Size-fractionated primary productivity and the phytoplankton-bacteria relationship in the Taiwan Strait

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ABSTRACT: Size-fractionated phytoplankton biomass, primary productivity, photosynthetic dissolved organic carbon (PDOC), vertical distribution of pico-, nano-, and microphytoplankton, and the relationship with bacteria were studied in the Taiwan Strait during 2 cruises conducted in August 1994 and February-March 1995. Nanophytoplankton (3 to 20 µm) dominated the community in the northern Taiwan Strait (NTS) while picophytoplankton (0.2 to 3 µm) dominated in the southern Taiwan Strait (STS). Nanophytoplankton accounted for 60 and 57% of biomass, and 77 and 36% of productivity in summer and winter in the NTS, respectively. Picophytoplankton contributed to 54 and 63% of biomass, and 85 and 48% of productivity in summer and winter in the STS, respectively. The vertical distribution pattern in the Taiwan Strait consisted of microphytoplankton (20 to 200 µm) mainly at the surface, nanophytoplankton in the middle and picophytoplankton at the bottom of the euphotic zone. Regression analysis indicated that bacterial abundance and biomass were positively significantly correlated with phytoplankton biomass and productivity, respectively, implying that the phytoplankton was an important organic carbon source for supporting bacterial growth. All the results suggested that the microbial loop played an important role in carbon cycling in the study areas, especially in the STS. The factors controlling the size structure, PDOC and vertical distribution of picophytoplankton are discussed.

KEY WORDS: Size-fractionation · Phytoplankton · Biomass · Productivity · Bacteria · Microbial loop · Taiwan Strait

INTRODUCTION

Many physiological processes occurring in planktonic ecosystems are size dependent. Plankton ecologists have paid progressively more attention to the ecology of small cell size organisms in pelagic communities in aquatic ecosystems. Data on the size structure of phytoplankton biomass and productivity are documented in more and more studies in oceanic ecosystems (Malone 1980, Takahashi & Bienfang 1983, Davis et al. 1985, Larry & El-Sayed 1987, Chavez 1989, Ning et al. 1993, 1996, Hong & Huang 1994, Liu et al. 1998). Nanophytoplankton accounts for a high proportion of the biomass and primary productivity in most phyto-

plankton communities. With the development of new techniques, such as flow cytometry, electronic microscopy and epifluorescence microscopy, picophytoplankton (smaller than 2 to 3 µm) was found to be of considerable quantitative significance in many parts of the world's oceans (Platt et al. 1983, Stockner & Antia 1986, Waterbury et al. 1986, Ray et al. 1989, Li 1994, Iriate & Purdie 1995).

Bacteria are not only decomposers, but also producers (secondary producers); the microbial loop plays a very important role in the cycling of organic carbon in aquatic ecosystems (Anderson 1988, Bjørnsen et al. 1988, Jumars et al. 1989, Rieman et al. 1990, Middelboe et al. 1992). Phytoplankton and bacteria have a close relationship in aquatic ecosystems.

The present study focuses on the size-fractionated phytoplankton biomass and productivity, photosyn-

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thetic dissolved organic carbon, vertical distribution of 3 phytoplankton categories and the phytoplankton-bacteria relationship in the Taiwan Strait.

DESCRIPTION OF STUDY AREAS

The Taiwan Strait is a channel on the continental shelf between the East China Sea and the South China Sea (Fig. 1). With irregular bottom topography, the water in this region is mostly less than 100 m deep. The climate is affected by the subtropical monsoon, which comes from the southwest in summer and from the northeast in winter. Due to the corresponding NE-SW trend of the Strait and the mountains along the 2 sides, the 'Narrow Pipe Effect' is quite distinct, which leads to high wind speeds. Upwelling, resulting from the effect of the monsoon and its topography, is common in the Strait (Hong et al. 1991, Liang 1997). There are several currents such as the Zhejiang-Fujian Coastal Current, the Strait Warm Current and Kuroshio water in this region (Hong et al. 1991).

METHODS

Study site and sampling. Two cruises were carried out in the Taiwan Strait (21 to 27° N, 116.5 to 122.5° E) in August 1994 and February-March 1995. Fig. 1 shows the location of transects and 24 stations in the northern and southern Taiwan Strait. The CTD, chemical and biological oceanographic parameters were measured at all stations. Diurnal variations of size structure of chlorophyll a (chl a) were measured at Stn NC1 (25° 39.00' N, 120° 29.10' E) in February 1995, with a sampling interval of 6 h. Water samples were taken with 5 l Niskin bottles at depths of 0, 10, 20, 30, and 50 m.

