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Spatial variability of phytoplankton production and the implications of its controlling mechanisms in the coastal zone near the river mouth of the Lanyang Hsi

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Abstract. Spatial patterns of phytoplankton properties, including primary production, chlorophyll a concentrations and normalized production indices in the coastal zone near the river mouth of the Lanyang Hsi were investigated during high tide in September of 1994. Concentrations of inorganic nutrients (nitrate and phosphate) and particulate organic carbon were also measured simultaneously. Three types of water— including river mouth water, seawater, and mixed water —were categorized due to the patchiness of measured variables in the study area. Extremely low values of phytoplankton properties observed in the nutrient-laden and turbid river mouth water indicates that light intensity is the major limiting factor on photosynthesis processes. In contrast, nutrient availability may limit the growth of phytoplankton in the seawater area where nutrient concentrations were lower than the half saturation constants for nutrient uptake. Nutrient data which deviated from the conservative mixing line indicated that the mixed water area may be a source of nutrients via sediments diagenensis processes. The coincidence of the high nutrient concentrations and high phytoplankton properties in the mixed water area suggests phytoplankton growth rates are probably not limited by nutrient supply. Since the mouth of the Lanyang Hsi is very narrow and shallow, nutrient-laden river water can be rapidly mixed with seawater. The relatively short residence time of riverine nutrients combined with the low phytoplankton activities in the river mouth may lead to more nutrients available for the growth of phytoplankton in the marine part.

Keywords: Coastal zone; Inorganic nutrients; Phytoplankton growth rates; Spatial variability; Tide; Turbidity; Wave.

Introduction

Studying the temporal and spatial variability of primary production and its controlling mechanisms is essential to understand the biogeochemical cycle of carbon in the ocean (Cullen et al., 1992; Knauer, 1991; Longhurst and Harrison, 1989). Phytoplankton constitute the base of the marine food webs and thus may affect the dynamics of higher trophic levels such as fishery yields due to the variability in their biomass and production. More importantly, the sinking of dead phytoplankton into the deep ocean (i. e. export production) acts as an important sink for atmospheric CO_2 (i.e. the biological pump). When compared with the open ocean, the coastal and estuarine ecosystems may be much smaller, either in terms of area or volume, but the amount of organic carbon exported to the deep ocean (13.7×10^{15} ton C y^{-1}) through these systems can be equal to that of the open ocean system (13.2×10^{15} ton C y^{-1}, Berger et al., 1989; Bienfang and Ziemann, 1992). In recognition of this, several large inter-disciplinary research programs, such as LMER (Land Margin Ecosystem Research) and LOICZ (Land-Ocean Interactions in the Coastal Zone) have been initiated to address the importance of estuarine and coastal ecosystems.

From a scaling point of view, there are two basic strategies for studying phytoplankton properties (biomass and production) in coastal and estuarine ecosystems. One is to address the spatial variability by holding the time factor constant (i. e. this study, see below), and the other is to investigate the temporal variability emphasizing the changes at diel, seasonal, and interannual scales (see Malone, 1991 for review). Both types of investigation are essential for the study of coastal ecology; however, until recently, information about them was quite rare in Taiwan.

Many studies have demonstrated that the plankton community's spatial variability is usually most intense at the margins of land and ocean and tends to be correlated with physical and hydrographic factors (see Mackas et al., 1988 for review). The regulation of the planktonic ecosystem by chemical and physical processes and the form and intensity of this dependence are often strongly signaled in the spatial distribution patterns of plankton properties. Light, temperature, nutrient availability, and zooplankton grazing are the four major factors considered important in regulating phytoplankton properties in aquatic ecosystems (for review, see Cullen et al., 1992). The spa-

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tial distribution patterns of these four factors can be quite heterogeneous in coastal systems under the influence of physical forces such as waves and tides. From a physiological and ecological point of view, coastal ecosystems may be a good experimental ground to investigate controlling mechanisms on phytoplankton structure (i.e. species composition) and function (i.e. production and turn-over rates).

