

Summer Phytoplankton Community Structure in the Kuroshio Current-Related Upwelling Northeast of Taiwan

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ABSTRACT

Observations of chlorophyll *a* concentration and phytoplankton assemblage were conducted during the summer of 1990 on 19 stations along two parallel transects across the Kuroshio Current front off the northeastern coast of Taiwan. The 0-100m seawater chlorophyll *a* content varied between 8.63 and 41.80mg·m⁻² in August and between 8.88 and 94.70mg·m⁻² in September. High nitrate content, low temperature, high salinity and high chlorophyll *a* concentrations were observed at the stations along the front. The vertical distribution of chlorophyll *a* was characterized by a shallower subsurface maximum of between 0 and 25m in the stations associated with the upwelling, while those of the non-upwelling stations were between 50-75m. Diatoms, *Skeletonema costatum* in August and *Thalassionema nitzschioids* in September, dominated the upwelled surface water because significant amounts of nutrients are supplied to surface or near-surface waters.

1. INTRODUCTION

The response of phytoplankton in upwelled waters can be conceptualized in various ways. Increases in production (Barber and Smith, 1981; Guillen *et al.*, 1971; Reid *et al.*, 1970) and/or standing crop (Guillen *et al.*, 1971; Reid *et al.*, 1970) in the nutrient-rich upwelling waters were observed either immediately or with a lag period due to the variation of upward speed and/or the chelation of trace metals of the upwelled water. Rapid vertical speed may lead to decreased production. The speed of water drifting away from the upwelling zone will, thus, in part determine the richness and the positioning of the productive belt.

Increases in the netphytoplankton fraction are closely coupled with the occurrence of coastal upwelling. In both temperate (Gilmartin, 1964; Anderson, 1965) and tropical (Saijo and Takesue, 1965; Malone, 1971a) marine environments, the nanophytoplankton are usually responsible for 80% to 100% of the observed phytoplankton productivity and standing crop. Netphytoplankton, on the other hand, exceeds nanophytoplankton in productivity and standing crop during periods of strong upwelling (Malone, 1971b). This shift in phytoplankton assemblages during upwelling was suggested to be caused by the retention of larger

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particles in strong vertical advection, and by the increases in ambient $\text{NO}_3\text{-N}$ concentrations. The relative importance of these two size groups of phytoplankton thus can be an effective tool to describe an upwelling process.

Large populations of phytoplankton dominated by diatoms were observed in many upwelled waters (Tont, 1976; Yoder *et al.*, 1981; Takahashi and Kishi, 1984). In Peruvian upwelling area, a low diversity of phytoplankton population was illustrated by the observation that eight species of diatom comprised 83% of the population (Ryther *et al.*, 1970).

The Kuroshio Current originates from east of the Philippines and flows north along the east coast of Taiwan. After leaving Taiwan, the Kuroshio Current turns northeast along the edge of the East China Sea and frequently intrudes over the continental shelf (Chern *et al.*, 1990). In contrast to the oligotrophic Kuroshio Current surface water, a rather constant nutrient front is observed near the shelf break (Liu *et al.*, 1988). Like other upwelling systems, this topographic process brings nutrient-rich water onto the shelf, and may promote primary production. The shallow water on the continental shelf off northeastern Taiwan has been a major fishing ground. The physical (Fan, 1980; Liu, 1983; Liu and Pai, 1987; Chern *et al.*, 1990) and chemical (Liu *et al.*, 1988; Wong *et al.*, 1991) aspects of the upwelling process have been described. There is, however, no paper published on attempts to establish the biological aspects.

The present study investigated the chlorophyll *a* distribution and characteristics of the phytoplankton assemblages in the upwelled waters of the Kuroshio Current and the East China Sea. The relative importance of nannophytoplankton versus netphytoplankton in contributing to the phytoplankton standing crop, the distribution of chlorophyll *a* concentration, and the characteristics of the phytoplankton community structure were used as indicators to describe the upwelling phenomena.

