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The coupling of oligotrich ciliate populations and hydrography in the East China Sea: spatial and temporal variations

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Abstract

Variations in the spatial and temporal distribution of oligotrich ciliate populations in the East China Sea were investigated during four cruises of the R/V *Ocean Researcher I* between December 1997 and October 1998. Over the entire continental shelf, a seasonal cycle was found with a distinct 3–5-fold increase in the abundance of oligotrich ciliates in summer. This increase appeared to be induced by the tremendous summertime runoff from the Changjiang. A radial-type spatial distribution pattern also was observed in summer, with population densities higher toward the Changjiang plume but highest of all in the margins of the plume. In spring and fall, the spatial distribution of the oligotrich ciliates was closely correlated to the abundance of cyanobacterium *Synechococcus.* In summer in the plume region, mixotrophic ciliates accounted for over 50% of the total ciliate population, compared to less than 30% outside the plume or that in other seasons. We propose a model in which these ciliates constitute part of the pathway through which the particulate and dissolved organic carbon in the runoff water is incorporated into the oceanic food web.

1. Introduction

For some years now, researchers have recognized that bacteria and protists play essential roles in marine pelagic ecosystems (Pomeroy, 1974). Planktonic ciliates are an important component in the microbial food chain, which is also referred to as the microbial loop (Azam et al., 1983), and they may help bring about trophic flux and nutrient cycling (Laybourn-Parry, 1992). In a typical oligotrophic oceanic ecosystem, organic exudates, or dissolved organic carbon (DOC), from phytoplankton are used by bacteria, and these, in turn, are consumed by protistan predators, such as planktonic microflagellates (Fenchel, 1982; Sherr et al., 1991) and ciliates (Sherr and Sherr, 1987; Fenchel and Jonsson, 1988). Such picoautotrophs as *Prochlorococcus* and *Synechococcus* similarly make a significant contribution to phytoplankton biomass and productivity in marine ecosystems (Stockner and Antia, 1986; Shiomoto et al., 1997). Typically, in the subtropical shelf water of the East

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China Sea (ECS), picophytoplankton comprise 25–86% of all chlorophyll *a* and 19–72% of primary production (Chen, 2000; Chiang et al., 2002). However, picophytoplankton are too small to be effectively utilized by metazoan grazers. Picophytoplankton have to be repacked via the microbial food chain before their production can enter the grazing food chain (Marshall, 1973).

The ECS, the largest marginal sea in the western North Pacific, is a vast area of shallow water into which flows the tremendous river runoff from the Changjiang (Yangtze River; see Fig. 1). With an annual mean of about $3\times10^3\,\mathrm{m}^3\,\mathrm{s}^{-1}$, water discharge reaches its maximum in summer (Beardsley et al., 1985). The fact that phytoplankton productivity is less than likely sufficient to support the demand made by bacteria in the shelf area of the ECS has led Shiah et al. (2000) to suggest that the substantial shortfall is made up by non-phytoplanktonic, allochothonous sources. The discharged fresh river water, therefore, might, ultimately affect the spatial and temporal patterns of the ciliate populations and, as a consequence, the microbial food web in these shelf waters. New highly supportive evidence for this theory is presented in this paper.

Oligotrich ciliates are known to be a major component of ciliate community in the ECS (Ota and Taniguchi, 2003). For the first time, their spatial and temporal variations are examined in the study, and the relationships between ciliate population density and surface salinity, particulate organic carbon (POC), and bacterial productivity (BP) in summer were analyzed. Besides these, this study discusses variations in the population of mixotrophic ciliates (MC) and the standing stock of cyanobacteria.

2. Materials and methods

During four cruises of the R/V *Ocean Researcher I* in December (winter) 1997, and March (spring), June (summer), and October (fall) 1998, surface temperatures and salinity were measured at a total of 31–36 sampling stations along seven cross-shelf transects (Fig. 1). Water samples were collected at 16–22 sampling stations along four of

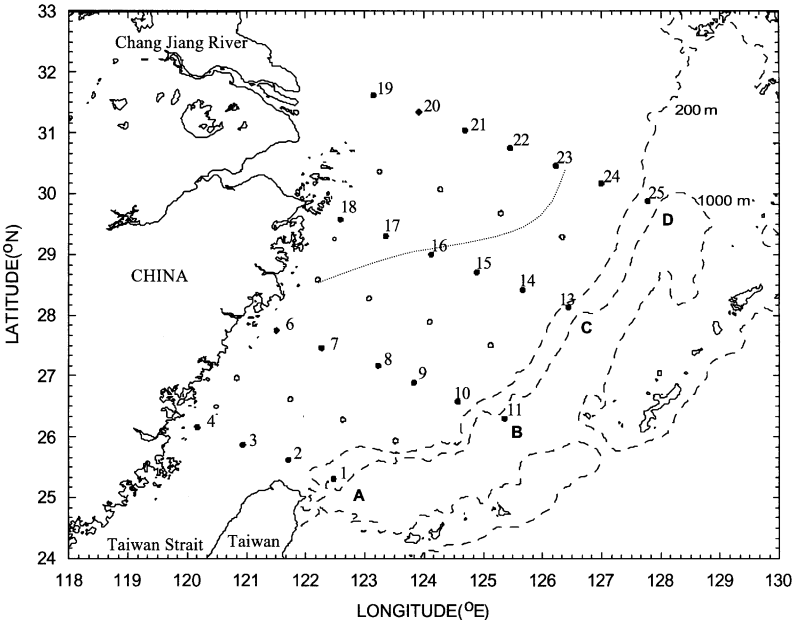

Fig. 1. ECS survey stations were located along seven cross-shelf transects (white and dark circles) on the four sampling cruises of 1997 and 1998. Dark circles indicate the stations where water samples were collected for the present study. Dashed lines indicate the Changjiang plume margin.

the cross-shelf transects, indicated as Transects A, B, C and D (Fig. 1). A Sea Bird-General Oceanic Rosette assembly with 20 l Go-Flo bottles were then employed to record temperature and salinity as well as to collect water samples from 5 to 11 different depths in the water column (2 m-bottom or 100 m). The seawater samples were subsequently fixed in neutralized formalin (2% final concentration). To prevent degradation of the pigments in the plastids that had been ingested intact by the ciliates, the fixed samples were stored in a cool (4°C), dark place until they could be examined under microscope.

Oligotrich ciliate cells in a 100-ml sample were concentrated following the Utermöhl method and were identified and thoroughly counted in each sample using an inverted epifluorescence microscope (Nikon-Tmd 300) at 200 × or 400 × (Hasle, 1978). All of the oligotrich ciliates were classified as heterotrophic ciliates (HC) or MC based on their autofluorescence. Plastids that had been retained intact by the mixotrophic oligotrich ciliates were recognizable by red fluorescence they emitted when excited with light at 450–490 nm (blue light).

