

# Comparative analysis of bacterioplankton and phytoplankton in three ecological provinces of the northern South China Sea

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**ABSTRACT:** The association between heterotrophic bacterioplankton and phytoplankton was examined in the northern region of the South China Sea where 3 marine biogeochemical provinces adjoin. The relationship between bacterial abundance and total chlorophyll *a* concentration was significant in the oceanic Archipelagic Deep Basin Province and in the China Sea Coastal Province, but not so in the Beibu Gulf (Sunda-Arafura Shelves Province). The importance of different phytoplankton groups (netplankton, nanoplankton and picoplankton, *Synechococcus* spp., *Prochlorococcus* spp. and pico-eukaryotes) to bacteria was examined by multiple linear regression analysis. We found that bottom-up control on bacteria depended strongly on the picoplankton size class of the phytoplankton, and particularly on the picocyanobacteria *Synechococcus* spp. Possible carbon transfer mechanisms suggest a plausible basis for the linkage of *Synechococcus* spp. to bacteria.

**KEY WORDS:** Phytoplankton · Photosynthetic picoplankton · Bacterioplankton · Northern South China Sea

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## INTRODUCTION

The South China Sea (SCS) is a vast marginal sea constituting one of the world's 50 so-called 'large marine ecosystems' (Sherman 2001). In geographic extent, the SCS covers 3.5 million km<sup>2</sup>, and comprises the waters bounded in the north by a horizontal line between Taiwan and mainland China at 25°N, in the east by a vertical line between Taiwan and the Philippines at 121°E and a diagonal line above the Sulu Sea between the Philippines and Borneo, in the south by a horizontal line between Borneo and Sumatra at 3°S, and in the west by a vertical line across the Malacca Strait at 103°E (Pauly & Christensen 1993). The SCS comprises almost equal areas of the continental shelf (54 %) and the open ocean (46 %), partitioned by the 200 m isobath.

For the purpose of harvest fisheries management, the SCS can be divided into 10 subsystems: 2 in

nearshore waters (<10 m), 6 on the shallow shelf (10 to 50 m), 1 in the deep shelf (50 to 200 m), and 1 in the open ocean beyond the shelf (Pauly & Christensen 1993). However, for the purpose of investigating the response of plankton to regional oceanographical features, it is sufficient to differentiate merely 3 ecological provinces (Longhurst 1998, Ning et al. 2003)—the China Sea Coastal Province (CHIN), the Beibu Gulf (Sunda-Arafura Shelves Province, SUND), and the Archipelagic Deep Basin Province (ARCH). The first 2 overlie the continental shelf in a common coastal biome, the third the deep ocean in a trade wind biome.

It has been suggested that as a whole, the SCS sustains an average annual catch that is substantially below potential fish production (Pauly & Christensen 1993, Sherman 2001). However, it is conceivable that an active microbial loop may divert primary production away from fisheries, leading to lower harvests than would presumably be otherwise possible. Unfor-

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tunately, the roles of heterotrophic bacterioplankton and photosynthetic picoplankton in the lower trophic levels of these waters have not been explicitly addressed. These microbial plankton are ubiquitous but have been little studied in the SCS until recently (Cai et al. 2002, Yang & Jiao 2002, Agawin et al. 2003, Ning et al. 2003). In contrast, many studies in the neighbouring East China Sea (ECS), also belonging to the CHIN province, have confirmed the importance of photosynthetic picoplankton (Liu et al. 1997, Chen 2000), including species of cyanobacteria in the genera *Synechococcus* and *Prochlorococcus* (Vaulot & Ning 1988, Ning et al. 1997, Chiang et al. 2002, Jiao et al. 2002, Chang et al. 2003a, Furuya et al. 2003). In the ECS, heterotrophic bacterial production is probably controlled interactively by substrate supply and temperature (Shiah et al. 2000, 2003).

In the portion of the SCS north of 17° N, the 3 ecological provinces adjoin each other. West of Hainan Island, the continental shelf is part of SUND; to the east, the shelf is part of CHIN, whilst the deep open ocean is part of ARCH (Fig. 1). We have recently described the summer distribution pattern of pico-phytoplankton in this area (Ning et al. 2003). Herein, we examine the relationship between heterotrophic bacteria and phytoplankton to infer the relative degree

to which these microbes are linked. Since bacteria are able or obliged to use the organic substrates originating from phytoplankton in various forms (e.g. excreted photosynthates, protistan egesta, cell lysates, etc.), these trophic groups are coupled to lesser or greater extents depending on the availability of substrates from other sources. A recent study suggested that a strong dependence of bacteria on algal extracellular production can only be expected in open ocean environments removed from allochthonous sources (Morán et al. 2002). Our study of the SCS investigated whether the bacteria–phytoplankton relationship is the same in all 3 provinces and found that it is not. We also determined which phytoplankton group had the greatest effect on this relationship and found this to comprise the picocyanobacteria *Synechococcus* spp.

## MATERIALS AND METHODS

From 10 to 16 August 1999, we sampled 22 stations in the northern SCS, south of continental China (Fig. 1) from the RV 'Xiangyanghong' No. 14. West of Leizhou Peninsula and Hainan Island lies the Beibu Gulf (SUND), a semi-enclosed tropical bay running from NE to SW, and no greater than 60 m in depth. The