Size-fractionation. Size-fractionation of chl a and photosynthetic rate were conducted according to the procedure reported by Wang et al. (1997). Phytoplankton in this present study were divided into 3 categories named micro- (20 to 200 μm), nano- (3 to 20 μm) and picophytoplankton (0.2 to 3 μm), water samples were fractionated by filtering with a 20 μm mesh, 3 and 0.2 μm Nuclepore filters (Costar®).

Chlorophyll a. The determination of chl a was performed by fluorescence analysis (Parsons et al. 1984), with a slight modification. 150 ml seawater sample was filtered under a pressure of less than 50 KPa, and extracted for 24 h in 90% acetone in 0°C, and the fluorescent value was measured before and after acidifying in a Hitachi 850 Fluorospectrometer with the excitation and emission wavelength set at 430 and 670 nm. Chl a could then be calculated from the formula,

$$\text{Chl } a = F_d \times [r/(r-1)] \times (R_b - R_a) \times (V_1/V_2) \qquad (1)$$

where Chl a = concentration of chl a (mg m^{-3}); F_d = calibration factor (mg m^{-3}); r = ratio of fluorescent value before and after acidifying for standard chl a; R_b = fluorescent value before acidifying; R_a = fluorescent value after acidifying; V_1 = volume for extracting sample (ml); V_2 = volume of water sample filtering.

F_d and r could be measured from standard pure chl a

$$F_d = \text{CHLA}_{STD}/(R_1 - R_2) \qquad r = R_1/R_2$$

where CHLA_{STD} = concentration (known) of standard pure chl a (mg m^{-3}); R_1 = fluorescent value before acidifying; R_2 = fluorescent value after acidifying.

Photosynthetic rate. Phytoplankton photosynthetic rate was measured by the ^{14}C method based on Parsons et al. (1984).

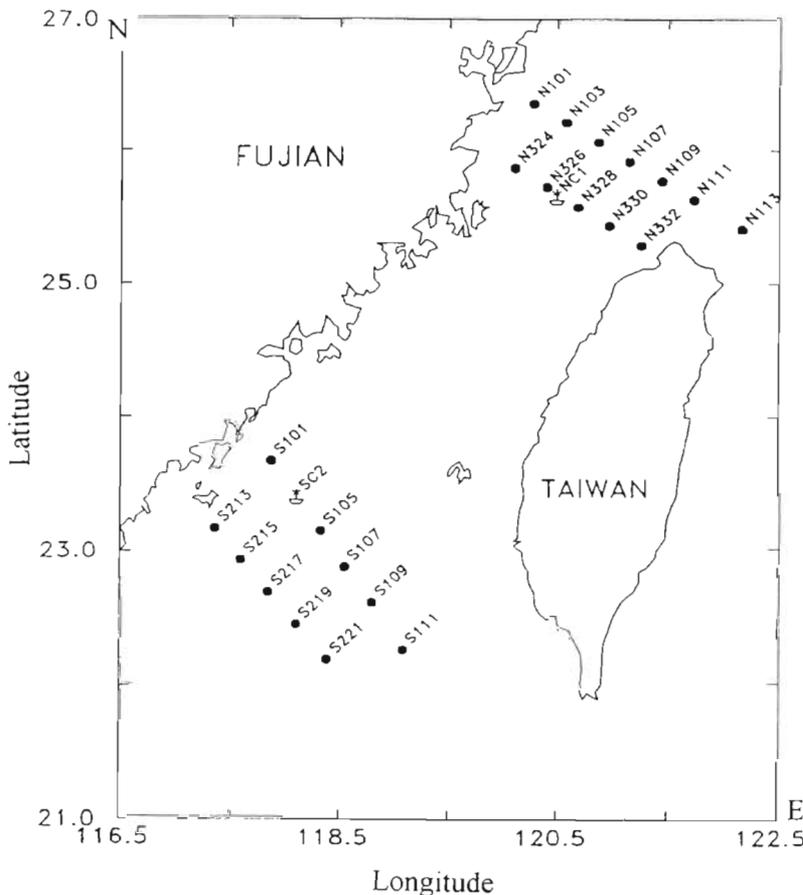Fig. 1. Location and sampling stations in the Taiwan Strait

120 ml seawater sample was incubated after the addition of ^{14}C-NaHCO$_3$ (185 KBq); the incubation was carried out on deck for 3 h with running seawater, which provided temperature control. At the end of incubation, the samples were filtered onto Nuclepore filters (Costar®) according to the size fractionation above, and the filters were fumed with concentrated hydrochloric acid to remove inorganic ^{14}C, then dried and stored in darkness, scintillation cocktail (Optiphase 'Hisafe') was added, and the radioactivity was measured using a Pharmacia-LKB 1409 liquid scintillation counter.

