African Journal of Marine Science 2009, 31(3): 373–380

AFRICAN JOURNAL OF MARINE SCIENCE
ISSN 1814–232X EISSN 1814–2338
doi: 10.2989/AJMS.2009.31.3.10.998

Variations in the dominant algal bloom-forming species in the western South China Sea from 1993 to 2007

CL Liu[1,2], DL Tang[1]*, SF Wang[1] and L Nguyen-Ngoc[3]

[1] *Key Laboratory of Tropical Marine Environmental Dynamics, and Key Laboratory of Marine Bio-resources Sustainable Utilization, South China Sea Institute of Oceanology, Chinese Academy of Sciences, Guangzhou 510301, China*
[2] *Marine College, Shandong University at Weihai, Weihai 264209, China*
[3] *Institute of Oceanography, 01 Cauda, Nha trang, Vietnam*
** Corresponding author, e-mail: lingzistdl@126.com*

Manuscript received May 2009; accepted September 2009

The study investigated the spatial and temporal variations of harmful algal bloom (HAB) species in the western South China Sea (SCS) for the period 1993–2007, using *in situ* HAB and remotely sensed datasets. A significant change in the dominant bloom species occurred during the study period. *Trichodesmium erythraeum* (Cyanophyta) was the dominant species from 1993 to 1999, usually occurring between March and July in the coastal waters of Binh Thuan Province, South Vietnam. *Phaeocystis globosa* (Haptophyta) dominated blooms from 2002 to 2007, usually occurring between June and September in the coastal waters of Ninh Thuan Province. Furthermore, most HAB species observed in the earlier period (1993–1999) were absent in latter period (2002–2007). These changes are attributable to environmental influences. Warm oligotrophic conditions likely favoured *T. erythraeum* whereas cooler eutrophic conditions favoured *P. globosa*.

Keywords: Chl *a* concentration, harmful algal blooms (HABs), *Phaeocystis globosa,* South China Sea, *Trichodesmium erythraeum*, upwelling

Introduction

Harmful algal blooms (HABs) in both fresh and marine water bodies impact negatively on other organisms, ecosystems, human health, recreation and/or fisheries (Smayda 1997), and have therefore become an important global issue (Veldhuis and Wassmann 2005). Several of the HAB-forming species produce toxins, while others are considered harmful only because of the exceptionally high cell abundances that they may attain (Hallegraeff 1993). The prymnesiophyte, *Phaeocystis globosa*, is an example of a HAB species with the potential to generate a very high biomass, to dominate the phytoplankton community for extended periods and to affect fisheries, the tourist industry and local ecosystems (Lancelot et al. 1994, Brussaard et al. 1996, 2005). A better understanding of changes in bloom-forming algal species is important in addressing aquatic ecosystem health.

Owing to their damaging effects, toxic algal species of the South China Sea (SCS) have been widely studied in order to improve detection and monitoring (Qi et al. 1992, 2004, Hodgkiss and Ho 1997, Tang et al. 1998, 1999, Nguyen and Doan 1996, Nguyen 1999). Some researchers have focused on algal species identification (Hodgkiss and Lu 2004, Azanza et al. 2005, Masuda et al. 2001) whereas others have reported on environmental factors influencing the development of HABs (Tang et al. 2003a, 2003b, Usup et al. 2002). The harmful species, *Phaeocystis globosa*, was observed for the first time in the northern SCS in 1997 (Chen et al. 1999). However, the absence of previous records may merely be a consequence of the lack of long-term records. Assessment variations in algal species requires long-term records and the studies referred to above provide a good base for further investigation of the frequency and magnitude of specific algal bloom species over longer periods of time.

The purpose of this study was to examine the algal bloom species in the coastal waters of the western SCS for the period 1993–2007 to establish: (1) which bloom species were present; (2) how these bloom species changed with time; and (3) the probable causes for these changes. The results of this study may be of use to better ascertain the potential threat that algal blooms pose to coastal foodwebs and human health.

Study area and data

The SCS is a marginal sea of the western Pacific Ocean, located in the tropical monsoon zone between the equator and the Tropic of Cancer (Figure 1a). The study area (Figure 1b) was located in the western SCS along the eastern Vietnamese coast, into which the Mekong River discharges. The region experiences seasonally reversed

