Phuket marine biological Center Special Publication 22: 39–50 (2000)

PELAGIC CARBON FIXATION AND HETEROTROPHY IN SHALLOW COASTAL WATERS OF SAWI BAY, SOUTHERN THAILAND

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ABSTRACT

Sawi Bay is a shallow, moderately impacted embayment that quickly becomes turbid during strong wind events. Measurements of nutrients, light, and plankton production indicate that while primary production in some bay locations is light-limited, nutrient availability may have some impact on variability of phytoplankton production. Mean depth-integrated phytoplankton production in the bay ranged from 342 to 862 mgC $m^{-2}d^{-1}$ on a typical sunny day and from 223 to 531 mgC $m^{-2}d^{-1}$ on a typical cloudy day. Depth-integrated phytoplankton production (mean: 330 mgC $m^{-2}d^{-1}$) in one of the mangrove creeks was not much different than in Sawi Bay. Extrapolated to the entire bay, daily and annual totals of phytoplankton production were 68 tC and 25,000 tC, respectively. In the wet season, bacterioplankton production was high (mean: 119 mg C $m^{-3}d^{-1}$; range: 34–397 mg C $m^{-3}d^{-1}$) with rapid growth rates and turnover (mean: 7 days). Rapid bacterial activity was reflected in rapid water-column respiration in I Laet Creek (mean: 487 mg C $m^{-3}d^{-1}$) and in the bay proper (mean: 642 mg C $m^{-3}d^{-1}$). Integrated by depth, mean pelagic respiration rates (682 mg C $m^{-2}d^{-1}$ in I Laet Creek; 1490 mg C $m^{-2}d^{-1}$ in the bay) exceeded phytoplankton production by ~ two fold, indicating that Sawi Bay waters were net heterotrophic. The ratio of bacterioplankton to phytoplankton production ranged from 35–87% compared with ratios ranging from 17–30% in other aquatic ecosystems, indicating that bacterial activity was high relative to phytoplankton production in the bay. Both the rapid respiration rates and the bacterioplankton/ phytoplankton production ratios imply that other sources of organic matter (sewage, aquaculture effluent, mangrove debris, river runoff) sustain the high levels of heterotrophic activity in Sawi Bay, at least in the wet season.

INTRODUCTION

The extreme diversity of estuarine types has been a major constraint on elucidating factors controlling phytoplankton production. Generally, the availability of nitrogen is considered to limit phytoplankton production (*e.g.* Boynton *et al.*, 1982; Dortch and Whitledge, 1992). However, some studies have indicated phosphorus (Myers and Iverson, 1981; Harrison *et al.*, 1990) and silicon (D'Elia *et al.*, 1983) limitation of phytoplankton production. In turbid estuaries, phytoplankton production is controlled mainly by the availability of light, although the upper limit may ultimately be determined by the availability of nutrients (Cole and Cloern, 1984; Lohrenz *et al.*, 1990). Cole and Cloern (1987) have demonstrated for several turbid estuaries that reasonable estimates of phytoplankton production can be obtained from field measurements of phytoplankton biomass and light attenuation.

As part of a larger project on carbon fixation and storage in a turbid coastal ecosystem, this study focused on the role of phytoplankton and bacterioplankton on carbon cycling in Sawi Bay, a shallow (2–3 m depth) embayment in southern

