed between 11 ciliated species and 13 microalgal species. Among these, eight species (*Strombidium globosaneum*, *Leprotintinnus bottnicus*, *Strombidinopsis cheshiri*, *Strombidium compressum*, *Stenosemella nivalis*, *Tontonia antarctica*, *Tintinnopsis tubulosoides* and *Strombidium sulcatum*) were found correlated with two or more microalgal species in abundance. For example, *S. globosaneum*, was not only positively correlated with two dinoflagellates (*Alexandrium tamarense* and *Prorocentrum minimum*) and two diatoms (*Coscinodiscus asteromphalus* and *Guinardia delicatula*) but also negatively correlated with the diatom *Actinoptychus senarius*. Only three species, however, *Pseudotontonia cornuta*, *Strombidium montagnesi* and *Strombidium acutum*, were associated with only one microalgal species (Table 2).

Results obtained by linear regression also indicated that the abundances of 11 microalgal species were correlated with that of 11 planktonic ciliates (Table 3). Six species (*Ceratium tripos*, *Skeletonema costatum*, *Actinoptychus senarius*, *Guinardia delicatula*, *Bacillaria paxillifera* and *Coscinodiscus oculus-iridis*) were found correlated with not only one species; however, five species (*Prorocentrum lima*, *Alexandrium tamarense*, *Ditylum brightwellii*, *Dictyocha fibula* and *Ceratium furca*) were associated with only one ciliate species (Table 3).

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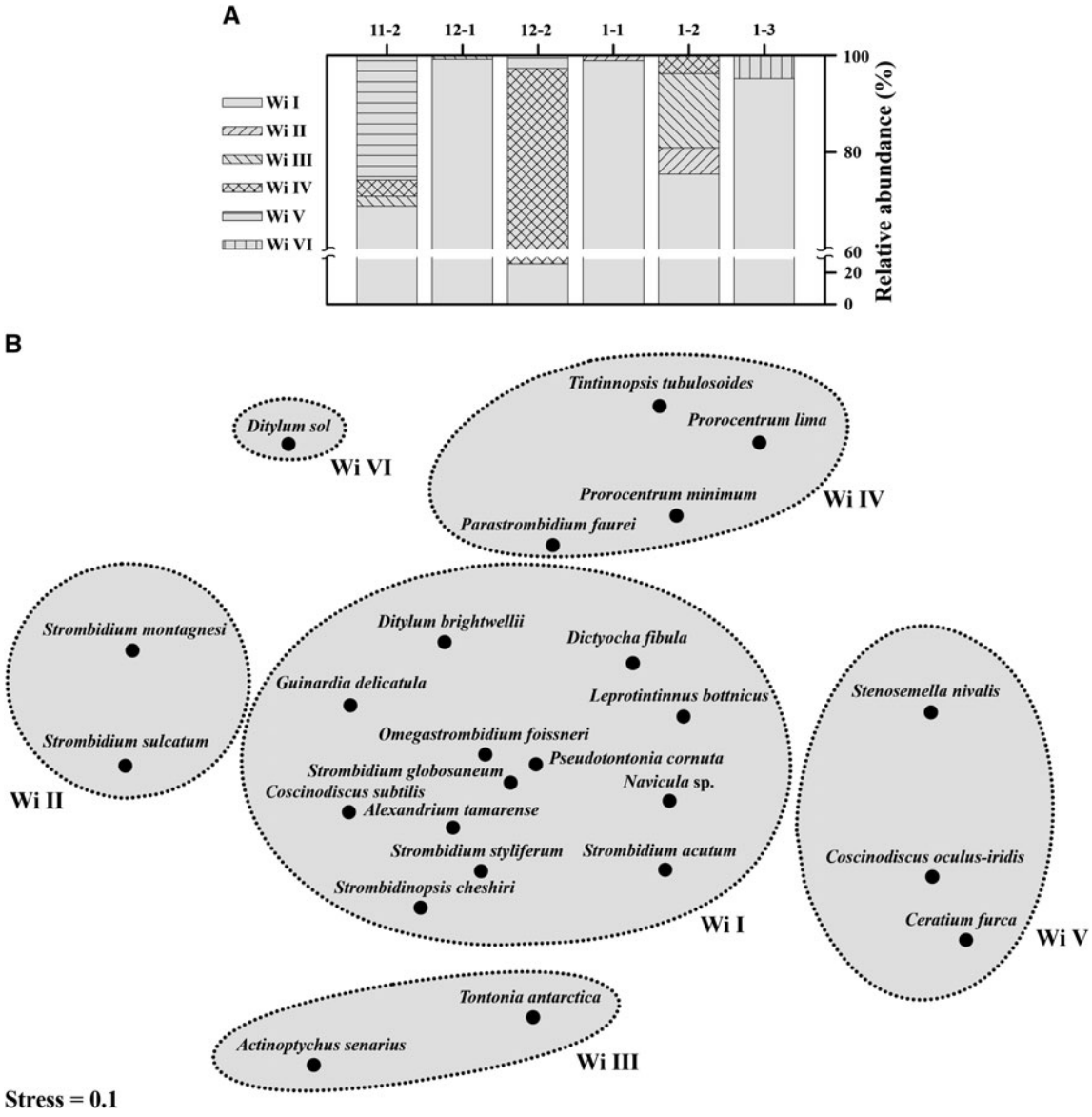