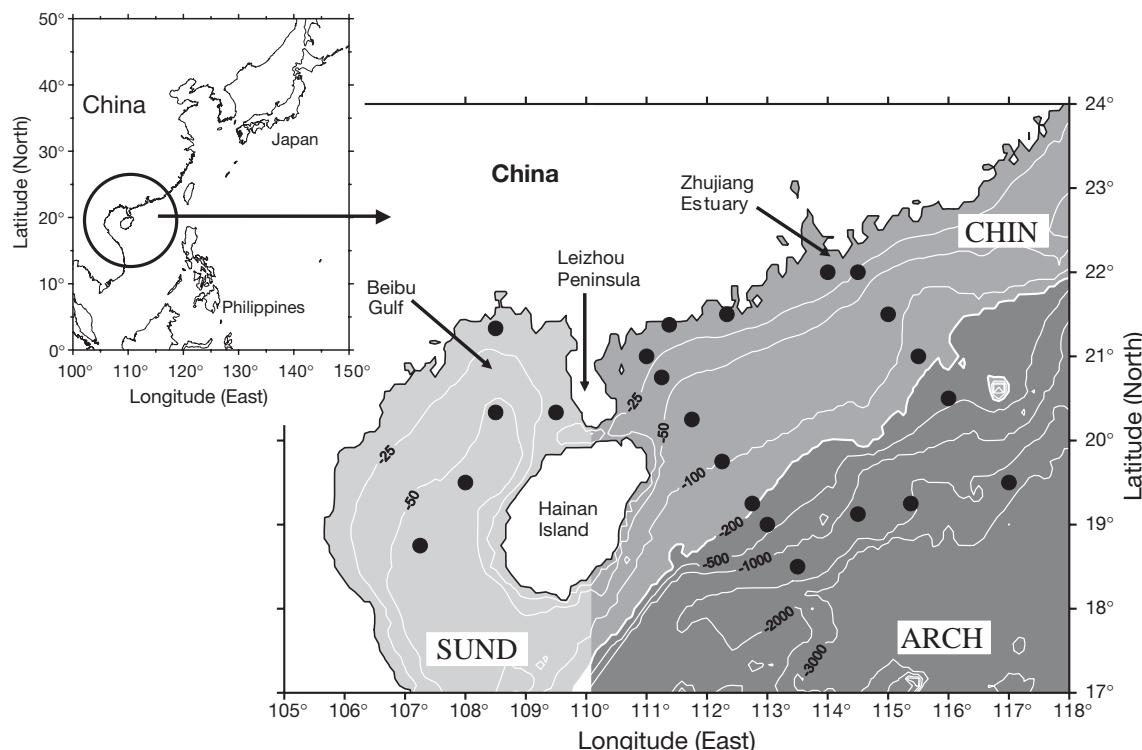


Fig. 1. South China Sea, showing 5 stations in the Sunda-Aratura Shelves Province (SUND), 10 stations in the China Sea Coastal Province (CHIN), and 7 stations in the Archipelagic Deep Basin Province (ARCH) sampled in present study

Qiongzhou Strait connects these waters to the region east of Hainan Island, comprising the Zhujiang (Pearl River) Estuary, the Guangdong coastal zone and the extensive continental shelf (CHIN). The slope and open ocean lie SE beyond the 200 m isobath (ARCH). We occupied 5 stations in SUND, 10 in CHIN and 7 in ARCH.

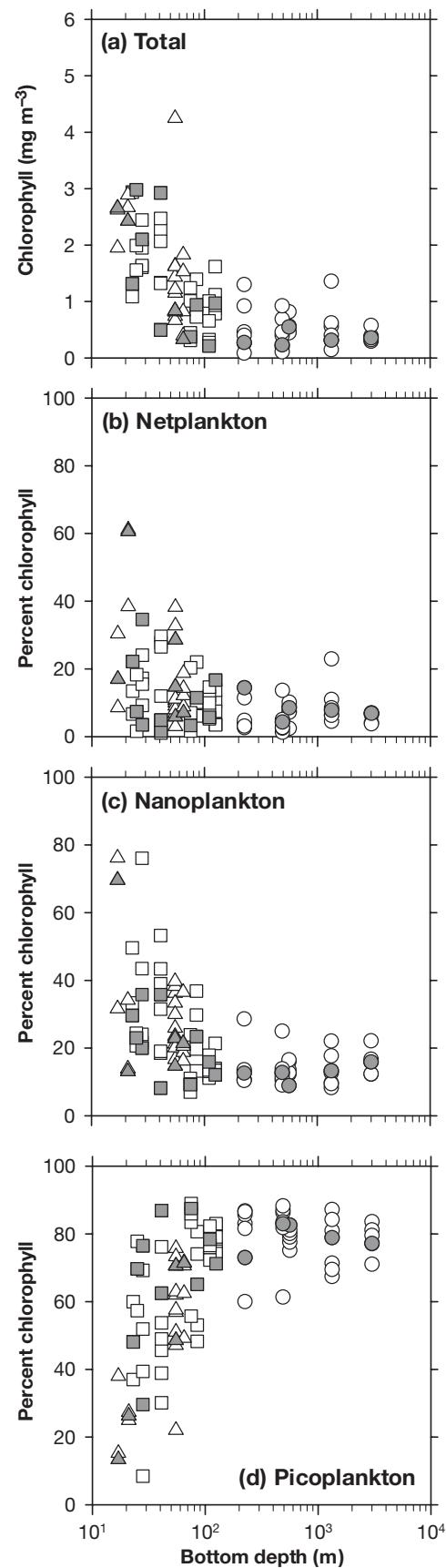
At the deep-water stations, samples were collected in 5 dm<sup>3</sup> Niskin bottles from the surface and at depths of surface, 10, 30, 50, 75, 100 and 150 m. At the shallow-water stations, fewer depths were sampled, but never less than 3 per station (0, 10 and 20 m). Aliquots of 1.8 cm<sup>3</sup> were filled into cryogenic vials and fixed with 0.2 cm<sup>3</sup> paraformaldehyde (1% final concentration) for 10 min at room temperature, quick-frozen in liquid nitrogen, and stored at -80°C until analysis (Marie et al. 1999). Picophytoplankton cells (the genera *Prochlorococcus* and *Synechococcus*, and picoeukaryotes) and heterotrophic bacteria were enumerated by flow cytometry using standard protocols (Marie et al. 1999) as previously described (Li et al. 1992, Li 1995, Li & Dickie 2001). Briefly, picophytoplankton were detected by red autofluorescence of chlorophyll *a*, and the 3 groups identified by relative cell size (forward light scatter) and the presence of phycoerythrin (orange fluorescence). Bacteria were detected by green fluorescence after staining with the nucleic acid binding fluorochrome SYBR Green-1.

Chlorophyll *a* content was determined in the various size fractions of the plankton by filtering 150 cm<sup>3</sup> seawater through 20 µm mesh net (netplankton), a 2.0 µm Nuclepore membrane filter (nanoplankton), and a Whatman GF/F glass fibre filter (picoplankton). The plankton thus retained was extracted in 90% acetone, and fluorescence was measured according to JGOFS protocol (Knap et al. 1996) using a Turner Designs model 10 fluorometer. Multiple linear regression analysis was performed according to Sokal & Rohlf (1995) on log-transformed variables.

