Influence of hydrographic conditions on picoplankton distribution in the East China Sea

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ABSTRACT: An investigation was made on picoplankton distributions in relation to physical and chemical conditions in the East China Sea, a marginal sea of the Northwest Pacific, in July 1998. *Synechococcus*, pico-eukaryotes and heterotrophic bacteria were ubiquitous, with average abundance at the order of 10^4, 10^2 and 10^5 cells ml^{-1}, respectively. *Prochlorococcus* was present at most locations beyond the 50 m isobath at around 10^4 cells ml^{-1}. Responses of these picoplankters to the hydrographic conditions were evident in both vertical and horizontal distributions. *Prochlorococcus* were basically associated with oceanic warm currents, and sudden changes in cell abundance often occurred within a relatively short distance of the currents. In the surface mixed layer, *Prochlorococcus* were usually present only when temperature was >26°C, salinity > 30 psu, total inorganic nitrogen < 3 μM and phosphate < 0.4 μM in the study period. Vertically, however, *Prochlorococcus* were distributed down where temperature was as low as 16°C and nutrient levels were also higher. No pronounced subsurface peaks in *Prochlorococcus* abundance were recorded in the oceanic warm currents although *Prochlorococcus* outnumbered *Synechococcus* by at least an order of magnitude. *Synechococcus* were most abundant in the coastal area associated with high nutrient levels. Pico-eukaryotes usually developed very well in the front areas on the continental shelf. Along offshore directions, pico-eukaryotes often centered farther from the shore and deeper in the water column than did *Synechococcus*. Heterotrophic bacteria showed the least variation in abundance among the 4 picoplankters, but still decreased distinctly in offshore directions, following a similar trend in the total biomass of pico-eukaryotes and *Synechococcus*. In the Yangtze River plume area, light availability was also important in regulating picoplankton distribution patterns. The relationship between *Prochlorococcus* and bacteria biomass was negative along gradients in the marginal sea.

KEY WORDS: *Prochlorococcus* · *Synechococcus* · Pico-eukaryotes · Heterotrophic bacteria · Picoplankton · East China Sea

INTRODUCTION

Prochlorococcus, divinyl chlorophyll containing tiny photoautotrophs (Chisholm et al. 1988, 1992) together with *Synechococcus*, pico-eukaryotes and heterotrophic bacteria are the principal components of the marine picoplankton community, and can be identified and quantified by flow cytometry (Olson et al. 1988, Marie et al. 1997). Ecological studies on *Prochlorococcus* and the other groups of picoplankton have been carried out extensively in oceanic waters of the Pacific (e.g. Campbell & Vaulot 1993, Binder et al. 1996), Atlantic (e.g. Olson et al. 1990, Li 1995, Buck et al. 1996), Mediterranean Sea (e.g. Vaulot et al. 1990, Bustillos-Guzman et al. 1995), and Arabian Sea (e.g. Campbell et al. 1998). Picoplankton have been considered to play critical roles in marine ecosystems. Although *Prochlorococcus* have been found in the plume of the Rhône River in the

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Mediterranean Sea (Vaulot et al. 1990), such coastal studies are still rare. Questions remain as to whether *Prochlorococcus* can grow actively in coastal waters or are simply advected from oceanic water (Partensky et al. 1999). The features of picoplankton distribution in marginal seas and the controlling factors remain unclear. The East China Sea is one of the largest continental marginal seas in the world, with nutrient-replete water in the coastal areas and oligotrophic oceanic waters along the Kuroshio Current coming from the western equatorial Pacific. It is thus ideally suited for ecological studies (Furuya et al. 1996, Hama et al. 1997). However, little is known about the structure and dynamics of the picoplankton communities in this area. *Prochlorococcus* have been verified to be present in certain areas of this sea (Jiao et al. 1998, Jiao & Yang 1999), but its regulation mechanisms remain largely unknown. A few reports of *Synechococcus* and heterotrophic bacteria exist but simultaneous observations of the 4 picoplankton groups are absent. The purpose of this study was to investigate population dynamics of these 4 groups of picoplankton as well as relevant physical and chemical factors in an attempt to understand the factors that affect the distribution of *Prochlorococcus* and other picoplankters in the temperate marginal sea.

Fig. 1. Location of the East China Sea, the main currents, and sampling stations in July 1998. 1: Kuroshio Current; 2 and 2′: Taiwan Warm Current; 3: Tsukuma Current; 4: Yellow Sea Warm Current; 5: the Yellow Sea Coastal Current; 6: Yangtze River diluted water; 7: the East China Sea Coastal Current. The locations of the currents are after Su (1989) with modifications according to the temperature and salinity data of the present cruise. Transects 1, 2, 4, 7 and 9 are indicated by the first digits of the corresponding sampling stations

MATERIALS AND METHODS

The East China Sea (ECS) is located on the western edge of the Northwest Pacific Ocean, and is characterized by a vast continental shelf and diverse environmental conditions. The main water masses are the Yangtze River diluted water in the west, the Yellow Sea Coastal Current from north to south along the northwest coast of the sea, the Yellow Sea Cold Eddy (Sawarh 1974) in the north, the Kuroshio Current coming from the western equatorial Pacific in the east, and the Taiwan Warm Current in the south. Thus, the ECS can be divided into 3 regions by the main currents and water masses. The coastal region is affected strongly by the Yangtze River water and the coastal currents.
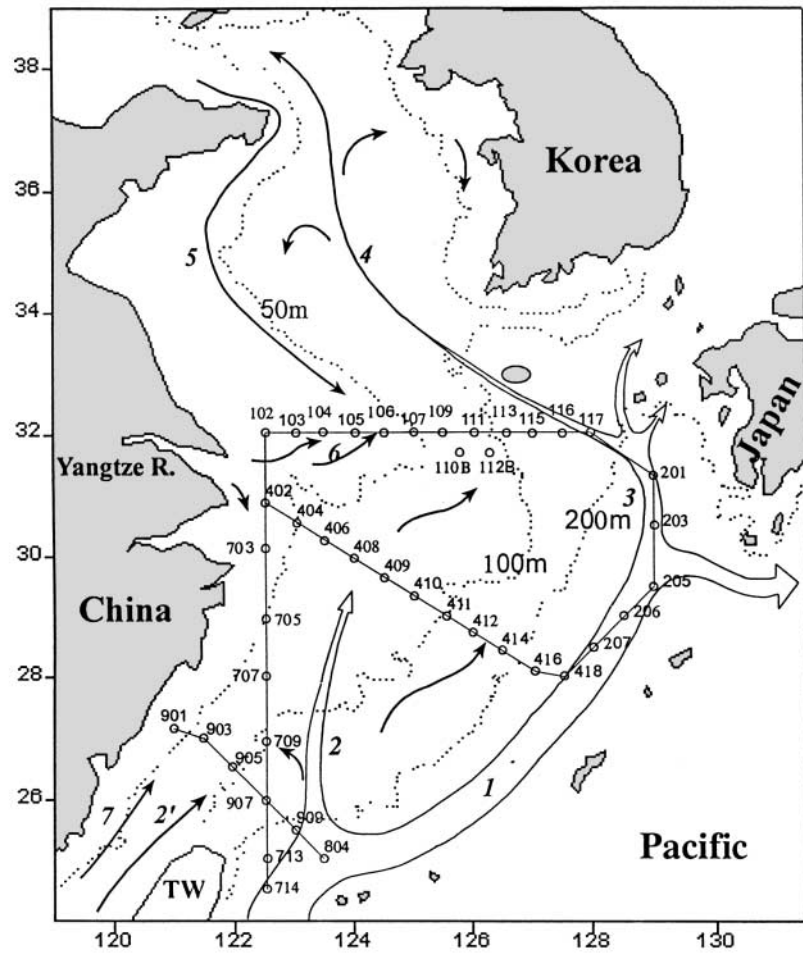
The deep water region along the east edge of the sea is strongly affected by the Kuroshio Current and Taiwan Warm Current and characterized by relatively low nutrients and high temperature; the transitional region between the 2, where currents and water masses meet, mix and interact, makes up the most important part of the continental shelf. Forty-two stations along 5 transects (1, 2, 4, 7 and 9) were investigated in July 1998 (Fig. 1).