Fig. 6. Ordination of the typical species on the multi-dimensional scaling-diagram (B) and temporal variation in relative abundance (A) in winter. Wi I–VI, group Wi I–VI.

As specified above, the linear regression analyses on modelling the species-specific correlations between 12 planktonic ciliate species and 15 microalgal species are summarized as a microbial correlation web in Figure 8.

Relationship between microplankton and environmental variables

The Mantel test demonstrated that the temporal variations in microplankton community structures were significantly correlated with those of environmental variables ($P < 0.001$).

For the temporal cycle, the correlations between microplankton abundances and environmental variables were established by multivariate biota–environment (BIOENV) analysis (Table 4). The results showed that the best matching with the planktonic ciliates occurred with the combination of temperature, salinity and NO_3-N, while the best matching with microalgae occurred with the combination of temperature, pH and NO_3-N. It was also notable that temperature and NO_3-N were included in most correlations (Table 4).

DISCUSSION

So far, there has been a growing interest on the interspecies correlations of planktonic ciliated protozoan with microalgae especially in field studies, although many researches have analysed various aspects of growth and feeding of ciliate species in culture with many ingeniously designed to study the interactions of specifically ciliates with demonstrated microalgal species (Bernard & Rassoulzadegan, 1990; Dolan & Simek, 1997; Montagnes & Lessard, 1999; Granéli & Johansson, 2003; Clough & Strom, 2005). For example, several tintinnids and non-loricate ciliates (Heinbokel, 1978; Jeong *et al.*, 1999; Maneiro *et al.*, 2000; Jakobsen *et al.*, 2001; Stoecker *et al.*, 2002; Gransden & Lewitus, 2003; Rosetta & McManus, 2003; Kamiyama & Matsuyama, 2005; Setälä *et al.*, 2005) are