## RESULTS

Following a first order pattern chlorophyll *a* concentration decreased with increasing bathymetric depth over the 3 ecological provinces (Fig. 2a). In shallow waters, there was generally more chlorophyll in the netplankton (Fig. 2b) and the nanoplankton (Fig. 2c)

Fig. 2. Relationship between chlorophyll (*chl a*) of phytoplankton and bathymetric depth. (a) *Chl a* concentration for entire phytoplankton assemblage; (b) % *chl a* in netplankton; (c) % *chl a* in nanoplankton; (d) % *chl a* in picoplankton. (●, ○) ARCH (n = 33); (■, □) CHIN (n = 43); (△, △) SUND (n = 23); grey symbols: samples collected at sea surface (nominal 0 m depth); open symbols: samples collected below sea surface



than in the picoplankton (Fig. 2d). Conversely, pico-plankton accounted for the majority of chlorophyll *a* in deep waters (Fig. 2d). Also in a first order pattern, abundance of different picoplankton cells was related to increasing bathymetric depth; decreasing for *Synechococcus* (Fig. 3a), picoeukaryotes (Fig. 3c) and heterotrophic bacteria (Fig. 3d), and increasing for *Prochlorococcus* (Fig. 3b). Much of the variability in these first order trends was associated with factors related to the depth at which the plankton were collected—mainly irradiance, temperature and nutrient concentrations. The depth-related variability in these measurements can be circumvented by considering only those samples collected near the sea surface at (nominal) 0 m depth. After doing so, it becomes evident (Fig. 4) that the phytoplankton community changed from picoplankton dominance (ca. 85%) in low biomass waters ( $0.2 \text{ mg chl } a \text{ m}^{-3}$ ) to even representation by all 3 size classes (ca. 33%) in high biomass waters ( $13 \text{ mg chl } a \text{ m}^{-3}$ ).

These whole region trends of a concurrent decrease in phytoplankton and bacteria from nearshore to offshore indicate statistically significant positive relations between bacterial abundance and chlorophyll *a* content of each of the phytoplankton size fractions (Fig. 5), and between bacterial abundance and each of the 3 picophytoplankton groups (Fig. 6). The weakest relationship was that between bacteria and *Prochlorococcus* (Fig. 6b), indicative of their opposing cross-shelf trends (Fig. 3).

A different pattern for the bacteria–phytoplankton relationship was seen when each ecological province was examined separately. In ARCH, the relationship was positive for chlorophyll *a* content of all phytoplankton size fractions (Fig. 7a,d,g,j) and for all pico-phytoplankton groups (Fig. 8a,d,g). However, in CHIN, bacterial abundance was not related to netplankton chlorophyll (Fig. 7e) and *Prochlorococcus* (Fig. 8e), and only weakly related to nanoplankton chlorophyll (Fig. 7h). The greatest difference between the trend for the whole region and that for a particular province was in SUND. Here, bacterial abundance did not increase with increasing chlorophyll *a* content of the various size fractions (Fig. 7c,f,i,l). Regional differences were reflected by Model II linear regression slopes of log bacteria on log total chlorophyll, which were 0.59 for the region as a whole, slightly higher (0.66) in ARCH, slightly lower (0.51) in CHIN, and not statistically significant ( $p > 0.05$ ) in SUND.

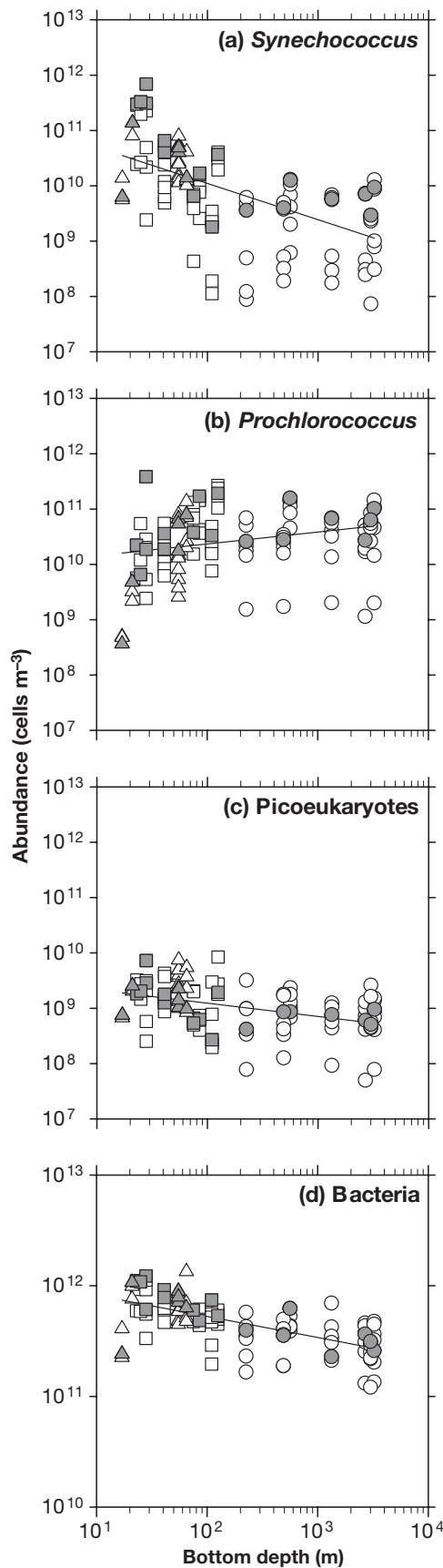


Fig. 3. Relationship between picoplankton cell abundance and bathymetric depth. (a) *Synechococcus* spp.; (b) *Prochlorococcus* spp.; (c) picoeukaryotic algae; (d) heterotrophic bacterioplankton. Further details as in Fig. 2, except that here for ARCH  $n = 49$