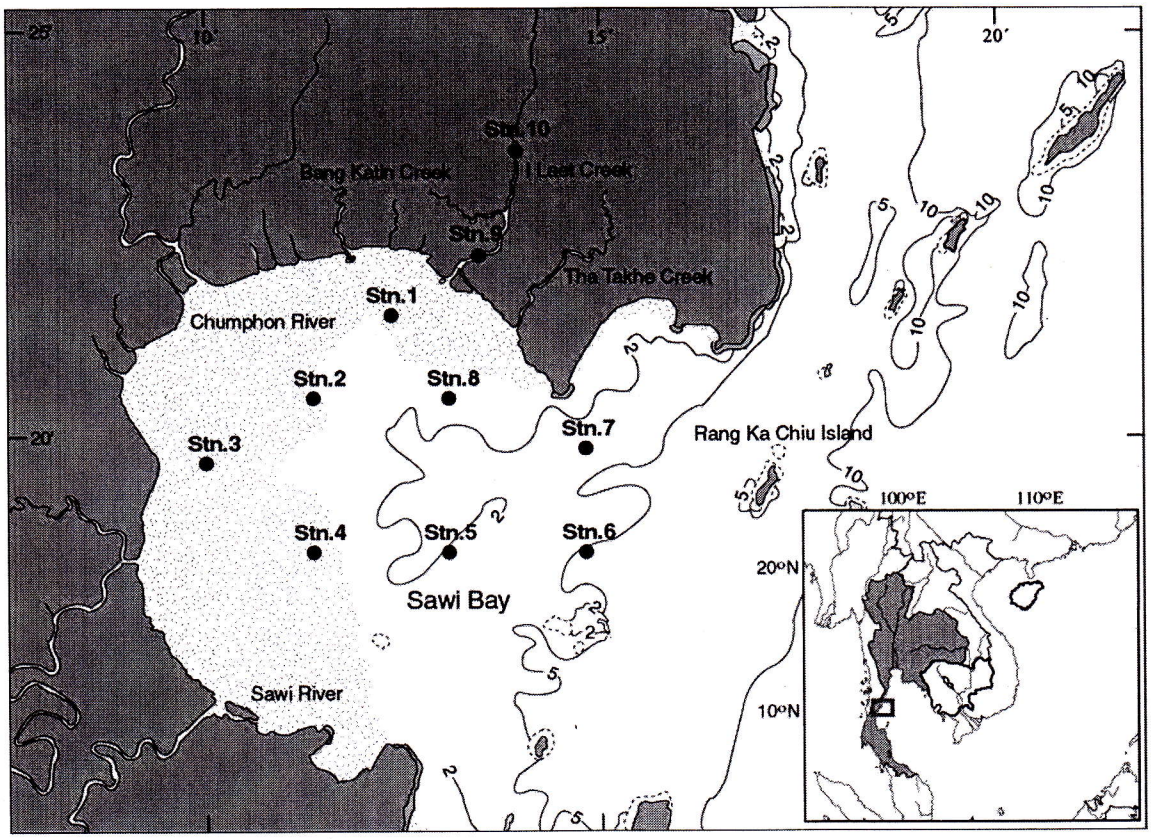

Figure 1 Map of pelagic stations in Sawi Bay and in I Laet Creek. Insert indicates location of Sawi Bay in relation to the southern coast of Thailand

Thailand (Fig. 1). Being shallow, the bay quickly becomes turbid during strong wind events (Wolanski *et al.*, 2000). There is no record of phytoplankton studies in the bay. However, the bay appears nutrient-rich and productive, supporting large-scale green mussel and baitfish fisheries. Considering these circumstances, this study focused on the establishment of the relationship between light and phytoplankton production rate and the relationship between phytoplankton and bacterioplankton activity. Phytoplankton production rates in the whole bay were estimated from the observed distributions of light and phytoplankton biomass measured as chlorophyll.

MATERIALS AND METHODS

Station locations

Ten stations were established within Sawi Bay: eight stations (Stns. 1–8) evenly distributed within the bay proper and two stations at the lower (Stn. 9) and upper (Stn. 10) reaches of I Laet Creek (Fig. 1). Each of these stations was visited for 3–8 day periods in June, October and December 1999 to measure primary production and in April, June and October 1999 to measure the distribution of chlorophyll and light. On each day, water for primary production experiments was collected from the sea surface. Sampling usually took place between 0900 and 1000 hrs.

Measurements for bacterioplankton abundance and production and pelagic respiration were conducted in October 1999 at Stns. 6, 8, 9 and 10 (Fig. 1).

Phytoplankton production

Water collected was dispensed into 100-ml polycarbonate bottles and inoculated with 5–10 μCi of ^{14}C sodium bicarbonate (specific activity: 57 mCi $mmol^{-1}$). Two sets of 3 light- and 2 dark-bottles were prepared for each water sample, set

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on racks and suspended just below the surface and at 1 m depth. The variation in underwater PAR (photosynthetically active radiation) during incubation was monitored using a natural fluorescence meter (Biospherical Instrument INF-300). After 2–3 hr incubation, bottles were placed in a dark box and brought back to the field laboratory. The contents of the bottles were filtered through Whatman GF/F glass fiber filters. These filters were placed in scintillation vials and acidified with 100 µl of 1 N HCl to remove excess ^{14}C bicarbonate (Lean and Burnison, 1979). Radioactivity left on the filters was measured by liquid scintillation spectrometry. Phytoplankton production rates were calculated according to Parsons *et al.* (1984).

Water was also filtered (25–100 ml) through Whatman GF/F glass fiber filters and the filters were kept frozen until laboratory analysis by fluorometry for chlorophyll-a (Strickland and Parsons, 1972). Replicate 10-ml sub-samples were filtered through 0.4-µm glass fiber filters (Sartorius), kept frozen and analysed in the laboratory for dissolved inorganic nutrients using a multi-channel autoanalyzer (Ryle *et al.*, 1981). In June, 20-l of water was filtered through a 20-µm plankton net, preserved with neutralized formalin (5% final concentration) and kept for later counting of phytoplankton cells (Ayukai, 1992).

Distributions of chlorophyll and light

At each station, vertical profiles of salinity, temperature and stimulated fluorescence were measured using a SeaBird CTD profiler with a WetLab fluorometer. The CTD cast was followed by a cast using the fluorescence meter to measure the profile of underwater PAR and to determine the light attenuation coefficient. In April 1999, the light attenuation coefficient was estimated from Secchi depth measurements.

Bacterioplankton Abundance and Production

Quadruplicate 20 ml samples for bacterioplankton abundance were taken immediately below the surface at each location using a 50-ml sterile plastic syringe. Each sample was gently decanted into a sterile glass scintillation vial and fixed with 500–1000 µl filtered, buffered formaldehyde. Samples were kept cool and dark until return to the laboratory. Bacteria were stained and counted using the DAPI method (Velji and Albright, 1993). Bacterial abundance were converted to biomass assuming 25 fgC cell^{-1} (Bell, 1993).

Bacterioplankton production was estimated via incorporation of tritiated thymidine (Bell, 1993). Briefly, 15–20 ml water samples (n= 4–5) collected in the same manner as for cell counts were spiked with 18.4 µl of undiluted thymidine (specific activity: 41.0 Ci mmol^{-1}) to give a final concentration of ~30 nM thymidine. The samples were incubated for 25 min in clear acrylic tubes just below the surface. Triplicate blanks containing 1 ml HCHO were run concurrently. Initial isotope dilution and time course experiments indicated that a final thymidine concentration of 30nM and an incubation time of 25 min were optimal. After incubation, samples were processed as described in Bell (1993) to estimate isotope incorporation into bacterial DNA.

