Phytoplankton Biomass and Production in Subtropical Hong Kong Waters: Influence of the Pearl River Outflow

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Abstract The size-fractionated phytoplankton biomass and primary production were investigated in four contrasting areas of Hong Kong waters in 2006. Phytoplankton biomass and production varied seasonally in response to the influence of the Pearl River discharge. In the dry season, the phytoplankton biomass and production were low ($<42 \text{ mg chl m}^{-2}$ and $<1.8 \text{ g C m}^{-2} \text{day}^{-1}$) in all four areas, due to low temperatures and dilution and reduced light availability due to strong vertical mixing. In contrast, in the wet season, in the river-impacted western areas, the phytoplankton biomass and production increased greater than five-fold compared to the dry season, especially in summer. In summer, algal biomass was 15-fold higher than

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X. Yuan · L. He LED, South China Sea Institute of Oceanology, CAS, Guangzhou, China in winter, and the mean integrated primary productivity (IPP) was 9 g C m^{-2} day⁻¹ in southern waters due to strong stratification, high temperatures, light availability, and nutrient input from the Pearl River estuary. However, in the highly flushed western waters, chl a and IPP were lower (<30 mg m⁻² and 4 g C m⁻² day⁻¹, respectively) due to dilution. The maximal algal biomass and primary production occurred in southern waters with strong stratification and less flushing. Spring blooms (>10 μ g chlaL⁻¹) rarely occurred despite the high chl-specific photosynthetic rate (mostly >10 µg C µg chl a^{-1} day⁻¹) as the accumulation of algal biomass was restricted by active physical processes (e.g., strong vertical mixing and freshwater dilution). Phytoplankton biomass and production were mostly dominated by the >5-µm size fraction all year except in eastern waters during spring and mostly composed of fast-growing chain-forming diatoms. In the stratified southern waters in summer, the largest algal blooms occurred in part due to high nutrient inputs from the Pearl River estuary.

Keywords Phytoplankton biomass · Primary production · Pearl River discharge · Stratification · Vertical mixing · Hong Kong

Introduction

The increased input of nutrients from riverine outflow and domestic sewage effluent into coastal waters stimulates primary production and nuisance algal blooms, which results in hypoxia or anoxia in the bottom water (Cooper and Brush 1991; NRC 2000). Substantial attention has been paid to phytoplankton dynamics in temperate systems such as Chesapeake Bay (Harding 1994; Kemp et al. 2005). However, comparatively few studies have been conducted in subtropical estuaries (Murrell et al. 2007). Coastal environments vary considerably in their physical and hydrographic properties, such as tidal stirring, depth, and freshwater runoff, which makes phytoplankton dynamics complex (Cloern 1996). Freshwater inputs may produce two distinctly different effects on phytoplankton growth: promote an algal bloom by stratifying the water column and retain phytoplankton cells in the euphotic zone (Simpson et al. 1991), or reduce phytoplankton growth by dilution during advection out of the estuary (Delesalle and Sournia 1992).

Hong Kong subtropical waters are located on the south coast of China, facing the northwestern part of the South China Sea (SCS) and lying to the southeast of the Pearl River estuary (PRE). As a result of the influence of the PRE discharge, local Hong Kong sewage effluent, and coastal/ shelf water from the SCS, there are several contrasting environments in Hong Kong waters: (1) western watersclose to the PRE; (2) eastern waters—far away from the PRE; (3) at Stonecutters Island and Victoria Harbor (SCI-VH)local sewage discharge; and (4) southern waters-a transition zone which receives water from the PRE, sewage effluent from Hong Kong, and oceanic seawater from the SCS. The seasonal variations in monsoon winds, rainfall, and temperature further complicate the hydrodynamics in these regions with different topography and bathymetry. Hong Kong waters receive high inputs of nutrients from sewage effluent all year, while the Pearl River discharge occurs mainly in summer (Xu et al. 2008; Ho et al. 2008). Consequently, algal blooms mainly occur in summer during the period of the maximal Pearl River discharge (HKEPD 2001; Yin et al. 2001). Little is known about the effect of the Pearl River outflow on primary productivity and phytoplankton biomass in eutrophic Hong Kong waters.

The present study investigated the seasonal dynamics of size-fractionated phytoplankton biomass and primary production in Hong Kong waters to evaluate the influence of the Pearl River outflow on phytoplankton growth. This is the first study to examine the contribution of different phytoplankton size classes to chl *a* biomass and primary production in Hong Kong waters in relation to anthropogenic nutrient inputs mainly from the Pearl River.