Next, water samples (0.5–2.0 l) for POC measurements were first filtered through a 200 μm mesh to remove zooplankton and then through a pre-combusted (550°C) 25 mm GF/F filter for 1 h (pumping pressure <100 mm Hg). The GF/F filters were then wrapped in pre-combusted aluminum foil in the next stage, and stored at −4°C. After being dried and acid fumed, the POC concentrations were measured with a CHN analyzer (Fisons; NA1500). Finally, a one-way ANOVA was used for statistical analysis and these results were compared using the least significant difference (LSD) method.

3. Results

3.1. Ciliate community

In ECS, the cell size of the ciliate community showed a gradual decrease from inner to outer shelf in all seasons (Fig. 2). The mean cell size also showed significant seasonal variations, especially

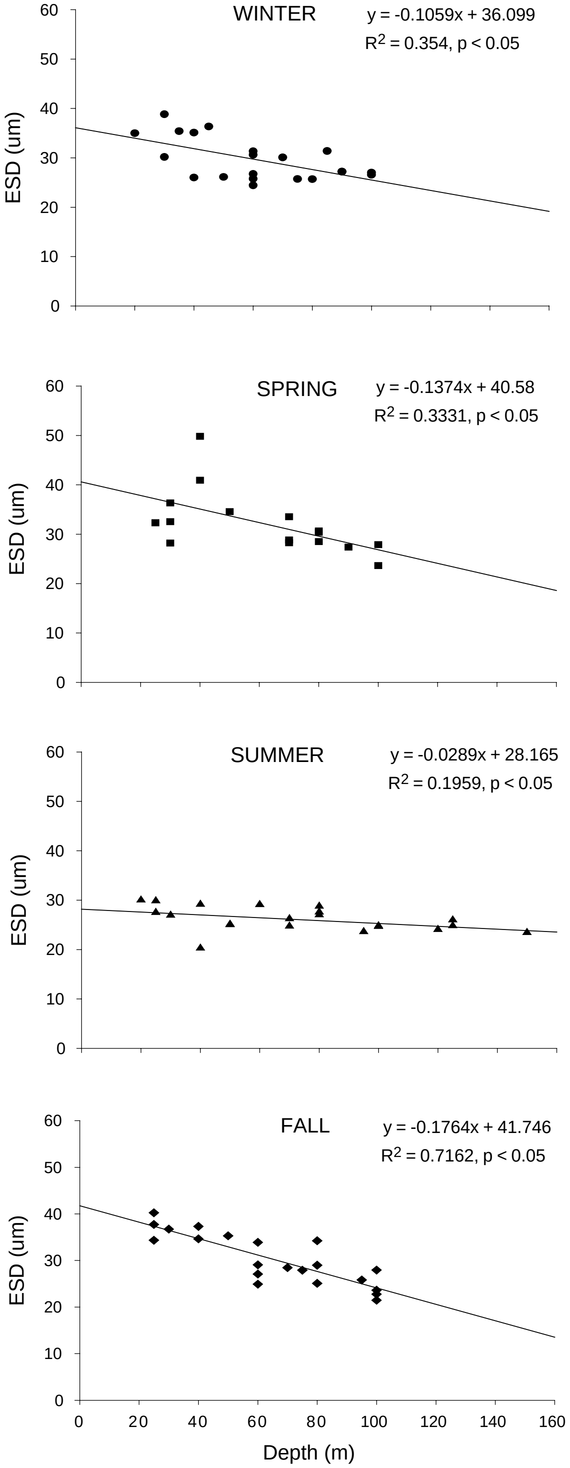

Fig. 2. The cross-shelf distribution of ESD of oligotrich ciliate in all four seasons in the ECS.

in summer. The equivalent spherical diameter (ESD) in winter, spring, and fall were 29.6±0.93, 32.1±1.51, and 30.4±1.21 μm, respectively. In contrast, Summer ciliates had a smaller size at 26.1±0.52 μm ESD ($P<0.05$, ANOVA and LSD analysis).

During the fall cruise, extra effort was made to obtain a general picture of species composition. On the basis of morphological characteristics, the ciliates were classified into three groups (Song et al., 1999): Strombilidiids, *Tontonia* in *Strobilidiidae*, and Strombilidiids species other than *Tontonia*. The most dominant component was Strombilidiids, making up 66.6%±15.6%, followed by other Strombilidiids at 31.2%±14.7%, and *Tontonia* at 2.1%±2.7%.

3.2. Horizontal distribution

In winter, spring and fall, the distributions pattern of surface salinity and temperature in the entire ECS ran roughly parallel to the coastline (Fig. 3), and salinity ranged between 32 and 34 psu at almost all stations. By contrast, during summer, a radial distribution pattern appeared in front of the mouth of the Changjiang, and in the center of the radial pattern, salinity was as low as 25 psu. The hydrographic features of the ECS, therefore, appeared to be significantly influenced by summer runoff from the Changjiang. It was also found that the extent and location of the plume closely approximated the typical Changjiang plume, as determined by Gong et al. (1996) in which they defined the temperature and salinity of the summer plume as >23°C and <31 psu, respectively. In the present paper, the plume is defined as $T = 22-26°\mathrm{C}$ and salinity as <31 psu.

In the same vein, the horizontal density distribution of total oligotrich ciliates (TC) made pronounced seasonal change (Fig. 4). From winter to spring, relatively few ($1–50\times10^4$ cells m^{-3}) ciliates existed in the water column. Nevertheless, abundance tended to increase from the inner shelf to the outer shelf, with the maximum population density observed at the northeast outer shelf. Ciliate abundance increased in summer ($30–180\times10^4$ cells m^{-3}), distributed in a pattern that matched that of radial surface salinity, again with a high density ($>60\times10^4$ cells m^{-3}) area in the Changjiang plume (<26°C; <31 psu). Then, in the fall, ciliate abundance generally decreased ($<20\times10^4$ cells m^{-3} at most sampling stations), but a high ciliate abundance was still found in the center of the continental shelf ($>70\times10^4$ cells m^{-3}).

In winter, spring and fall, HC and MC had a similar distribution pattern to that of TC. HC were the most abundant components of the oligotrich ciliates, representing between 70.5% and 92.2% of the total number of oligotrich ciliates. In summer, MC abundance was high within the margin of the Changjiang plume ($>120\times10^4$ cells m^{-3}), where it accounted for >50% of the total number compared to <30% comprised outside the plume.