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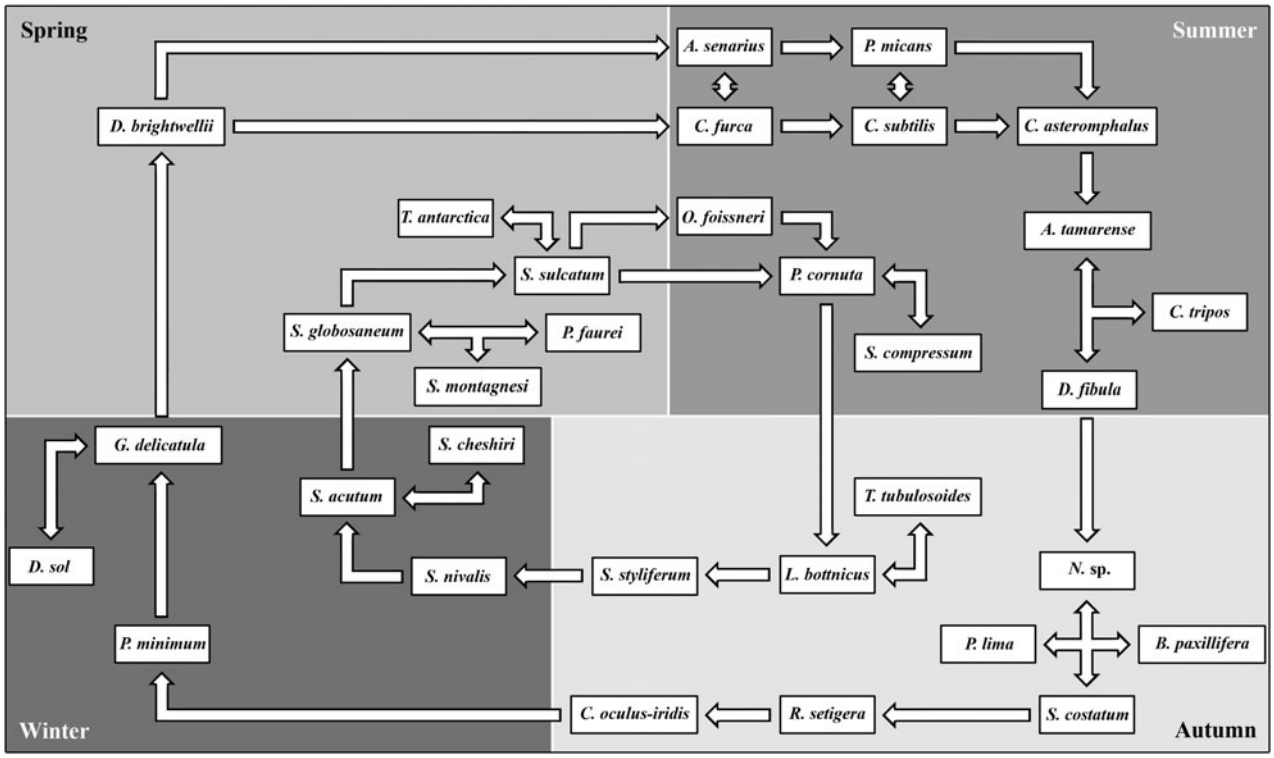

Fig. 7. 1-year loop of 14 dominant ciliate species and 18 microalgae species in abundance. Species abbreviations: *A. senarius*, *Actinoptychus senarius*; *A. tamarense*, *Alexandrium tamarense*; *B. paxillifera*, *Bacillaria paxillifera*; *C. furca*, *Ceratium furca*; *C. tripos*, *Ceratium tripos*; *C. asteromphalus*, *Coscinodiscus asteromphalus*; *C. oculus-iridis*, *Coscinodiscus oculus-iridis*; *C. subtilis*, *Coscinodiscus subtilis*; *D. fibula*, *Dictyocha fibula*; *D. brightwellii*, *Ditylum brightwellii*; *D. sol*, *Ditylum sol*; *G. delicatula*, *Guinardia delicatula*; *L. bottnicus*, *Leprotintinnus bottnicus*; *N.* sp., *Navicula* sp.; *O. foissneri*, *Omegastrombidium foissneri*; *P. faurei*, *Parastrombidium faurei*; *P. lima*, *Prorocentrum lima*; *P. micans*, *Prorocentrum micans*; *P. minimum*, *Prorocentrum minimum*; *P. cornuta*, *Pseudotontonia cornuta*; *R. setigera*, *Rhizosolenia setigera*; *S. cosatum*, *Skeletonema costatum*; *S. nivalis*, *Stenosemella nivalis*; *S. acutum*, *Strombidium acutum*; *S. cheshiri*, *Strombidinopsis cheshiri*; *S. compressum*, *Strombidium compressum*; *S. globosaneum*, *Strombidium globosaneum*; *S. montagnesi*, *Strombidium montagnesi*; *S. styliferum*, *Strombidium styliferum*; *S. sulcatum*, *Strombidium sulcatum*; *T. antarctica*, *Tontonia antarctica*; *T. tubulosoides*, *Tintinnopsis tubulosoides*.

known to ingest dinoflagellates or other bloom-forming microalgae, and may be important in controlling their blooms (Montagnes & Lessard, 1999; Tillmann, 2004). In other cases, toxic dinoflagellates or other microalgae appear to have deleterious effects on ciliates such as changes in swimming behaviour, reduced ingestion, inability to support growth or even causing mortality (Jakobsen *et al.*, 2001; Kamiyama & Arima, 2001; Granéli & Johansson, 2003; Rosetta & McManus, 2003; Clough & Strom, 2005). Moreover, several mixotrophic dinoflagellates ingesting ciliates have been described (Jacobson & Anderson, 1996; Li *et al.*, 1996). For instance, *Ceratium furca* preys mainly on choreotrich ciliates (Smalley *et al.*, 1999; Smalley & Coats, 2002). Thus, a predatory ciliate may become the prey of the dinoflagellate it tried to consume (Tillmann, 2004).