Materials and Methods

Study Sites and Sampling

Twelve stations were chosen that were the same as the monitoring stations of the Environmental Protection Department (EPD) of Hong Kong (Fig. 1). The equivalent EPD station number is given in Table 1, and the longitude and latitude for each station are given in HKEPD (2001). Based on nutrient sources and salinity, the 12 stations represent four main regions: western waters (S1-S2), which are close to the PRE; SCI-VH region (S3-S6), which is close to the sewage discharge outfall sites near SCI and VH; eastern waters (S7-S8), which are close to Mirs Bay and are generally dominated by high salinity coastal/shelf seawater; and southern waters (S9-S12), which are representative of the transition region between the influence of the PRE from the west, local sewage effluent from the north, and coastal/shelf seawater from the south next to the northern SCS.

Four cruises in winter (February), spring (April), summer (July), and fall (November) were conducted in 2006. Vertical profiles of salinity, temperature, dissolved oxygen, and turbidity were measured by a YSI 6600 submersible probe (YSI Incorporated, USA). In this study, the stratification index (SI) was calculated as follows:

$$SI = \frac{\Delta \sigma_t}{h} \tag{1}$$

where $\Delta \sigma_t$ (kg m⁻³) is the difference in the seawater density (σ_t) between surface and bottom densities and *h* is the depth (meter) of the water column. Seawater density (σ_t) is calculated based on Fofonoff and Millard (1983) using the monthly average salinity and temperature. The depth of the upper mixed layer was determined as the first depth where the change in $\Delta \sigma_t$ was $\geq 0.2 \text{ m}^{-1}$ (Therriault and Levasseur 1985).

Photosynthetic available radiation (PAR) in the water column was measured using a Li-Cor underwater spherical quantum sensor (LI 193SA, USA), while the solar radiation in the air was measured using a LI-Cor pyranometer (LI-200SZ, USA). The photic zone (1% of light depth) was estimated from light meter measurements of PAR in the water column.

The mean light intensity in the mixed layer, I_m , was estimated using the following equation (Riley 1957):

$$I_{\rm m} = \frac{I_0 \left(1 - \mathrm{e}^{-kz}\right)}{kz} \tag{2}$$

where I_0 (W h m⁻²)=mean daily solar radiation at the surface water (average of 7 days prior to sampling date), k= coefficient of extinction (K=1.44/Secchi depth, Holmes 1970), and z=the mixed layer depth. I_0 was obtained by multiplying the mean daily solar radiation in the surface air by 70% using average of 7 days prior to sampling date from monitoring data from the Hong Kong Observatory (http://www.weather.gov.hk/cis/). The conversion factor of 70% from the light intensity in the surface air to that under the surface of the water was estimated from our in situ light measurements (K. Yin, unpubl data).

Water samples were taken at three depths: surface (1 m below the surface), middle (4 m below the surface), and bottom (1 m above the bottom) using a 10-L polyvinyl

Fig. 1 Twelve sampling stations in Hong Kong waters. *SCI* Stonecutters Island, *VH* Victoria Harbor. The four contrasting areas are western waters (*S1* and *S2*), SCI-VH (*S3*, *S4*, *S5*, and *S6*), southern waters (*S9*, *S10*, *S11*, and *S12*), and eastern waters (*S7* and *S8*)



chloride Go-flo sampler (General Oceanics, USA). At S9 where the water depth was only 6 m, only surface and bottom samples were taken. The sample from each depth was aliquoted to small acid-washed plastic/glass bottles for measurement of the following parameters.

Inorganic Nutrients

Samples for nutrient determinations were taken with a 60-ml syringe and filtered through a pre-combusted 0.7- μ m GF/F filter (Whatman Inc., USA) mounted in a Swinnex filter holder (Swinnex, USA) into 30-ml Nalgene bottles. All plastic wares were pre-cleaned with 10% HCl. The filtered water samples were placed in a deep freezer at -20°C and frozen immediately. Nutrients including ammonium (NH₄), nitrate (NO₃), nitrite (NO₂), phosphate (PO₄), and silicate (SiO₄) were analyzed in the shore laboratory within 2 weeks, using a Skalar San Nutrient Analyzer, and following JGOFS Protocols (Knap et al. 1996).

Size-Fractionated Chlorophyll a

Samples (270 ml) were successively filtered through a 5- μ m polycarbonate filter (Millipore, USA) and then a 0.7- μ m GF/F filter, using vacuum pressure <400 mm Hg. The filters were kept frozen at -20°C. Later, they were extracted in 90% acetone in the dark at 4°C for 24 h and then measured in a pre-calibrated fluorometer (Turner Designs) in order to determine in vitro chl *a* concentrations (Parsons et al. 1984).