Water samples were collected at 0, 10, 20, 30, 50, 75, 100 and 150 m depths using Niskin bottles (Oceanic). Samples for flow cytometry analysis were fixed with glutaraldehyde (final conc.: 1%, Vaulot et al. 1989), quick-frozen in liquid nitrogen and stored in a freezer at −20°C for later analysis. Samples were run on a

FACSCalibur flow cytometer (Becton-Dickinson), equipped with an external quantitative sample injector (Harvard Apparatus PHD 2000). Procedures were as described by Olson et al. (1990). The 3 autotrophs were distinguished according to their positions in plots of red fluorescence (FL3) versus 90° angle light scatter (SSC), and orange fluorescence (FL2) versus SSC. Pico-eukaryotes were identified by their large size and red fluorescence. SYBR Green I (Molecular Probes) was applied as the nucleic acid stain (Marie et al. 1997) for bacteria identification in plots of FL3 versus green fluorescence (FL1). Samples for flow cytometry enumeration of autotrophs were run separately from those for heterotrophic bacteria. Flow cytometry data were collected in list mode, and analyzed with CytoWin 4.1 software provided by D. Vaulot (Station Biologique, Roscoff, France. Software is available from www.sb-roscoff.fr/Phyto/cyto.html). Data for nutrients, temperature, salinity, and transparency were from the Chinese JGOFS cruise project reports of the same cruise.

RESULTS

Physical and chemical conditions

During the study period, surface water temperature ranged from 30°C in the oceanic water to 25°C in the northwest coastal area. Nutrient levels in the coastal region were high. Total inorganic nitrogen (TIN) was usually higher than 4 µM and reached up to 13 µM; PO_4-P was usually higher than 0.3 µM and reached up to 1.0 µM. Nutrient levels in the deep water region were usually low (TIN < 2 µM, PO_4-P ca. 0.2 µM). The transitional region was variable with TIN from 1 to 10 µM and PO_4-P from 0.2 to 0.8 µM). Salinity ranged from more than 34 psu in the southeast region to less than 20 psu in the Yangtze River estuary. Transparency was 0.8 to 3.5 m in the estuarine area, and more than 40 m in the clear waters of the Kuroshio Current region. Most of the investigation sites were stratified and nitraclines usually developed (Figs. 2 & 3).

Picoplankton distribution patterns and affecting factors

In the Yangtze River plume, there were strong horizontal and vertical gradients in nutrients, salinity, temperature and transparency from the river mouth to the adjacent radiation areas, and pronounced responses in picoplankton distribution were recorded (Fig. 4; also see Fig. 5a,c), e.g. at Stn 103, transparency was only 2.5 m, salinity increased from 25 psu at the surface to 32 psu below 20 m. The surface layer was obviously
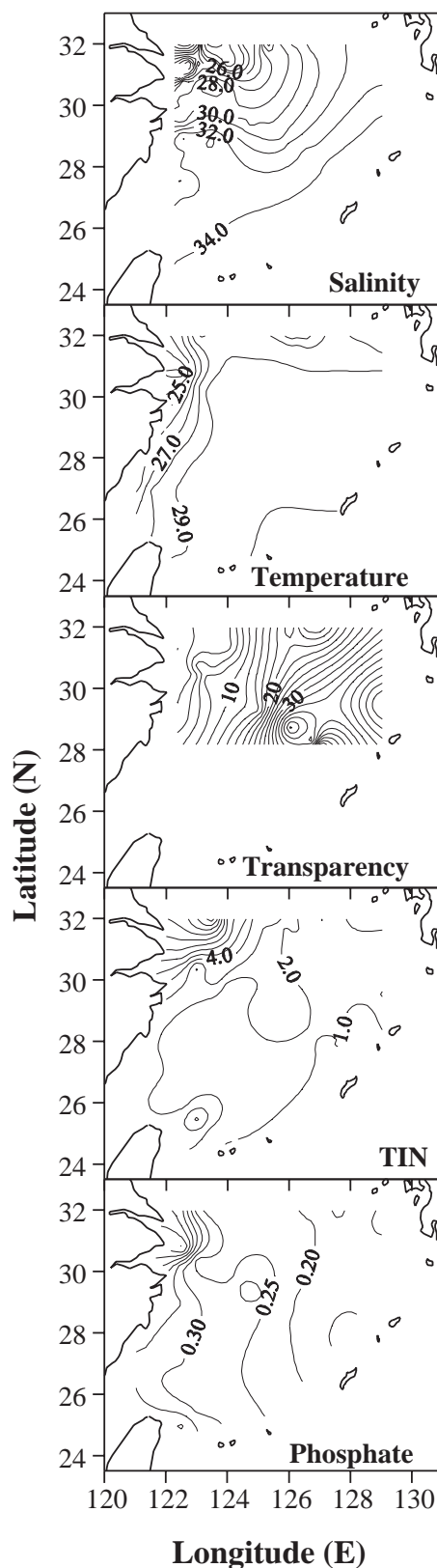