In our study, a total of 64 ciliate species and 100 diatoms and dinoflagellates were identified during an annual cycle in Jiaozhou Bay from June 2007 to May 2008. The data are basically consistent with historical reports (Shen, 2001; Zhang & Wang, 2001) in this area. 14 ciliates and 18 microalga species, which in combination successfully described their own assemblages respectively, were sought out by multivariate analyses. Furthermore, the annual variations in ciliated and microalgal assemblages all presented a clear temporal pattern and a definitely significant correlation between these two assemblage structures has been proved by the Mantel test ($P = 0.001$). This seasonal variation pattern in microbial community was also in agreement with the previous studies in other regions (Gomez & Gorsky, 2003; Kchaou *et al.*, 2009).

In addition, our study indicated that the community structures of microplankton were different between the four seasons of a whole 1-year period and complex interspecies correlations are presented among the ciliated and microalgal species. Furthermore, in each season, planktonic ciliates and microalgae exhibited their special functions on structuring community pattern in the microbial ecosystem during each month or sample. And it is impressive that the microalgal blooms were obviously suppressed or shortened by planktonic ciliates, which has been revealed by many previous investigations (Admiraal & Venekamp, 1986; Bochstahler & Coats, 1993; Jeong *et al.*, 1999; Kamiyama & Arima, 2001; Tillmann, 2004).

Moreover, 32 microplankton species represented a clear succession process and formed a circulation. Although the complexity of microbial ecosystems is enormous, with hundreds of species interacting in a number of ways from competition and predation to facilitation and mutualism (Montagnes & Lessard, 1999; Maneiro *et al.*, 2000; Tillmann, 2004; Sapp *et al.*, 2007). Based on our data, in this microbial loop especially in each season, the specific interspecies succession process revealed the potential relationships between ciliates and microalgal species.

Numerous previous studies have documented the species-specific correlations by laboratory or field studies (Maneiro *et al.*, 2000; Jakobsen *et al.*, 2001; Stoecker *et al.*, 2002; Gransden & Lewitus, 2003; Rosetta & McManus, 2003) but

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Table 2. Linear regression analysis; abundance of protozoan grazer related to algival protists. *F* of the model is only shown when the model is multiple.

Phagotrophic species	R^2	Variables	Regression coefficients	*t*	*P*
		Constant	−0.262	−0.344	0.735
		Actinoptychus senarius	−0.642	−4.277	<0.001
Strombidium globosaneum $F_{(5,23)} = 14.732$; $P < 0.001$	0.804	*Alexandrium tamarense*	0.58	4.628	<0.001
		Prorocentrum minimum	0.472	4.889	<0.001
		Coscinodiscus asteromphalus	0.306	3.512	0.002
		Guinardia delicatula	0.162	2.27	0.036
		Constant	0.808	1.527	0.142
Leprotintinnus bottnicus $F_{(3,23)} = 14.709$; $P < 0.001$	0.688	*Dictyocha fibula*	0.486	3.332	0.003
		Prorocentrum lima	0.779	3.975	0.001
		Actinoptychus senarius	0.683	2.649	0.015
		Constant	0.231	1.159	0.26
Strombidium cheshiri $F_{(3,23)} = 14.453$; $P < 0.001$	0.684	*Guinardia delicatula*	0.371	6.407	<0.001
		Ditylum sol	−0.567	−3.906	0.001
		Rhizosolenia setigera	−0.436	−3.114	0.005
		Constant	3.171	6.958	<0.001
Strombidium compressum $F_{(3,23)} = 13.223$; $P < 0.001$	0.665	*Ceratium tripos*	0.808	4.433	<0.001
		Ditylum brightwellii	−0.279	−2.305	0.032
		Dictyocha fibula	0.353	−2.256	0.035
		Constant	3.409	4.568	<0.001
Stenosemella nivalis $F_{(3,23)} = 11.411$; $P < 0.001$	0.631	*Alexandrium tamarense*	−0.605	−4.734	<0.001
		Rhizosolenia setigera	0.432	2.516	0.021
		Dictyocha fibula	0.193	2.162	0.043
		Constant	0.231	8.604	<0.001
Tontonia antarctica $F_{(3,23)} = 8.407$; $P = 0.001$	0.558	*Dictyocha fibula*	0.371	−3.026	0.007
		Actinoptychus senarius	−0.567	−2.628	0.016
		Ceratium furca	−0.436	−2.435	0.024
		Constant	0.054	0.177	0.861
Tintinnopsis tubulosoides $F_{(2,23)} = 12.599$; $P < 0.001$	0.545	*Ceratium tripos*	0.406	3. 438	0.002
		Prorocentrum lima	0.377	2.715	0.013
		Constant	4.365	7.282	<0.001
Strombidium sulcatum $F_{(2,23)} = 6.135$; $P = 0.008$	0.369	*Coscinodiscus oculus-iridis*	−0.667	−2.770	0.011
		Dictyocha fibula	−0.375	−2.226	0.037
		Constant	3.282	7.843	<0.001
Pseudotontonia cornuta	0.212	*Ceratium furca*	0.547	2.434	0.024
		Constant	2.335	5.073	<0.001
Strombidium montagnesi	0.192	*Actinoptychus senarius*	−0.683	−2.284	0.032
		Constant	4.188	9.836	<0.001
Strombidium acutum	0.189	*Actinoptychus senarius*	−0.626	−2.263	0.034