Size-Fractionated Primary Productivity

Seawater samples for the primary productivity measurements were pre-screened through a 200- μ m mesh, and then a 50-ml sample was transferred to acid-washed glass tubes to which 0.4–2 μ Ci (14.8–74 kBq) of ¹⁴C-labelled sodium bicarbonate (NaH¹⁴CO₃) was added. Duplicate tubes were wrapped with different layers of screening providing light fields corresponding to approximately 100%, 55%, 30%, 10%, and

Station num	ber	Water depth (m)	Winter				Spring				Summer				Fall			
This study	EPD		PZ _{dep}	ы	SI	$I_{ m m}$	PZ _{dep}	ы	SI	I_{m}	$\mathrm{PZ}_{\mathrm{dep}}$	ы	SI	$I_{ m m}$	$\mathrm{PZ}_{\mathrm{dep}}$	ы	SI	I_{m}
SI	NM2	11	9	11	0.007	143	8	5	0.169	858	5	$\overline{\vee}$	1.516	1888	~	11	0.12	66
S2	WM4	29	8	29	0.002	44	12	29	0.037	171	6	1	0.476	1981	10	29	0.00	31
S3	WM3	20	7	20	0.001	74	10	9	0.054	709	12	1	0.515	2016	10	20	0.01	51
$\mathbf{S4}$	VM7	11	6	11	0.005	134	6	٢	0.028	741	11	1	0.633	2004	8	11	0.00	93
S5	VM5	13	13	13	0.008	175	8	13	0.008	379	8	3	0.608	1902	7	13	0.01	100
S6	VM2	13	13	13	0.000	159	7	13	0.014	412	6	Э	0.569	1227	10	13	0.00	91
S7	EM3	24	24	20	0.012	108	21	24	0.011	409	11	7	0.185	1580	15	24	0.00	61
S8	MM8	30	I	I	I	Ι	14	30	0.000	384	13	7	0.136	1765	15	30	0.01	69
S9	SM10	9	4	9	0.008	258	5	4	0.040	848	5	1	1.010	1860	4	9	0.00	179
S10	SM9	6	6	6	0.000	233	7	б	0.079	1202	8	1	0.989	1955	6	8	0.00	162
S11	WM1	33	10	33	0.005	62	13	33	0.060	209	6	7	0.351	1578	12	33	0.00	37
S12	SM6	15	15	15	0.009	178	15	б	0.113	1509	7	1	0.795	2076	8	11	0.00	150

1% of surface irradiance, and hence, this provided a simulated ambient vertical light profile. Since the water column in Hong Kong waters is very shallow (10-20 m), a surface water sample (1 m below the surface) was used for the 100% and 55% light incubation; a middle water sample (4 m below the surface) was used for 30% and 10% light incubation, while a near-bottom water sample (1 m above seabed) was used for the 1% light incubation. In situ ¹⁴C incubation experiments were conducted at all five light levels at S1, S3, S5, S7, S10, and S12, while only one light level (100%) was conducted at the remaining six stations (S2, S4, S6, S8, S9, and S11) for a general comparison of surface primary production at 12 diverse stations in Hong Kong waters. Samples were incubated for 4 h between 10:00 to 14:00 on-deck in running surface seawater. The incubation was terminated after 4 h by filtering sequentially through a cascade filtering apparatus with a 5-µm PC filter (i.e., >5 µm size fraction) and then through a GF/F filter (i.e., <5 µm size fraction). Filters were put into a scintillation vial and stored in the dark at -20°C. HCl (0.25 ml, 0.1 N) was added to the scintillation vials and left overnight to remove the inorganic NaH14CO3. Three milliliters of Optiphase Hisafe II Scintillation fluid was added to the samples and left for another 24 h in the scintillation cocktail. Counting was carried out using a liquid scintillation counter (LKB Rack Beta), and counts were quenched using the external standard channels ratio method. NaH¹⁴CO₃ was added to duplicate surface samples and immediately filtered sequentially through a 5-µm PC filter and then through a GF/F filter to provide a blank correction value that was subtracted from the light bottle uptake values. Subsamples of the NaH¹⁴CO₃ working solution were assayed before and after each cruise to determine the isotopic activity added. Primary productivity at each depth was calculated according to Jassby and Platt (1976), as described in Gong et al. (2003). Daily primary production was estimated by multiplying by the ratio of the whole day's irradiance to the irradiance during the incubation period, in order to minimize the bias caused by differences in irradiance for the incubations conducted at the different time of the day. Finally, light depths were determined to give 100%, 55%, 30%, 10%, and 1% of the surface radiation. The integrated primary production (IPP) was calculated by averaging the measured production between two depths and multiplying by the depth interval (Ichimura et al. 1980).

Statistical Analyses

All percentage data were subject to angular and log transformations, respectively, before statistical analysis (Zar 1999). Parametric correlation methods and the Pearson test in the software package Statistical Package for the Social Sciences for Windows were used to obtain a correlation coefficient and the significance of the correlation between

the contribution percentage of the $>5-\mu m$ fractions to total primary production and photosynthetic active radiation.