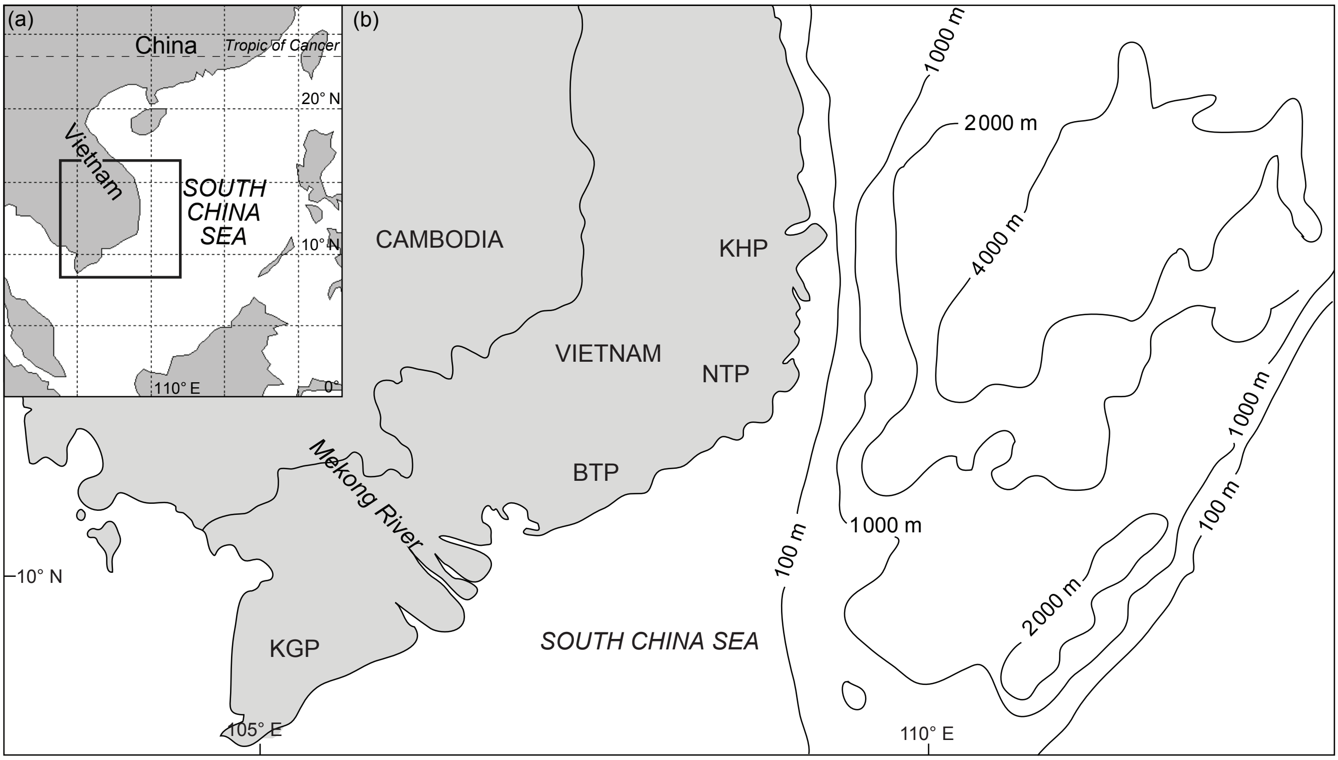

Figure 1: Map of the location of the study area in the western South China Sea, showing the Khanh Hoa Province (KHP), Ninh Thuan Province (NTP), Binh Thuan Province (BTP) and Kien Giang Province (KGP)

tropical monsoons: a south-westerly monsoon first appears in May and expands to cover the entire basin of the SCS during July and August, whereas a north-easterly monsoon appears in late September (Shaw and Chao 1994). The region is complex in physical, chemical and ecological characteristics, and several newly recorded algal species have caused massive fish and marine mammal kills in addition to posing a threat to human health.

HAB data were collected and compiled from various sources, including government statistical reports from China and Vietnam, reliable websites, research journals, conference proceedings, newspapers, etc. A single HAB event was regarded as a reported observation that was separated both temporally and spatially from other events. There were no HAB records available for the study area prior to 1990, so our effort was focused on HAB events reported or recorded during the period 1993–2007. Our study analysed the regional distribution and monthly incidences of algal bloom species, with particular attention to changes in the dominant algal bloom species.

Chlorophyll *a* (Chl *a*) images of 1 km × 1 km spatial resolution were derived from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) and processed through the SeaWiFS Data Analysis System (SeaDAS) using the Ocean Color 4-band algorithm (OC4, 4) (O'Reilly et al. 1998). Sea surface temperature (SST) data from the Advanced Very-High Resolution Radiometer (AVHRR) Pathfinder Version 5 SST Project (resolution 4 km, monthly averaged daytime data) were obtained from the website of the Physical Oceanography Distributed Active Archive Center (PODAAC) of the Jet Propulsion Laboratory (JPL), NASA (http://www.podaac.jpl.nasa.gov/sst). Wind speed and direction over the ocean surface were sourced from the NASA satellite Quick Scatterometer (QuikScat) measurements of backscattered power (Wentz et al. 2001). Monthly averaged QuikScat wind vector images were produced by remote sensing systems sponsored by the NASA Ocean Vector Winds Science Team (http://www.ssmi.com/qscat/qscat_description.html).

Results

Spatial and temporal distribution of algal species

A total of 22 confirmed HAB events were recorded from 1993 to 2007 in the western SCS (Table 1), the first of which was attributed to the cyanophyte *T. erythraeum* in 1993 in the coastal waters of Binh Thuan Province (BTP) (Nguyen and Doan 1996). However, the actual number of HAB events is likely to be considerably higher, taking into account the number of unconfirmed observations of HABs by local fishers (Nguyen et al. 2003).

Of the 22 HAB events, nine were located in the coastal waters of BTP and seven in the waters of Ninh Thuan Province (NTP) (Figure 2). Of the nine HABs occurring in the coastal waters of BTP, eight were caused by *T. erythraeum* during the period 1993–1999. In contrast, only one bloom of *T. erythraeum* was recorded in the coastal waters of NTP, which occurred in 1999. Most blooms off this province occurred after 2002 and were dominated by the haptophyte *Phaeocystis globosa*.