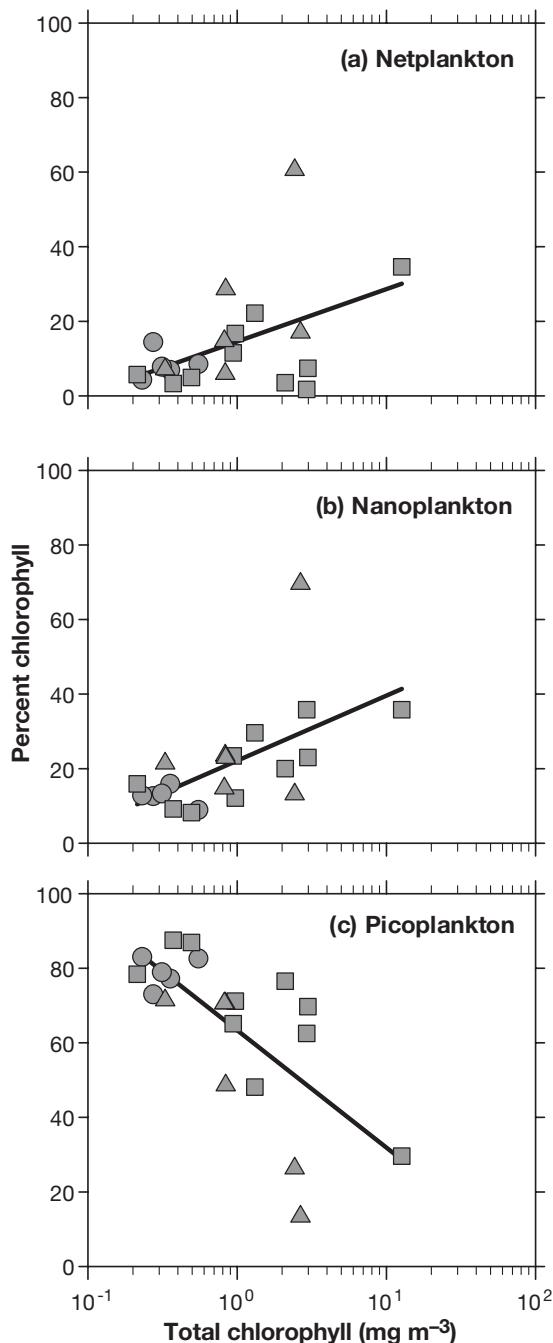


Fig. 4. Percentage contribution of (a) netplankton, (b) nanoplankton and (c) picoplankton to chlorophyll *a* biomass as a function of total chlorophyll *a* concentration in surface waters of the South China Sea (SCS). (●) ARCH; (■) CHIN; (▲) SUND

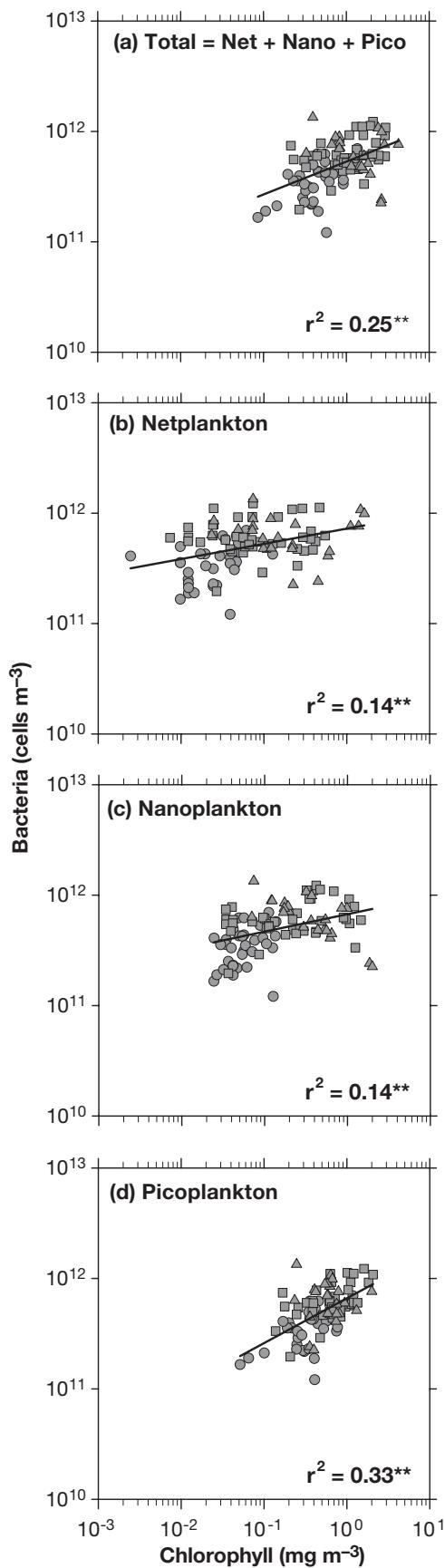


Fig. 5. Bivariate relationship between bacterial abundance and chlorophyll *a* content of different size fractions of phytoplankton in the entire SCS study region. (a) Total phytoplankton; (b) netplankton; (c) nanophytoplankton; (d) picophytoplankton. Proportion of explained variation is given by coefficient of determination ( $r^2$ ). \*\*Statistically significant at  $p < 0.01$  ( $n = 99$ ).