Step-wise regression analysis was performed individually for each region to assess the relative impact of different variables, with chl *a* concentration as the dependent variable and temperature, turbidity, Secchi disk depth, SI, chl-specific photosynthesis rate (Pchl), and mean water column PAR averaged for the previous 7 days.

Results

Physical Parameters

Daily solar irradiance varied seasonally. Daily solar irradiance at the surface air was on average 17.3 MJ m⁻² in winter and 24.6 MJ m⁻² in summer during the cruise in 2006, higher than the respective normal level (11.2 MJ m⁻² in February and 19.2 MJ m⁻² in July). In spring, daily solar irradiance was on average 12.2 MJ m⁻², comparable to the normal level (13.1 MJ m⁻² in April). In fall, daily solar irradiance was on average 6.5 MJ m⁻² during the cruise, 54% lower than the normal level (14.0 MJ m⁻² in November).

Temperature at the surface exhibited a clear seasonal variation in the four regions, with the lowest (approximately 18°C) in winter and the highest (approximately 27°C) in summer (Fig. 2). Surface salinity fluctuated seasonally, with the lowest at all regions in summer when strong stratification occurred. In contrast, strong vertical mixing occurred in all regions during the dry season and SCI-VH and eastern

waters in spring (Fig. 2). Turbidity at the surface was the lowest (close to zero) in summer and the highest (up to 10) in winter. The Secchi disk depth fluctuated between 1.5 and 2.2 m in all areas, except in eastern waters where the Secchi disk depth was >2 m and a maximum (4.8 m) in spring.

Nutrients

A clear temporal and spatial variation in NO₃ and SiO₄ concentrations was observed in all seasons in response to the PRE discharge. Their concentrations were relatively low (<12 μ M NO₃ and <16 μ M SiO₄) in all regions in the dry season when there was little input from the Pearl River discharge. In the summer wet season, NO₃ and SiO₄ concentrations were the highest (up to 60 and 75 μ M, respectively) in western waters, intermediate in southern and SCI-VH waters and seven to 15 times higher in western than eastern waters (Fig. 3).

Anthropogenic NH₄ and PO₄ inputs were mainly from local sewage effluent (SCI-VH) and, thus, they shared similar spatial and seasonal variations (Fig. 3). In general, NH₄ concentrations were high (approximately 10 μ M) in the western waters (except spring) and the SCI-VH all year (except winter), and always low (<5 μ M) in eastern waters. PO₄ concentrations were near or >0.5 μ M in all regions in fall and winter and approximately 1 μ M in the SCI-VH region in spring and summer and in western waters in summer. They were near or <0.5 μ M in western waters in spring and in eastern and southern waters in summer (Fig. 3).



Fig. 2 Seasonal changes in surface, middle, and bottom water temperature, salinity, turbidity, and Secchi depth at 12 stations in four regions in Hong Kong waters in 2006. SCI-VH Stonecutters Island and Victoria Harbor. Error bars= ± 1 SD and n=2 to 4



Fig. 3 Seasonal changes in surface, middle, and bottom inorganic nutrients including nitrate (NO_3) , silicate (SiO_4) , ammonium (NH_4) , and phosphate (PO_4) in four regions in Hong Kong waters in 2006.

SCI-VH Stonecutters Island and Victoria Harbor. Note the different scale for NO₃, SiO₄, and NH₄. Error bars= ± 1 SD and n=2 to 4

Surface Phytoplankton Biomass and Primary Production

There was a clear seasonal variation in the surface chl *a* biomass and primary productivity, with the highest (6–34 mg m⁻³ and 0.6–2.7 g C m⁻³ day⁻¹, respectively) in summer, intermediate (1–6 mg m⁻³ and 0.1–0.5 g C m⁻³ day⁻¹, respectively) in spring and fall, and the lowest (<1–5 mg m⁻³ and <0.10 g C m⁻³ day⁻¹, respectively) in winter (Fig. 4).

There was little spatial variability in fall and winter since surface chl *a* varied over a small range (mostly 2–4 and 0.7–1.6 mg m⁻³, respectively; Fig. 4). In the river-impacted areas such as western and southern waters during spring, the surface chl *a* was higher (>2 mg m⁻³). In southern waters (Stn S12) in summer, the surface chl *a* was highest (up to 70 mg m⁻³).