Table 1: Harmful algal bloom events reported between 1993 and 2007 in the study area

Event	Year	Month	Location (Province)	Dominant species	Phylum
1	1993	March	Binh Thuan	*Trichodesmium erythraeum*	Cyanophyta
2	1995	February	Khanh Hoa	*Noctiluca scintillans*	Dinophyta
3	1995	February	Khanh Hoa	*Noctiluca scintillans*	Dinophyta
4	1995	May	Binh Thuan	*Trichodesmium erythraeum*	Cyanophyta
5	1996	March	Binh Thuan	*Trichodesmium erythraeum*	Cyanophyta
6	1996	March	Khanh Hoa	*Noctiluca scintillans*	Dinophyta
7	1996	April	Binh Thuan	*Trichodesmium erythraeum*	Cyanophyta
8	1996	May	Binh Thuan	*Trichodesmium erythraeum*	Cyanophyta
9	1996	June	Binh Thuan	*Trichodesmium erythraeum*	Cyanophyta
10	1996	July	Binh Thuan	*Trichodesmium erythraeum*	Cyanophyta
11	1999	March	Binh Thuan	*Trichodesmium erythraeum*; *Trichodesmium thiebautii*	Cyanophyta
12	1999	March	Ninh Thuan	*Trichodesmium erythraeum*; *Trichodesmium thiebautii*	Cyanophyta
13	2002	June	Ninh Thuan	*Phaeocystis globosa*	Haptophyta
14	2002	July	Binh Thuan	*Phaeocystis globosa*	Haptophyta
15	2002	July	Khanh Hoa	*Heterosigma* sp.	Xanthophyta
16	2002	July	Ninh Thuan	*Phaeocystis globosa*	Haptophyta
17	2002	July	Ninh Thuan	*Phaeocystis globosa*	Haptophyta
18	2002	December	Kien Giang	*Microcystis* sp.	Cyanophyta
19	2003	August	Kien Giang	*Microcystis* sp.	Cyanophyta
20	2005	August	Ninh Thuan	*Phaeocystis globosa*	Haptophyta
21	2006	August	Ninh Thuan	*Phaeocystis globosa*	Haptophyta
22	2007	September	Ninh Thuan	*Phaeocystis globosa*	Haptophyta

Sources: Nguyen and Doan (1996), Nguyen (1999), Nguyen et al. (2003), Tang et al. (2004a, 2004c), Wang et al. (2008)

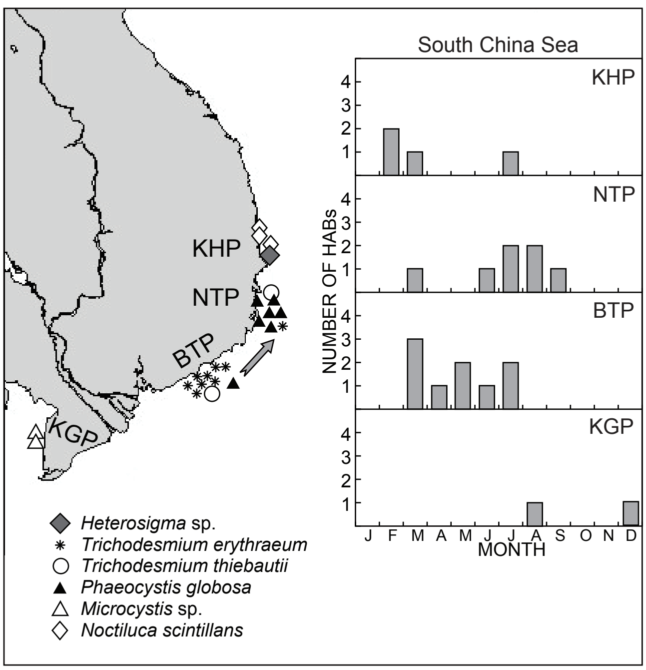

Figure 2: Distribution of HABs by species and monthly occurrence by region from 1993 to 2007 in the western coastal waters of the South China Sea. Abbreviations as in Figure 1

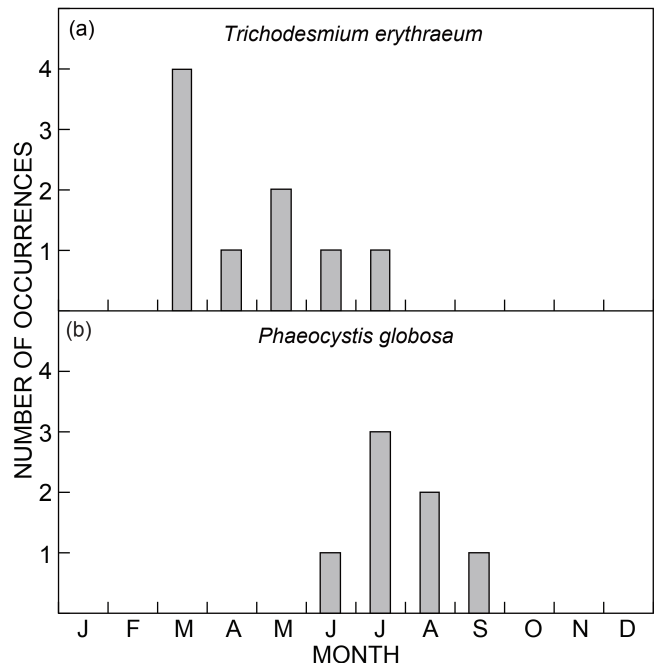

Figure 3: Comparative numbers of occurrences of (a) *Trichodesmium erythraeum* and (b) *Phaeocystis globosa* by month during 1993–2007

HABs caused by species occurring less often, such as those of *Noctiluca scintillans*, *Trichodesmium thiebautii* and *Heterosigma* sp., were observed mainly between February and July, with the exception of two blooms of *Microcystis* sp. in August and December in the coastal waters of Kien Giang Province (KGP). All blooms of *T. erythraeum* occurred between March and July (Figure 3a), whereas those of *P. globosa* were observed between June and September (Figure 3b). The decay of blooms of *P. globosa* can cause excessive production of foam, which can be detrimental to activities related to tourism and fisheries (Orton 1923).