Recovery efficiency was 93 %. Internal standards were used to correct for quenching. The rate of thymidine incorporation was converted to carbon production assuming a thymidine conversion factor of 2×10^{18} cells mol^{-1} and assuming 25 fgC cell^{-1} (Bell, 1993). Specific daily growth rate (µ) was calculated by dividing the mean production estimates by the mean standing crop.

Oxygen flux measurements

Pelagic respiration was estimated from rates of oxygen consumption in unfiltered water taken at each location from immediately below the surface (Alongi *et al.*, 1999). Water from each location was returned to the field laboratory and six blackened glass bottles containing a magnetic stirrer bar were gently filled. An oxygen probe was sealed into a custom-made cap on the top of each bottle. The bottles were then placed into a magnetic stirrer within a large plastic bin containing ambient seawater. The stirrers were run using propellers powered by an electric water pump. The water in each bottle was stirred continuously. Each oxygen probe was connected to a TPS Model WP82 oxygen meter. The electrodes were calibrated as per factory instructions. The experiments were incubated in the shade just long enough (normally 12–18 hr) so as to obtain a linear decline in oxygen

concentration while minimizing bottle effects. Bin water was replenished often to mimic in situ temperatures. The data were converted to carbon equivalents assuming an RQ of 1.

RESULTS AND DISCUSSION

The variation in chlorophyll concentrations (Fig. 2) in outer Sawi Bay (2.7 to 5.1 mg m^{-3}, Stn. 8) was small relative to that in the inner bay (2.6–12.8 mg m^{-3}, Stn. 1) where peak chlorophyll and cell densities were measured. Peak phytoplankton densities were most likely a reflection of enhanced phytoplankton growth in response to nutrients released from resuspended sediments or from pulses of creek outflow. Cell densities in the outer bay ranged from 5,000–15,000 cells l^{-1}, but cell densities in the inner bay varied 8-fold, from 6,000 to 48,000 cells l^{-1} (Fig. 3). Diatoms such as *Nitzschia* spp., *Pseudonitzschia* spp. and *Chaetoceros* spp., dominated the phytoplankton community. Some dinoflagellate species, such as *Ceratium* spp., *Protoperidinum* spp. and *Prorocentrum* spp., occurred in many samples but

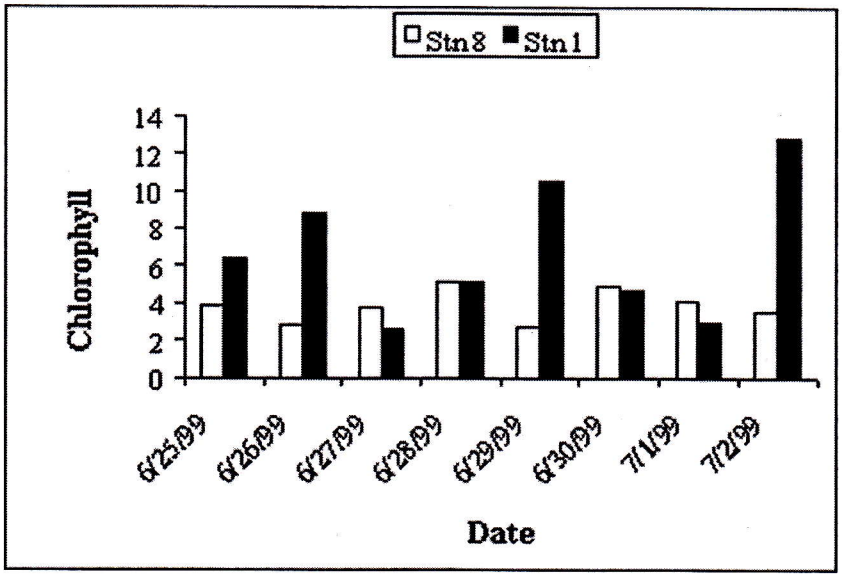

Figure 2 Variation in mean chlorophyll-a concentration (mg m^{-3}) at Stn. 1 (inshore) and Stn. 8 (offshore) in Sawi Bay, late June-early July 1999.

Table 1 Mean nutrient concentration (μM) in the phytoplankton production experiments in Sawi Bay and I Laet Creek. Values are mean±1S.E.

		PO_4	NO_3+NO_2	NH_4	Si
Sawi Bay					
Jun 99	Stn. 1	0.17±0.08	0.25±0.05	2.30±0.91	47.69± 9.34
	Stn. 8	0.18±0.08	0.14±0.13	1.23±0.75	36.72± 5.11
Oct. 99	Stn. 1	0.09±0.04	0.21±0.13	1.02±0.45	18.70± 8.09
	Stn. 8	0.11±0.03	0.32±0.29	0.89±0.17	18.58±17.77
I Laet Creek					
Oct 99	Stn. 9	0.41±0.09	5.63±3.53	6.21±1.11	112.78±27.62
	Stn. 10	0.50±0.04	7.07±3.54	8.98±3.12	143.36± 8.66
Dec 99	Stn. 9	0.19±0.13	3.72±0.58	2.37±1.73	113.99±43.61
	Stn. 10	0.29±0.09	5.50±1.17	4.06±0.62	152.25±15.31

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were rare (500 cells l^{-1}). Size fractionation of some samples showed that picoplankton accounted for only 11–28 % of the total phytoplankton population.