To address the necessity of integrating physical and chemical data for the interpretation of the spatial variability of the biological results, we conducted a field survey on the coast near the mouth of the Lanyang Hsi to examine how phytoplankton properties were related to the spatial distribution patterns of inorganic nutrients and the physical forces such as tides and waves. The volume of data obtained from one cruise might be low, but the results and implications derived could complement those of the ongoing LOICZ program in Taiwan.

Materials and Methods

Study Area and Sampling

The Lanyang Hsi, located in the northeastern part of Taiwan (Figure 1), is a typical subtropical island-type river with high precipitation (3,000 mm y^{-1}), a small drainage area, and a steep slope (mean gradient 1 : 21; Kao, 1995). The Lanyang Hsi is about 70 km in length and 0.5 km in width with a drainage basin area of 820 km^2. The river mouth is quite narrow and shallow (<2 m). Freshwater from the Lanyang Hsi discharges into this area and mixes with seawater very quickly (Kao, 1995). This study was conducted in September of 1994 during high tide. A total of 40 stations were deployed in an area of 3.0 × 4.5 km^2 (Figure 1) so the spatial variability of measured variables (see below) could be analyzed on a finer scale. Primary production and chlorophyll a concentrations were measured at every other station. Surface water was collected by clean 2.0 liter polycarbonate bottles. Surface water temperature was uniformly distributed within the study area ranging from 23 to 25°C. Water depth recorded by sonar increased seaward from <5 to 75 m. In addition, all variables inside the river mouth were measured at the Gor Mar Lang Bridge (station G; Figure 1) which was about 500 m away from the river mouth.

Primary Production

The phytoplankton photosynthesis rate was measured using the ^{14}C-HCO$_3^-$ assimilation method (Parsons et al., 1984). For details see also Shiah et al. (1995). In brief, seawater samples collected before dawn were filtered through 200 μm nylon mesh to remove large zooplankton. Immediately thereafter, aliquots of 250 ml water samples were transferred to polycarbonate bottles, including three clear bottles and one dark one, and then inoculated with 0.1 ml ^{14}C-HCO$_3^-$ solution (final specific activity, 10 μCi). One clear bottle was immediately filtered as the time zero sample. Duplicate light bottles and one dark bottle were incubated at sea surface light intensity (i.e. 100% I_0) in a plastic tank maintained at ambient temperature with surface seawater running through. All samples from 21 sampling stations were collected in one night. Neither light intensity nor PAR (photosynthetic available radiance) were monitored during the cruise. Following retrieval after dusk, the water samples were filtered through 25 mm GF/F filters using vacuum <100 mmHg to avoid damage to cells. The filters then were placed in scintillation vials with 0.5 ml of 0.5 N HCl to remove residual ^{14}C-HCO$_3^-$. After being returned to the laboratory, the vials containing filters were left open and dried in a hood at room temperature overnight. Samples were counted in a liquid scintillation counter (Packard 1,600) after addition of 10 ml scintillation cocktail to the vials. Normalized production index (P^B; mgC mgChl^{-1} h$^{-1)}$was calculated by dividing production (mgC m^{-3} d^{-1}) by chlorophyll a concentration (mgChl m^{-3}) and daylight incubation time (i.e. 12 h).