2. MATERIALS AND METHODS

2.1 Cruises

The present research was based on data collected during two cruises (cruise 248: August 1-8, 1990 and cruise 254: September 17-22, 1990) on the R/V Ocean Researcher I of the National Science Council, Republic of China. Observations were made on two parallel transects, A and B (Figure 1), across the Kuroshio Current front off the northeastern coast of Taiwan. Transect A had nine sampling stations and B had ten. Adjacent stations in each transect were 28.3km apart in distance. At the 200-m isopleth, where the shelf front is located, one additional station was added in each transect. They were station 542A between stations 5422 and 5323 on the transect B and station 512A between stations 5121 and 5022 on the transect A. The Kuroshio main current flows through stations 5125, 5030, 4531 in transect B and stations 4523, 4424 in transect A.

2.2 Sample Collection and Analysis

A rosette multi-sampler was lowered to collect water samples from 3, 10, 25, 50, 75 and 100m. Surface water (0m) was collected with a bucket. One half liter of seawater from each depth was preserved with neutralized formalin for species identification. Two 1-l samples were taken for chlorophyll *a* measurement with several drops of MgCO_3 added. In order to understand the relative importance of phytoplankton of different size-groups in contributing to standing crop, phytoplankton were divided into two size groups based on their retention by fine-mesh nets. The water samples for chlorophyll *a* measurement were sieved through two stacked filters, a 10- μm mesh cloth (Nytex, Switzerland) on top of a Whatman GF/C

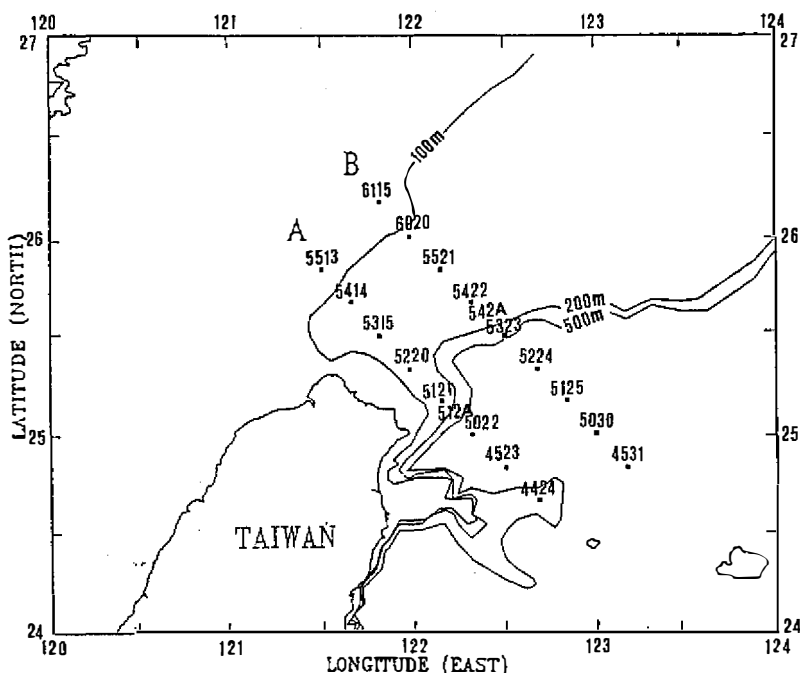


Fig. 1. Location of study site off northeastern Taiwan: numbers indicate sampling stations.

glass fibre filter (Yamamoto *et al.*, 1988). Those phytoplankton retained on the cloth screen were regarded as the netphytoplankton. Those on the GF/C filter were regarded as the nanrophytoplankton. The filtration procedure was finished on board and samples were frozen at -20°C in darkness until analysis. The use of GF/C glass-fiber filters leads to no more than 10% underestimation of nanrophytoplankton chlorophyll *a* (Venrick *et al.*, 1987).