The relationship between PAR ($\mu E\ m^{-2}s^{-1}$) and assimilation number, AN (mgC mg $chl^{-1}h^{-1}$), was expressed using the following Michaelis-Menten type equation (Fig. 4):

$$AN = (12.38 \times PAR) / (627 + PAR),\ r^2 = 0.699$$

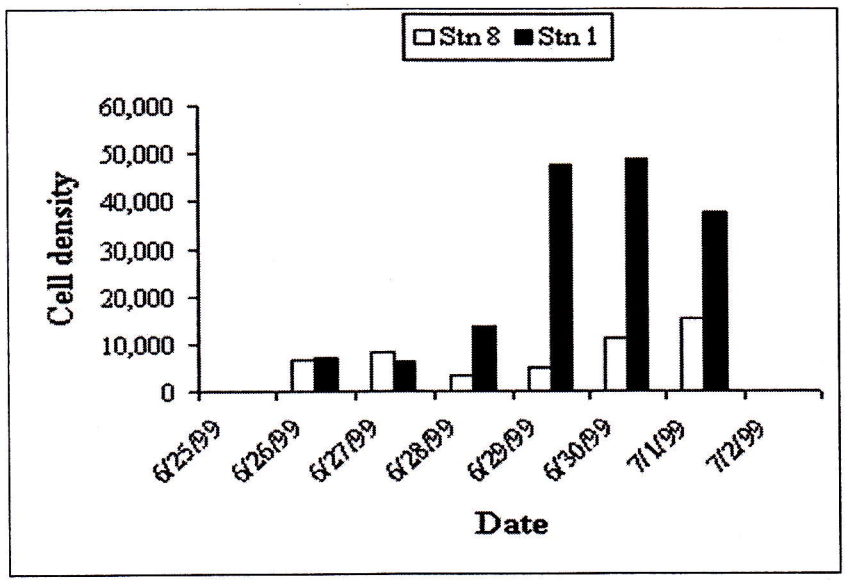

Figure 3 Variation in mean phytoplankton cell density (cells l^{-1}) at Stn. 1 (inshore) and Stn. 8 (offshore) in Sawi Bay, late June-early July 1999.

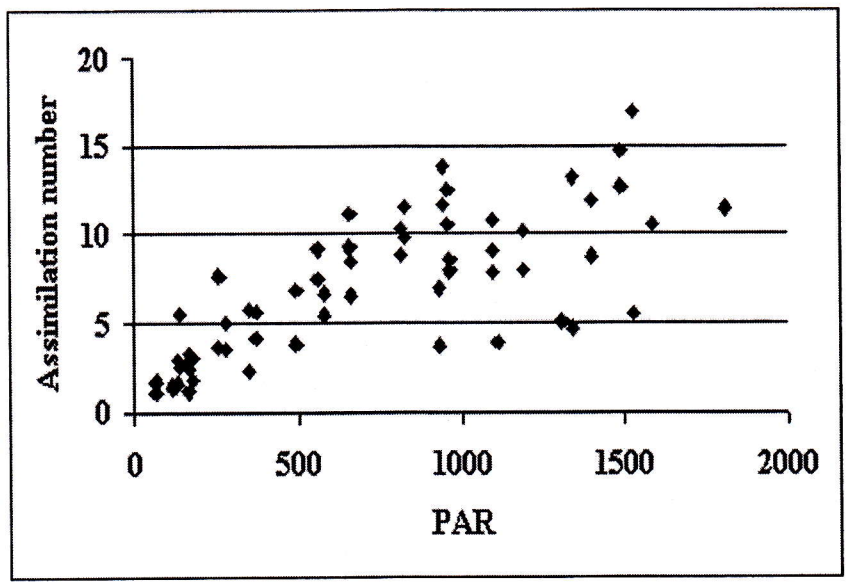

Figure 4 Relationship between underwater PAR (mE m^{-2} s^{-1}) and assimilation number, AN (mgC $mgChl^{-1}$ h^{-1}) for phytoplankton populations in Sawi Bay. Data from all seasons and stations combined. See text for Michaelis-Menten type equation.