Variation of algal species

The HAB events recorded during this study were attributed to six species (Table 1, Figure 4a). The six blooms of 2002 were attributed to three previously unrecorded algal species, *P. globosa, Heterosigma* sp. and *Microcystis* sp. (Box B in Figure 4a). In contrast, there were few new records of previously unrecorded species in other years (Table 1 and Figure 4a). It is therefore noteworthy that there was no overlap in those HAB species that dominated from 1993 to 1999 with those that dominated from 2002 to 2007.

In all, 12 HAB events were observed between 1993 and 1999 (Figure 4b, Table 1), with *T. erythraeum* responsible for nine of these events (Box C in Figure 4a). There were no observed HAB events in 2000 and 2001. However, these years were succeeded by another eventful year in 2002, in which six blooms were recorded, of which four were dominated by *P. globosa* (Box B in Figure 4a). Two *P. globosa* blooms appeared in July of 2002 causing an estimated mortality of 90% of the animal and plant species around the tidal reefs of NTP. Since 2002, *P. globosa* has been the dominant HAB species responsible for seven of the blooms between 2002 and 2007 (Box D in Figure 4a).

Chl a*, SST and wind in March 1999 and July 2002*

During the period of study, the incidence of blooms was recorded in March 1999 and July 2002. Most of these blooms were dominated by species previously unknown to cause blooms within the region (Figure 4a and Table 1). Satellite data was used to characterise the environmental conditions of March 1999 and July 2002.

In 2002, a widespread algal bloom, depicted by high Chl *a* concentrations (red arrow in Figure 5d), was evident near the coasts of NTP and BTP. Moreover, a band of high Chl *a*, extending offshore from the NTP coastline to 116° E, was formed in association with a cold plume of water. These satellite-observed blooms are considered to correspond to the reported *P. globosa* blooms during July 2002 (Table 1). However, SeaWiFS images for March 1999 (Figure 5a) indicated an absence of high Chl *a* in the coastal waters off NTP where *Trichodesmium* sp. had been reported to bloom at that time (Table 1). QuikScat data showed that the prevailing winds for July 2002 (Figure 5b) were strong south-westerly winds blowing parallel to the South Vietnamese coastline (red oval inset in Figure 5e). In contrast, in March 1999, the prevailing winds were weak north-easterly winds (Figure 5b). SST imagery implicated upwelling as an important mechanism in the development of HAB events. The image for July 2002 showed distinctly low-temperature waters (24–26 °C) on the coasts of the