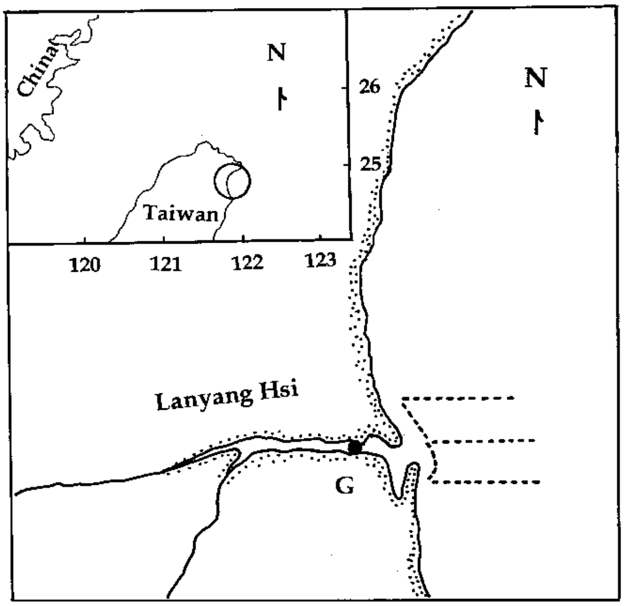

Figure 1. Map of the study area showing sampling stations. Dashed lines indicate the four transects with 10 sampling stations along each transect. G, sampling station at the Gor Mar Lang bridge.

Salinity, Chlorophyll a, Particulate Organic Carbon, Nitrate and Phosphate

Salinity samples were measured with an Autosal salinometer as practical salinity units (psu). Chlorophyll a (Chl.), nitrate and phosphate concentrations were measured following the methods of Parsons et al. (1984). Water samples for Chl. measurements were filtered through 47 mm Whatman GF/F filter sand then stored at -20°C. Chl. concentrations were determined fluorometrically. The filters were ground in 10 ml 90% acetone followed by extraction in a 4°C shaking incubator for 2 h. After centrifugation at 1000 rpm for 5 min, Chl. concentrations in the supernatant were measured on a Turner fluorometer (model 10-AU-005). Water samples (0.5 liter) for particulate organic carbon (POC) measurement were filtered through 200 µm mesh to remove zooplankton and then Whatman 25 mm GF/F filters. After filtration, samples were wrapped in aluminum foil and stored at 4°C. Both filters and aluminum foil were pre-combusted at 550°C for 1 h before filtration processes. POC concentrations were measured by combustion method (HORIBA) after samples were dried and acid-fumed. Filtrates for inorganic nutrient analyses were collected with polyethylene bottles and frozen in liquid N_2 immediately. Nitrate concentrations were determined by reducing nitrate to nitrite with a cadium wire which was activated with a copper sulfate solution, and the nitrite was converted to the pink azo dye for colorimetric determination. Phosphate concentrations were measured by mixing seawater samples with a composite reagent containing molybdic acid, ascorbic acid, and trivalent antimony. The resulting blue solution then was measured by spectrophotometer at 880 nm.

Results

As Figures 2a–c show, the spatial patterns of salinity and nutrient concentrations in the coastal water outside the Lanyang river were quite heterogeneous. Basically, the coastal water could be categorized into three types according to distinct physical, chemical, and biological characteristics. The mesohaline river mouth was characterized by low salinity (19–25 psu) and high concentrations of NO_3^- (>10 µM) while concentrations of NO_3^- in seawater (>32 psu) were low (most values < detection limit of 0.1 µM; Figure 3a). A water mass with intermediate salinity (25–31 psu) and high concentrations of NO_3^- was observed at the north and northeast of the study area. Since there are no other rivers flowing into this area and it was high tide when the survey was conducted, we believed that this water mass (i.e. the mixed water) was derived from the Lanyang river which had been isolated and then mixed with seawater that was moving northwestward during high tide.