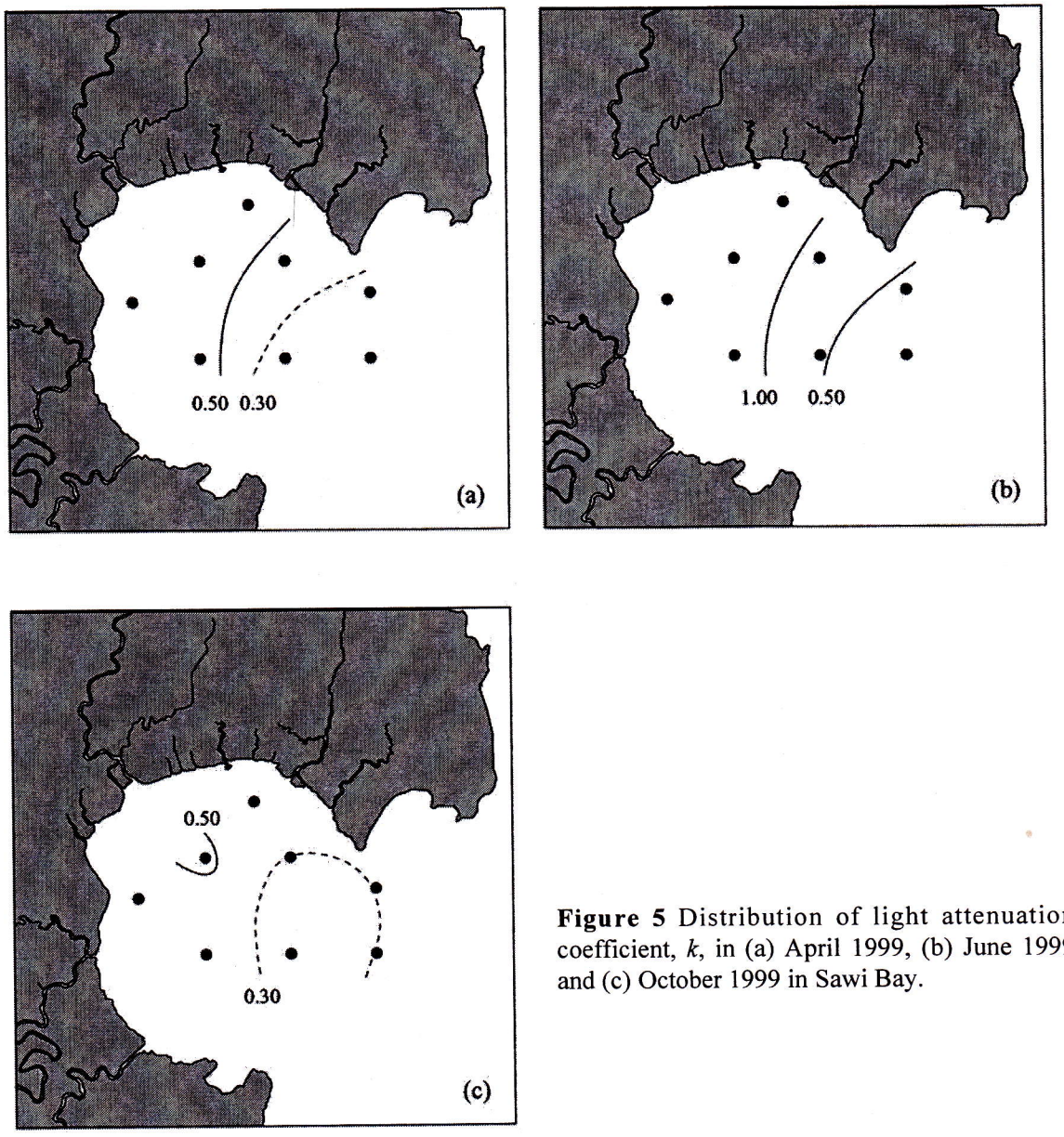

Figure 5 Distribution of light attenuation coefficient, *k*, in (a) April 1999, (b) June 1999 and (c) October 1999 in Sawi Bay.

There are large deviations from data points around this equation. This may reflect the fact that the experiments in Sawi Bay and I Laet Creek were conducted over a 6 mo period, and may represent changes in light response characteristics of different phytoplankton populations over time. There is also a practical problem in conducting phytoplankton production experiments in such a turbid environment—occasional samples contained a large amount of suspended sediments causing coagulation of particulate matter during the incubations.

Nutrient concentrations in the bay were low (Table 1) compared with nutrient concentrations in other mangrove creeks and estuaries in Asia (Alongi *et al.*, 1992), indicating some possibility of nutrient limitation of phytoplankton production. This is somewhat contrary to the expectation that the availability of nutrients would be of minor importance in determining the variability of phytoplankton production in such a shallow-water bay. Nutrient concentrations (mainly nitrate +

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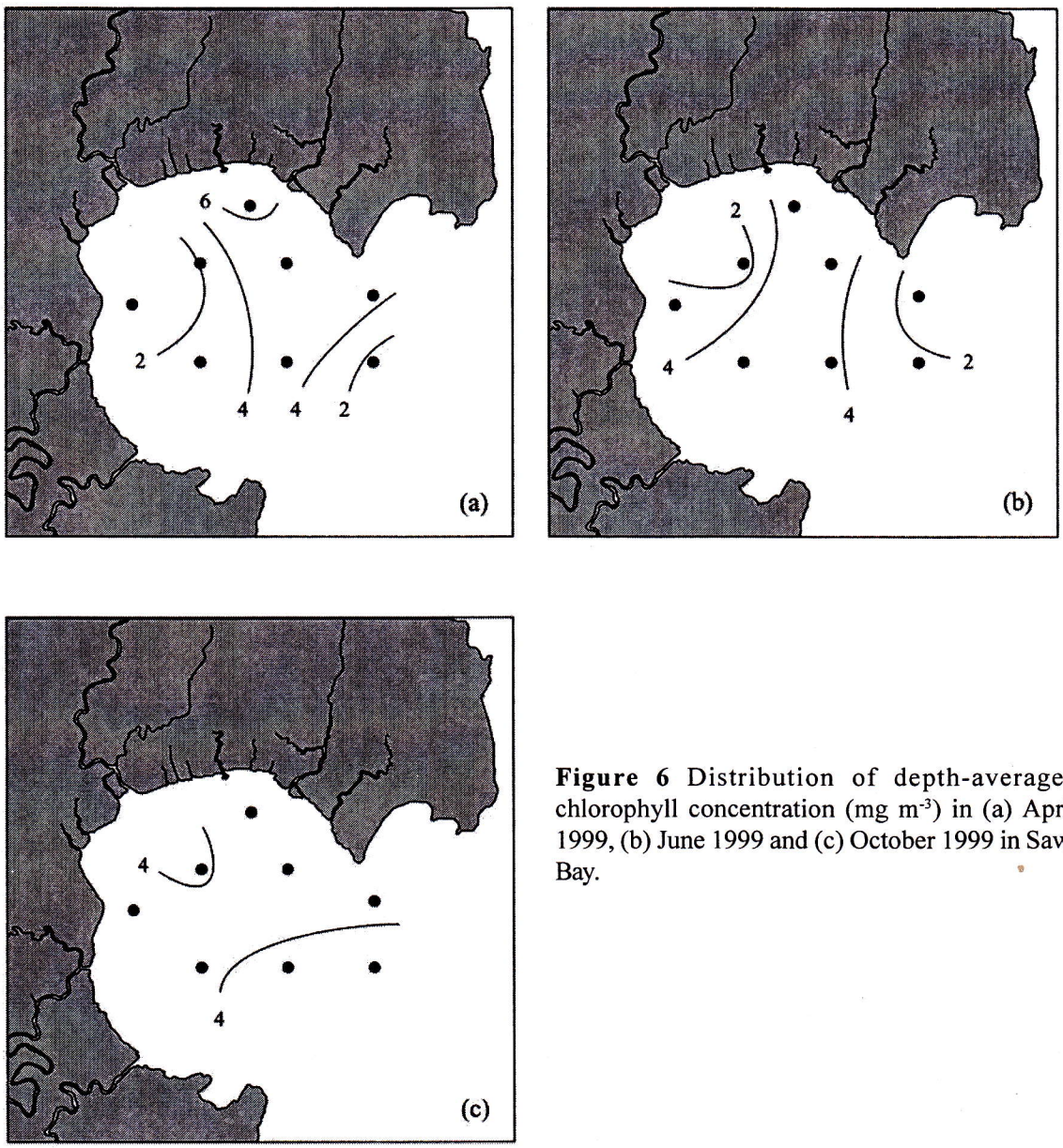