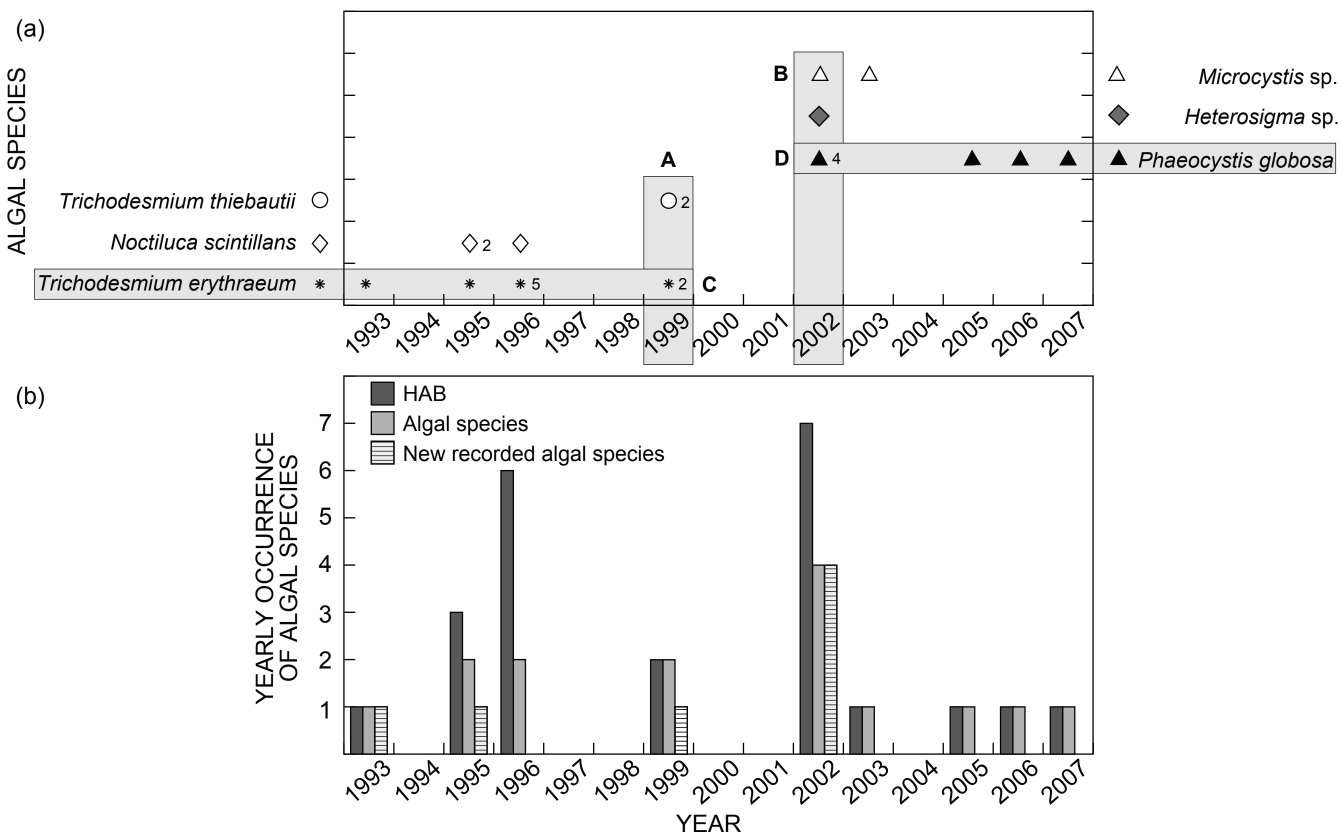

Figure 4: (a) Annual HAB species occurrence in the western South China Sea, 1993–2007. *Trichodesmium erythraeum* was the dominant bloom in most years during 1993–1999 (Box C); *Phaeocystis globosa* bloomed in most years during 2002–2007 (Box D). More species were found in both 1999 and 2002 (Boxes A and B); (b) annual HAB and algal species occurrences in the study area

BTP and NTP (red arrow in Figure 5f) coincident with the location, shape, and timing of algal blooms (Table 1 and Figures 2, 5d).

Discussion

Comparsion of the T. erythraeum *and* P. globosa *blooms*

Our data revealed a distinct change in the species responsible for HABs during the study period. *Trichodesmium erythraeum* dominated from 1993 to 1999 in the coastal waters of BTP (Table 1, Figure 2) and in March 1999, and blooms of this species extended into the coastal waters of NTP (Table 1, and depicted by an arrow in Figure 2). However, from 2002, *P. globosa* dominated blooms in these waters (Tables 1, 2, Figure 4a). Ecologically, several factors contribute to a bloom of one or another species, specifically the combination of the

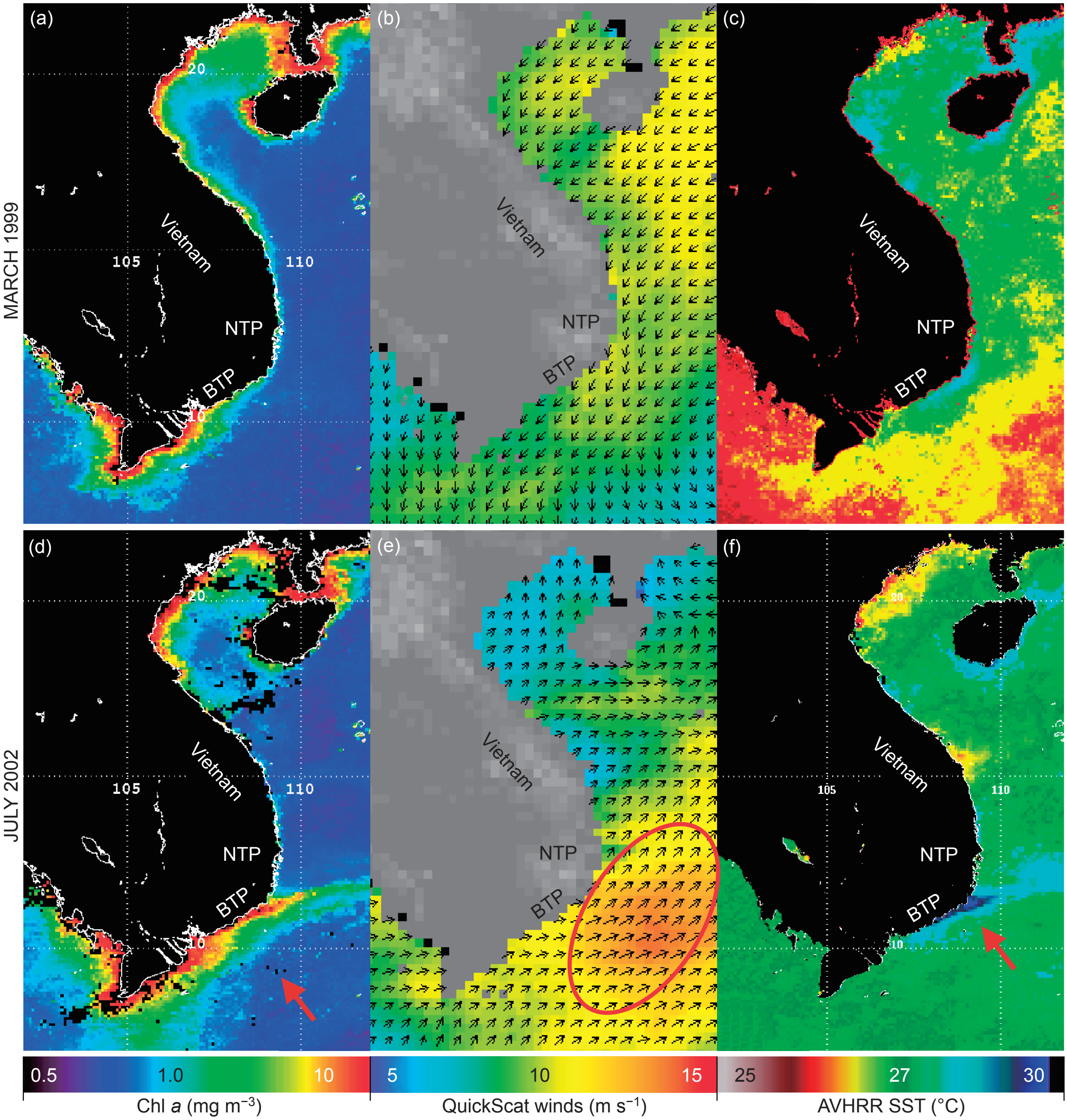

Figure 5: Remotely sensed images for Chl *a*, wind and SST for the study area in March 1999 (a, b, c) and July 2002 (d, e, f)

physiological characteristics of the phytoplankton and the temporary habitat conditions (Yamamoto and Okai 2000).