Fig. 2. Distribution of surface salinity (psu), temperature (°C), transparency (m), total inorganic nitrogen (TIN, µM) and phosphate (µM)
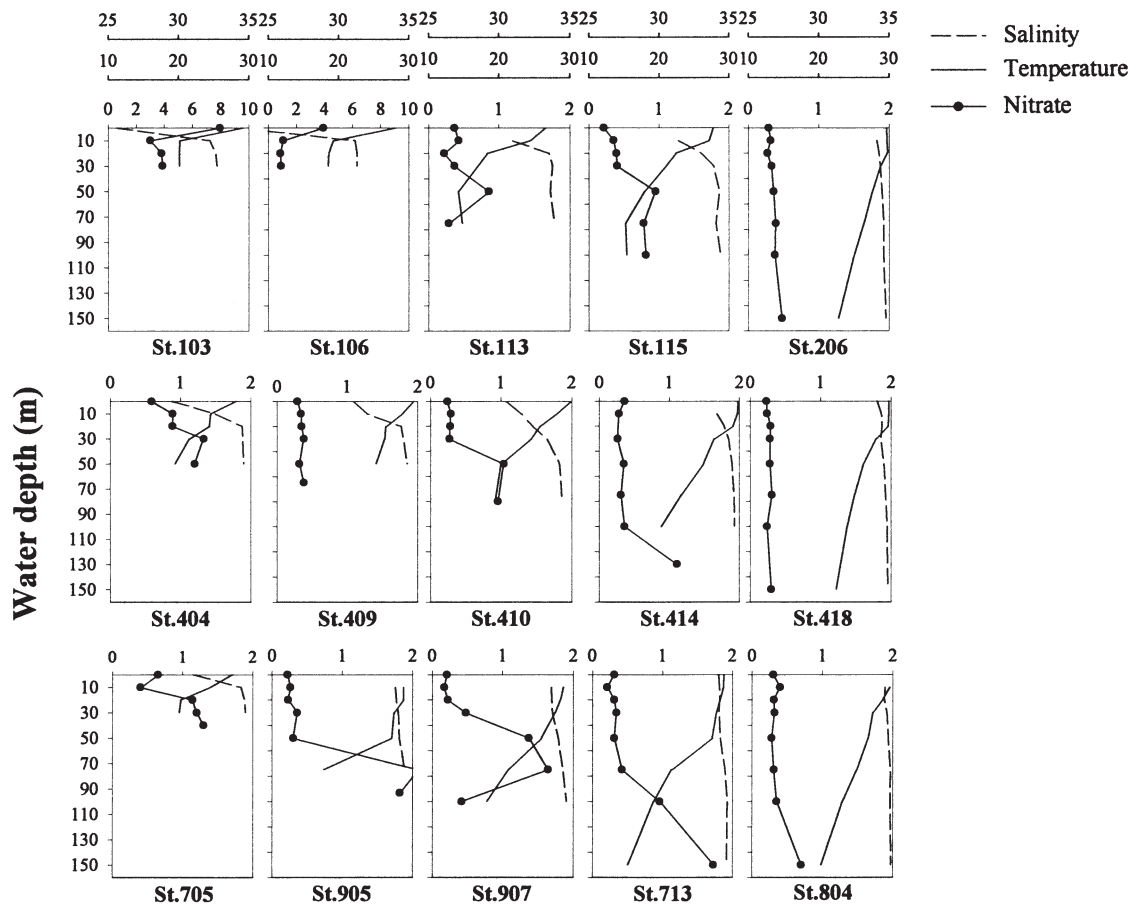
Fig. 3. Depth profiles of salinity (psu), temperature (°C) and nitrate (µM) at some typical stations (St.)

diluted by freshwater. Nitrate was about 8 µM at the surface and reduced abruptly to 3 µM within 10 m. Abundance maxima of *Synechococcus* and bacteria occurred at the surface. Bacteria were very abundant, with depth-weighted average cell abundance reaching a level of 1.2×10^6 cells ml^{-1}. Cell abundances of *Synechococcus* and pico-eukaryotes were relatively low, with depth-weighted averages of 1.0×10^4 and 1.1×10^2 cells ml^{-1} respectively. At Stn 106 (where both nutrient and turbidity were lower than at Stn 103), situated on the outer edge of the plume, cell abundances of *Synechococcus* and pico-eukaryotes were 8- and 5-fold higher, respectively, than those at Stn 103, and the abundance peaks deepened to 10 m. However, cell abundance of bacteria decreased to 1.0×10^6 cells ml^{-1} due to less availability of organic carbon from the river input (Zhao 2000). At Stn 404 (which is opposite Stn 103 on the other side of the plume, although with similar distance to the Yangtze River mouth), the transparency was much higher and nutrients were much lower than those at Stn 103 because of the lesser impact of land input. *Synechococcus* and pico-eukary-

otes were more abundant (5.0×10^4 and 8.6×10^2 cells ml^{-1}, respectively) and bacteria were less abundant (5.4×10^5 cells ml^{-1}) at Stn 404 compared with at Stn 103 (Figs. 3 & 4). On the other hand, while light limitation was less influencing here, nutrient availability became stressing. Picoplankton at this station followed the nitrate depth profile and peaked at a subsurface layer deeper than that at Stn 106, where turbidity was similar but nutrient was much higher at the surface (Figs. 3 & 4). There was no *Prochlorococcus* present in this region. Light as well as nutrient availability seemed to play a critical role in determining picoplankton distribution patterns in the plume area.