Figure 6 Distribution of depth-averaged chlorophyll concentration (mg m^{-3}) in (a) April 1999, (b) June 1999 and (c) October 1999 in Sawi Bay.

nitrite) in the creeks were considerably higher than in Sawi Bay (Ayukai *et al.*, 2000). Consequently, the dissolved N:P ratio was lower in the bay than in the creeks.

The meaning of molar nutrient ratios in relation to the Redfield ratio has been debated repeatedly (Bauerfeind *et al.*, 1990, Fisher *et al.*, 1992), but it appears that the availability of nitrogen considerably exceeds the demand of phytoplankton, especially in I Laet Creek. I Laet Creek was heavily used for shrimp aquaculture in the past, so it is likely that the effluent from shrimp ponds as well as untreated sewage from fishing villages lining the creek has significantly altered nutrient stoichiometry in the creek.

The measurements of light attenuation coefficient (k) in Sawi Bay showed that relatively turbid water was present in the inner bay, at Stns. 1–4 (Fig. 5) particularly during the wet season in October 1999 (Fig. 5c). This was partly due to the discharge of freshwater and sediments from the Chumpon and Sawi Rivers, but due largely to

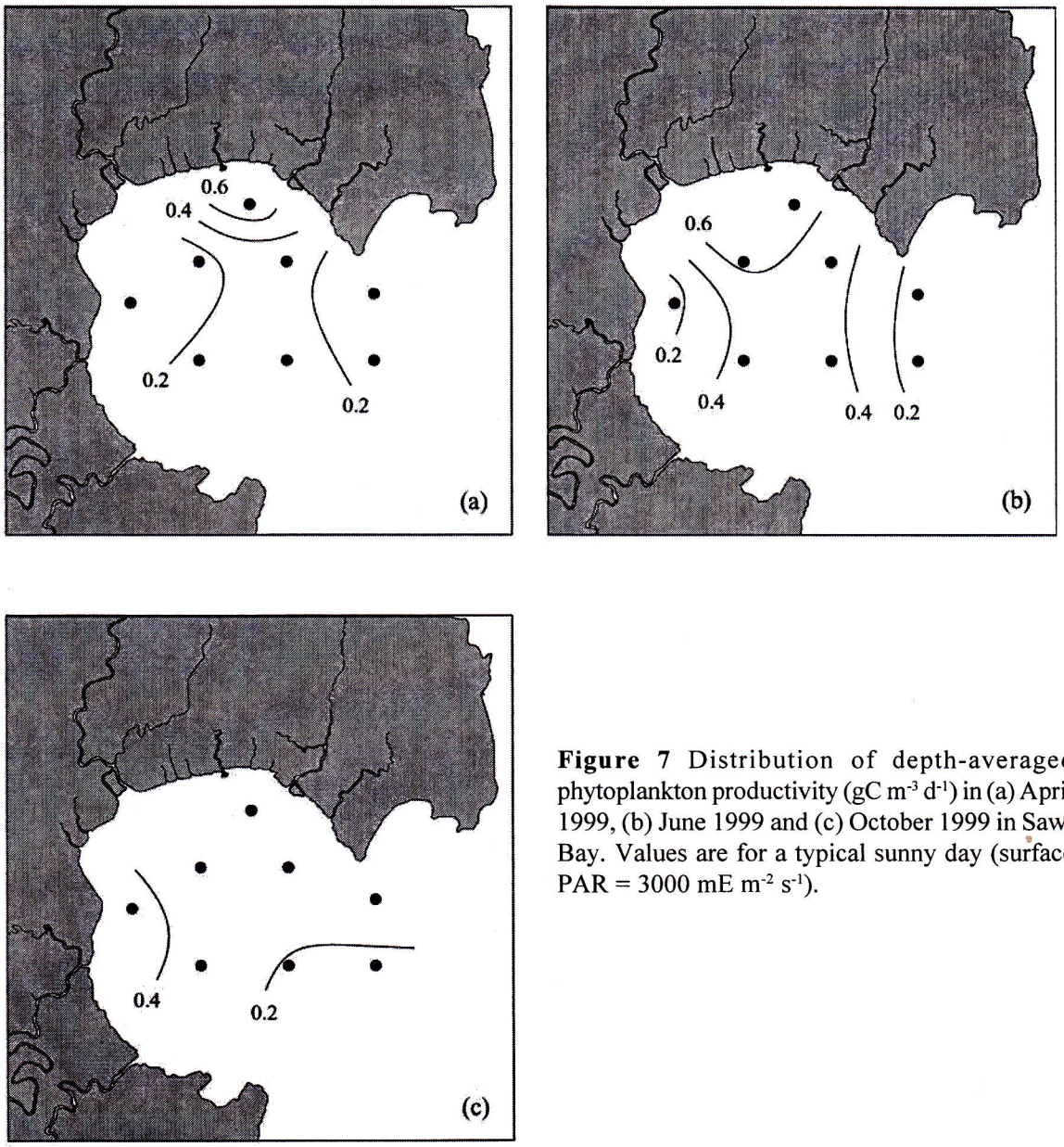

Figure 7 Distribution of depth-averaged phytoplankton productivity (gC m^{-3} d^{-1}) in (a) April 1999, (b) June 1999 and (c) October 1999 in Sawi Bay. Values are for a typical sunny day (surface PAR = 3000 mE m^{-2} s^{-1}).

resuspension of bottom sediments by strong winds (Wolanski *et al.*, 2000).

The area of highest chlorophyll concentration was most often found outside the turbid inshore boundary in the middle of the bay (Fig. 6). In April, the highest chlorophyll concentration was observed at Stn. 1, close to I Laet Creek. This suggests that the high chlorophyll value observed was due to flushing of chlorophyll-rich creek water during low tide(Ayukai *et al.*, 2000)

Phytoplankton production rates were estimated based on the field measurements of chlorophyll and light, and using the empirical relationship between PAR and assimilation number,

$$P_z = C_z \times [12.38 \times (PAR_0 \times e^{(-kz)})] / (627 + (PAR_0 \times e^{(-kz)})]$$

where P_z is phytoplankton production rate at depth z, C_z is chlorophyll concentration at depth

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z, PAR_0 is photosynthetically active radiation just below the sea surface, k is the light attenuation coefficient. For PAR_0, the values on typical sunny and cloudy days (3,000 and 1,000 μE $m^{-2}s^{-1}$, respectively) were chosen. Like the distribution of chlorophyll-a, higher values of depth-averaged phytoplankton production rate were most often found in the middle to northern reaches of Sawi Bay (Fig. 7).