Photosynthetic dissolved organic carbon. Photosynthetic dissolved organic carbon was measured using the acid bubbling method (Wood & Vaalen 1990, Jiao & Wang 1994), with slight modifications: 5 ml filtrate (passing through 0.2 µm filter) of incubation samples, adjusted to pH < 1 with 1:1 (v/v) hydrochloric acid (HCl) and distilled water, was bubbled with nitrogen (N$_2$) for 30 to 45 min at a speed of 300 ml min^{-1}, then adjusted to pH = 7 with 1 N sodium hydroxide and bubbled again with carbon dioxide (CO$_2$) for 15 to 20 min, then 5 ml modified scintillation cocktail (8:2 [v/v] scintillation cocktail [Optiphase 'Hisafe'] and Triton X-100) was added.

Bacterial biomass. Bacterial biomass was calculated from bacterial abundance, which was measured with the AODC method (Parsons et al. 1984). Bacterial volume was measured by scanning electronic microscopy and converted to carbon biomass assuming a transfer factor of 0.121 pg C µm^{-3} (Watson et al. 1977).

Bacterial productivity. Bacterial productivity was determined by thymidine incorporation based on the method of Fuhrman & Azam (1982). 9.25 KBq (Methyl-^{3}H)-thymidine was added to 20 ml samples. Triplicate samples and controls (formalin-killed, final conc. 0.5%) were incubated at in situ temperature in the dark for 30 min, the incubations were stopped with formalin (final conc. 0.5%). To each 20 ml sample and control, an equal volume of ice-cold 10% (wt/v) TCA was added and the mixtures were kept on ice for

10 min. The TCA-insoluble fraction was collected by filtering the sample through a 0.2 µm Nuclepore filter (25 mm) (Costar®). The filters were rinsed 5 times with 1 ml of ice-cold 5% (wt/v) TCA and then dried, dissolved in 10 ml scintillation cocktail (Optiphase 'Hisafe'), the radioactivity was measured using a Pharmacia-LKB 1409 liquid scintillation counter.

Bacterial heterotrophic activity. Bacterial heterotrophic activity was measured by radio-labeled D-Glucose uptake (Parsons & Strickland 1962, Wright & Hobbie 1966): 183 KBq ^{14}C-D-glucose was added to 125 ml water sample and incubated at in situ temperature in the dark for 1 h; it was then filtered under a pressure of less than 50 KPa, filters were dried and radioactivity was measured using a Pharmacia-LKB 1409 liquid scintillation counter.

RESULTS

Size structure of biomass and productivity of phytoplankton

Nanophytoplankton dominated the phytoplankton biomass (chl a) in the northern Taiwan Strait (NTS) while picophytoplankton were dominant in the southern Taiwan Strait (STS) in both summer and winter (Table 1). Nanophytoplankton accounted for 60 and 57% of biomass in summer and winter in the NTS, respectively, and picophytoplankton constituted 54 and 63% of biomass in summer and winter in the STS, respectively.

Size structure of primary productivity is similar to that of biomass (Table 2). Nanophytoplankton and picophytoplankton dominated primary productivity in the NTS and the STS, respectively; however, their dominance decreased in winter compared to that in summer, with nanophytoplankton accounting for only 36% of the total primary productivity in winter, as opposed to 77% in summer in the NTS, and picophytoplankton only constituting 48% of total primary productivity in winter, while this was 85% in summer in the STS.