Comparing *T. erythraeum* and *P. globosa* in terms of physiological characteristics and environmental preferences (Table 2), it is evident that the former species occurs and is more abundant in oligotrophic tropical and subtropical surface waters such as the Red Sea (Karl et al. 1997, Lugomela et al. 2002). In contrast, *P. globosa* is more common in coastal and oceanic temperate waters, such as the North Sea, and tends to bloom under eutrophic conditions (Baumann et al. 1994). *Phaeocystis globosa* also differs from *T. erythraeum* in that it has a polymorphic life cycle with a flagellated unicellular form, which favours eutrophic surface waters associated with upwelling. The flagellated unicellular form of *P. globosa* is able to swim to depth to obtain dissolved nutrients. Therefore, in 2002, when nutrients were distributed throughout the surface layers as a result of intense upwelling, *P. globosa* could obtain more nutrients than *T. erythraeum*, which lacks the ability to obtain nutrients at depth, enabling *P. globosa* to dominate the HAB. In contrast, due to the influence of the post-1998 *El Niño* event, upwelling was weak in the western SCS in 1998/1999 (Zhao and Tang 2007), which resulted in relatively lower levels of nutrients in the surface waters, and these oligotrophic conditions favoured *T. erythraeum* in 1999 (Yamamoto et al. 2002).

Another possible factor accounting for the absence of reported *T. erythraeum* blooms in the latter part of the time-series may be the more turbulent mixing of surface waters, generated by the greater wind speeds occurring in 2002 (Figure 5e). Bloom formation of *T. erythraeum* is inhibited by turbulence (Table 2) as it is relatively fragile and is found in abundance only in surface waters during calm periods (Karl et al. 1992), whereas *P. globosa* readily thrives in well mixed waters.

Nutrient enrichment and other environmental factors

Apart from the physiological characteristics of phytoplankton, many others factors influence phytoplankton composition (Yamamoto et al. 2002). There is considerable evidence that certain phytoplankton tend to dominate during periods of relative nutrient enrichment and associated environmental regimes (Paerl 1988, Lomas and Glibert 1999, Smayda 2000).

In this study, the *T. erythraeum* blooms were observed many times between March and July in the coastal waters of BTP, where the Mekong River is the major source of freshwater. The high nutrient discharge associated with this river results in increased nitrate and ammonium concentrations along the coast (Zhu et al. 2003) and enhanced biological activity. As a consequence, BTP coastal waters frequently experienced spring and summer phytoplankton blooms, when these nutrient increases were at their highest levels as a result of increased river flow rates.

In contrast, wind-induced upwelling forced by the south-westerly monsoon may be responsible for the different algal blooms frequently observed in the coastal waters of NTP from June to September (Corrales and Crisostomo 1996, Lim et al. 2005). In that region, upwelling enriches the surface water layers of both the coast and open sea, favouring increased phytoplankton biomass and the high frequency of HABs (Tang et al. 2004b).

Other complex interactions between nutrient levels and oceanic environmental factors are likely to affect HAB occurrence, especially during *El Niño* and *La Niña* events, as well as during the transitional periods between them. However, the processes involved are not easily identified and explained without further in-depth research into the nature of the environmental conditions associated with measured nutrient levels and types.

Summary

Our investigations have shown a significant change of the dominant bloom-forming algae during the period 1993–2007. From 1993 to 1999, *T. erythraeum* dominated blooms, typically between March and July. Subsequently, *P. globosa* dominated during the period 2002–2007 and

Table 2: Comparison between two algal species *Trichodesmium erythraeum* and *Phaeocystis globosa*

Previous study		*Trichodesmium erythraeum*	*Phaeocystis globosa*
Biological features	Phylum	Cyanophyta	Haptophyta
	Colour of cell	Grey or brown	Yellow-brown
	Shape of cell	Filamentous	Spherical motile cell
	Flagellate	No	Two flagella and a short haptonema
	Toxin	Release sulphureted hydrogen after death	Release sulphureted hydrogen when bloom
Environmental factors	Temperature range	Tropical and subtropical waters	Temperate waters
	Nutrient	Oligotrophic surface waters	Eutrophic surface waters
	Physical factors	Stable water mass	Upwelling
Distribution and occurrence	Distribution in the world	Tanzania coastal waters, Australia	Denmark, Norway, Arabian Bay
	Typical distribution	Red Sea	The North Sea
	Distribution in China	Fujian Province, East Sea, Northern SCS	East Sea, South China Sea
	First occurrence in China	Fujian Province in 1962	Guangdong Province in 1997
Present study	Year of occurrence	1993, 1995, 1996, 1999	2002, 2005, 2006, 2007
	Month of occurrence	March, April, May, June, July	June, July, August, September
	Distribution region	Binh Thuan Province, Ninh Thuan Province	Ninh Thuan Province
	Environmental factors	Meikong River discharge	Wind-induced upwelling

Sources: Baudoux and Brussaard (2005), Chang et al. (2000), Lugomela et al. (2002), Karl et al. (1992)

usually between June and September. In 2002, multiple blooms were observed and were dominated by species atypical to the region.