3.3. Vertical distribution

Water column profiles revealed very different patterns of vertical distribution of TC and MC between Kuroshio Water (St. 11), Shelf Mixing Water (St. 16), and the Changjiang plume (St. 19). In Kuroshio Water, the abundance of TC was, for the most part, uniform in the first 100 m and MC was rarely apparent in every season (Fig. 5). In the middle part of the continental shelf (shelf mixing water), a decrease in abundance was observed with depth and a subsurface ciliate maximum layer was observed in the bottom of euphotic zone (euphotic zone = 42 m). MC was mostly evident in the euphotic zone in the fall and also had a maximum abundance at 40 m. In summer, the abundance of TC was significantly higher than in other seasons in the Changjiang plume, and the vertical distribution pattern of TC differed considerably from that in other seasons. A maximum abundance of TC was observed at 2 m, but TC then decreased with depth. A similar vertical profile to that of TC was observed in the case of MC, while the abundance ranged from $40–160\times10^4$ cells m^{-3}, again being highest relative to that in other areas or seasons in the ECS.

3.4. Seasonal variations

Over the entire ECS, an annual pattern of surface salinity clearly emerged (Fig. 6A). In

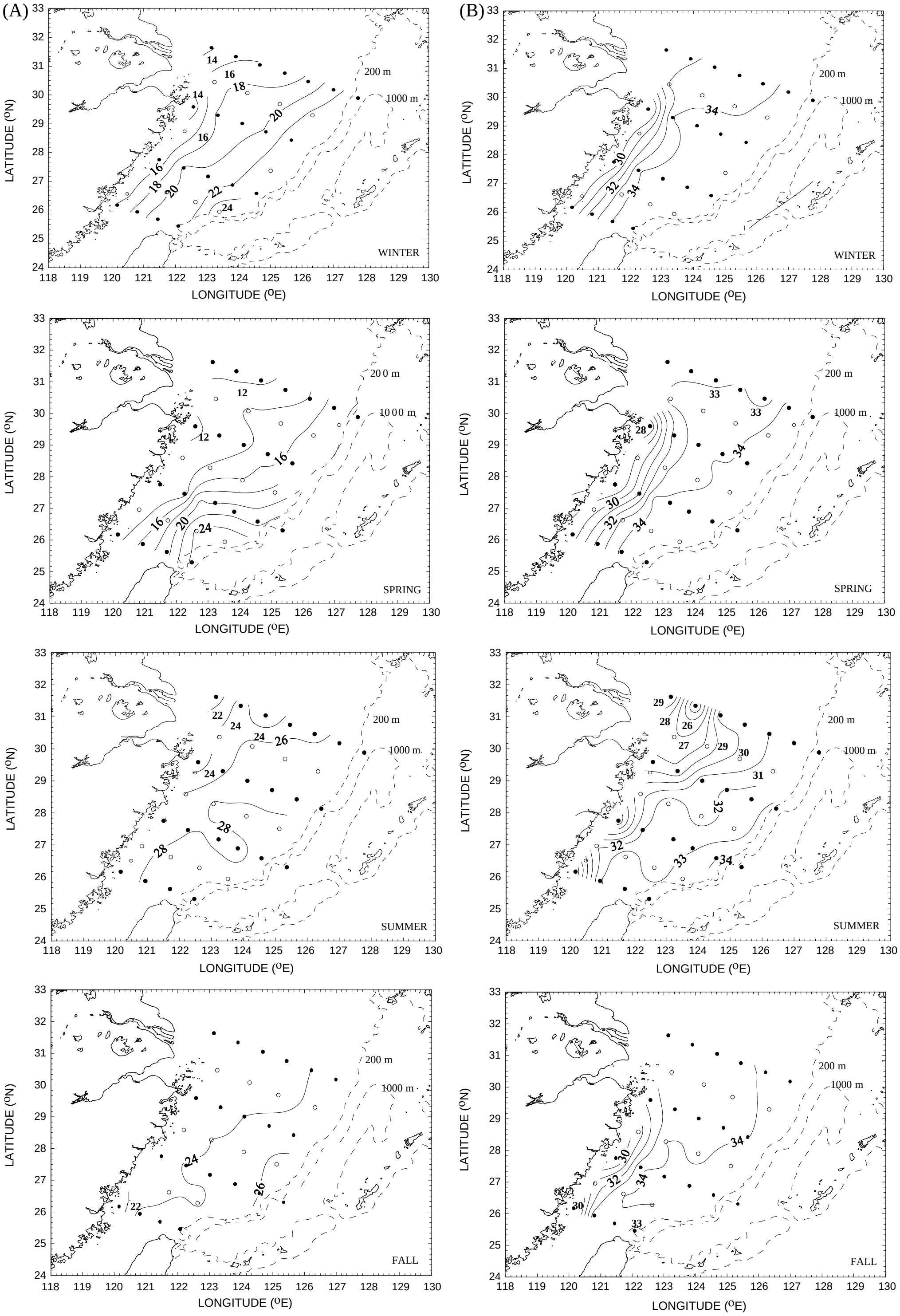

Fig. 3. Horizontal distribution of (A) surface temperature (°C, 2 m depth); and (B) salinity (psu) in all four season in the ECS.

winter, spring and fall, the average surface salinity was greater than 33.0 psu, unlike that in summer when it was lower than 31.0 psu.

The fluctuations in depth-weighted average TC abundance from surface to bottom or 100 m were generally parallel to seasonal variations in surface salinity (Fig. 6A). A low standing stock of TC ($11.41–18.43 \times 10^4$ cells m^{-3}) was observed during seasons of high salinity, namely winter, spring and fall, whereas the standing stock sharply increased