Chlorophyll *a* and phaeopigments concentration were measured according to the procedures described by Strickland and Parsons (1972). The fluorescence was measured with a Hitachi F3000 fluorescence spectrometer. Each observation was duplicated and the mean of the replicates was reported. Integrated water column chlorophyll *a* (*Chl* - *a*) concentration ($\text{mg}\cdot\text{m}^{-2}$) to 100m was estimated by the following equation:

$$\text{Chl} - a = \Sigma^{100\text{m}}(C_{i+1} + C_i)(D_{i+1} - D_i)/2$$

where C_i and C_{i+1} are the chlorophyll *a* concentrations ($\text{mg}\cdot\text{m}^{-3}$) and D_i and D_{i+1} are the depths of the upper and lower limit of sample *i*.

Species identification and cell count were done on the surface samples obtained in all stations on the B transect. At least 500 cells per sample were examined. This sorting procedure ensured the bias of the community diversity statistics estimation, H' , to be negligible (McIntire and Overton, 1971). The filamentous blue-green algae, *Trichodesmium* spp. were counted by their filament numbers.

Water temperature, salinity and nutrient data were adopted from the Chemical Oceanography Data Bank of the National Science Council R. V. Ocean Researcher I Regional Instrument Center. Water samples collected concurrently with those for the chlorophyll *a* measurements were used to determine the nitrate concentrations (Gong and Liu, 1991). Hydrographic results of temperature, salinity and nitrate along the transects A and B (Figures 2 and 3) were adopted partially from Gong and Liu (1991).

2.3 Data analysis

Series of diversity numbers presented by Hill (1973) were used to describe the phytoplankton assemblages and were calculated based on the observed number of species in each sample. They are:

$$N_o = S$$

where S is the total number of species,

$$N_1 = e^{H'}$$

where H' is Shannon's index and defined as:

$$H' = -\sum(p_i \ln p_i)$$

p_i is the proportional abundances of the i th species at the sample,

$$N_2 = 1/\lambda$$

where λ is Simpson's index and defined as $= \sum P_i^2$

These diversity numbers, which are in units of number of species, measure the "effective number" (Hill, 1973) of species present in a sample. N_o is the number of all species in the sample; N_1 is the number of abundant species in the sample; and N_2 is the number of very abundant species.

The averaged linkage method of cluster analysis from SAS package program was used to compare the species composition between sampling stations.

The "aging index of upwelling" (AIU) proposed by Takahashi *et al.* (1986) was used to evaluate the aging status of upwelled water mass and is defined as:

$$AIU = 0.7X/(Y + 0.7X)$$

where X is concentrations of chlorophyll *a* ($\text{mg}\cdot\text{m}^{-3}$) and Y is the concentrations of nitrate plus nitrite (μM) in seawater. AIU has a range of between 0 and 1. In newly upwelled water where there are insignificant amounts of phytoplankton, AIU will be 0. In old upwelled water where there are high levels of chlorophyll and low levels of nutrients due to active phytoplankton uptake, AIU will be 1. In the present study, AIU was calculated based on data from surface samples.

3. RESULTS

The 0-100m seawater chlorophyll *a* contents (netphytoplankton plus nanophytoplankton) varied between 8.63 and 41.80 $\text{mg}\cdot\text{m}^{-2}$ in August and between 8.88 and 94.79 $\text{mg}\cdot\text{m}^{-2}$