Regionally, from 1993 to 1997, the HAB blooms occurred mainly in the BTP coastal waters, where nutrient inputs from the Mekong River are considered to have favoured blooms of *T. erythraeum*. The only observation of *T. erythraeum* outside of the BTP was in NTP coastal waters in March 1999. *P. globosa* dominated HAB events, where upwelling may have been a major factor from 2002 onwards and these occurred mainly in NTP coastal waters. The reason for the shift in algal blooms from the coastal waters of BTP to those of NTP requires further investigation.

Acknowledgements — The present work was supported by the following research grants: (1) National Natural Sciences Foundation of China (40976091, 2010); (2) Foundation of Key Laboratory of Marine Biology (LMB/LAMB and LMM) (LMB081004) and Key Laboratory of Tropical Marine Environmental Dynamics (LED) (LED0801) of Chinese Academy of Sciences and Guangdong; (3) the CAS/SAFEA International Partnership Program for Creative Research Teams KZCX2-YW-T001. We would like to thank Mr David Warrington of the State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau for his advice in preparing the manuscript. We are also grateful to two reviewers for their helpful suggestions, which greatly improved the manuscript.

References

Azanza RV, Fukuyo Y, Yap LG, Takayama H. 2005. *Prorocentrum minimum* bloom and its possible link to a massive fish kill in Bolinao, Pangasinan, Northern Philippines. *Harmful Algae* 4: 519–524.

Baudoux AC, Brussaard CPD. 2005. Characterization of different viruses infecting the marine harmful algal bloom species *Phaeocystis globosa*. *Virology* 341: 80–90.

Baumann MEM, Lancelot C, Brandini FP, Sakshaug E, John DM. 1994. The taxonomic identity of the cosmopolitan prymnsiophyte Phaeocystis: a morphological and ecophysiological approach. *Journal of Marine System* 5: 5–22.

Brussaard CPD, Gast GJ, van Duyl FC, Riegman R. 1996. Impact of phytoplankton bloom magnitude on a pelagic microbial food web. *Marine Ecology Progress Series* 144: 211–221.

Brussaard CPD, Kuipers B, Veldhuis MJW. 2005. A mesocosm study of *Phaeocystis globosa* population dynamics I. Regulatory role of viruses in bloom control. *Harmful Algae* 4: 859–874.

Chang J, Chiang KP, Gong GC. 2000. Seasonal variation and cross-shelf distribution of the nitrogen-fixing cyanobacterium, *Trichidesmium*, in southern East China Sea. *Continental Shelf Research* 20: 479–492.

Chen JF, Xu N, Jiang TJ, Wang Y, Wang ZH. 1999. A report of *Phaeocystis globosa* bloom in coastal water of Southeast China. *Journal of Jinan University (Natural Science)* 20: 124–129 (in Chinese with English abstract).

Corrales RA, Crisostomo R. 1996. Variation of Pyrodinium cyst density in Manila Bay, Philippines. In: Yasumoto T, Oshima Y and Fukuyo Y (eds), *Harmful and toxic algal blooms*. Paris: Intergovernmental Oceanographic Commission of UNESCO. pp 181–183.

Hallegraeff GM. 1993. A review of harmful algal blooms and their apparent global increase. *Phycologia* 32: 79–99.

Hodgkiss IJ, Ho KC. 1997. Are changes in N:P ratios in coastal waters the key to increased red tide blooms? *Hydrobiologia* 352: 141–147.

Hodgkiss IJ, Lu SH. 2004. The effects of nutrients and their ratios on phytoplankton abundance in Junk Bay, Hong Kong. *Hydrobiologia* 173: 213–227.

Karl DM, Letelier R, Hebel DV, Bird DF, Winn CD. 1992. *Trichodesmium* blooms and new nitrogen in the North Pacific gyre. In: Carpenter EJ, Capone DG, Rueter JG (eds), *Marine pelagic cyanobacteria*: Trichodesmium *and other diazotrophs*. Dordrecht: Kluwer Academic Publishers. pp 219–237.

Karl DR, Letelier L, Tupas DJ, Christian J, Hebel D. 1997. The role of nitrogen fixation in biogeochemical cycling in the subtropical North Pacific Ocean. *Nature* 388: 533–538.

Lancelot C, Wassmann P, Barth H. 1994. Ecology of *Phaeocystis*-dominated ecosystems. *Journal of Marine Systems* 5: 1–4.

Lim PT, Usup G, Leaw CP, Ogata T. 2005. First report of *Alexandrium taylori* and *Alexandrium peruvianum (*Dinophyceae) in Malaysia waters. *Harmful Algae* 4: 391–400.

Lomas MW, Glibert PM. 1999. Temperature regulation of nitrate uptake: a novel hypothesis about nitrate uptake and reduction in cool water diatoms. *Limnology and Oceanography* 44: 556–572.

Lugomela C, Lyimo TJ, Bryceson I, Bergman B. 2002. *Trichodesmium* in coastal waters of Tanzania: diversity, seasonality, nitrogen and carbon fixation. *Hydrobiologia* 477: 1–13.

Masuda M, Abe T, Kawaguchi S, Phang SM. 2001. Taxonomic notes on marine algae from Malaysia. VI. Five species of Ceramiales (Rhodophyceae). *Botanica Marina* 44: 467–477.

Nguyen NL, Doan NH. 1996. Harmful marine phytoplankton in Vietnam waters, In: Yasumoto T, Oshima Y, Fukuyo Y (eds), *Harmful and toxic algal blooms*. Paris: Intergovernmental Oceanographic Commission of UNESCO. pp 45–48.