Out of the estuarine area in the north part of the sea, the Yellow Sea Coastal Current met the Yangtze River plume and turned to the east, together with the eddy, centered at around Stn 111, and formed a cold water mass west of Stn 113 (Figs. 1 & 5a, Temp). Beyond Stn 113, water temperature was distinctly higher because a branch of Kuroshio Current passing though Stns 116 and 117 (Fig. 1). In the front area in between the cold and warm water masses at Stn 113, tempera-
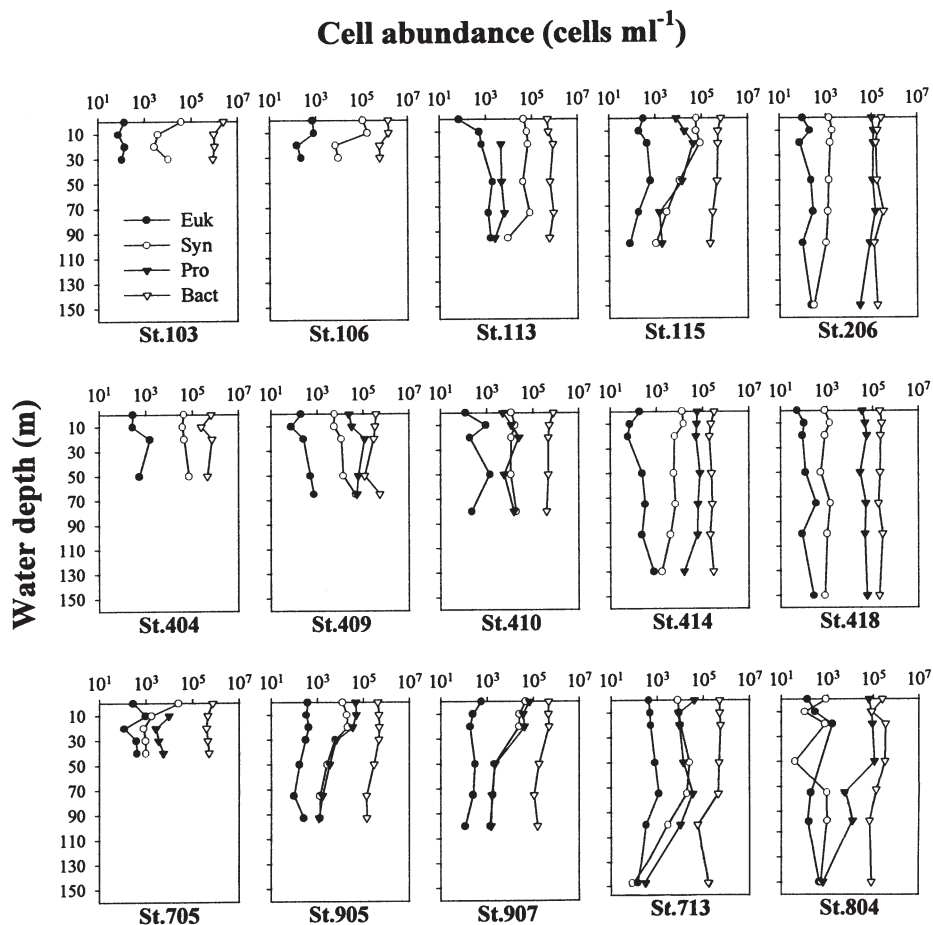
Cell abundance (cells ml⁻¹)

Fig. 4. Picoplankton depth profiles at some typical stations. *x*-axis in logarithmic scale. Euk: picoeukaryotes; Syn: *Synechococcus*; Pro: *Prochlorococcus*; Bact: heterotrophic bacteria

ture was 26.5°C at the surface, 18°C at 20 m and down to less than 14°C at 50 m (Fig. 3, Stn 113). Depth-weighted average of pico-eukaryotes reached 1.2×10^3 cells ml⁻¹, with maximum abundance (2×10^3 cells ml⁻¹) occurring at around 50 m, corresponding to the maximum nitrate concentration depth (Fig. 4, Stn 113). This was one of the 2 high abundance zones of pico-eukaryotes; the other one was at another front area, Stn 406 (see below). *Synechococcus* and bacteria were also more abundant at the subsurface layer (down to 80 m) than at the surface 20 m layer. *Prochlorococcus* began to appear at Stn 113. From here eastward along this transect, *Synechococcus*, pico-eukaryotes and bacteria all decreased dramatically; *Prochlorococcus*, in contrast, increased up to 1.2×10^5 cells ml⁻¹ at the east end of the transect. Distinct differences in the distributions of different picoplankters can be seen from Transect 1 (Fig. 5a). *Prochlorococcus* was confined to the outer region (east of Stn 113), where a branch of Kuroshio Current passes through (Fig. 1). *Synechococcus* peaked in the outer part of the plume, where nutrients were still replete but turbidity was not that high

(around Stn 105, transparency was more than 6 m), while pico-eukaryotes peaked immediately outside the plume (Stn 107) and formed another high abundance zone in the front area (Stn 113). A high abundance of bacteria was associated with coastal waters.

On the main continental shelf of the ECS, picoplankton distributions were more complex because of interacting water masses. Transect 4 passed through 2 main warm water currents in a perpendicular direction. One was the Kuroshio Current principal in the outer region of the sea (affecting Stns 414, 416 and 418), the other was Taiwan Warm Current main branch coming from the northeast of Taiwan island affecting Transect 4 at around Stns 408 and 409 (Figs. 1 & 5c, Temp, NO₃). In these 2 areas, stratifications were weak and nutrient levels were very low (nitrate was down to 0.2 µM) and nitraclines were deep (down to 100 m) or absent (Fig. 3). Abundance of *Prochlorococcus* was around 5×10^4 cells ml⁻¹, much higher than those of the other 2 autotrophs (Fig. 4, Stns 409, 414 and 418). In between the 2 warm water masses, there was a transitional region around Stns 410 to 412, where the thermocline
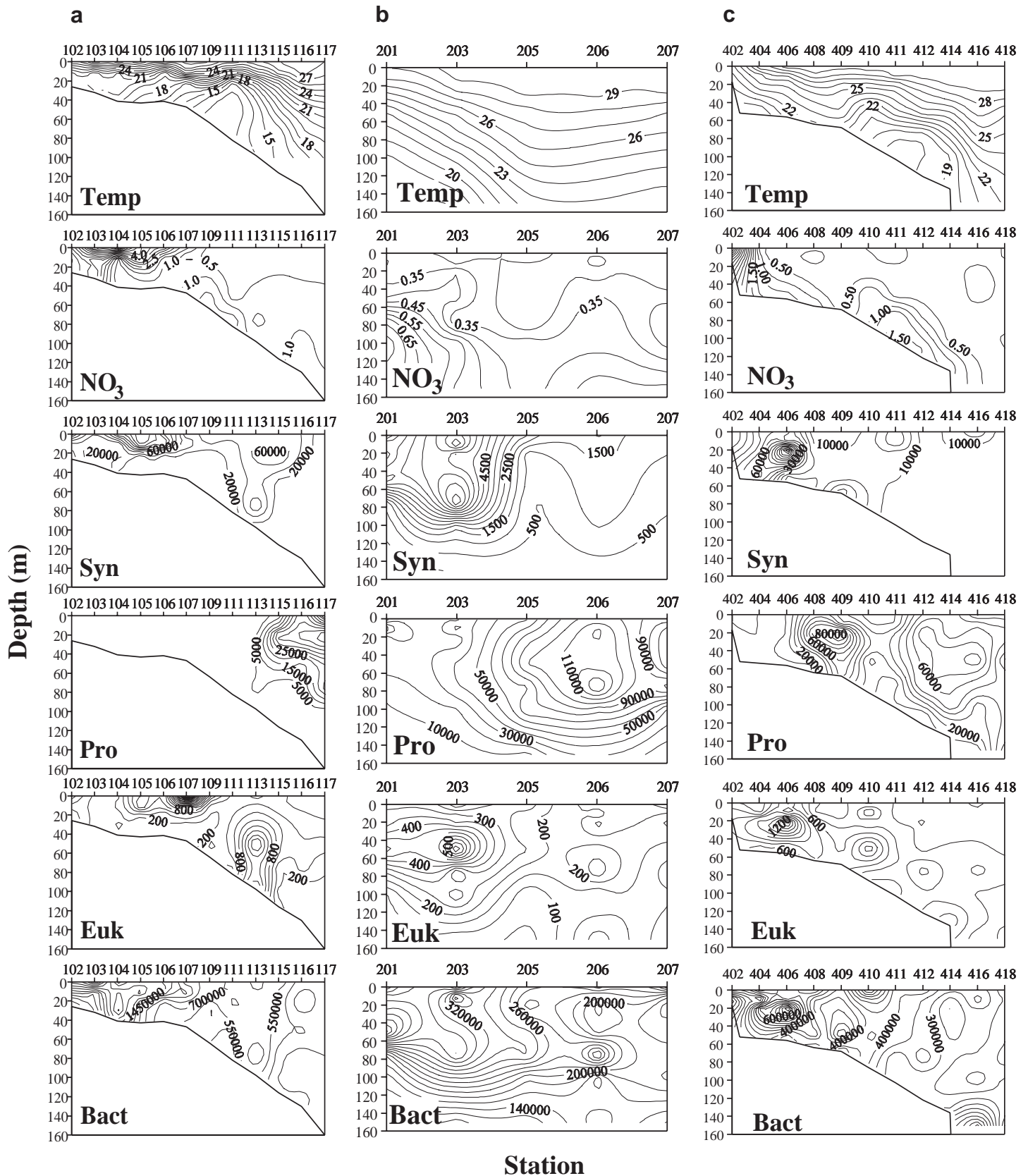
a