Symbols as in Fig. 4

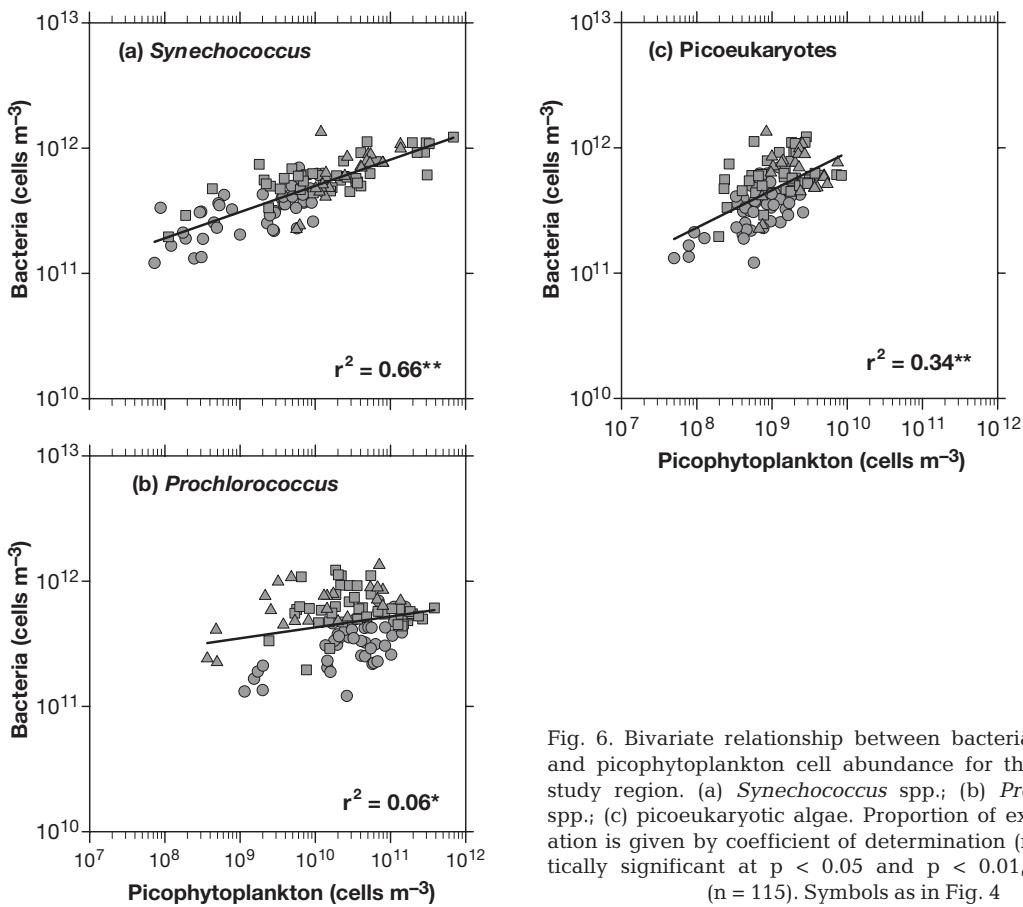


Fig. 6. Bivariate relationship between bacterial abundance and picophytoplankton cell abundance for the entire SCS study region. (a) *Synechococcus* spp.; (b) *Prochlorococcus* spp.; (c) picoeukaryotic algae. Proportion of explained variation is given by coefficient of determination ( $r^2$ ). \*,\*\*Statistically significant at  $p < 0.05$  and  $p < 0.01$ , respectively ( $n = 115$ ). Symbols as in Fig. 4

The bivariate correlations (Figs. 5 to 8) do not reveal the underlying separate dependence of bacterial abundance on the individual phytoplankton groups (chlorophyll size class or picophytoplankton cell type), because there is intercorrelation amongst the phytoplankton themselves. Multiple linear regression analysis (Sokal & Rohlf 1995) is required to determine which of the phytoplankton groups affect bacteria significantly and appreciably, and to estimate the relative magnitude of the contributions of these groups. In short, we computed partial regression coefficients on

the log-transformed variables, and present both the standard and conventional forms of these coefficients. The standard form ('beta coefficients') expresses the average change in standard deviation units of log bacteria for 1 SD change in log units of a particular phytoplankton group, all others being held constant. The conventional form expresses the average change in the variables in non-standardised measurement units. Because log-transformed variables are used, a rescaling of the untransformed measurements using fixed multiplicative factors (such as converting cell abundance to

Table 1. Multiple linear regression analysis of log bacterial abundance ( $y$ ) on log net-chlorophyll ( $x_1$ ), log nano-chlorophyll ( $x_2$ ), and log pico-chlorophyll ( $\log x_3$ ) in 3 biogeochemical provinces of the South China Sea. Standard partial regression coefficients are designated  $b'$ ; conventional partial regression coefficients  $b$ ; period in subscript separates dependent from independent variables that are held constant.  $R^2$ : coefficient of multiple determination;  $F_s$ : sample statistic of the  $F$ -distribution;  $p$ : probability.  $n = 33$  data points for ARCH, 43 for CHIN, 23 for SUND and 99 for the whole region (combined)

Province	Standard partial regression coefficients			$y$ -intercept	Conventional partial regression coefficients			$R^2_{y,1,2,3}$	$F_s$	$p$
	$x_1 = \text{net chl}$	$x_2 = \text{nano chl}$	$x_3 = \text{pico chl}$		$x_1 = \text{net chl}$	$x_2 = \text{nano chl}$	$x_3 = \text{pico chl}$			
ARCH + CHIN + SUND	0.16	-0.14	0.56	11.83	0.054	-0.055	0.38	0.32	15.10	<0.0001
ARCH	0.17	-0.63	0.98	11.31	0.092	-0.52	0.60	0.40	6.35	<0.01
CHIN	-0.43	0.24	0.56	11.75	-0.12	0.072	0.29	0.33	6.29	<0.01
SUND	0.55	-1.15	0.22	11.72	0.19	-0.54	0.19	0.79	24.06	<0.0001