it should be addressed that especially in field studies, the connections between the ciliates and microalgae cannot be proven because of a lack of a statistical resolution. In the present study, the approach of multivariate analyses basically indicates the potential relationships between dominant ciliates and dominant microalgae. Then, linear regression finally calculated the relationships and formed an interspecies correlation network. In this microbial web, it is clear that in field studies the interspecies correlations were very complex and cannot simply be defined by several species. The results showed that most ciliates and microalgae were correlated with two or more species and only in fewer cases one species was associated with another one. In a lot of previous laboratory studies, which is consistent with our results, the interspecies correlation hypotheses were examined by processing the different types of ingested matter. For example, in the study of Montagnes *et al.* (1996), the planktonic ciliate *Strombidinopsis cheshiri* was proved to feed on diatoms and in our study *S. cheshiri* was definitely related to the three diatom species *Guinardia delicatula*, *Ditylum sol* and *Rhizosolenia setigera*. Moreover, in the studies of Smalley *et al.* (1999) and Smalley & Coats (2002), the dinoflagellate *Cerarium furca* was determined grazing on choreotrich ciliates, which is also proven in our study with the connections among *C. furca*, *Totonia antarctica* and *Pseudotontonia cornuta*. So, the microbial interspecies correlation web calculated by the linear regression between ciliates and microalgal species could be used as a robust guide for future studies especially after more and more information is gathered to verify this conclusion by further investigations on a range of marine habitats and over extended time periods. Furthermore, the Mantel and BIOENV analyses demonstrated that the temporal variations in microplankton community structures were significantly correlated with certain environmental variables, especially nutrients in combination with temperature. These findings suggest that the microplankton communities accurately reflect the water quality and have the potential for use in marine water monitoring. Moreover, the evidence supplied by multivariate analyses could guide the designs of culture researches in future. So, to discover information about complex ecological systems efficiently, this multivariate tool could be used as a powerful approach for inferring the interspecies correlations from field data in marine ecosystems.

In summary, the results of this study demonstrated that: (1) species distributions of planktonic ciliates and microalgae

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Table 3. Linear regression analysis; abundance of algival protists related to protozoan grazer. *F* of the model is only shown when the model is multiple.