b

c

Depth (m)

Station

Fig. 5. (Above and facing page.) Vertical distributions of temperature (Temp, °C), nitrate (NO_3, µM), *Synechococcus* (Syn), *Prochlorococcus* (Pro), pico-eukaryotes (Euk) and heterotrophic bacteria (Bact) along transects (a) 1, (b) 2, (c) 4, (d) 7 and (e) 9. Unit of picoplankton: cells ml^{-1}
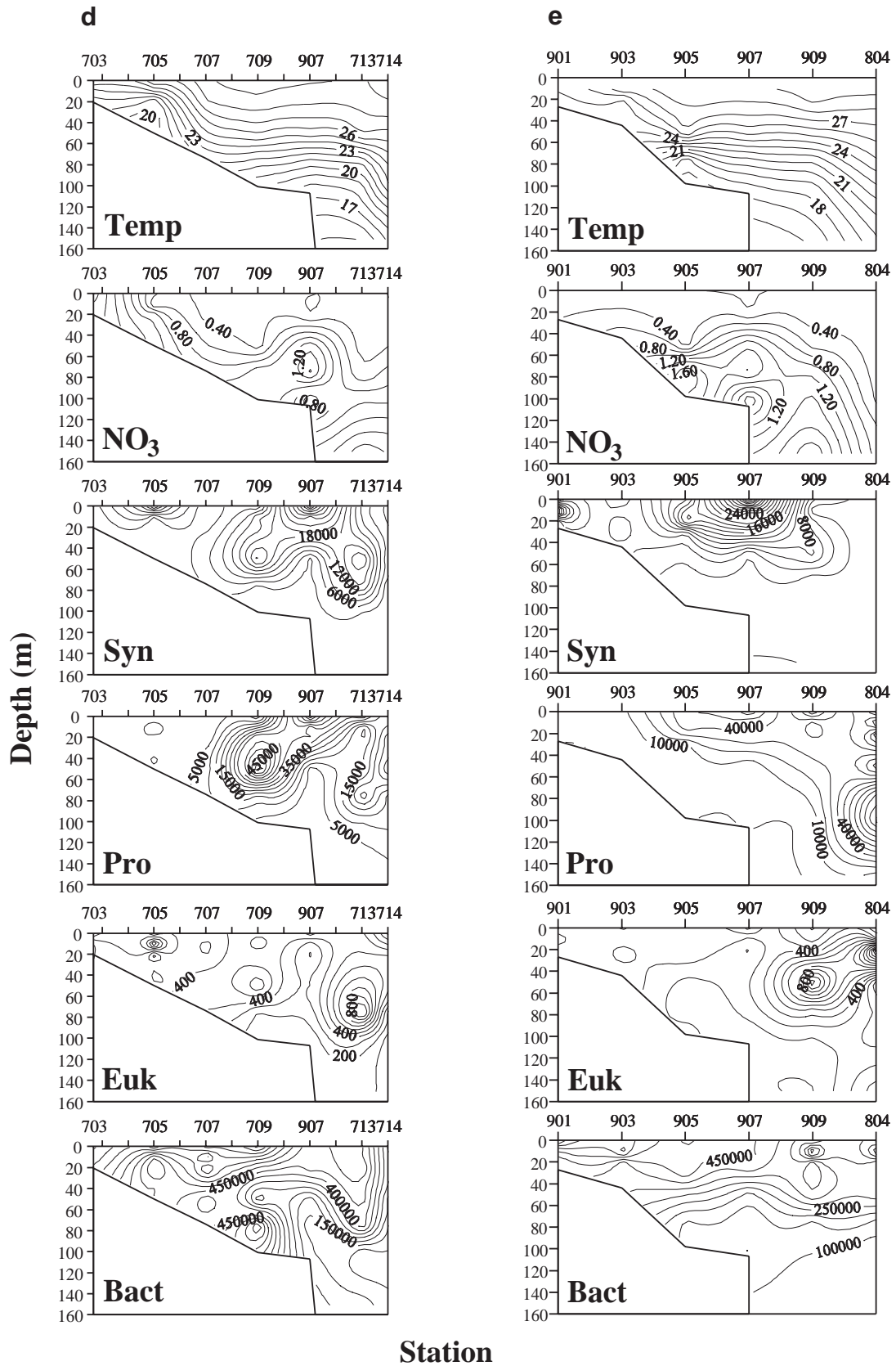
Fig. 5 (continued)

and nitracline developed at around 50 m (Fig. 3, Stn 410). A significant biological feature of this region was that pico-eukaryotes thrived to a high abundance just next to the highest of 1.4×10^3 cells ml^{-1} recorded in the further coastal area Stn 406 (Fig. 5c, Euk). Distinct patterns in picoplankton distribution can be seen along Transect 4 (Fig. 5c). *Prochlorococcus* was associated with the warm currents, dominating numerically in the center and east edge of the sea. *Synechococcus* was abundant in the estuarine adjacent waters but not the high turbidity area. Pico-eukaryotes displayed a pattern similar to *Synechococcus* but were more deeply distributed (Fig. 5c, Euk). Bacteria, presumably unaffected by light availability, centered closest to the river input of high turbidity and high nutrients.