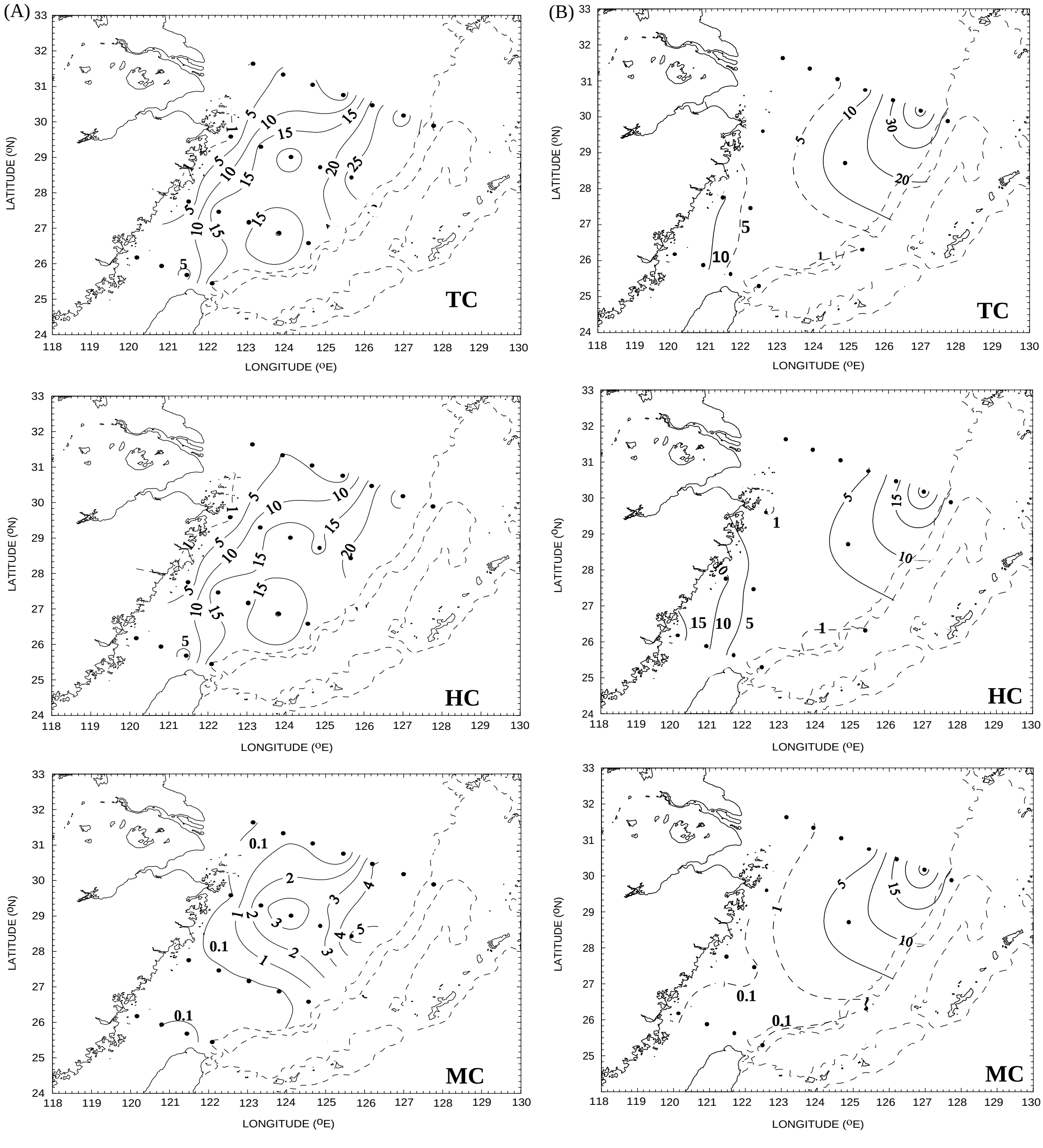

Fig. 4. Horizontal distribution of total ciliate (TC), heterotrophic ciliate (HC) and mixotrophic ciliate (MC) abundance ($\times 10^4$ cells m^{-3}) in the ECS in (A) winter (December 1997); (B) spring (March 1998); (C) summer (June 1998); and (D) fall (October 1998).

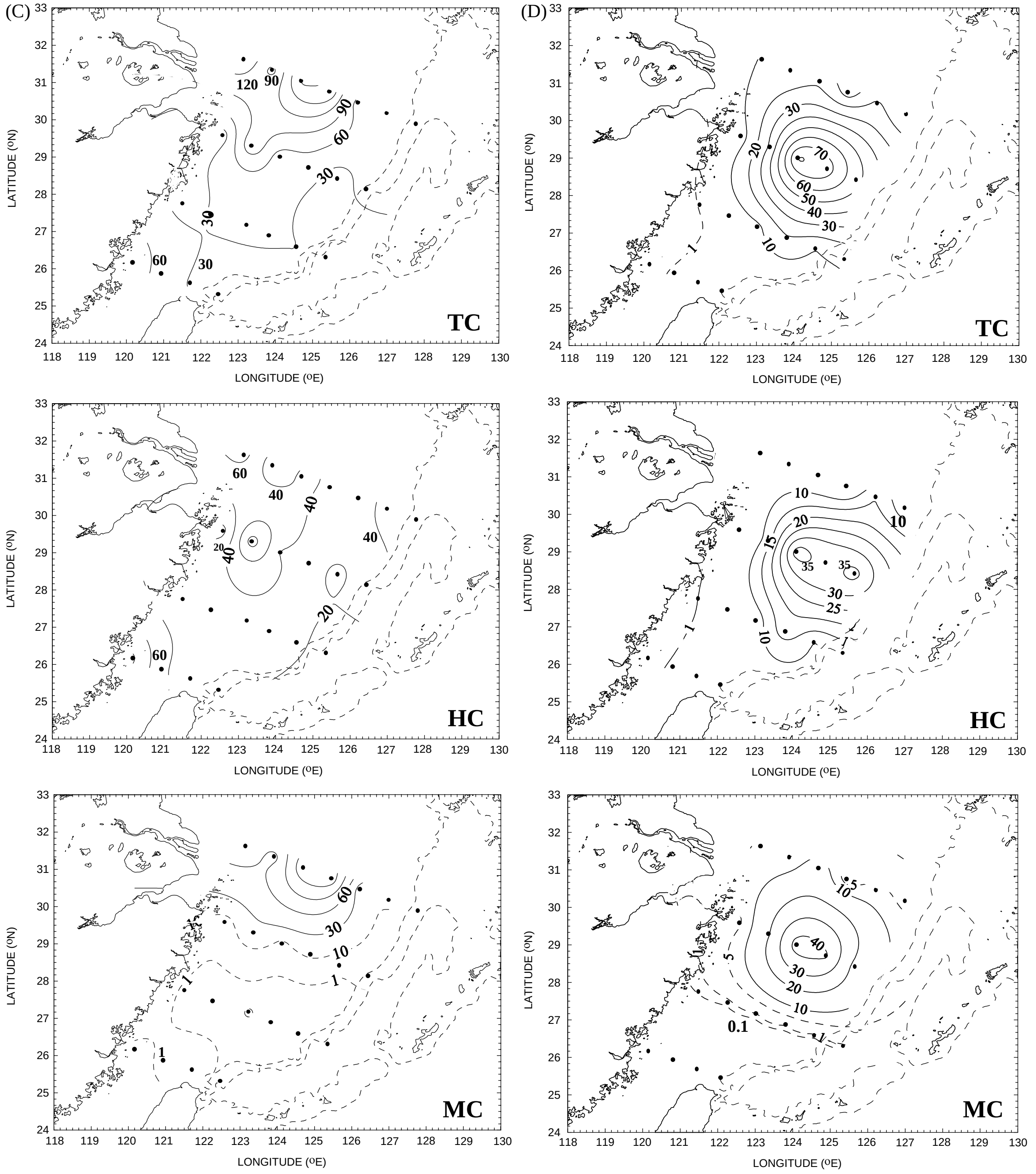

Fig. 4 (*continued*).