Mean depth-integrated phytoplankton production in Sawi Bay ranged from 342 to 862 mgC $m^{-2}d^{-1}$ on a typical sunny day and from 223 to 531 mgC $m^{-2}d^{-1}$ on a typical cloudy day (Table 2). Since the depth of individual stations affects these values, the distribution of depth-integrated phytoplankton production rate becomes somewhat different from that of depth-averaged phytoplankton production rate, with the highest value occurring in the outer bay rather than in the middle of the bay (Table 2). Low depth-integrated phytoplankton production rates in June were likely due to turbid water occupying a larger area of the bay.

The water in I Laet Creek was nutrient-rich, particularly in the availability of nitrogen (Table 1). Chlorophyll concentrations in the creek were slightly higher (5.1 and 13.5 mg m^{-2}; Table 3) than in the inner bay (5.66 and 25.29 mg m^{-2}; Fig. 2). Depth-integrated phytoplankton production rates in the creek were not significantly different than in the bay, with a mean value of 330 mgC m^{-2} d^{-1} (Table 3). Water was far more turbid in the creeks than in the bay, so presumably, the light limitation of phytoplankton production was more

Table 2 Depth-integrated phytoplankton production rate (mgC $m^{-2}d^{-1}$) in Sawi Bay. Values were estimated for typical sunny and cloudy days (surface PAR, 3,000 and 1000 mE $m^{-2}s^{-1}$, respectively).

		Stn. 1	Stn. 2	Stn. 3	Stn. 4	Stn. 5	Stn. 6	Stn. 7	Stn. 8	Grand mean
Apr. 99	PAR3000	451	230	20	433	1,389	784	1,989	568	733
	PAR1000	311	147	14	268	917	401	1,070	353	435
Jun. 99	PAR3000	190	81	275	356	647	459	167	562	342
	PAR1000	129	53	168	230	438	311	103	350	223
Oct.99	PAR3000	402	338	363	421	958	896	2,365	1,154	862
	PAR1000	267	220	249	281	583	484	1,391	777	531

Table 3 Light attenuation coefficient (k), chlorophyll stock (mg m^{-2}) and depth-integrated phytoplankton production rate (mgC $m^{-2}d^{-1}$) in I Laet Creek Values were estimated for typical sunny and cloudy days (surface PAR, 3000 and 1000 mE $m^{-2}s^{-1}$, respectively) . NA= not measured.

			Depth (m)	k	Chl	Production	
						PAR3000	PAR1000
Oct. 99	I	Stn. 9	2.4	3.5	NA	NA	NA
		Stn. 10	1.3	3.8	NA	NA	NA
	II	Stn. 9	2.4	3	NA	NA	NA
		Stn. 10	1.3	2.8	NA	NA	NA
	III	Stn. 9	2.5	5.1	25.29	439	239
		Stn. 10	1.3	3.9	10.65	424	235
Dec. 99	I	Stn. 9	2.1	3.9	15.03	384	211
		Stn. 10	1.4	2.6	5.66	281	159
	II	Stn. 9	2.2	3.5	12.33	357	194
		Stn. 10	1.4	3.2	9.30	374	201
	III	Stn. 9	2.5	4.3	11.86	342	189
		Stn. 10	1.5	4.4	20.30	713	407

Table 4 Abundance (cells ml^{-1}), carbon production (mgC $l^{-1}d^{-1}$= mg C $m^{-3}d^{-1}$), daily specific growth rate (μ, d^{-1}) of bacterioplankton in I Laet Creek (Stns 9 and 10) and in Sawi Bay (Stns 6 and 8) in October 1999. BP/PP ratio = ratio of bacterial production to primary production (both depth-integrated, mg C $m^{-2}d^{-1}$). Values are mean ± 1 S.E.