Table 1. Size-fractionated biomass (average chl a, mg m^{-3}) and percentage of 3 sizes of phytoplankton (average % and standard deviation, SD) in the Taiwan Strait

Season	Size	Northern Taiwan Strait				Southern Taiwan Strait			
		Average chl a	Average %	SD	n	Average chl a	Average %	SD	n
Summer	Micro-	0.135	20	17	11	0.160	22	22	6
	Nano-	0.379	60	15	11	0.157	24	19	6
	Pico-	0.115	20	18	11	0.448	54	22	6
Winter	Micro-	0.227	26	21	27	0.043	5	5	14
	Nano-	0.446	57	16	27	0.301	32	10	14
	Pico-	0.137	17	14	27	0.599	63	11	14

Table 2. Size-fractionated primary productivity (average PR, mg C m^{-3} h^{-1}) and percentage of 3 sizes of phytoplankton (average % and standard deviation, SD) in the Taiwan Strait

| Season | Size | Northern Taiwan Strait | | | | Southern Taiwan Strait | | | |
		Average PR	Average %	SD	n	Average PR	Average %	SD	n
Summer	Micro-	0.185	20	36	8	0.062	6	3	6
	Nano-	1.166	77	39	8	0.108	9	7	6
	Pico-	0.038	3	6	8	0.889	85	5	6
Winter	Micro-	0.307	34	22	6	0.161	23	18	8
	Nano-	0.383	36	20	6	0.178	29	6	8
	Pico-	0.302	30	24	6	0.242	48	19	8

Diurnal variation of size-fractionated biomass varied with depth (Fig. 2). Microphytoplankton changed sharply in the upper 30 m. It showed high concentration in the day and low value in the night at depths of 0, 10, and 20 m, whereas it showed low concentration in the day and high value in the night at a depth of 30 m, and slight variation at a depth of 50 m. The vertical migration and grazing pressure of mesozooplankton is a probable cause of this variation.

Photosynthetic dissolved organic carbon

The percentage of photosynthetic dissolved organic carbon (PDOC) was measured at Stns NC1 and S213 in February 1995. The average PDOC was 24.8%. Total photosynthetic rate (TPR) was the sum of photosynthetic particulate organic carbon (PPOC) and PDOC (Table 3).

Vertical distribution of micro-, nano- and picophytoplankton

There were different vertical distribution patterns between summer and winter. In summer, the vertical distribution pattern of the 3 size fractions of phytoplankton was significantly different within the euphotic zone. For example, at Stn N330, the high picophytoplankton biomass was at depths of 20 and 35 m, while the high nanophytoplankton biomass was at 20 m and that of microphytoplankton at 0 and 20 m (Fig. 3). The distribution pattern showed microphytoplankton in surface and near-surface waters, nanophytoplankton in the middle and picophytoplankton at the bottom of
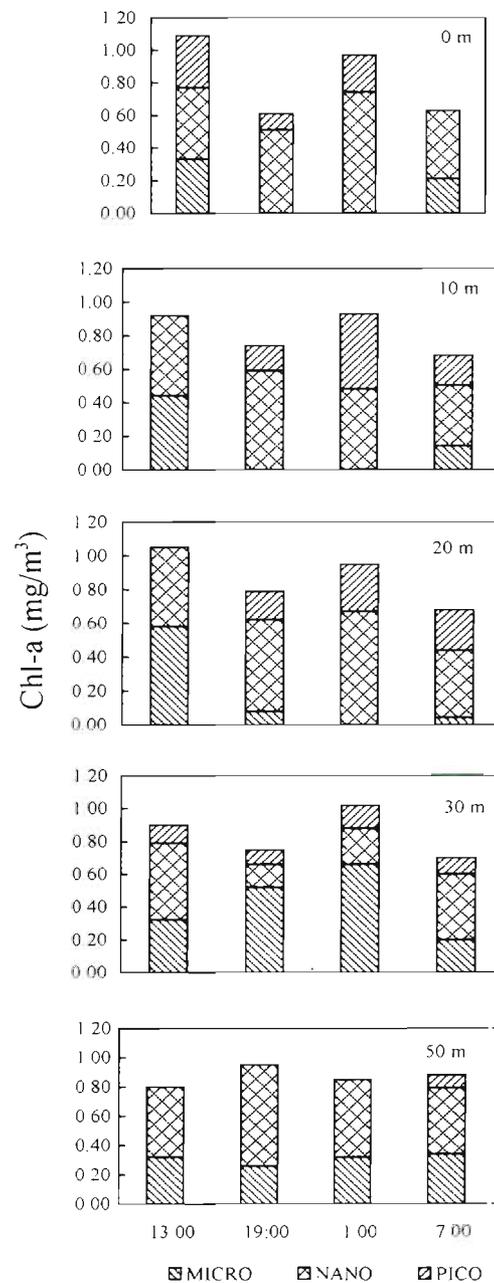

Fig. 2. Diurnal variation of size-fractionated biomass (chl a) in winter in the Taiwan Strait at Stn NC1. MICRO: microphytoplankton; NANO: nanophytoplankton; PICO: picophytoplankton