Integrated Phytoplankton Biomass and Primary Production

The integrated chl *a* (Ichl *a*) and primary production (IPP) exhibited a similar seasonal and spatial variation as surface phytoplankton production. A seasonal comparison revealed that Ichl *a* and IPP were the lowest (<20 mg m⁻² and 0.2–1.2 g C m⁻² day⁻¹) in winter, moderate (18–93 mg m⁻² and 0.7–3.0 g C m⁻² day⁻¹) in spring and fall, and the highest (up to 560 mg m⁻² and 25 g C m⁻² day⁻¹) in summer (Fig. 5).

For the river-impacted areas such as western and southern waters in spring, Ichl *a* and IPP (approximately 60 mg m⁻² and 2.5–3.0 g C m⁻²day⁻¹, respectively) were



Fig. 4 Seasonal changes in size-fractionated chl *a* and primary productivity (size fractions >5 and <5 μ m) in the surface layer in four regions in Hong Kong waters in 2006. *SCI-VH* Stonecutters Island and Victoria Harbor. The *number above the bars* is the percent contribution of the size fraction >5 μ m. Error bars=±1 SD and *n*=2 to 4



Fig. 5 Seasonal changes in size-fractionated (>5 and <5 μ m) integrated chl *a* (Ichl *a*) and integrated primary production (IPP) in four regions in 2006. *SCI-VH* Stonecutters Island and Victoria Harbor. The *number above the bars* is the percent contribution of the size fraction >5 μ m. Error bars=±1 SD and *n*=2 to 4

more than twofold higher, compared to the other regions (approximately 20 mg m⁻² and <1.2 g C m⁻²day⁻¹, respectively; Fig. 5). In southern waters in summer, Ichl *a* and IPP were the highest (up to 1,010 mg m⁻² and 40 g C m⁻²day⁻¹ at S12, respectively). In contrast, in western waters, Ichl *a* and IPP were relatively low (28 mg m⁻² and <1.2 g C m⁻²day⁻¹, respectively; Fig. 5). The percent contribution of the >5-µm size fraction to total phytoplankton biomass and production was >50% all year, except for spring when the <5-µm size fraction dominated the algal biomass and production (<50%) in eastern waters (Figs. 4 and 5).

Chl-specific Photosynthetic Rate

The mean chl-specific photosynthetic rate was low (generally <8 μ g C μ g chl a^{-1} day⁻¹) in all regions in the dry season, except for (approximately 12 μ g C μ g chl a^{-1} day⁻¹) SCI-VH in fall and eastern waters in winter and relatively high (10–14 μ g C μ g chl a^{-1} day⁻¹) in the wet season in all regions, except in western waters (<6 μ g C μ g chl a^{-1} day⁻¹; Fig. 6). In the dry season, the <5- μ m fraction had a higher chl-specific photosynthetic rate. In contrast, in the wet season, the >5- μ m fraction had higher chl-specific photosynthetic rate (Fig. 6).

Regression Analysis

The step-wise regression analysis showed that the SI explained 71%, 80%, and 54% of the variability in the chl a concentration in SCI-VH, eastern, and southern waters, respectively (Table 2). In contrast, chlorophyll-specific primary productivity (Pchl) explained 70% of variability in the chl a concentration in western waters (Table 2).

Discussion

Effect of the Pearl River Discharge on Phytoplankton Biomass and Production

Temporal Variability

Hong Kong waters are subjected to seasonal exchange between the Pearl River discharge in the wet season and coastal/oceanic water in the dry season induced by the seasonal alteration between southwest monsoon wind in summer and northeast monsoon wind in winter (Yin 2002; Xu et al. 2008). Biological processes are strongly coupled with physical processes (Harrison et al. 2008). The clear seasonal variability in the



Fig. 6 The seasonal mean chl-specific photosynthetic rate for all light levels (100%, 55%, 30%, 10%, and 1% surface irradiance) for two phytoplankton size fractions in four regions. Error bars= ± 1 SD and n=1 to 2

 Table 2 Step-wise regression analysis performed for each region separately

Variables	r^2	р
Western waters ^a		
Pchl	0.70	0.006
SCI-VH ^b		
SI	0.71	0.000
Im	0.84	0.003
Pchl	0.89	0.029
Eastern waters ^c		
SI	0.80	0.004
Turb	0.93	0.033
SDD	1.00	0.000
Southern waters ^d		
SI	0.54	0.001

Chlorophyll a concentration is the dependent variable

T temperature (°C), *Turb* turbidity, *SDD* Secchi disk depth (meter), *Pchl* chl-specific photosynthetic rate (μ g C (μ g chl)⁻¹ day⁻¹), *SI* stratification index (kg m⁻⁴), *I*_m mean daily water column irradiance (W h m⁻² day⁻¹) for an average of 7 days prior to the sampling date ^a *T*, Turb, SDD, SI, and *I*_m did not contribute significantly to the ability to predict chl

 $^{\rm b}$ T, Turb, and SDD did not contribute significantly to the ability to predict chl

^c *T*, SI, and $I_{\rm m}$ did not contribute significantly to the ability to predict chl ^d *T*, Turb, SDD, Pchl, and $I_{\rm m}$ did not contribute significantly to the ability to predict chl

chl *a* concentration and primary production in Hong Kong waters appeared to be related to seasonal exchange between the Pearl River discharge and coastal/oceanic water. Step-wise regression analysis suggested that seasonal variability in the chl *a* concentration in Hong Kong waters, except for western waters, was primarily attributed to the degree of stratification in the water column.