Algival species	R^2	Variables	Regression coefficients	*t*	*P*
		Constant	−1.305	−2.444	0.024
		Strombidium compressum	0.595	6.405	<0.001
Ceratium tripos $F_{(4,23)} = 27.168$; $P < 0.001$	0.851	*Tintinnopsis tubulosoides*	0.544	4.395	<0.001
		Parastrombidium faurei	−0.350	−4.008	0.001
		Strombilidium acutum	0.353	3.47	0.003
		Constant	−1.913	−1.866	0.076
Skeletonema costatum $F_{(2,23)}$=17.641; $P < 0.001$	0.627	*Leprotintinnus bottnicus*	0.873	4.521	<0.001
		Strombidium compressum	0.817	3.267	0.004
		Constant	2.075	3.758	0.001
Actinoptychus senarius $F_{(3,23)}$=10.693; $P < 0.001$	0.616	*Strombidium globosaneum*	−0.433	−3.990	0.001
		Stenosemella nivalis	−0.414	−3.327	0.003
		Leprotintinnus bottnicus	0.218	3.145	0.005
		Constant	3.264	2.74	0.012
Guinardia delicatula $F_{(2,23)}$=9.400; $P = 0.001$	0.472	*Strombidinopsis cheshiri*	1.571	3.865	0.001
		Pseudotontonia cornuta	−0.600	−2.154	0.043
		Constant	−0.513	−2.080	0.05
Bacillaria paxillifera $F_{(2,23)}$=8.678; $P = 0.002$	0.453	*Tintinnopsis tubulosoides*	0.344	3.95	0.001
		Tontonnia antarctica	0.147	2.262	0.034
		Constant	−0.432	−0.955	0.35
Prorocentrum lima	0.412	*Leprotintinnus bottnicus*	0.421	3.926	0.001
		Constant	5.877	18.276	<0.001
Alexandrium tamarense	0.398	*Stenosemella nivalis*	−0.675	−3.814	0.001
		Constant	1.21	2.334	0.030
Coscinodiscus oculus-iridis $F_{(2,23)}$=6.167; $P = 0.008$	0.370	*Strombidium sulcatum*	−0.462	−3.385	0.003
		Parastrombidium faurei	0.326	2.237	0.036
		Constant	3.922	5.376	<0.001
Ditylum brightwellii	0.318	*Strombidium compressum*	−0.659	−3.206	0.004
		Constant	1.02	1.519	0.143
Dictyocha fibula	0.260	*Leprotintinnus bottnicus*	0.443	2.783	0.011
		Constant	−0.607	−0.900	0.378
Ceratium furca	0.212	*Pseudotontonia cornuta*	0.388	2.434	0.024