Table 3. Photosynthetic particulate organic carbon (PPOC), photosynthetic dissolved organic carbon (PDOC), total photosynthetic rate (TPR) and percentage of PDOC in the Taiwan Strait

Station	Relative Irradiation ($\% I_0$)	PPOC (mg m^{-3} h^{-1})	PDOC (mg m^{-3} h^{-1})	TPR (mg m^{-3} h^{-1})	PDOC (%)
	100	1.012	0.283	1.295	21.9
NC1	10	0.509	0.180	0.689	26.1
	1	0.169	0.083	0.252	32.9
S213	100	1.459	0.533	1.992	26.8
	10	0.934	0.181	1.115	16.2

Table 4. Contribution of picophytoplankton to total phytoplankton (in biomass) in summer (%)

Depth (m)	0	10	20	35	40
Stn N330	30		31	54	
Stn NC1	0		40		16
Stn S215	75	77	82		

the euphotic zone, which was 36 m at this station. In addition, the contribution of picophytoplankton to total phytoplankton (in biomass) also increased with depth from the surface to the bottom (Table 4). However, in winter, the vertical distribution pattern of the 3 size fractions of phytoplankton was different from that in summer. For example, the higher microphytoplankton occurred at the bottom, the picophytoplankton was mainly at depths of 10 to 20 m and the nanophytoplankton was uniformly distributed (Fig. 4). The pattern during winter may be due to strong mixing of seawaters.

Phytoplankton-bacteria relationship

The results showed that bacterial abundance (TB, $\times 10^6$ ind ml^{-1}) was positively significantly correlated with phytoplankton biomass (chl a, mg m^{-3}) (Fig. 5),

$$TB = 1.201 + 0.827 \text{ Chl } a \quad (p < 0.01, r = 0.502, n = 68)$$

Bacterial productivity (BP, mg C m^{-3} d^{-1}) was positively significantly correlated with photosynthetic rate (PR, mg C m^{-3} d^{-1}) (Fig. 6),

$$BP = 0.93 + 0.106 \text{ PR} \quad (p < 0.01, r = 0.655, n = 20)$$
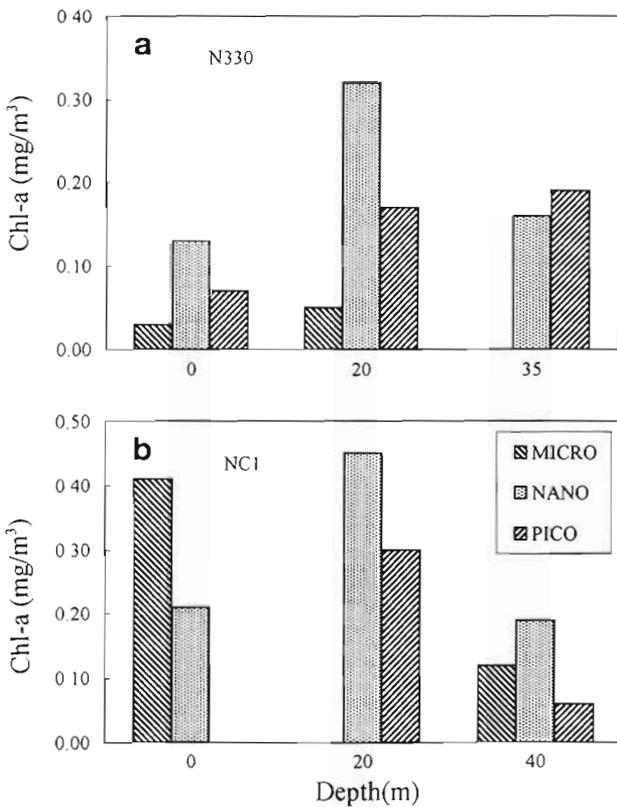