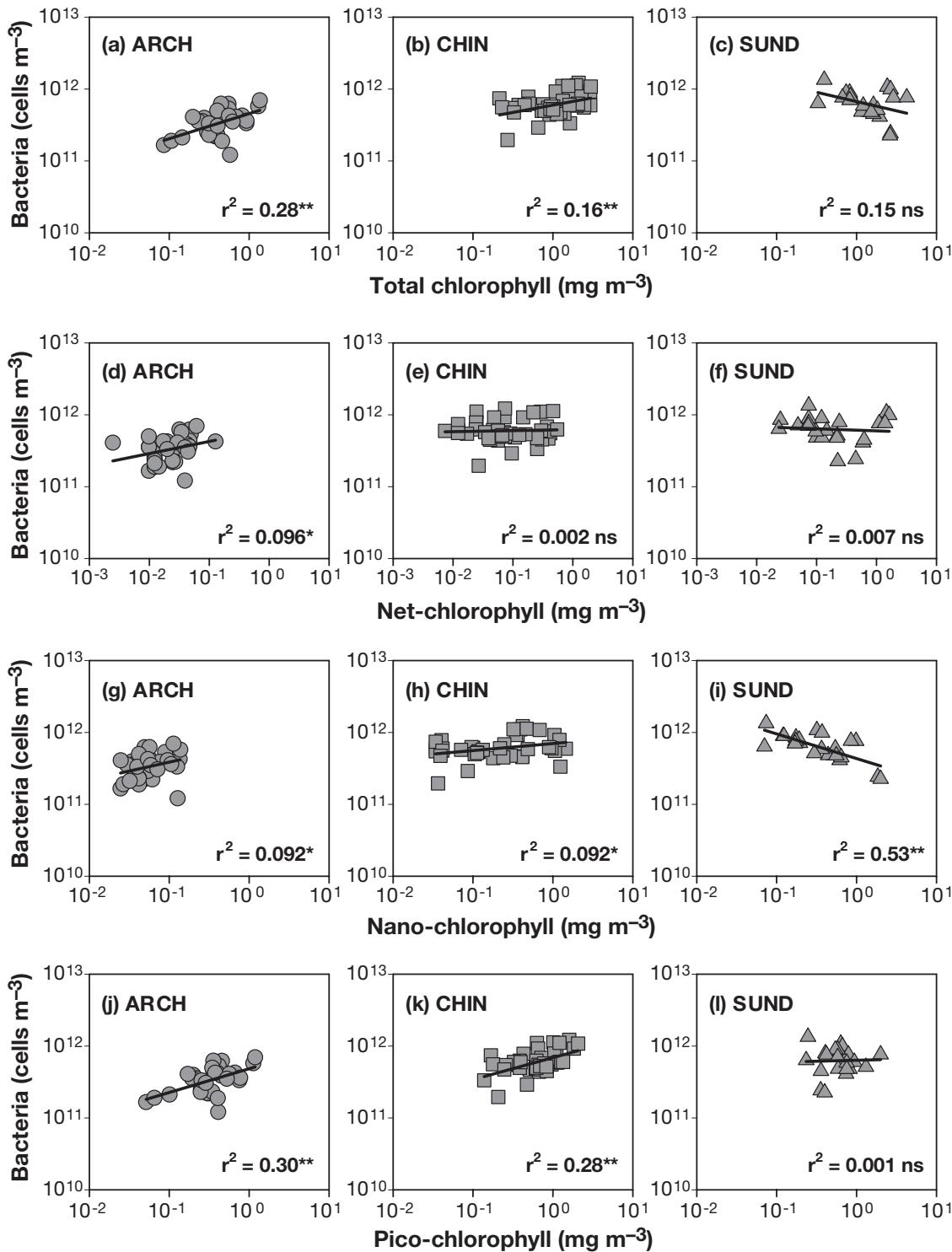


Fig. 7. Bivariate relationship between bacterial abundance and chlorophyll *a* content of different size fractions of phytoplankton in separate ecological provinces of SCS: ARCH (●, n = 33), CHIN (■, n = 43), and SUND (▲, n = 23). Further details as for Fig. 6

carbon biomass using carbon cell quota) affects only the *y*-intercept, and not the regression coefficients.

Multiple regression analysis revealed picophytoplankton to have the main effect on bacteria (Table 1).

In the study area as a whole, the beta coefficient for picoplankton chlorophyll (0.56) was the highest amongst the 3 size classes. On a regional basis, this coefficient was highest in ARCH (0.98), intermediate

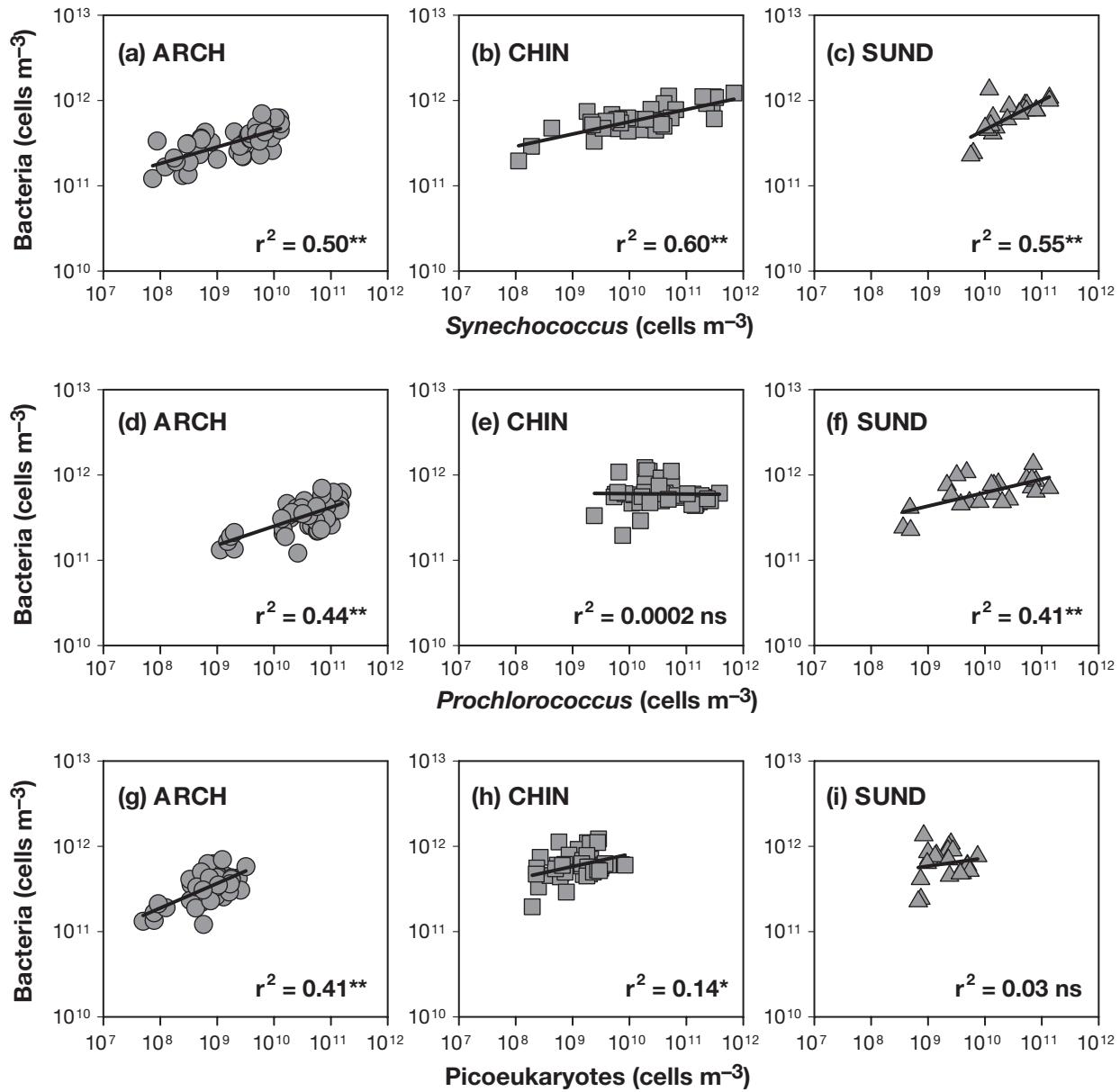


Fig. 8. Bivariate relationship between bacterial abundance and picophytoplankton cell abundance in separate ecological provinces of SCS: ARCH (●, n = 49), CHIN (■, n = 43), and SUND (▲, n = 23). Further details as for Fig. 6