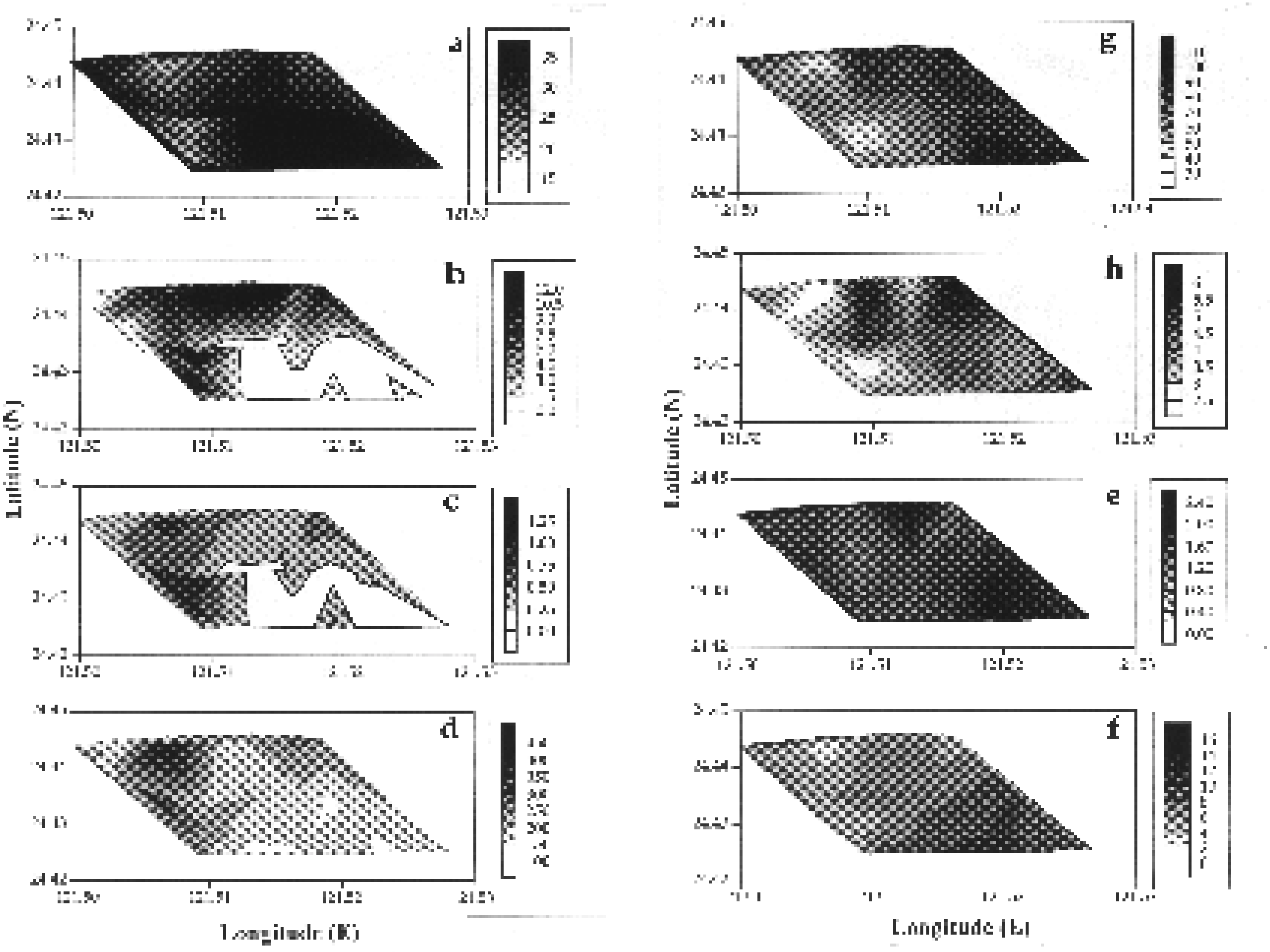

Figure 2. Spatial distribution patterns of salinity (a, psu), nitrate (b, µM), phosphate (c, µM), particulate organic carbon (d, mgC m^{-3}), chlorophyll a (e, mg m^{-3}), ratios of chlorophyll a to particulate organic carbon (f), primary production (g, mgC m^{-3} d^{-1}) and normalized production indices (h, mgC mgChl^{-1} h^{-1}) measured in the Lanyang Hsi coastal area. Note the blank regions in (b) and (c) marked by lines indicate areas where nitrate and phosphate limitation might occur, respectively (see text for details).