Transect 7, set from out of the Yangtze River estuary to the south edge of the sea (Fig. 1), was mainly affected by the Kuroshio Current (Stn 714) and Taiwan Warm Current in the southern part (Stn 709, Figs. 1 & 5d). *Prochlorococcus* centered at around 50 m of the 2 currents correspondingly. *Synechococcus* showed a very interesting pattern along this transect, peaking in between the 2 warm water masses at the surface of Stn 907 along with another center at the surface around Stn 705. On the other hand there were also 2 subsurface high *Synechococcus* abundance centers similar to those of *Prochlorococcus* at Stns 709 and 713. Pico-eukaryotes formed one center at the surface of Stn 705 and another at 75 m of Stn 713, which was deeper than that of *Synechococcus* and similar to that of *Prochlorococcus*. Distribution of bacteria along this transect seemed to follow the overlay of autotrophs.

Transect 9 together with Stn 804 formed another gradient from coastal water to oceanic Kuroshio Current water (Figs. 1 & 5e). In between the coastal water and the Kuroshio water, another branch of Taiwan Warm Current passed through this transect at around Stn 905. *Prochlorococcus* were sparse in the coastal water but very abundant (maximum of 1.2×10^5 cells ml^{-1} at 50 m at Stn 804) in the oceanic water. Again *Synechococcus* centered at the very coast and in between the 2 warm waters at Stn 907 (around 1.5×10^4 cells ml^{-1}). Pico-eukaryotes were less abundant in the coastal area and were quite different in distribution pattern in terms of their relationship to *Synechococcus* and other picoplankton. They centered at the subsurface layer of Stn 909, and the front area and surface layer of Stn 804. The distribution pattern of bacteria at this transect was not typical but somewhat similar to that of the overlay of autotrophs.

In depth profile, 3 typical patterns can be seen at Stns 905, 907 and 804 (Figs. 3 & 4). At Stn 907, nitracline occurred at about 20–40 m, and temperature decreased gradually from the surface to the bottom of the euphotic zone. Picoplankton peaked at the very

surface. In contrast, at Stn 905, strong thermocline and nitracline deepened to 50–70 m. *Prochlorococcus*, *Synechococcus* and bacteria were distributed down to the same depth and peaked at about 20 m. At Stn 804, where nitrate was low (around 0.2 µM) in the whole water column, *Prochlorococcus* abundance was at least an order of magnitude higher than the other autotrophs and was abundant at all the sampling depths in the upper 100 m, reflecting a typical oligotrophic condition.

Along the Kuroshio Current branch from Stn 207 to Stn 201, water column structure was relatively uniform and similar to that at Stn 804 in the far south (Fig. 3) but the oceanic current became weaker and shallower (Fig. 5b). Correspondences in picoplankton were seen from their abundance. *Prochlorococcus* gradually decreased from a magnitude of 10^5 cells ml^{-1} in the south to less than half of that in the north. All the other 3 picoplankters, especially pico-eukaryotes, were increasing in the same direction (Fig. 5b, Syn, Pro, Euk and Bact).

DISCUSSION

Impacts of the Yangtze River and picoplankton distribution patterns along trophic gradients

The Yangtze River is one of the largest rivers in the world. Tremendous amounts of nutrients and other materials carried by the freshwater runoff input into the sea greatly impacting the estuarine ecosystem. In conjunction with the oligotrophic Kuroshio Current on the other side of the sea, distinct gradients in nutrients, turbidity and salinity are formed across the continental shelf (Fig. 2). Corresponding patterns in picoplankton distribution could be recognized.

Prochlorococcus were very abundant in the southern and eastern regions of the sea where warm currents pass through, and declined gradually in abundance along warm water radiations to inshore direction on the continental shelf, and then disappeared in the Yangtze River estuarine area. By plotting cell abundance against nutrients, it can be seen that *Prochlorococcus* were only present where TIN was less than 3 µM and phosphate less than 0.4 µM (Fig. 6a,b). As in the Arabian Sea (Campbell et al. 1998), *Prochlorococcus* in the ECS were inversely correlated with macronutrients (Table 1). However this relationship may not be causative since *Prochlorococcus* can tolerate elevated nutrient concentrations (Chavez et al. 1991, Vaulot & Partensky 1992). There are several possible interpretations of the inverse relationship. First, high nutrients in marginal seas are usually associated with coastal waters where other factors (including land
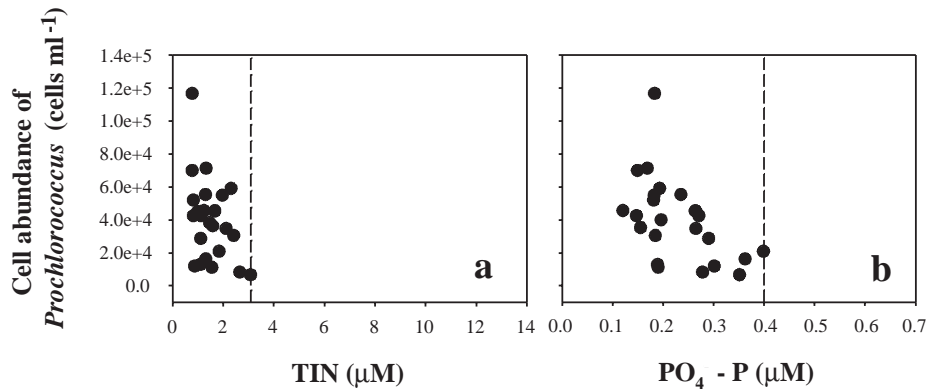
Fig. 6. Relationship between *Prochlorococcus* and (a) total inorganic nitrogen (TIN) and (b) PO$_4$-P in the East China Sea, indicating the corresponding thresholds above which *Prochlorococcus* disappeared. (Only data from the surface mixed layer were included to avoid possible interference by high nutrient concentrations at the bottom of the euphotic zone.) *x*-axis scales up to nutrient levels recorded in the surface mixed layer

input materials) may also be important in regulating picoplankton dynamics. Secondly, high nutrient conditions favor those whose maximum growth rates are higher than *Prochlorococcus*, such as *Synechococcus* (Moore et al. 1995). Furthermore, recent work has revealed that only the low-light ecotype *Prochlorococcus* strain can take up nitrite and that none of the *Prochlorococcus* strains in culture can utilize nitrate due to lack of nitrate reductase genes (Moore et al. 2002). Thus, high nitrate concentration favors other picoplankters other than *Prochlorococcus*. Therefore, the observed inverse relationship between *Prochlorococcus* and macronutrients is due either to non-causal correlation or to *Prochlorococcus* being outcompeted where nutrients are replete but in an unavailable form to *Prochlorococcus* (López-Lozano et al. 2002, Moore et al. 2002); furthermore, the maximum growth rate of *Prochlorococcus* is lower than that of other species such as *Synechococcus* (Moore et al. 1995, Cavender-Bares et al. 2001).