Fig. 3. Vertical distribution of size-fractionated biomass in summer (a) at Stn N330 and (b) at Stn NC1 (see Fig. 2 for abbreviations)
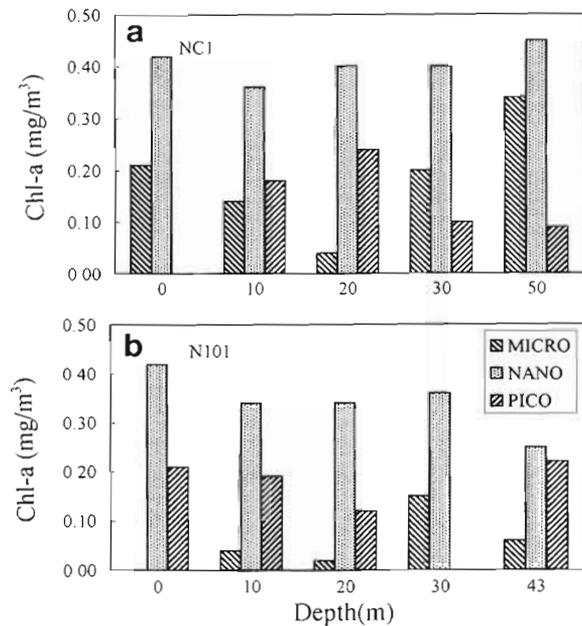

Fig. 4. Vertical distribution of size-fractionated biomass in winter (a) at Stn NC1 and (b) at Stn N101 (see Fig. 2 for abbreviations)
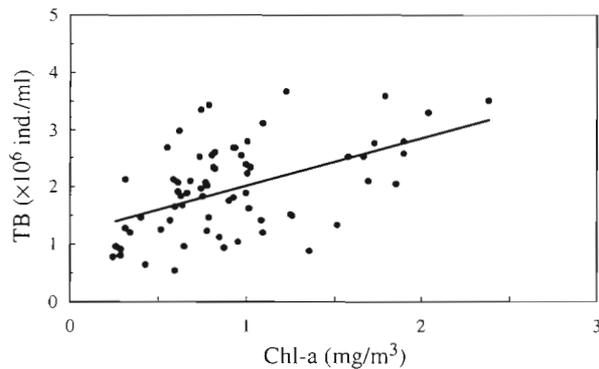
Fig. 5. Relationship between bacterial abundance (TB) and chl *a* biomass (Chl-*a*)

Fig. 7. Relationship between bacterial heterotrophic activity (BHA) and photosynthetic dissolved organic carbon (PDOC)

Therefore, TB and BP coupled very closely with primary processes (phytoplankton biomass and primary productivity), implying that phytoplankton was an important organic carbon source for supporting the growth of bacteria. Bacterial heterotrophic activity (BHA, mg C m^{-3} d^{-1}) positively correlated with PDOC (mg C m^{-3} d^{-1}) (Fig. 7),

$$BHA = 3.395 + 0.186 \, PDOC \quad (r = 0.555, n = 8)$$

implying that photosynthetic product (especially PDOC) could be utilized by bacteria.

DISCUSSION

Factors controlling the size structure of phytoplankton and PDOC

The data in this study showed that phytoplankton size structure had remarkable differences between the the NTS and the STS; picophytoplankton dominated in the STS while nanophytoplankton prevailed in the NTS.

It is known that the size structure of phytoplankton is correlated with latitude (mainly temperature), light
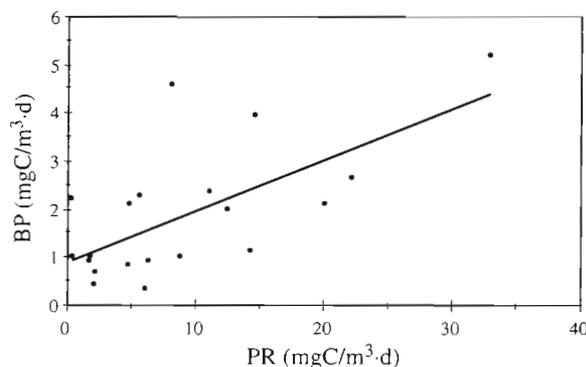

Fig. 6. Relationship between bacterial production (BP) and primary productivity (PR)
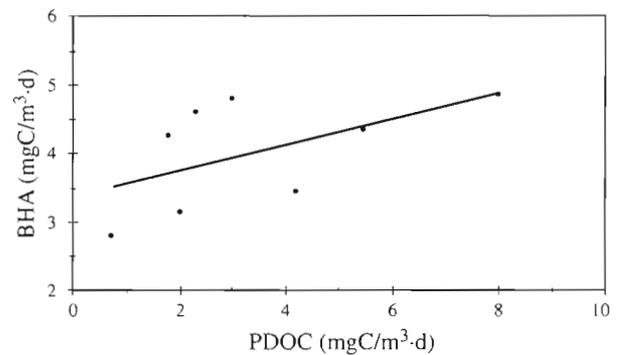
intensity and nutrient level. Murphy & Haugen (1985) concluded that microphytoplankton abundance increased while picophytoplankton decreased as latitude increased. In addition, the nutrient level also affected the size structure of phytoplankton; as we know that the Michelis-Menten constant of phytoplankton depends on cell size, the smaller the cell is, the lower the constant. Thus, picophytoplankton should dominate the phytoplankton community in oligotrophic waters.