In the dry season, with the domination of the coastal/ oceanic waters, Hong Kong waters are characterized by strong vertical mixing, as indicated by the low SI. Strong vertical mixing not only diluted the phytoplankton biomass by mixing the phytoplankton cells throughout the water column but the vertical mixing also resulted in light limitation by transporting the algal cells out of the euphotic zone. In the dry season, low phytoplankton biomass and production were primarily attributed to strong vertical mixing. The same results were observed in tropical Gulf of Carpentaria in winter (Burford and Rothlisberg 1999). During winter, primary production in this study was comparable to that in Gulf of Carpentaria. In winter, the temperature was much lower than the optimal temperature, which might be responsible for the two to threefold lower chl a concentrations than fall. The relatively low temperature (18°C) contributed to the low chl-specific photosynthetic rate in winter since incident light during the incubation period was high and similar to that in spring. Similarly, temperature regulation of primary production has been reported in subtropical Moreton Bay in winter (O'Donohue and Dennison 1997). Previous studies have shown that photosynthetic carbon assimilation is enzymatically controlled and is a temperature-dependent process Falkowski and Raven (1997). During this period, low primary production was likely the result of low chl *a* concentrations, temperature, and light intensity.

In contrast, in fall, temperature was not the limiting factor for phytoplankton growth since temperature was comparable to the optimal temperature (23–27°C) for the growth of several dominant phytoplankton species in Hong Kong waters (Ho 2007). In fall, the low chl-specific photosynthetic rate was more likely attributed to the low light availability.

In contrast, in the wet season, the input of the Pearl River outflow stratified the water column and reduced the mixed layer depth. In summer, during the period of the maximal Pearl River discharge, the mixed layer generally decreased to <3 m which is much shallower than the photic zones in all regions (Table 1). Strong stratification also helps to maintain the phytoplankton cells in the euphotic zone and increase the light intensity. Therefore, the Pearl River inputs triggered phytoplankton growth most likely by increasing the light intensity and retaining the algal cells in the euphotic zone and not by supplying large amounts of nutrients since nutrients were not limiting in the river-impacted western waters.

The maximal chl a concentrations always occurred in summer during the period of the strongest stratification in all regions except for western waters. Chl a concentrations increased dramatically (up to 15-fold) from winter to summer. In summer, the combination of strong stratification, high temperature, and nutrient inputs results in higher primary production, compared to other coastal areas (Table 3). For example, in summer, phytoplankton biomass and production in Hong Kong waters were nearly tenfold higher than tropical Gulf of Carpentaria (Burford and Rothlisberg 1999) due to high nutrient inputs. High temperature led to higher primary production and Chl-specific photosynthetic rate $(2-25 \text{ g C m}^{-2} \text{day}^{-1} \text{ and }$ approximately 10 µg µg chl a^{-1} day⁻¹) than for temperate Chesapeake Bay $(0.8-2.4 \text{ g C m}^{-2} \text{day}^{-1} \text{ and } 4.2-$ 8.2 µg µg chl a^{-1} day⁻¹) which is also subjected to the high nutrient loading (Table 3). Our Chl-specific photosynthetic rates (10–14 μ g μ g chl a^{-1} day⁻¹) in summer were comparable to values $(8.9\pm3.8 \ \mu g \ \mu g \ chl a^{-1} day^{-1})$ observed for the subtropical Mississippi River plume (Lohrenz et al. 1992). Bioassays have also shown that net phytoplankton growth rate was up to 2.4 day^{-1} or more than 3 doublings day^{-1} in the Pearl River river-impacted areas

Location	IPP $(gCm^{-2}day^{-1})$	Period	Citations
Hong Kong	Mean 9 (range, 1.2-18.5)	July	This study
Pearl River estuary	3-4.3	July	Yin et al. (2004)
Japan (Amur Bay)	2.5-4.0	July	Zvalinskii et al. (2005)
Mississippi River	<1.5–11	July-August	Lohrenz et al. (1999)
Mississippi River	0.3–3.8	January–December	Lohrenz et al. (1997)
Amazon River	1.09-8.2	March	Smith and DeMaster (1996)
Chesapeake Bay	1.7–2.5	July–August	Harding et al. (2002)
Gulf of Carpentaria	0.96	December-February	Burford and Rothlisberg (1999)

 Table 3
 Comparison of integrated primary production (IPP) between Hong Kong waters and other coastal waters with high nutrient loading

during summer (Xu 2007). These results suggest that Hong Kong waters are very productive during summer due to the input of the Pearl River discharge.