Along trophic gradients from the estuary to the oceanic water, pico-eukaryotes showed a very similar pattern for the different transects. High abundance occurred immediately out of the river plume, where nutrients were still abundant but turbidity was fairly low (Stns 107, 406, 705 and 903) and another high abundance zone formed in the front areas of cold and warm water masses (Stns 113, 410, 713 and 909).

Synechococcus showed a general pattern similar to that of pico-eukaryotes, but its high abundance usually centered shallower in depth and closer to shore than did pico-eukaryotes. The distribution of *Synechococcus* can be understood in terms of nutrient availability and light availability. Generally, *Synechococcus* is positively correlated with nitrogen concentrations (Table 1), but in the Yangtze River estuary area, although nutrient level was very high, *Synechococcus* abundance could be very low due to low transparency, e.g. at Transects 1 and 4, *Synechococcus* abundance increased dramatically with increasing transparency and reached their peak values where transparence was about 5 to 8 m (Fig. 7). *Synechococcus* decreased with increasing transparency as nutrient availability became more limiting than light availability. This pattern is similar to that in previous studies of the Yangtze River estuary (Vaulot & Ning 1988), although the observation scale is not the same.

Table 1. Correlation coefficients between picoplankton cell abundances and physical and chemical factors in the East China Sea in July 1998. (Data from all sampling depths are included for the statistics in this table; only coefficients of significance at the $p < 0.01$ level are shown; + and –: positive and reverse relationship respectively.) Syn: *Synechococcus*; Pro: *Prochlorococcus*; Euk: picoeukaryotes; Bact: heterotrophic bacteria; TIN: total inorganic nitrogen

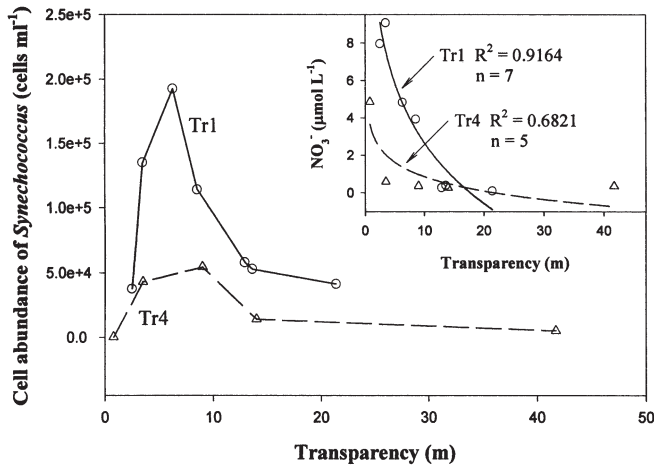| Picoplankton	Temp. (°C)	Salinity (psu)	PO$_4$-P	SiO$_4$-Si	NO$_2$-N	NO$_3$-N	NH$_4$-N	TIN	TIN:P
Syn (n = 220)	+	−0.46	−	+0.27	+	+0.38	+	+0.33	+0.44
Pro (n = 161)	+0.39	+	−0.44	−0.48	−0.30	−0.42	−	−0.35	−
Euk (n = 220)	+	−	−	+	+	+	+	+	+
Bact (n = 220)	−	−0.44	+	+0.54	+0.42	+0.50	+0.45	+0.64	+0.56

Fig. 7. Variation of cell abundance of *Synechococcus* with transparency. The upper-right inner chart indicates the inverse correlation between transparency and nutrient at Transects 1 and 4 (Tr1 and Tr4). Notice that the *Synechococcus* abundance peak values at Transect 1 were higher than those at Transect 4, due to higher nutrient availability at Transect 1 than at Transect 4

Bacteria, presumably uninfluenced by light, were most abundant in the plume area where nutrients were replete and dissolved organic carbon resources were rich (Zhao 2000) although light availability was low.

The species composition of pico-eukaryotes may have changed over regions and water masses in the ECS, as we noticed subtle variations in the location of 'pico-eukaryote groups' in flow cytometry plots of samples from different areas. The high abundance zone at the subsurface of Stn 804 was probably formed by oceanic species rather than coastal species. Therefore, the geographic distribution pattern of pico-eukaryotes in the ECS should not be simply attributed to effects of physical-chemical factors.

Similarly the 2 high abundance zones of *Synechococcus* at Stns 709 and 713 were likely formed by oceanic populations different from the one centered near the coast. We were able to discriminate the 'high cellular phycourobilin to phycoery-throbilin (PUB:PEB) ratio population' in oceanic waters from the 'low PUB:PEB ratio population' (Wood et al. 1985, Olson et al. 1988, Campbell et al. 1998) in the coastal water for the winter cruise in the same area of the sea. Because cytographic overlaps between the 2 populations were severe for the summer samples, we treated the 2 as a single group for the present study to simplify the comparison between *Synechococcus* and others.

In contrast to *Prochlorococcus*, which was basically associated with oligotrophic conditions, *Synechococcus*, pico-eukaryotes and bacteria populations seem to be associated more with eutrophic conditions. By converting cell abundance to cell biomass using the factors widely applied — 53 fg C cell[-1] for *Prochlorococcus*, 250 fg C cell[-1] for *Synechococcus*, 2100 fg C cell[-1] for pi-coeukaryotes and 20 fg C cell[-1] for heterotrophic bacteria (Morel et al. 1993, Campbell et al. 1994, Buck et al. 1996) — it can be seen that biomass of bacteria is positively correlated with the sum of that of *Synechococcus* and pico-eukaryotes in the study area out of the estuary (Fig. 8a), while it is negatively correlated with that of *Prochlorococcus* (Fig. 8b). Such an inverse relationship between *Prochlorococcus* and bacteria was also found in the Arabian Sea (Campbell et al. 1998). Since *Prochlorococcus* can flourish in stratified nutrient-deplete waters (Olson et al. 1990, Campbell & Vaulot 1993, Lindell & Post 1995), and bacteria is generally more abundant in the nutrient-rich coastal areas (Fuhrman 1999), the inverse relationship between the two seems to be another feature of the transitional zones between oligotrophic and eutrophic regimes.