Based on the Michaelis-Menten constant (K) measured by Eppley et al. (as cited in Chen & Qian 1992) for microphytoplankton, K of phosphate and nitrate was 0.12 to 0.55 µmol l^{-1} and 0.1 to 6.5 µmol l^{-1}, respectively. The phosphate concentration was smaller than the K of microphytoplankton in both the NTS and the STS in summer (Table 5), so it must limit their growth. The average phosphate concentration in the surface water was only 0.07 µmol l^{-1} in the STS, which may limit the growth of nanophytoplankton, therefore, picophytoplankton predominated the community. Nitrate could not limit the 3 size fractions of phytoplankton because its concentration was higher than the K of nitrate uptake in the study area. Data showed that N/P ratios were higher than the Redfield value (24 for yearly average and 46 for summer average in

Table 5. Nutrient level of surface waters in the Taiwan Strait (µmol l^{-1}) (Wu et al. 1997a,b). NTS: northern Taiwan Strait; STS: southern Taiwan Strait

Location	Nutrients	Summer	Winter
NTS	Phosphate	0.12	0.42
	Nitrate	4.75	9.15
	n	12	11
STS	Phosphate	0.07	0.18
	Nitrate	5.70	2.55
	n	12	7

the surface water), phosphate played a more important role than nitrate in controlling phytoplankton growth in this region (Wu et al. 1997a,b).

It has been well recognized that healthy algal cells released PDOC during photosynthesis, which could support bacterial growth (Wood & Vaalen 1990, Jiao & Wang 1994). The PDOC yield was affected by many external factors such as light intensity, temperature and nutrient status. Among these, light intensity had the most significant effect. The data showed that PDOC percentage increased when being exposed to extreme conditions such as low light intensity (1 % of incident light (I_0) in NC1) (Table 3) (Zlotnik & Bubinsky 1989, Jiao & Wang 1994). Bjørnsen (1988) pointed out that algae could passively release DOC, which is uncorrelated with the photosynthetic process, but positively correlated with biomass and ratio of the surface area versus the volume of alga, therefore, the smaller the alga, the higher the PDOC; more PDOC would flow to the microbial loop if nano- and picophytoplankton dominated the phytoplankton community. Anderson (1988) concluded that the microbial loop played a much more significant role in pico- and nanophytoplankton-dominated communities. However, Baines & Pace (1991) summarized results from an *in situ* investigation and pointed out that the PDOC yield was not mainly affected by algal biomass, especially in coastal areas and estuaries, and that PDOC was positively lineally correlated with primary productivity. PDOC was quite high (24.8 % on average) in the Taiwan Strait (Table 6), which might be due to the dominance of nano- and picophytoplankton in the study area, especially in the STS where picophytoplankton predominated significantly in biomass and productivity.

Factors affecting vertical distribution of picophytoplankton

The result in this study indicated that the high picophytoplankton occurred at the bottom or near the bottom of the euphotic zone. This is consistent with the results reported by Platt et al. (1983) and Li (1994), but it is different from those reported by Happey-Wood (1993), Waterbury et al. (1986) and Joint (1989), who observed that the picophytoplankton maximum was in surface and near-surface waters. Sournia (1982) and Glover et al. (1985) concluded that the picophytoplankton belonged to 'shade flora' and were most abundant at the bottom of the euphotic zone. Based on research of vertical distribution and diurnal variation

Table 6. Percentage of photosynthetic dissolved organic carbon (PDOC) in different study areas

Study Area	Method	PDOC (%)	Source
Coastal Seawaters	–	12	Baines & Pace (1991)
Knebel Vig (Denmark)	12 h	15	Baretta-Bekker et al. (1994)
Baltic Sea	4 h *in situ*	10–20	Larsson & Hagström (1982)
Wood Hole (USA)	10 d	23	Norrman & Zweifel (1995)
Lake in Germany	–	10	Weisse et al. (1990)
Jiaozhou Bay (China)	4 h *in situ*	24.3	Jiao & Wang (1994)
Xiamen Harbour (China)	2 h *in situ*, microalgae	10	Zheng et al. (1992)
Taiwan Strait (China)	3 h *in situ*	24.8	This study

of picophytoplankton, Stockner & Antia (1986) concluded that the contribution of picophytoplankton to total phytoplankton tended to increase with the depth of the euphotic zone, and that picophytoplankton had the ability to absorb blue-green light for phototsynthesis. The present study supported the result that picophytoplankton belonged to 'shade flora'.