Station	Date	Bacterial Numbers	Bacterial Production	μ	BP/PP ratio
Stn. 6	20 October	9.3 (±0.2)×10^5	50 ± 4	2.2	46%
	22 October	1.1 (±0.02)×10^6	103 ± 34	3.7	
	24 October	9.2 (± 0.01)×10^5	36 ± 4	1.6	
Stn. 8	20 October	9.7 (± 0.6)×10^5	397 ± 15	16.4	35%
	22 October	9.9 (± 0.06)×10^5	83 ± 6	3.4	
	24 October	8.9 (± 0.1)×10^5	34 ± 5	1.5	
Stn. 9	21 October	2.0 (± 0.08)×10^6	193 ± 3	3.9	87%
	25 October	9.2 (± 0.3)×10^5	52 ± 2	2.3	
Stn. 10	19 October	2.8 (±0.1)×10^6	120 ± 10	1.7	48%
	21 October	4.7 (±1.8)×10^6	167 ± 13	1.4	
	25 October	9.2 (±0.2)×10^6	77 ± 2	0.3	

Table 5 Depth-integrated water column respiration rate (mgC $m^{-2}d^{-1}$) in Sawi Bay (Stns. 6 and 8) and I Laet Creek (Stn. 10) in October 1999. Values are mean±1S.E.

	Date	Respiration rate
Sawi Bay		
Stn. 8	18 Oct 99	317 ± 38
Stn. 8	20 Oct 99	1589 ± 50
Stn.8	24 Oct 99	567 ± 26
Stn.6	22 Oct 99	3490 ± 133
	Grand mean =	1490 ± 510
I Laet Creek		
Stn. 10	19 Oct 99	689 ± 20
Stn. 10	21 Oct 99	889 ± 30
Stn. 10	25 Oct 99	469 ± 16
	Grand mean =	682 ± 70

severe in the creek. The mean value of depth-integrated phytoplankton production in Sawi Bay was 520 mgC $m^{-2}d^{-1}$, similar to or slightly lower than those reported for other tropical mangrove creeks and estuaries (Robertson and Blaber, 1992). Extrapolated to the entire bay (total water area: 130 km^2), daily and annual totals of phytoplankton production are 68 tC and 25,000 tC, respectively.

In October 1999, bacterioplankton densities and production (Table 4) and water-column respiration rates (Table 5) were measured at four phytoplankton production stations. Bacterioplankton densities were, on average, greater within I Laet Creek (Stns. 9 and 10) than within the bay proper, probably a reflection of higher nutrient and particle loads within the creek. Bacterioplankton production rates varied at each site from day-to-day, most likely in relation to the state of the tide during sampling. Specific growth rates of bacteria were very rapid (μ ranged from 0.2–16.4) with a grand mean turnover time of 7 hrs. In comparison with other tropical estuaries, our bacterioplankton data indicate low- to mid-range standing stocks but high rates of production and turnover (Robertson and Blaber, 1992; Ducklow and Shiah, 1993; Robertson *et al.*, 1993; 1998).

The rapid rates of bacterioplankton growth are reflected in rapid pelagic respiration rates. Mean depth-integrated respiration rates averaged 682 ± 172 mg C $m^{-2}d^{-1}$ in I Laet Creek and 1490 ± 1249 mg C $m^{-2}d^{-1}$ in the bay proper, converted to carbon equivalents (Table 5). The comparison of these values with depth-integrated phytoplankton production rates (Table 2) suggests that the consumption of organic carbon exceeded the production of fixed carbon throughout the bay during the wet season.

A comparison of the ratio of bacterioplankton to phytoplankton production (Table 4) indicates a greater proportion (48–87%) of bacterial

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production relative to primary production in creek waters compared with somewhat lower (35–46%) ratios in the bay proper. These ratios are greater than those estimated for many estuaries (17%, Ducklow and Shiah, 1993) and marine and freshwater bodies (30%, Cole *et al.*, 1988). This can be reasonably interpreted as high bacterial activity relative to the amount of primary production in Sawi Bay. This may be due to several interrelated factors, including enhancement of bacterial growth associated with untreated sewage and crude processing of fish in villages lining the creeks, as well as inputs from shrimp ponds, green mussel and baitfish fisheries, mangroves, and agricultural runoff from adjacent catchments. Assuming a bacterial conversion efficiency of 50%, bacterioplankton in bay water would be utilizing ~70–92% of the primary production on a daily basis. In creek water the figure is >100%, indicating that other sources of organic matter (as listed above) sustain the measured rates of bacterioplankton growth and production, at least in the wet season.

ACKNOWLEDGEMENTS

This study was supported by funds provided by the Kansai Electric Power Company of Japan. The authors thank Paul Dixon, Cassie Payn and Cary McLean at the Australian Institute of Marine Science and colleagues from Chulalongkorn University for their assistance. Diane Brinkman and the staff of the AIMS Analytical Services analysed the chlorophyll and nutrient samples. Contribution No. 1028 from the Australian Institute of Marine Science.

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