The temperature was optimal for the algal growth in other seasons. The chl-specific photosynthetic rates in spring were comparable to summer. The high chl-specific photosynthetic rate implied that temperature, light, and nutrients were optimal for high phytoplankton growth at most stations provided that vertical mixing and horizontal dilution are eliminated as occurred in the bottle incubations. However, the chl a concentrations in spring were much low than summer. The contrast between high chl a-specific photosynthetic rates observed in the incubation experiments and the low in situ chl a concentrations in spring suggested that the processes (e.g., dilution, mesozooplankton grazing, and vertical mixing) that were excluded in the incubation experiments were the primary factors that were responsible for the relatively low in situ chl a concentrations. This suggestion was supported by a series of simultaneous nutrient enrichment bioassays, which showed that the ambient nutrients could support algal growth for a few days, and the algal biomass increased several times when dilution and vertical mixing were reduced in the bottle incubations (Xu et al. 2009).

In spring, Hong Kong waters were dominated by weak stratification (e.g., western and southern waters) or strong vertical mixing (e.g., SCI-VH), as indicated by the low SI. Tidal currents and mixing also exerted an important impact on the stability of the water column, and the weak stratification was easily destroyed, especially in VH that is a narrow channel (Fig. 1). Chen et al. (2009) found that the microzooplankton grazing rate was low (approximately 0.7 day^{-1}) relative to growth rate (1.8 day^{-1}) in April, while grazing rate was up to 1.2 day^{-1} in May, comparable to phytoplankton growth rate. Hence, active physical processes were responsible for low phytoplankton biomass in early spring. However, grazing may be one of the factors that are responsible for the lack of the algal bloom in late spring in Hong Kong waters that routinely occurs in temperate waters.

In our study, the effect of microzooplankton grazing on algal biomass and primary production was not examined since only grazers >200 µm were excluded before the incubations. A previous study showed that there is low microzooplankton biomass, and grazing rates are 0.5 and 0.8 day^{-1} in the river-impacted areas in Hong Kong waters in June and July during the period of the maximum Pearl River discharge, respectively, which contributes approximately 30% of the phytoplankton production (Chen et al. 2009). In February (winter), microzooplankton grazing rate is approximately 0.2 day⁻¹, accounting for <20% of phytoplankton production. During this period, microzooplankton grazing makes a smaller contribution (<20%) to algal production in Hong Kong waters, relative to the dilution and light limitation induced by strong vertical mixing (Chen et al. 2009), since the decrease in temperature results in a sharper decrease in the herbivorous protists than that of phototrophic protists (Rose and Caron 2007).

Spatial Variability

There were no apparent variations in the phytoplankton biomass and primary productivity in the dry seasons because of the strong vertical mixing in all regions. By comparison, in the wet season, spatial variability was obvious in response to the influence of the Pearl River discharge. In spring, phytoplankton biomass and primary production in the river-impacted areas (e.g., western and southern waters) was greater than twofold higher than other areas with little/no influence from the Pearl River discharge. A good correlation between salinity and chl a concentrations at the surface (Fig. 7) suggested that an increase in the phytoplankton standing stock along the east to west transect was a result of stratification caused by the invasion of the Pearl River outflow. This observation was in agreement with the result obtained from the step-wise regression analysis.

In summer, the phytoplankton standing stock at the surface also varied spatially in response to different hydrodynamics. In western waters that are strongly influenced by the Pearl River discharge, the high freshwater input increases the horizontal flushing and reduce the residence time, despite



Fig. 7 Chl a versus salinity at the surface along the west to east transect (S1 to S8) in spring. The correlation coefficient, r, is given

strong stratification. Furthermore, the movement of water through the narrow channel (Ma Wan Channel, Fig. 1) in the western waters enhances the flushing effect (Lee et al. 2006). As a result, the phytoplankton biomass was diluted and was lower than other regions. This flushing effect on algal biomass was similar to that in the Hudson River estuary (Howarth et al. 2000).