Nguyen NL. 1999. *Trichodesmium erythraeum* bloom. *Harmful Algae News* 19: 13. Available at http://ioc.unesco.org/iocweb/IOCpub/iocpdf/han19.pdf.

Nguyen NL, Doan NH, Nguyen TMA, Ho VT. 2003. A summary of HAB studies in Vietnam, paper presented at Workshop on Red Tide Monitoring in Asian Coastal Waters, University of Tokyo, Tokyo.

O'Reilly JE, Maritorena S, Mitchell BG, Siegel DA, Carder KL, Garver SA, Kahru M, McClain C. 1998. Ocean color chlorophyll algorithms for SeaWiFS. *Journal of Geophysical Research* 103: 24937–24953.

Orton JH. 1923. The so-called "Baccy-juice" in the waters of the Thames oyster-beds. *Nature* 111: 773.

Paerl HW. 1988. Nuisance phytoplankton blooms in coastal, estuarine, and inland waters. *Limnology and Oceanography* 33: 823–847.

Qi YZ, Hong Y, Qian HL, Lu SH. 1992. Problems caused by harmful algal blooms in China. In: IOC Workshop Report No. 94. UNESCO. pp 22–24. Available at http://www.jodc.go.jp/info/ioc_doc/Workshop/w094.pdf.

Qi YZ, Chen JF, Wang ZH, Xu N, Wang Y, Shen PP, Lu SH, Hodgkiss IJ. 2004. Some observations on harmful algal bloom (HAB) events along the coast of Guangdong, southern China in 1998. *Hydrobiologia* 512: 209–214.

Shaw PT, Chao SY. 1994. Surface circulation in the South China Sea. *Deep Sea Research I* 41: 1663–1683.

Smayda TJ. 1997. Harmful algal blooms: their ecophysiology and general relevance to phytoplankton blooms in the sea. *Limnology and Oceanography* 42: 1137–1153.

Smayda TJ. 2000. Ecological features of harmful algal blooms in coastal upwelling ecosystems. *South African Journal of Marine Science* 22: 219–253.

Tang DL, Kawamura H, Dien TV, Lee MA. 2004a. Offshore phytoplankton biomass increase and its oceanographic causes in the South China Sea. *Marine Ecology Progress Series* 268: 3–41.

Tang DL, Kawamura H, Guan L. 2004b. Long-time observation of annual variation of Taiwan Strait upwelling in summer season. *Advance Space Research* 33: 307–312.

Tang DL, Kawamura HD, Hai N, Takahashi W. 2004c. Remote sensing oceanography of a harmful phytoplankton bloom (HAB) off the coast of southeastern Vietnam. *Journal of Geophysical Research* 109: C03014, doi:10.1029/2003JC002045.

Tang DL, Kawamura H, Lee MA, Dien TV. 2003a. Seasonal and spatial distribution of Chlorophyll *a* and water conditions in the Gulf of Tonkin, South China Sea. *Remote Sensing Environment* 85: 475–483.

Tang DL, Kester DR, Ni IH, Qi YZ, Kawamura H. 2003b. *In situ* and satellite observation of a harmful algal bloom and water condition at the Pearl River estuary in late autumn 1998. *Harmful Algae* 2: 89–99.

Tang DL, Ni IH, Kester DR, Müller-Karger FE. 1999. Remote sensing observations of winter phytoplankton blooms southwest of the Luzon Strait in the South China Sea. *Marine Ecology Progress Series* 191: 43–51.

Tang DL, Ni IH, Müller-Karger FE, Liu ZJ. 1998. Analysis of annual and spatial patterns of CZCS-derived pigment concentrations on the continental shelf of China. *Continental Shelf Research* 18: 1493–1515.

Usup G, Pin LC, Ahmad A, Teen LP. 2002. *Alexandrium* (Dinophyceae) species in Malaysian waters. *Harmful Algae* 1: 265–275.

Veldhuis MJW, Wassmann P. 2005. Bloom dynamics and biological control of a high biomass HAB species in European coastal waters: a *Phaeocystis* case study. *Harmful Algae* 4: 805–809.

Wang SF, Tang DL, He FL, Fukuyo Y, Azanza RV. 2008. Occurrences of harmful algal blooms (HABs) associated with ocean environments in the South China Sea. *Hydrobiologia* 596: 79–93.

Wentz FJ, Smith DK, Mears CA, Gentemann CL. 2001. Advanced algorithms for QuikScat and SeaWinds/AMSR. In: International Geoscience and Remote Sensing Symposium (IGARSS'01). IEEE conference proceedings, Sydney, Australia. pp 1079–1081.

Yamamoto T, Hashimoto T, Tarutani K, Kotani Y. 2002. Effects of winds, tides and river water runoff on the formation and disappearance of the *Alexandrium tamarense* bloom in Hiroshima Bay, Japan. *Harmful Algae* 1: 301–312.

Yamamoto T, Okai M. 2000. Effects of diffusion and upwelling on the formation red tides. *Journal of Plankton Research* 22: 363–380.

Zhao H, Tang DL. 2007. Effect of 1998 El Niño on the distribution of phytoplankton in the South China Sea. *Journal of Geophysical Research* 112: C02017, doi:10.1029/2006JC003536

Zhu GH, Ning XR, Cai YM, Liu ZL, Liu ZG. 2003. Studies on species composition and abundance distribution of phytoplankton in the South China Sea. *Acta Oceanologica Sinica* 25: 8–23 (in Chinese, with English abstract).