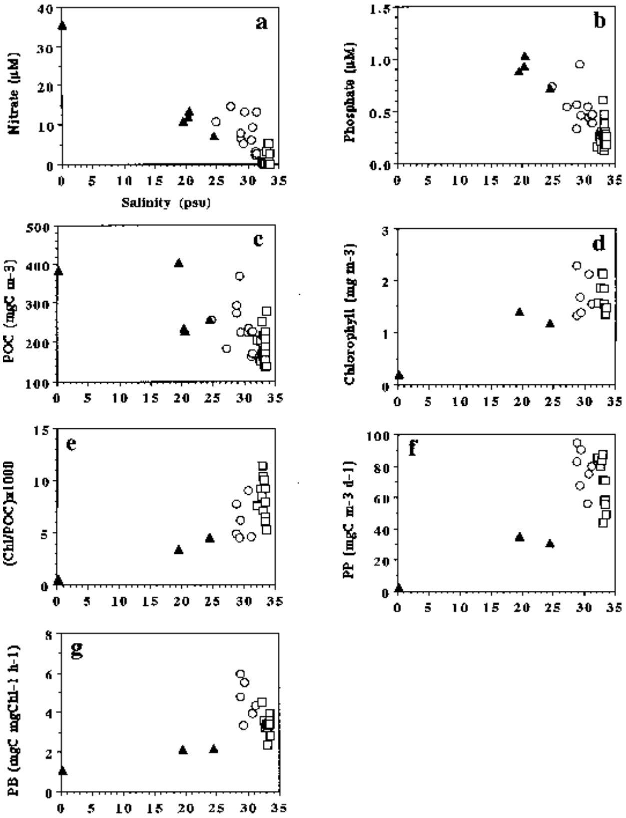

Figure 3. Scatter plot of measured variables vs. salinity in the study area. a, nitrate; b, phosphate; c, particulate organic carbon; d, chlorophyll a; e, ratios of chlorophyll a to particulate organic carbon; f, primary production; g, normalized production indices. Solid triangles, open circles and open squares represent the river mouth water, the mixed water and seawater, respectively. Noted that phosphate concentrations at station G were not determined.

Freshwater salinity and NO_3^- concentrations recorded at the Gor Mar Lang Bridge (station G) were 0.2 psu and 28 µM while those in the river mouth were 19–25 psu and 7.0–13.5 µM, respectively (Figure 3a). The distance between station G and the river mouth was about 500 m. Such rapid changes in salinity and NO_3^- concentrations indicated that the river water was mixing with seawater very quickly within the river mouth area. Concentrations of NO_3^- were negatively correlated with salinity (r = -0.75, $p<0.05$, n = 41) but with several data above and below the conservative mixing line (Figure 3a). Data of the former were recorded at stations located in the mixed water area, indicating that the mixed water contained an extra source of NO_3^- besides the Lanyang river water. In contrast, most of the NO_3^- concentrations measured in the seawater were below the conservative mixing line, suggesting that NO_3^- could be rapidly depleted by the uptake of marine phytoplankton. When compared with the former two water masses, NO_3^- concentrations of the river mouth water lay closer to the conservative mixing line, indicating that physical mixing might play a more important role in determining nutrient distribution in the river water. Note that NO_3^- concentrations of the river water with salinity in the range of 1.0–17 psu were not determined. The distribution pattern of PO_4^{-3} (Figures 2c, 3b; 0.12–1.03 µM) was very similar to that of NO_3^- (r = +0.63, $p<0.05$, n = 40). Concentrations of particulate organic carbon ranged from 138 to 405 mgC m^{-3}, the highest being in the river mouth area (Figure 2d) and then decreasing as salinity increased (Figure 3c; r = -0.71, $p<0.05$, n = 20).

Chlorophyll a concentrations (Chl.) varied two fold (1.18–2.28 mgChl m^{-3}; Figures 2e, 3d) with higher concentrations observed in the mixed water and seawater. Ratios of Chl. to POC (i.e. Chl./POC × 1,000; Figure 2f) which indicate relative amount of viable particulate organic matter were low (<5) around the river mouth area and were positively correlated with salinity (Figure 3e; r = +0.79, $p<0.05$, n = 20). This indicated that the POC collected at the river mouth contained a high proportion of detrital substance derived from the sediments via resuspension. Primary production (PP) ranged from 30.5 to 94.7 mgC m^{-3} d^{-1} and increased seaward (Figures 2g, 3f). The distribution pattern of PP was similar to but did not match exactly with that of Chl. Figures 2h and 3g show that higher values of normalized production indices (>4.20 mgC $mgChl^{-1}$ h^{-1}; P^B) were only observed in the mixed water while the P^B of the other two areas were low with most values <4.00 mgC $mgChl^{-1}$ h^{-1}.