Besides light intensity, the vertical distribution of picophytoplankton was also affected by the thermocline. For example, there was a thermocline between 20 and 40 m in Stn NC1 in summer (Fig. 8), and the picophytoplankton biomass above the thermocline was 5 times the biomass beneath it (40 m). This is similar to the result reported by Ning & Vaulot (1991) in the Yangtze River estuary.

Phytoplankton-bacteria interaction in coastal ocean

Nutrient levels can control the community structure of microorganisms. Generally, phytoplankton are the main contributors to living biomass in eutrophic areas,
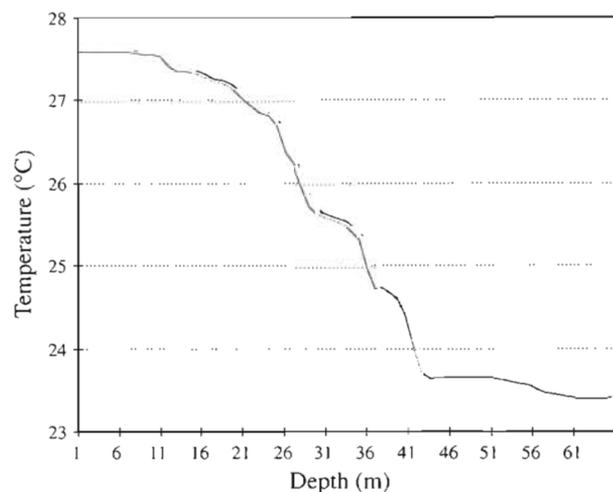

Fig. 8. Profile of temperature at Stn NC1 in summer

but bacteria and zooplankton dominate living biomass in oligotrophic waters (Dorth & Packard 1989). For instance, bacteria contributed 70% of planktonic carbon biomass in the oligotrophic Sargasso Sea (Fuhrman et al. 1989). Phytoplankton contributed about 27% POC, and bacteria only 2.5% in the Taiwan Strait. This was due to the relatively high nutrient levels, which resulted from upwelling (Liang 1997), the coastal current and land inputs in the Strait (Wu et al. 1997a,b); therefore, phytoplankton dominated the living biomass. Bacterial productivity contributed 5 to 52% (22% on average) of primary productivity in the Taiwan Strait, which was double that of the East China Sea and the northeast waters of Taiwan (Liu pers. comm. 1995). If bacterial growth efficiency was 13 to 24% (Linley & Newell 1984), then primary production (organic carbon) in the euphotic zone was almost utilized by bacteria. On the other hand, organic carbon from primary production could cover 60 to 100% bacterial growth, this result was similar to others in coastal oceans (Billen & Fontiguy 1987, Lancelot & Mathot 1987). As bacteria consumed most of the primary organic carbon, there was small output of organic carbon in both vertical and horizontal directions in the Taiwan Strait and shelf of the East China Sea, which was similar to the result of the Atlantic Ocean SEEP-II plan (Biscaye et al. 1994).

The importance of the microbial loop in the Taiwan Strait

The ecological significance of bacteria and protozoa has been recognized. Bacteria have played an important role in aquatic ecosystems since 1980 (Hobbie et al. 1977, Fuhrman & Azam 1980). It was estimated that some 10 to 57% photosynthetic organic carbon was released as a dissolved form (called PDOC) (Larsson & Hagström 1982, Jiao & Wang 1994). PDOC could be utilized by bacteria, and the latter was grazed on protozoa (ciliates and flagellates), which made an energy connection between bacteria and zooplankton; this energy flowing structure (PDOC → bacteria → protozoa → zooplankton) was called the microbial loop (Azam et al. 1983).

In the Taiwan Strait, the significant dominance of pico- and nanophytoplankton, the high PDOC yield and the bacterial productivity suggested that the microbial loop would play an important role in organic carbon transformation in this region. However, the study on the microbial loop had many limits. It is still uncertain whether the microbial loop was a sink or a link in carbon cycling (Ducklow et al. 1986, Sherr et al. 1987). In the Taiwan Strait, data on protozoa (ciliates and flagellates) are needed to estimate their role in organic carbon transformation and size grazing pressure of zooplankton on phytoplankton.

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