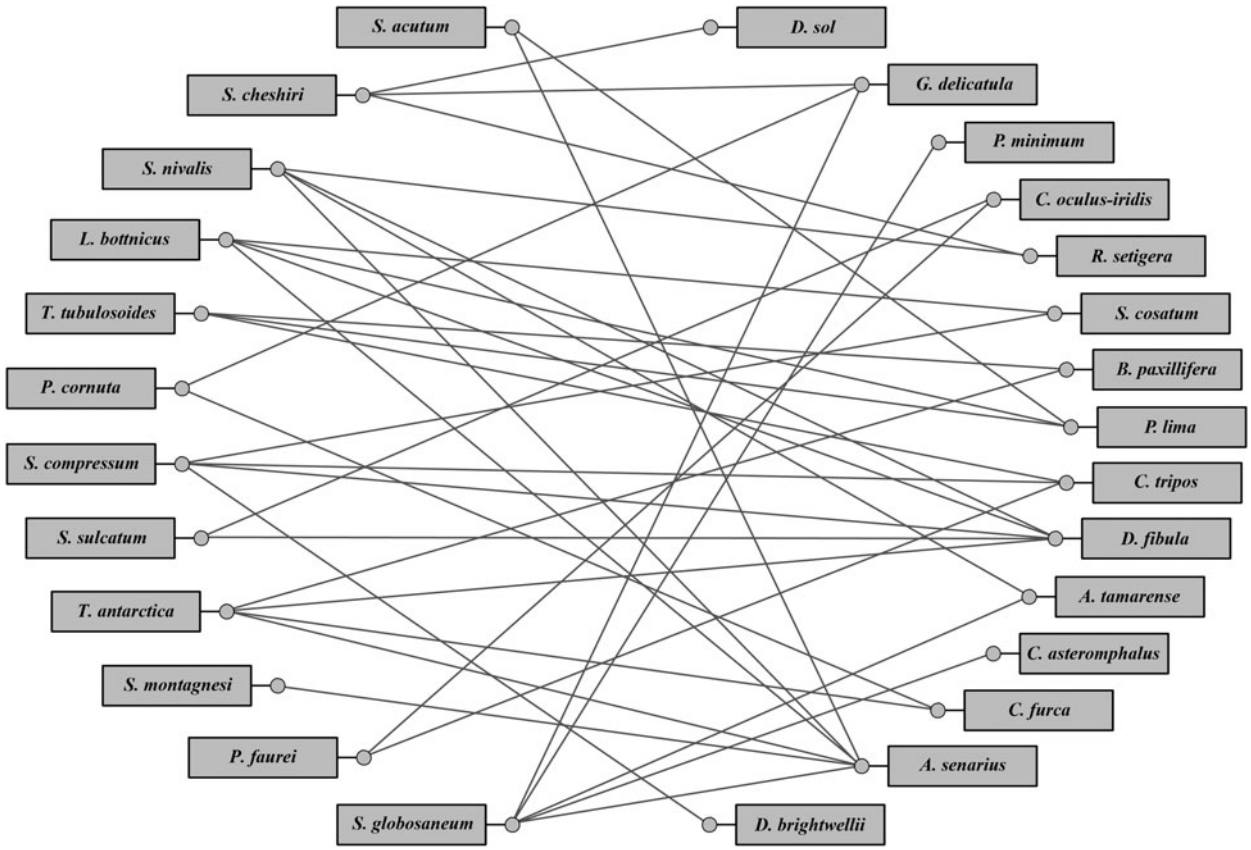

Fig. 8. Microbial correlation web formed by 12 ciliated protozoa species and 15 microalgal species. See Figure 7 for all abbreviations.

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Table 4. Summary of results from biota–environment (BIOENV) analysis showing the 10 best matches of environmental variables with temporal variations in ciliate and microalgae abundances in Jiaozhou Bay from June 2007 to May 2008.

Rank	Ciliates			Microalgae		
	R	Environmental variables	*P*	*R*	Environmental variables	*P*
1	0.306	Tem, Sal, NO_3-N	0.01	0.176	Tem, pH, NO_3-N	0.01
2	0.303	Tem, Sal, NO_3-N	0.01	0.171	Tem, pH, NH_3-N, NO_3-N	0.01
3	0.295	Tem, Sal, NO_3-N	0.01	0.168	Tem, pH, Sal, NO_3-N	0.01
4	0.294	Tem, pH, Sal, DO, NO_3-N	0.01	0.167	Tem, pH, NO_3-N, SRP	0.01
5	0.291	Tem, Sal, NO_3-N, NO_2-N	0.01	0.165	Tem, pH, Sal, NO_3-N, SRP	0.01
6	0.290	Tem, Sal, DO, NO_3-N, NO_2-N	0.01	0.163	Tem, pH, Sal, NH_3-N, NO_3-N	0.01
7	0.289	Tem, NO_3-N	0.01	0.162	Tem, pH, NH_3-N,	0.01
8	0.286	Tem, NO_3-N, NO_2-N	0.01	0.161	Tem, NO_3-N	0.01
9	0.282	Tem, pH, Sal, DO, NO_3-N, NO_2-N	0.01	0.159	Tem, pH, Sal, DO, NO_3-N, SRP	0.01
10	0.281	Tem, DO, NO_3-N	0.01	0.159	Tem, pH, Sal, NH_3-N, NO_3-N, SRP	0.01

Tem, temperature; Sal, salinity; DO, dissolved oxygen; NO_3-N, nitrate nitrogen; NO_2-N, nitrite nitrogen.

were both temporal in a 1-year cycle and the significant relationship between these two assemblages was represented; (2) complex interspecies correlations between planktonic ciliates and microalgae were summarized as a loop and proved by statistical evidence to form a microbial correlation web; (3) the temporal pattern of microplankton communities significantly related to the temporal changes of environmental variables; and (4) these findings suggest there is a clear temporal cycle of the microplankton communities in response to environmental changes in Jiaozhou Bay and provide basic referenced data for future field and laboratory studies and these multivariate methods have the potential to contribute a novel important tool for gaining deeper insight into the structure and stability of the microbial food web in marine ecosystems.

ACKNOWLEDGEMENTS

This work was supported by the Darwin Initiative Programme (Project No. 14-015) which is funded by the UK Department for Environment, Food and Rural Affairs, 'The Natural Science Foundation of China' (project number: 41076089) and a grant by the Research Group (Project No. RGP-VPP-083), King Saud University Deanship of Scientific Research. We thank Professor Weibo Song, Laboratory of Protozoology, Ocean University of China (OUC), China, for his helpful discussions.

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https://doi.org/10.1017/S0025315412001324 Published online by Cambridge University Press