to 57.81×10^4 cells m^{-3}, representing a 3–5 fold difference, in the low salinity season (summer). Although similar patterns were also found for HC and MC (Fig. 7A), one-way ANOVA and LSD showed that seasonal density fluctuations were significant only for TC and HC ($P < 0.05$), but not

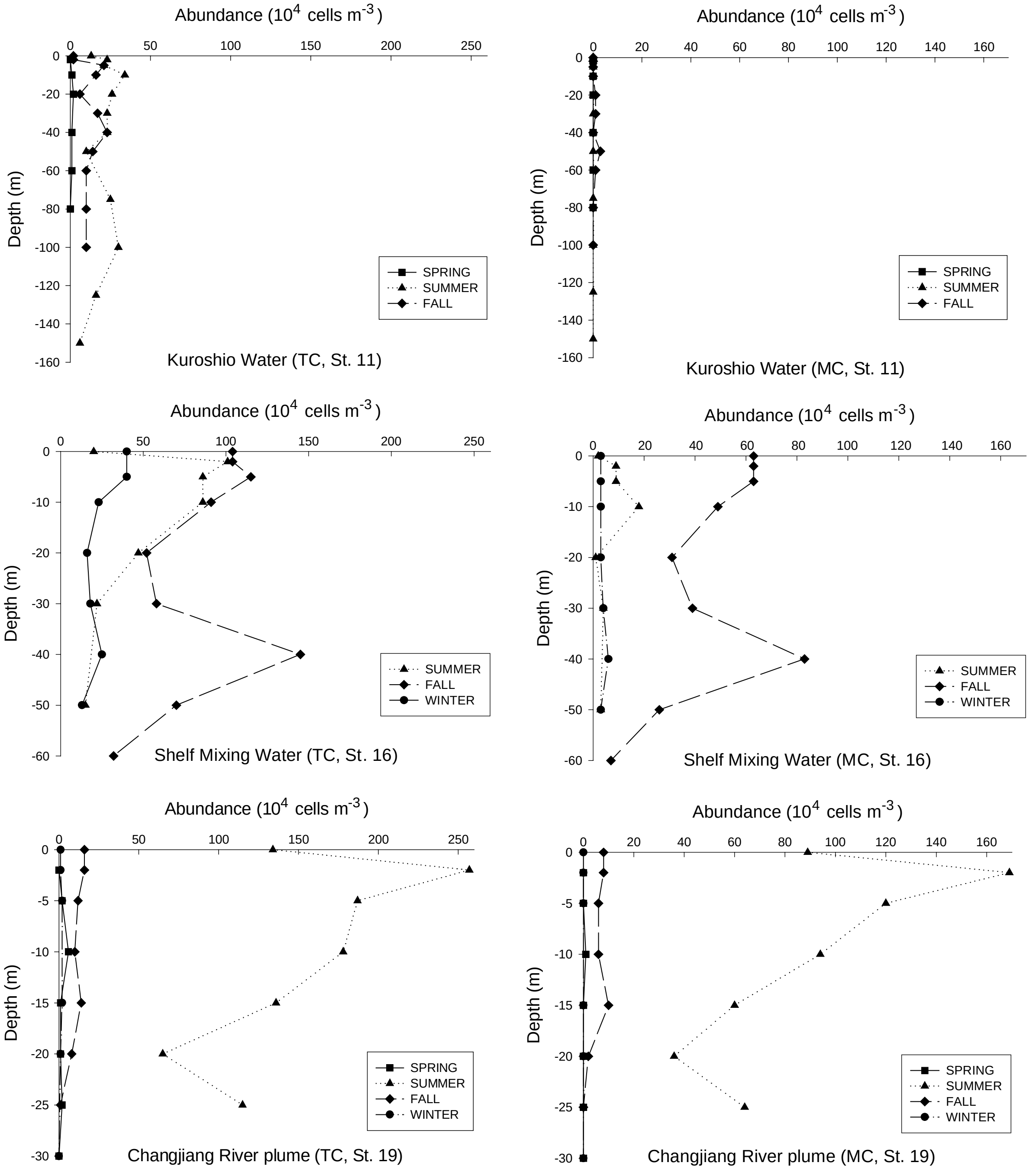

Fig. 5. Vertical distribution of TC and MC abundance ($\times 10^4$ cells m^{-3}) in the ECS in Kuroshio Water (St. 11), Shelf Mixing Water (St. 16) and the Changjiang plume (St. 19) in all four seasons.

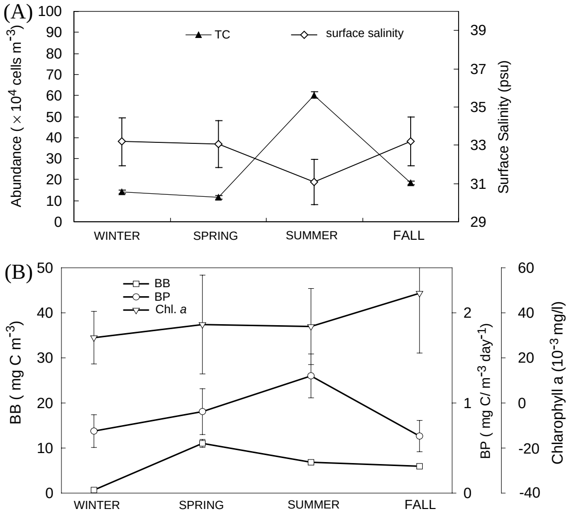

Fig. 6. Seasonal variations of (A) surface salinity and depth-weighted average TC abundance ($\times 10^4$ cells m^{-3}); and (B) bacterial productivity (BP, mg C m^{-3} day^{-1}), bacterial biomass (BB, mg C m^{-3}) and chlorophyll *a* (mg m^{-3}) (BP and BB data from Shiah et al., 2000).

for MC ($P > 0.05$). However, dividing the entire study area into the Coastal Water and Shelf Mixing Water (respective definitions; see Chiang et al., 2002) indicated that most of the seasonal fluctuations could be attributed to the population dynamics in the Coastal Water (Figs. 7B and C). The increases in the summer standing stocks of TC, HC and MC were, in fact, all statistically significant in the Coastal Water ($P < 0.05$), but was not true in the Shelf Mixing Water ($P > 0.05$).