The discrete physical, chemical, and biological characteristics observed in the three water types were summarized as follows: the river mouth water was characterized by high concentrations of inorganic nutrients and detritus (i.e. low Chl./POC ratios) and low salinity and biological parameters (Chl., PP, and P^B). On the other hand, the seawater was unique in high salinity, Chl., and PP but low in nutrient concentrations. High values for biological parameters and nutrient concentrations marked the area of the mixed water with intermediate salinity.

Discussion

Our study highlights the importance of physical forces in determining the spatial variability of hydrographic and biological variables in the coast adjacent to the Lanyang Hsi. The inverse correlation observed between salinity and inorganic nutrient concentrations indicated that mixing of freshwater and seawater was the primary factor in determining the spatial distribution patterns of chemical variables. The Lanyang Hsi served as one of the major sources of dissolved inorganic nutrients for the coastal area. Inorganic nutrients derived from the Lanyang Hsi were quickly mixed and diluted by nutrient-depleted seawater in the river mouth area. When plotted against salinity, all the NO_3^- data recorded in the river mouth area fitted right on the conservative mixing line (Figure 3a; solid triangles), suggesting the spatial distribution pattern of NO_3^- in this river mouth area was principally determined by mixing processes. Biological uptake probably was not very important in the river mouth area due to its high turbidity (see below) and low phytoplankton biomass and production.

In addition to inorganic nutrients, the export of detrital POC via the Lanyang Hsi might also have great ecological implications for the adjacent coastal ecosystems (Kao, 1995). Particulate materials can undergo continual decomposition with attendant regeneration of dissolved inorganic nutrients (making them available for phytoplankton assimilation). For many shallow estuarine and coastal systems, nutrient regeneration in bottom sediments constitutes an important recycling mechanism (Nixon, 1981; Kemp and Boynton, 1984). The high NO_3^- (Figures 2b, 3a) observed in the mixed water suggested that there was an extra source of NO_3^- in the study area. Since the Lanyang Hsi is the only river discharging into this area, a potential explanation for this extra NO_3^- source was sediment diagenesis (i. e. mineralization of organic detritus to inorganic nutrients). In the scheme of "new or export production" (the primary production supported by allochthonous inorganic nutrients), the Lanyang Hsi might fuel coastal phytoplankton growth via two routes. The direct supply of dissolved inorganic nutrients from river water inputs and the decomposition of riverine particulate organic matter into inorganic forms, which occurred at slower rates.

Primary production (PP) is a product of biomass (Chl.) and normalized production index (P^B). That is, PP = Chl. × P^B. Any factor which influences the latter two variables will also affect PP concomitantly. As mentioned in the previous section, temperature, light intensity, inorganic nutrient supply rates and grazing from zooplankton are the four major environmental factors considered to be important in regulating Chl. and hence PP. Note that grazing plays a very important role in regulating phytoplankton biomass, but does not have much effect on P^B which are indices of phytoplankton turnover rates.