Table 2. Multiple linear regression analysis of log bacterial abundance (y) on log *Synechococcus* ( $x_4$ ), log *Prochlorococcus* ( $x_5$ ) and log picoeukaryotes ( $\log x_6$ ) in 3 biogeochemical provinces of the South China Sea. Symbols as in Table 1. n = 49 data points for ARCH, 43 for CHIN, 23 for SUND and 115 for the whole region (combined)

Province	Standard partial regression coefficients			Conventional partial regression coefficients			$R^2_{y,4,5,6}$	$F_s$	p
	$x_4 = Syn$ $b'_{y4,5,6}$	$x_5 = Pro$ $b'_{y5,4,6}$	$x_6 = Euk$ $b'_{y6,4,5}$	y-intercept $a$	$x_4 = Syn$ $b_{y4,5,6}$	$x_5 = Pro$ $b_{y5,4,6}$	$x_6 = Euk$ $b_{y6,4,5}$		
ARCH+CHIN+SUND	0.71	0.061	0.14	8.97	0.18	0.022	0.074	0.67	76.84 <0.0001
ARCH	0.63	-0.21	0.52	8.57	0.17	-0.071	0.24	0.64	26.30 <0.0001
CHIN	0.84	-0.18	-0.055	10.95	0.16	-0.054	-0.021	0.63	22.21 <0.0001
SUND	0.63	0.48	-0.063	7.96	0.29	0.12	-0.038	0.76	20.27 <0.0001

in CHIN (0.56), and lowest in SUND (0.22). In contrast, the coefficient for netplankton chlorophyll was appreciable in SUND (0.55), but low in ARCH (0.17).

Within the picophytoplankton size class, *Synechococcus* had the main effect (Table 2). The beta coefficient for *Synechococcus* was high on a region-wide basis (0.71) and did not differ greatly amongst the provinces (0.62 to 0.84). In contrast, the beta coefficient for *Prochlorococcus* was very low on a region-wide basis (0.06), and even negative in ARCH and CHIN. The beta coefficient for picoeukaryotes was appreciably high only in ARCH (0.52).

## DISCUSSION

Comparative analysis in ecology (Cole et al. 1991) is the statistical evaluation of observations across nature's gradients aimed at identifying broad patterns and at inferring possible underlying rules. In aquatic microbial ecology, the comparative approach has provided much insight into food web structure, dynamics and function (Gasol & Duarte 2000). In particular, the regulation of bacteria by carbon resources has been extensively studied (Pace & Cole 1994). The basis of this regulation is the trophic dependence of bacteria on phytoplankton; i.e. heterotrophic bacteria require labile organic molecules for growth, and these are made available by phytoplankton.

In systems where bacteria are carbon limited, the extent to which dissolved primary production satisfies bacterial carbon demand is a direct and quantitative measure of trophic coupling (Morán et al. 2002). A less direct indication of coupling is the extent to which bacterial abundance changes in relation to bacterial production, the latter being a surrogate for the steady state flux of dissolved organic substrates (Billen et al. 1990, Ducklow 1992). An even less direct indication of coupling is the extent to which bacterial abundance changes in relation to chlorophyll concentration. Clearly, bacterial abundance is not a robust proxy for bacterial carbon demand, and neither is chlorophyll concentration a robust proxy for dissolved primary productivity. Nevertheless, the ease with which bacterial abundance and chlorophyll concentration can be measured has allowed an extensive examination of their statistical relationship to each other. This relationship, described by linear regression of the log-transformed variables, is always positive but less than proportional (Gasol & Duarte 2000). In a survey of 33 studies in different freshwater and marine ecosystems, the power slope ranged from 0.2 to 0.8, and averaged  $0.47 \pm 0.03$ , leading Gasol & Duarte (2000) to state that this is one of the few undisputed patterns in aquatic microbial ecology. A power slope of less than 1 indi-

cates that bacterial abundance is highest (in relation to phytoplankton biomass) in low chlorophyll waters. However, it is unclear whether this means that bacteria are more abundant than is supportable by the resources available in oligotrophic waters, or conversely that bacteria are too sparse for the resources available in mesotrophic waters (Gasol & Duarte 2000).

At the largest scale of our observation, which was a region covering the juncture of the 3 provinces of ARCH, CHIN and SUND, the first-order patterns in the distribution of chlorophyll *a* and microbial plankton were as expected from general considerations (Agawin et al. 2000, Cai et al. 2002), from studies in neighbouring areas (Chen 2000, Chiang et al. 2002, Jiao et al. 2002), and from climatological averages (Xie et al. 2003). Picophytoplankton comprised the greater portion part of phytoplankton biomass in warm, nutrient-poor offshore waters (Figs. 2d & 4c), but these waters sustained low absolute abundances of *Synechococcus*, picoeukaryotes and bacteria (Fig. 3). Also at this large scale, the expected coupling between bacteria and total chlorophyll was confirmed (Fig. 5a). The slope of the Model II bivariate regression (0.59) was slightly higher than the grand global mean of 0.46 (Li et al. 2004), but compared well with that in other ecosystems (Gasol & Duarte 2000). Since the carbon:chlorophyll *a* ratio of phytoplankton has been shown to increase from coastal to offshore waters in the ECS due to changes in species composition as well as in light and nutrient conditions (Chang et al. 2003b), it is possible that the actual coupling of bacterial carbon demand to dissolved primary production is weaker than indicated by the relationship of bacterial abundance to chlorophyll *a*.