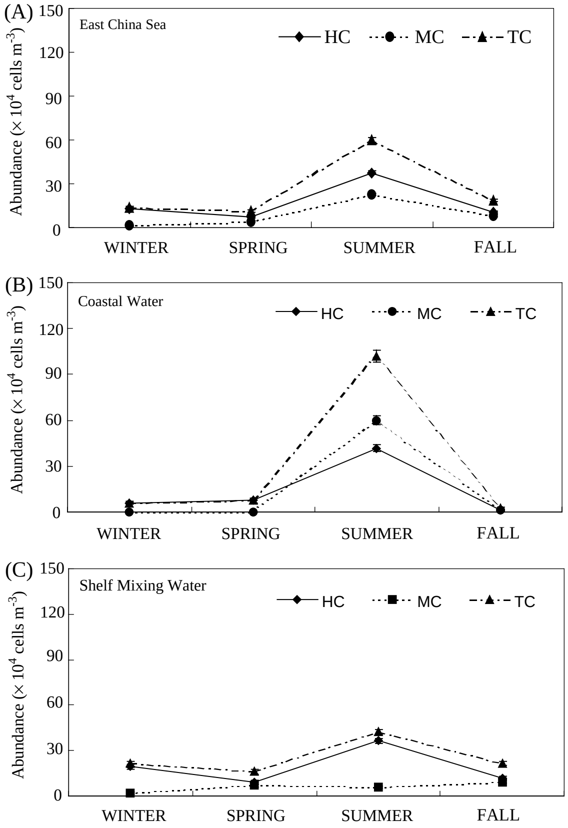

Fig. 7. Seasonal variations of the depth-weighted average abundance of HC ($\times 10^4$ cells m^{-3}), MC ($\times 10^4$ cells m^{-3}) and TC ($\times 10^4$ cells m^{-3}) in (A) the entire ECS; (B) Coastal Water; and (C) the Shelf Mixing Water.

4. Discussion

Ciliate abundance levels reported in the ECS ranged from 0.17 to 183.89×10^4 cells m^{-3}. This range is similar to ciliate abundance commonly found in other oceanic ecosystems (Table 1), but the degree of variation seems higher compared to the subarctic and subtropic oceanic waters in western Pacific (Suzuki et al., 1998). Although the formaldehyde-based fixative has been shown to underestimate ciliate abundance (Leakey et al., 1994a; Stoecker et al., 1987, 1994), our results are still within the commonly accepted range, and our own test indicated similar counts from samples fixed with formalin and with Lugol's (data not shown).

4.1. Spatial and temporal distribution

The ciliate distribution pattern showed a distinct variation with season. In spring and fall when *Synechococcus* abundance was not influenced by runoff from the Changjiang (summer) or the Yellow Sea Cold Water (winter), the ciliate and *Synechococcus* distributions seemed to match each other reasonably well (Chiang et al., 2002), and a positive correction could be established (Fig. 8) in the shelf area. This fact is indicative of a close coupling of *Synechococcus* and oligotrich ciliates in this subtropical shelf ecosystem, and it can be reasonably deduced that the coupling is caused by

Table 1
A comparision of oligotrich ciliate abundance data

Oceanic region	Sampling time	Sampling depths	Remark	Method	Abundance (10^4 cells/m^3)	Reference
Tropical neritic waters	Year-round	5 m	1 station	Bouin's	97–393	Lynn et al. (1991)
Antarctica nearshore water	Year-round	10 m	1 station	Lugol's	23–126	Leakey et al. (1994b)
Tropical oceanic water (Northwestern Indian Ocean)	Fall	5–9 depths	9 stations	Lugol's	3.1–82.3 (mean value)	Leakey et al. (1996)
Temperature neritic water	Winter	10 depths	21 stations	Lugol's	16.3–79.2 (weighted mean)	James and Hall (1995)
Subarctic oceanic water (Western Pacific)	Spring	6–12 depths	6 stations	Formaldehyde	55.73–148.88 (mean value)	Suzuki et al. (1998)
Subarctic of oceanic water (Western Pacific)	Fall	6–12 depths	3 stations	Formaldehyde	22.38–40 (mean value)	Suzuki et al. (1998)
Subtropic of oceanic water (Western Pacific)	Fall	6–12 depths	6 stations	Formaldehyde	5.38–44.88 (mean value)	Suzuki et al. (1998)
Subtropic of Western Pacific (East China Sea)	Three seasons	7–14 depths	7–14 stations	Formaldehyde	3–146 (weighted mean)	Ota and Taniguchi (2003)
Subtropic of Western Pacific (East China Sea)	Four seasons	5–11 depths	16–22 stations	Formaldehyde	0.17–183.89 (weighted mean)	This study

a prey–predator relation. This hypothesis is supported by Chen (2001), who reported that the grazing rate of oligotrich ciliates was controlled by *Synechococcus* abundance in the study area, which then had a significant influence on ciliate growth rate. In winter, the *Synechococcus*–ciliate relationship was disturbed when a higher *Synechococcus* abundance in Yellow Sea Cold water ($>10^{12}$ cells m^{-2}) was introduced into the study area (Chiang et al., 2002).

Of particular interest is that in summer, several biological processes other than *Synechococcus* abundance appeared to have become major controlling factors. Strong evidence suggests that the levels of terrestrial substrate had an effect on the spatial pattern of the ciliate standing stock in that period. A positive correlation between surface salinity and surface POC was noted (Fig. 9A), which strongly implies that the major source of POC was the discharge from the Changjiang. Although DOC data was not available for examination, Chiangjiang showed also brought significant amount of DOC. Furthermore, there was a good correlation between POC and BP (Fig. 9B). Shiah and Ducklow (1994) and Shiah et al. (2000) in fact have argued that this is highly indicative of the bottom-up control of bacteria. Finally, there was a positive correlation between BP and TC (Fig. 9C), suggesting that TC may be controlled by BP. We conclude from these findings that a very clear relationship exists between ciliate standing stock and the discharge of fresh water from the Changjiang (cf. Smetacek, 1981; Leakey et al., 1994b). We agree with Shiah et al. (2000) that this input of terrestrial material (i.e. POC and DOC) is in all likelihood crucial in supporting the microbial food web in the shelf water.