The role of water mass in determining the distribution of *Prochlorococcus* in the marginal sea

From Fig. 9, it can be seen that in the surface mixed layer, *Prochlorococcus* disappeared when temperature was below 26°C and salinity was less than 30 psu in the study period (Fig. 9a). While in the deep water below the mixed layer, the corresponding thresholds recorded were 16°C and 33.4 psu respectively (Fig. 9b). Obviously, temperature, the most crucial factor regulating *Prochlorococcus*'s distribution on a basin scale, was not a reliable criterion for the situation in marginal seas. It was most likely that the combination
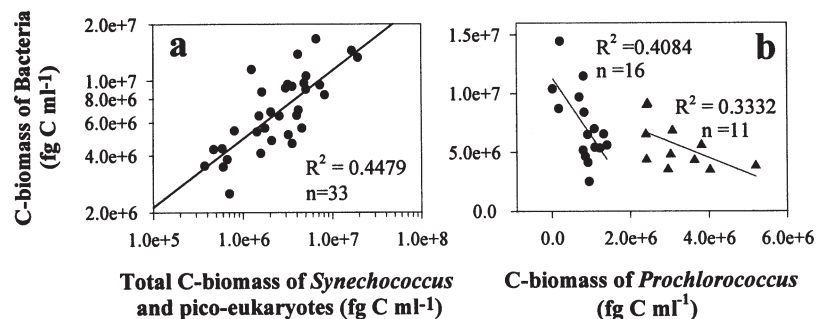

Fig. 8. Relationship between depth-weighted average carbon-biomass (fg C ml^{-1}) of bacteria and (a) the sum of *Synechococcus* and pico-eukaryotes at the stations out of the estuarine area, and (b) *Prochlorococcus* (▲: oceanic stations located in the main stream of Kuroshio Current and Taiwan Warm Current; ●: shelf stations or stations across trophic gradients)

of multivariables associated with water mass determined the distribution scope of *Prochlorococcus* in marginal seas.

The association of *Prochlorococcus* with particular water masses and currents is supported by the more shoreward distribution of *Prochlorococcus* along Transect 4, where the Taiwan Warm Current reached, than along Transect 1, where *Prochlorococcus* was present from Stn 113 eastward, much farther away from the estuary. This pattern was consistent with the distribution of water currents (Su 1989): the Taiwan Warm Current proceeded up to the Yangtze River estuary area but stopped by the Yellow Sea Cold Eddy in the summer time (Fig. 1). Meanwhile, the Yellow Sea Coastal Current from the north side proceeded southward along the 40 to 50 m isobath to 32° N (Transect 1) and, in conjunction with the 'cold eddy', formed the cold water system. In between the cold and warm water systems there was a boundary roughly paralleling the 50 m isobath near the river plume. *Prochlorococcus* suddenly disappeared at Stn 406 (cold water system), only about 60 km west of Stn 408 where the warm water current passes through and *Prochlorococcus* was very abundant. This is consistent with the situation of the Gulf Stream in the North Atlantic, where *Prochlorococcus* abruptly declined off the stream on both sides and dropped below the detection limit on the coastal water side (Cavender-Bares et al. 2001, Jiao unpubl. data).

The effects of water mass can also be seen from the relationship between abundances of *Prochlorococcus* and *Synechococcus* (Fig. 4). In the middle of the Kuroshio Current (typically Stns 206 and 804), *Prochlorococcus* were 2 orders of magnitude more abundant than *Synechococcus*. At the edge of the Kuroshio Current (typically Stns 418 and 714), or in the weaker branches of the warm current (e.g. Stn 409), abundance of *Prochlorococcus* was 1 order of magnitude greater than that of *Synechococcus*. In the front areas between the warm current branches and the shelf water masses (e.g. Stns 410, 115 and 907), abundances of the 2 genera were comparable. In the coastal waters (e.g. Stns 103, 106 and 404), *Prochlorococcus* were absent and *Synechococcus* were very abundant.

Given the environmental conditions in the ECS, the distribution of *Prochlorococcus* is most likely controlled fundamentally by oceanic currents and relevant water masses over a large spatial scale. Locally, temperature, nutrients and water column structures may also play additional roles. Unlike the situation in the oceans, the sudden change in cell abundance within a relatively short distance seems to be a typical feature of marginal seas.
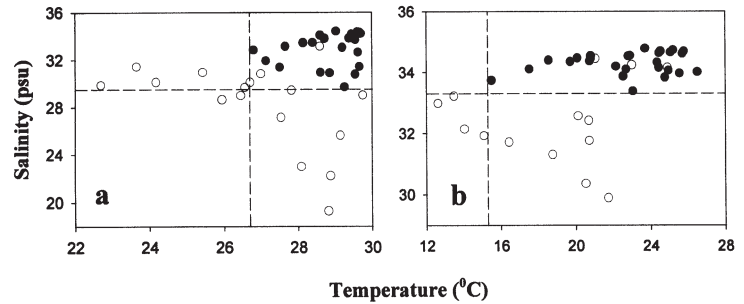

Fig. 9. Distribution of stations in a temperature-salinity plot, indicating corresponding thresholds below which *Prochlorococcus* disappeared. (a) Surface mixed layer; (b) deep layer below. ●: stations where *Prochlorococcus* were present; ○: stations where no *Prochlorococcus* were detected

Characteristics of depth profile of *Prochlorococcus* in the marginal sea

Partensky et al. (1999) summarized the worldwide data on *Prochlorococcus* and classified *Prochlorococcus* vertical distribution patterns into 3 types with respect to its depth profile shape and relative abundance to *Synechococcus*. In the present study, although there were no such typical patterns as in the oligotrophic tropical oceans, 2 types of *Prochlorococcus* depth profile can be roughly distinguished. One type allocated to the Kuroshio Current area was characterized by deep distribution of *Prochlorococcus* with abundance at least an order of magnitude higher than *Synechococcus* (typically Stns 206, 418 and 804, see Fig. 4). The other type was characterized by *Prochlorococcus* abundance peaking at the surface layer and dropping to an abundance comparable to that of *Synechococcus* above the nitracline (typically Stns 115, 410, 905 and 907). The latter type is similar to the description of Partensky et al. (1999) for the case of nearshore waters. There were also transitional types in the shelf waters. Unlike the situation of stratified oligotrophic waters, where *Prochlorococcus* maintain a maximum near the bottom of the euphotic zone (Olson et al. 1990, DuRand et al. 2001), the oceanic waters in the ECS were associated with the Kuroshio Current whose movements make the water column always mixed. Thus, there were no pronounced subsurface peaks in the depth profiles, although *Prochlorococcus* outnumbered *Synechococcus* by at least an order of magnitude, as is common in oceanic water (Campbell & Vaulot 1993). This seems to be a specific biological feature of the marine current system in the marginal sea areas.

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