In contrast, southern waters are less turbid and flushed more than western waters but more stratified than the SCI-VH region and eastern waters (Lee et al. 2006), which favors the phytoplankton growth and accumulation of phytoplankton cells. Consequently, southern waters are the most productive region in Hong Kong waters, as indicated by the high Ichl a and IPP. In addition, the Pearl River discharge might transport phytoplankton into southern waters and partially contribute to the high algal biomass in southern waters. An unusually large summer bloom (up to 73 μ g chl L⁻¹) was observed in this region (Stn S12), accompanied by a drawdown of PO_4 to limiting concentrations (Xu et al. 2009). The frontal region of the plume has also been found to have high chl a concentrations relative to inshore and offshore waters in other coastal waters such as Chesapeake Bay (Breitburg 1990; Harding 1994) and the Mississippi River plume (Grimes and Finucane 1991).

Dominance of Large Diatoms in Hong Kong Waters

Several field studies have demonstrated that vertically stratified oligotrophic waters are characterized by a low biomass of small and often motile phytoplankton, while eutrophic, turbulent, and partially mixed water columns are dominated by a high biomass of large cells (e.g., diatoms; Malone 1980; Legendre 1981; Cushing 1989; Trembly and Legendre 1994). In Hong Kong waters, the chl *a* biomass and primary productivity in both the surface layer and water column were mostly dominated by the $>5-\mu m$ size fraction, and occasionally by the $<5-\mu m$ fraction, mainly in eastern waters in spring (Figs. 4 and 5). Fast-growing chain-forming

diatoms such as *Skeletonema costatum*, *Chaetoceros curvisetus*, *Thalassiosira* sp., *Pseudo-nitzschia delicatissima* and *Pseudo-nitzschia pungens*, and dinoflagellates such as *Scrippsiella trochoidea* are the most common phytoplankton species in Hong Kong waters (Ho 2007; Xu et al. 2009). Therefore, diatoms are dominant in Hong Kong waters and in agreement with previous studies in other eutrophic and turbulent coastal waters (Trembly and Legendre 1994).

In Hong Kong waters, the strong vertical mixing in fall and winter and moderate mixing in spring can help these large diatoms remain suspended in the upper water column. The high nutrient concentrations in Hong Kong waters (except eastern waters in spring) might also be beneficial to fast-growing diatoms, since their growth rates are higher than small phytoplankton when nutrient concentrations are high (Furnas 1991; Jochem 2003).

It has been reported that large phytoplankton have higher chl a-specific photosynthetic rates than small phytoplankton (Cermeño et al. 2005). However, our results indicated that the chl a-specific photosynthetic rates varied seasonally with low rates in fall and winter due to relatively low temperatures and/or light availability and high rates in spring and summer due to high temperatures and light availability. Furthermore, during fall and winter, the chl a-specific photosynthetic rate for the small size fraction ($<5 \mu m$) is higher than the large size fraction (>5 μ m) at all stations. The same results were obtained in other coastal and oceanic waters (Howard and Joint 1989; Iriarte and Purdie 1994). This was likely due to the physiological advantages of a higher efficiency of photon absorption and nutrient uptake for the small-sized phytoplankton under low light and nutrient conditions (Raven 1986). Consequently, there was a higher contribution of the small size fraction to chl a concentrations in fall and winter relative to spring and summer. Large phytoplankton were the main contributor to total chl a and primary production in the fall and winter, possibly due to the relatively high light levels in subtropical Hong Kong waters.

Conclusions

This is the first study to measure primary productivity in Hong Kong waters and to examine the contribution of different phytoplankton size classes to chl *a* biomass and primary production. The Pearl River discharge clearly increased phytoplankton biomass and production in Hong Kong waters. In the dry season when there was little or no influence of the Pearl River discharge, phytoplankton biomass and production was lower since strong vertical mixing diluted the algal cells, and the mixing to depth resulted in light limitation. In winter, the lowest Ichl *a* and IPP occurred due to relatively low temperatures (18°C). In contrast, in the wet season, in the river-impacted areas, the phytoplankton biomass and production increased five-fold or more, especially in summer. In the summer wet season, phytoplankton production reached a maximum, due to strong thermohaline stratification, high light and temperature, and nutrient input from the PRE. In particular, large algal blooms formed in southern waters due strong stratification, and less flushing and turbulence. The mean IPP in July was 9 g C m⁻²day⁻¹ which was higher than many eutrophic coastal waters in Asia and comparable to that in the Mississippi and Amazon Rivers.

Hong Kong subtropical waters are generally shallow, and solar radiation is relatively high. Our results revealed that phytoplankton biomass and production in Hong Kong waters was mostly dominated (50–70%) by large phytoplankton (mainly diatoms) in all seasons, due to high nutrient loading from the PRE and overall relatively high light conditions in Hong Kong which favors fast-growing large diatoms. Furthermore, the shallow water column in Hong Kong waters can easily be mixed by winds and tidal currents, particularly in winter, spring, and fall. Therefore, large diatoms are kept suspended in the water column, and this may partially explain their dominance in eutrophic, turbulent ecosystems in subtropical coastal waters.

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