Ciliate standing stock in the shelf area equally displayed a distinctive temporal pattern (Fig. 6A). In temperate and polar inshore waters, planktonic ciliate populations also exhibited a clear seasonal cycle of high abundance during the spring and summer months but low abundance in the winter months, and since this cycle fully agrees with the fluctuations in chlorophyll *a* concentration and bacterial biomass (BB) (Smetacek, 1981; Montagnes et al., 1988; Leakey et al., 1994b), a tight trophic coupling between ciliates and organic

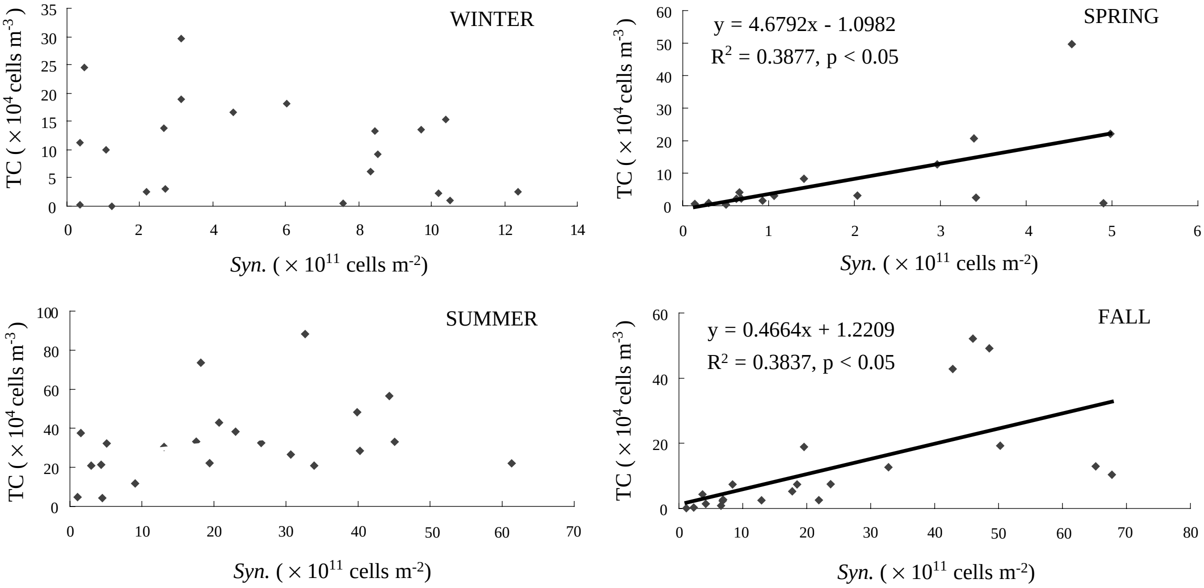

Fig. 8. Relationships between integrated *Synechococcus* abundance (× 10^{11} cells m^{-2}) and the depth-weighted average abundance of TC (× 10^4 cells m^{-3}) in winter, spring, summer and fall.

carbon from phytoplankton and bacteria seems quite apparent. In the ECS, it may well be that the peak ciliate population densities observed in summer were also driven by an increased availability of organic carbon, which in this case probably means bacteria rather than chlorophyll *a* sources in light of the absence of a chlorophyll *a* peak in summer (Fig. 6B) in the ECS. In a contemporaneous study of the ECS continental shelf area, we found that while depth-weighted average BP also did peak in summer, but the depth-weighted average BB reached its peak in spring (Fig. 6B), i.e. several months earlier. To explain the absence of a BB peak in summer, we suggest that a considerable amount of bacteria may have been consumed by phagoflagellates or phagociliates. This hypothesis is clearly consistent with, and helps to explain, the high summertime ciliate standing stock that was found in the present study.

4.2. Relationship between MC and phytoplankton in the Changjiang plume

Following Gong et al. (1996) who determined salinity in the plume as <31 psu, the summer surface salinity data along the northern transect (Transect D in Fig. 1) suggest that the center is located around at St. 20 with Sts. 19, 21 and 22 in the plume margins (Fig. 10A). Fig. 10A also shows that the abundance of total ciliates was higher within the plume region than outside it, although ciliate abundance was relatively low at the central station (St. 20). Within the plume region (but not outside it), mixotrophs made up the greatest share of the oligotrich ciliate population (Fig. 10B). Conversely, along the same transect at the same time, while the total BB remained constant, the standing stock of *Synechococcous* was low within the plume but it grew with increasing distance. Chang et al. (2003) also reported that the *Synechococcus* growth rate was 4–5 times higher within the plume than that outside it (Fig. 10D). The most likely explanation for these observations is that increased nutrient input from the Changjiang leads to an increase in *Synechococcus* productivity, but any increase in the abundance of these cyanobacteria is offset since *Synechococcus* are consumed by MC within the plume. The net result is, therefore, an increase in the number of MC. This hypothetical account is supported strongly by the tight relationship between MC and

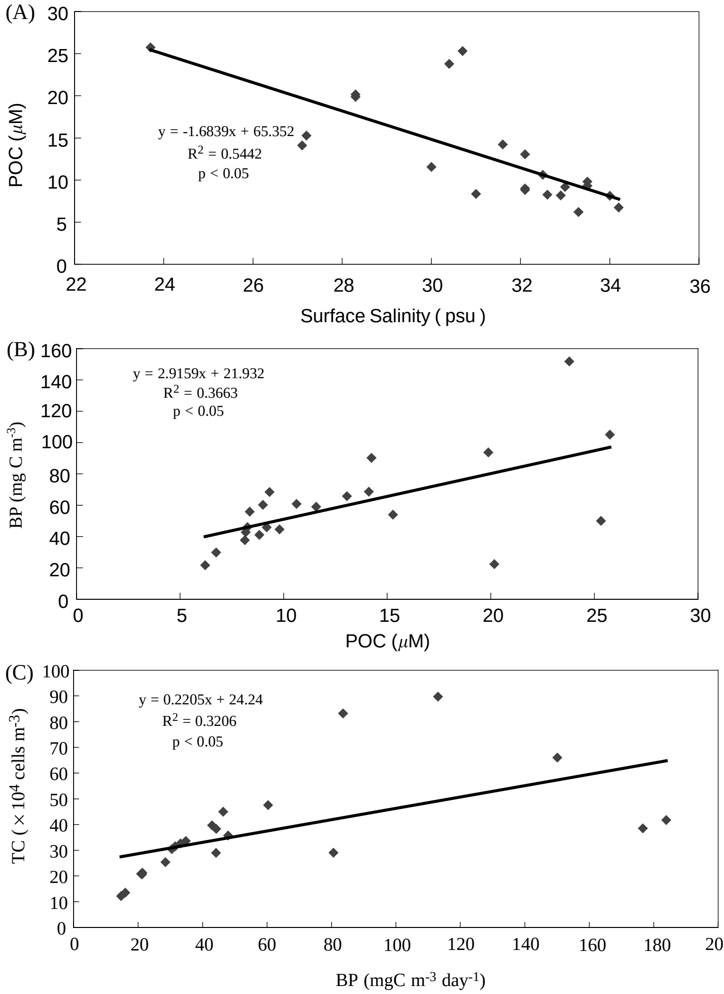

Fig. 9. Relationships between (A) surface salinity and POC; (B) POC; and BP and (C) BP and TC in summer (BP and BB data from Shiah et al., 2000).