At the finer level of individual provinces, the patterns were idiosyncratic. Most notably, the positive correlation between bacteria and total chlorophyll weakened from ARCH to CHIN to SUND (Fig. 7a,b,c). Less positive (including zero) slopes between bacteria and their resource supply are generally interpreted as evidence for stronger top-down control or allochthonous carbon subsidies (Ducklow 1992, Pace & Cole 1994, Gasol & Duarte 2000). Recent studies in the southern ECS suggest the importance of dissolved organic carbon from non-phytoplankton and allochthonous sources in supporting bacterial carbon demand (Shiah et al. 2000, 2003) and high rates of microbial plankton respiration (Chen et al. 2003). Further north, in the Yellow Sea, bacteria are also uncoupled from phytoplankton, apparently because strong tides mix the organic matter produced in the euphotic zone into the deeper water column (Cho et al. 1994). In both the SCS and ECS, it therefore appears that bacteria are coupled to phytoplankton most strongly in the offshore biome in a pattern stereotypic for open ocean waters

(Ducklow 1992). In the coastal biome, the hydrodynamic features are complex (Xue et al. 2001) and include estuarine plumes that carry heavy anthropogenic loads (Yin et al. 2001) and also the likelihood of enhanced bacterivore populations (Chiang et al. 2003). Furthermore, the shallow waters of the Beibu Gulf (SUND) contain substantial areas of coral reefs, mangroves and seagrasses. These additional potential sources of substrate supply or grazing pressure would reduce the apparent linkage of bacteria to phytoplankton.

Where the bacteria–chlorophyll relationship was significant, this was mainly attributable to the picoplankton. The proportion of bacterial variation explained solely by picoplankton chlorophyll in ARCH ( $r^2 = 0.30$ ) and in CHIN ( $r^2 = 0.28$ ) was only slightly less than that explained by joint consideration of all 3 chlorophyll size fractions ( $R^2 = 0.40$  and 0.33 respectively, Table 1). Since this relationship depended greatly on *Synechococcus*, and to some extent on picoeukaryotes, but not on *Prochlorococcus* (as indicated by the partial regression coefficients, shown in Table 2), the question arises as to whether these picoplankters differ in the efficiency with which they transfer carbon to bacteria via the dissolved carbon pool. An alternative explanation for the observed correlation between bacteria and phytoplankton is that they were responding independently to the same set of forcing factors. For example, conditions supporting high dissolved organic matter (DOM) supply to heterotrophs might also support selective alleviation of trace metal inhibition of phototrophs (Sherr et al. 2004). Be that as it may, the evidence for a causal link between picophytoplankton and bacteria is strong. The transfer processes include exudation of organic photosynthates by healthy picoplankters, the release of DOM in the egesta of protozoans that have consumed the picoplankters, and the liberation of cellular contents by viral lysis or autolysis (Nagata 2000).

Several lines of evidence point to a low transfer of carbon from *Prochlorococcus* to the dissolved pool. First, we surmise that the direct efflux of soluble carbon from *Prochlorococcus* is low. We are unaware of direct evidence on the rate of extracellular release by picophytoplankters, but group-specific primary production often decreases in the order picoeukaryotes, *Synechococcus*, *Prochlorococcus* (Li 1994, 1995), reflecting the same order in specific growth rate and cellular carbon content (Worden et al. 2004). Generally, phytoplankton release about 10 to 20% of primary production as exudates, but this is thought to be insufficient to meet bacterial carbon demand (Nagata 2000).

Second, there may be differences in the efficiency with which phagotrophic flagellates assimilate different picophytoplankters, implying that the non-

assimilated fraction is different. Guillou et al. (2001) found that although the stramenopile *Picophagus flagellatus* ingested both *Synechococcus* and *Prochlorococcus*, the former was poorly digested and supported less growth. The efficiency of carbon transfer was less than 1% for *Synechococcus* compared to 23% for *Prochlorococcus*. In other words, as a result of protozoan grazing on picophytoplankters, less of the carbon from *Prochlorococcus* (and more from *Synechococcus*) was potentially available for heterotrophic bacteria. The trophic flow model of Nagata (2000) suggested that grazers, particularly protozoans, are the major contributors to DOM production. If it is generally true that a substantial portion of *Synechococcus* spp. carbon is released to the dissolved organic pool and made available to bacteria, then this would be a plausible basis for their strong coupling observed in the SCS.

Third, although it is known that phytoplankton are susceptible to viral infection (Fuhrman 1999, Sullivan et al. 2003) and automortality (Berges & Falkowski 1998, Veldhuis et al. 2001), there is insufficient information to evaluate the relative extent to which *Synechococcus*, *Prochlorococcus* and picoeukaryotes would each contribute to the DOM pool upon lysis. On the basis of cell membrane integrity, it appears that populations of *Synechococcus* generally contain proportionately more viable cells than those of picoeukaryotes (Veldhuis et al. 2001, Agustí & Sánchez 2002) and *Prochlorococcus* (Agustí 2004). However, an assay of membrane permeability presumably does not distinguish between lysis induced by autogenic factors or by viruses. Other evidence suggests that viruses are likely to have a significant role in shaping phytoplankton species composition (Fuhrman 1999). Recent genomic analyses of marine picocyanobacteria indicate differences in genes that control cell surface chemistry, providing a basis for selective phage recognition, and possibly also selective recognition by protist grazers (Rocap et al. 2003). New information on viruses regarding their host strain specificity and titres (Sullivan et al. 2003) are consistent with a view that *Synechococcus* spp. are commonly susceptible to viral-induced mortality, and that this decreases along a trophic gradient from coastal to open ocean waters. The contribution of phytoplankton lysis to carbon flow in the microbial web can be modelled (Fuhrman 1999), but there is yet insufficient information for separate parameterisation of *Synechococcus*, *Prochlorococcus* and picoeukaryotes.

In the SCS as a whole, and in the provinces of ARCH, CHIN and SUND taken separately, *Synechococcus* spp. were the only picophytoplankters with a consistent strong relationship to heterotrophic bacteria (Table 2). The coupling mechanisms of photosynthate

exudation, protozoan egestion and cell lysis together provide a plausible basis for this particular linkage, but we cannot exclude the possibility that the correlations have no cause-and-effect basis. These inferences, arising from our comparative analysis, point to research questions that could be tested in future by direct experimentation.

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