A comparison of biological variables in the three water masses revealed that controlling mechanisms of phytoplankton properties in these three areas might be quite different. Light intensity (i.e. turbidity) might be the major factor causing the low P^B and Chl. concentrations (and thus low PP) in the river mouth area in spite of the high concentrations of inorganic nutrients (Wofsy, 1983; Harding et al., 1986). Evidence for this speculation came from the facts showing that both the P^B and Chl. values of the river mouth area (1.78 ± 0.61 mgC $mgChl^{-1}$ h^{-1}; 0.92 ± 0.63 mgChl. m^{-3}) were <50% and 60% of those measured in the mixed water (4.62 ± 0.97 mgC $mgChl^{-1}$ h^{-1}; 1.72 ± 0.39 mgChl. m^{-3}) and the seawater areas (3.40 ± 0.54 mgC $mgChl^{-1}$ h^{-1}; 1.63 ± 0.29 mgChl. m^{-3}), respectively. Although not measured directly, turbidity in the river mouth area must be higher than in the other two areas due to its shallowness (<10 m). Ward et al. (1984) demonstrated that the magnitude of POC resuspension in the coastal area was a function of water depth, the strength of wind velocity (i. e. waves), and tides. They showed that, in areas where water depth was <5 –10 m, the combined effects of waves and tidal motions resuspended large amounts of sediment. This might result in high turbidity and thus low light intensity in the river mouth's surface water. This could be inferred from the low Chl./POC ratios (Figures 2f, 3e) and high POC concentrations (Figures 2d, 3c) recorded in this area. The low Chl. concentrations recorded in the river mouth water might be ascribed to the high zooplankton grazing rate. We do not think this is the case since highly turbid water is not a suitable environment for the survival of zooplankton. Besides, the ready availability of organic detritus for herbivorous zooplankton may greatly reduce the grazing pressure on phytoplankton (Day et al., 1989). On the other hand, PP was high in the clearer deep water areas (i.e. the seawater and the mixed water). However, the cause of these high PP values in these two zones were not the same. Chl. concentrations in the seawater were higher than those of the mixed water while P^B values of the former were lower than those of the latter. The discrete P^B values recorded in these three waters coincided with the contrasting scenario of inorganic nutrient concentrations and Chl./POC ratios and these reflected the possibility of switching from light limitation in the river mouth water to nutrient limitation in the seawater. The high P^B values in the mixed water suggested less nutrient limitation in this area (see below).

The same phenomenon described above has been reported in an experiment performed in the southern East China Sea north of Taiwan (Shiah et al., 1995). It was observed that both the P^B values of the nutrient-laden and turbid China coastal water (<3.8 mgC $mgChl^{-1}$ h^{-1}) and the clear, nitrate-depleted Kuroshio water (<4.8 mgC $mgChl^{-1}$ h^{-1}) were low. In contrast, much higher P^B values (10.9 mgC $mgChl^{-1}$ h^{-1}) were recorded in the samples taken from the upwelling area where nutrients were supplied by the upwelling process. The three different types of water mass in their study (i.e. the China coastal, Kuroshio, and upwelling waters) could be viewed as equivalents of the three waters of this study (i.e. river mouth, seawater, and mixed water) respectively.

A rigorous test of nutrient limitation requires detailed measurements in bioassay or other experiments. A simpler and more limited method of evaluating nutrient limitation is to compare the in situ nutrient concentrations to the half-saturation constants (Ks) for nutrient uptake reported in the literature. The Ks represents the concentrations at which nutrient uptake is half of its maximum value. Concentrations below these values are associated with greatly reduced uptake rates, potentially enough to limit algal growth rates or biomass accumulation. In contrast, concentrations greater than the Ks have a relatively small positive effect on uptake rates. Typical values of Ks of NO_3^- and PO_4^{-3} for natural phytoplankton populations are ca. 1–2 μM and 0.1–0.5 μM respectively (for review, see Fisher et al., 1988). Here we used the average values of 1.5 μM for NO_3^- and 0.25 μM for PO_4^{-3} to evaluate nutrient limitation. As shown in Figures 3a and 3b, NO_3^- and PO_4^{-3} concentrations measured in the seawater area were all lower than their corresponding Ks values, indicating algal growth (i. e. P^B) might be limited by NO_3^- and/or PO_4^{-3} in the seawater (Figures 2b–c).