Synechococcus abundance within the plume (but not outside it) (Fig. 11).

Some independent external evidence is available to indicate that MC and *Synechococcus* have a predatory/prey relationship because phycoerythrin, a pigment unique to *Synechococcus* (Waterbury et al., 1979), has previously been identified in some mixotrophs (McManus and Fuhrman, 1986). On the other hand, picophtoplankton is also a major food source for mixotrophic nanoflgellate (Craon, 2000). Thus, we also argue that another hypothesis may be that the great part of picophyplankton was consumed by nanoflagellate. Then these pigment-containing nanoflagellates were transported to the ciliate community. It has been proposed elsewhere that the retained plastids in MC may come from cyanobacteria (Bernard and Rassoulzadegan, 1994) or photosynthesis nanoflagellate (Craon, 2000). All of the above observations support the conclusion that the discharged fresh water of the Changjiang plume significantly affects the microbial food web in the region.

4.3. Photosynthesis rate of MC and the production of TC

Putt (1990) has reported that the concentration of chlorophyll *a* ranged from 21 to 99 pg cell^{-1} in

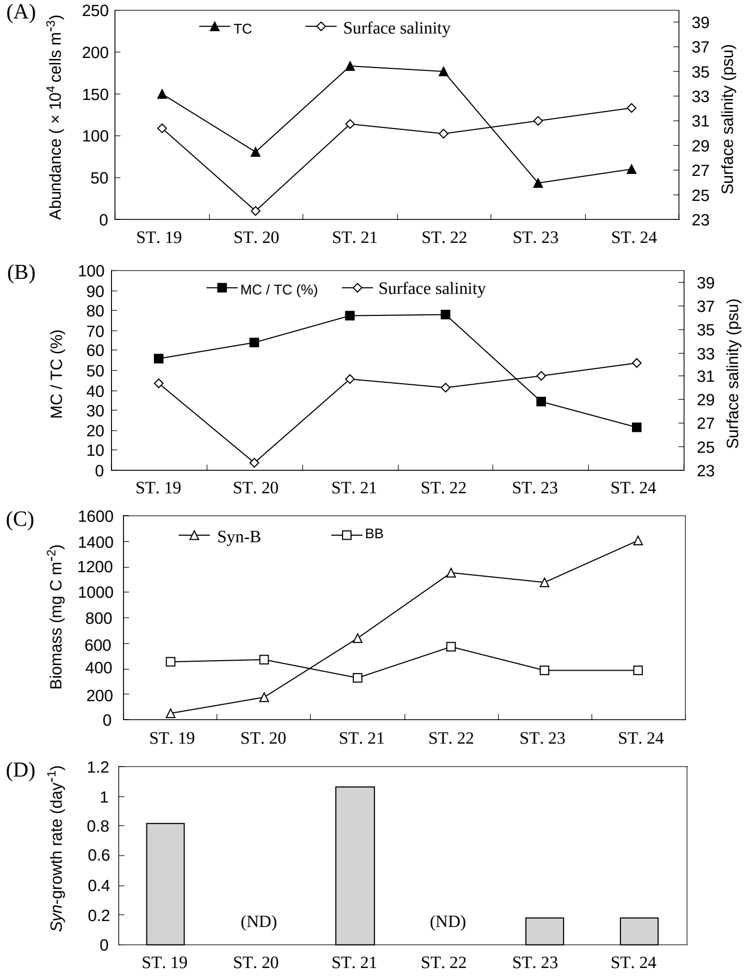

Fig. 10. Variations of (A) surface salinity (psu) and depth-weighted average abundance of TC ($\times\ 10^4$ cells m^{-3}); (B) MC/TC ratio (%); (C) *Synechococcus* biomass (mg C m^{-2}) BB (mg C m^{-2}); and (D) intrinsic growth rate of *Synechococcus* (day^{-1}) along the northern transect (*Synechococcus* and BB data from Shiah et al. (2000) and Chang et al. (2000), respectively).

mixotrphic oligotrich ciliates. Based on this figure, the maximum average contribution rate of MC to total chlorophyll *a* in winter, spring, summer and fall are 0.3%, 1.0%, 2.8% and 0.7%, respectively. From these results, we are confident that ciliate photosynthesis is likely negligible in the general continental shelf ecosystem of the ECS but that it does have relative importance in the Changjiang plume, where the average contribution rate is 7.7% with the highest value (24.2%) occurring in the margin, just as seen in the high contribution rate observed in the Nordic Sea in summer (24%, Putt, 1990). On the other hand, according to Lee (2000), the average seasonal ciliate production is 29.2 (winter), 8.8 (spring), 80.6 (summer), and 25.7 mg C m^{-2} d^{-1} (fall), and the rate of ciliate carbon demand for primary production is respectively 17.8%, 6.5%, 109.7%, and 25% in the ECS. From these results, we are reasonably sure that primary production cannot be sufficient to support the growth of the ciliate community in summer. It follows then that in summer, organic carbon from non-phytoplankton and allochothonous sources might play a very important role in

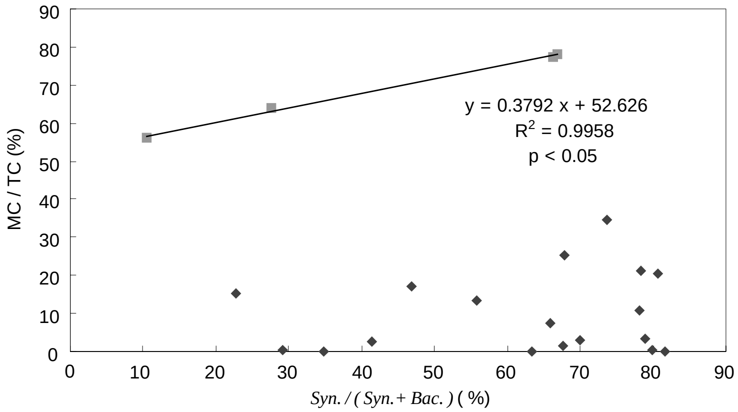

Fig. 11. Scatter plot of the contribution of *Synechococcous* bacteria to the microbial food web in summer: [*Synechococcous*/ (Bacteria + *Synechococcous*), %] versus the MC/TC ratio (%). Dark squares represent sampling stations located within the plume region (i.e. stations 19, 20, 21 and 22), Dark diamond stand for sampling station outside the plume region (*Synechococcous* and BB data from Shiah et al. (2000) and Chang et al. (2000), respectively).

the microbial carbon cycle in the shelf area of the ECS.

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