It is well known that estuaries are capable of trapping (i.e. removing) many kinds of nutrient before river water reaches the coastal areas. Fisher et al. (1988) showed that in Chesapeake Bay, the USA's largest estuary, about 50% of nitrogenous nutrients, phosphate and silicate were consistently removed from the water column by phytoplankton due to the long water residence time (several months) in the bay. Thus the actual amount of nutrient transported into the coastal and marine areas could be quite low. On the other hand, as mentioned above, the quick discharge and rapid mixing of the Lanyang river water with seawater (i.e. short residence time) due to the unique topography and low phytoplankton activities in the river mouth might lead to more nutrients available for the growth of phytoplankton in the marine part.

Many studies have shown that seasonal and interannual variability of estuarine phytoplankton biomass (and thus production) are related directly to the nutrient loading which is a function of riverine discharge (for review see Malone, 1991). An understanding of the temporal variations in the nutrient loading of the freshwater end member (i.e. the Lanyang Hsi) is therefore very important in understanding the seasonal changes of primary production in the coast of the Lanyang Hsi. Kao (1995) showed that the annual range of nitrate concentrations of the Lanyang Hsi was 10–40 μM with an average of 25 μM and that nitrate loading varied more than two order of magnitude ($5.4 \times 10^3 - 3.6 \times 10^6$ mol d^{-1}). Both concentrations and flux were higher during the northeast monsoon season (i.e. Oct. – Jan. of the next year) and sporadic typhoon events. The results of this study were obtained during the "normal" period and thus could not be extrapolated throughout the whole year. Therefore, it is vital to conduct similar surveys during different seasons. We predict that the phytoplankton biomass and production outside the Lanyang Hsi, at least in the mixed water and the seawater areas with low turbidity, will be greatly enhanced in correspondence with the high nutrient loading that occurs during the northeast monsoon season and after typhoons.

Conclusion

Our study demonstrated that the spatial distribution patterns of phytoplankton properties— including primary production, chlorophyll a concentrations, and normalized production indices—were quite heterogeneous outside the river mouth of the Lanyang Hsi. Such spatial patchiness might be caused by the uneven distribution of nutrients and turbidity via the influence of waves and tides. Inorganic nutrients delivered by the Lanyang Hsi could not be utilized efficiently by phytoplankton at the river mouth due to its high turbidity. This might result in more inorganic nutrients available for algal growth in the marine area. The controlling mechanisms for primary production switched from light limitation in the river mouth area to nutrient limitation in seawater, indicating the importance of studying spatial variability and the necessity of integrating the results of different environmental parameters.

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蘭陽溪口海岸區浮游植物生產力空間分布之機制研究

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本文報導浮游植物生產力，葉綠素濃度及單位葉綠素生產力在蘭陽溪河口海岸區之空間分布特徵。透過分析此三種生物參數與無機營養鹽（硝酸鹽、磷酸鹽），顆粒性有機碳濃度及鹽度之關係，探討浮游植物生長速率在此海域內之可能控制機制。依水體內各測量參數之分布特徵，研究區可分為三類水團，包括河口水（高營養鹽，低鹽度）、海水（低營養鹽，高鹽度）及混合水（高營養鹽，中鹽度）。前貳者之單位葉綠素生產力皆顯著的低於混合水；再經與營養鹽半飽和吸收常數及（葉綠素/顆粒性有機碳）之濃度比值的空間分布型態比對後，推斷浮游植物在河口水及海水內之生長控制因子分別為混濁度（即光照強度）及無機營養鹽之供應率。混合區水體之硝酸鹽濃度明顯地偏離並高於守恆混合線，顯示沈積物的有機物再生分解作用可為此區提供額外之營養鹽來源，而浮游植物在此區域內之生長可能不受營養鹽之限制。由於蘭陽溪出海口處窄而淺之特殊地型，使得富含無機營養鹽之河水得以迅速的與海水混合。此種短駐留期及河口水內之低浮游植物活性，使得海水內之浮游植物有更大的機會攝取生長所需之無機營養鹽。

關鍵詞：海岸區；無機營養鹽；浮游植物生長速率；空間變異度；潮汐；混濁度；波浪。