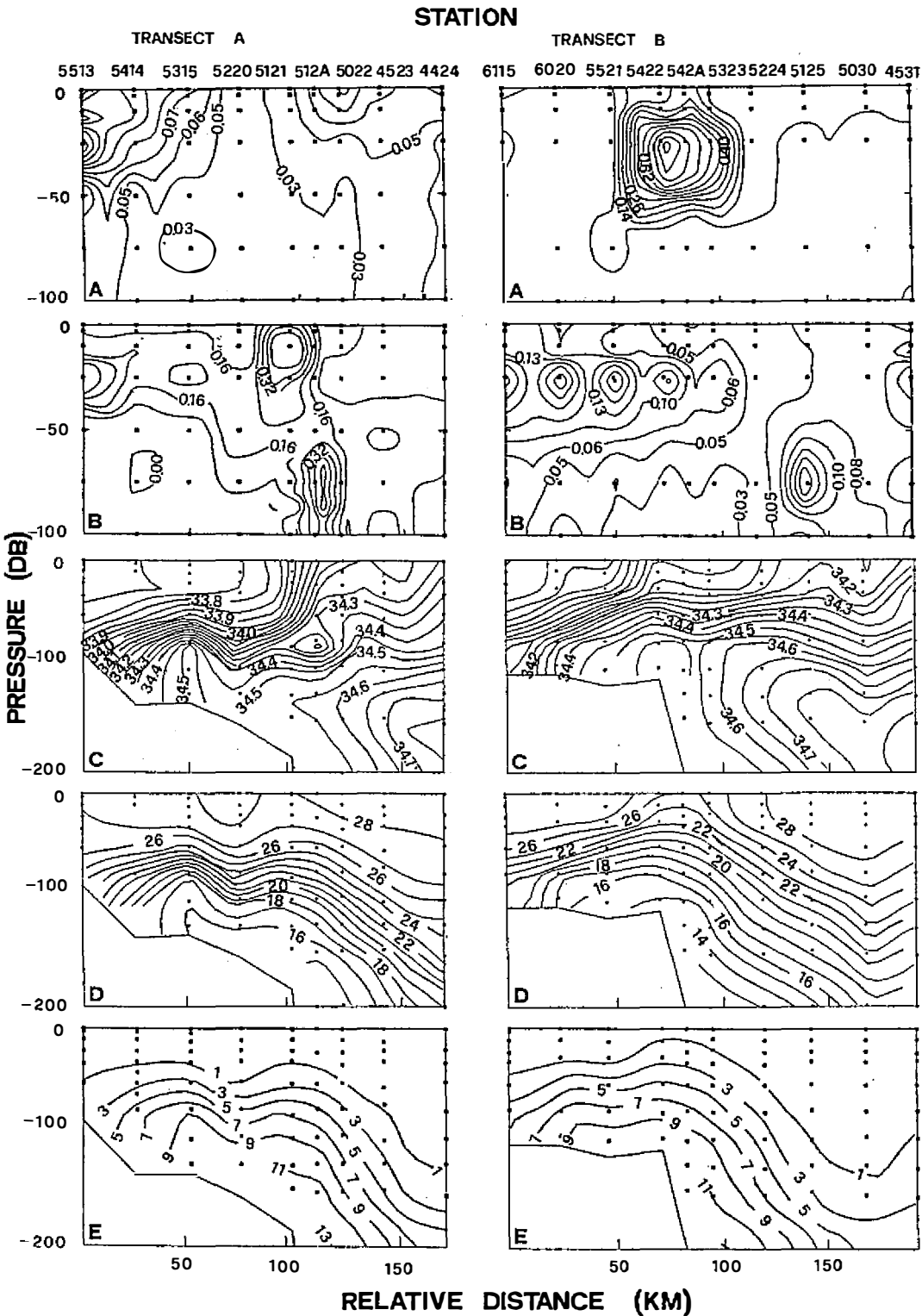


Fig. 2. Cross sections of (A) netplankton chlorophyll *a* ($\mu\text{g}\cdot\text{l}^{-1}$), (B) nannoplankton chlorophyll *a* ($\mu\text{g}\cdot\text{l}^{-1}$), (C) salinity (0/00), (D) temperature ($^{\circ}\text{C}$) and (E) nitrate (μM) along Transects A and B, August 1990. Temperature, nitrate and salinity results were adopted from Gong and Liu (1991).

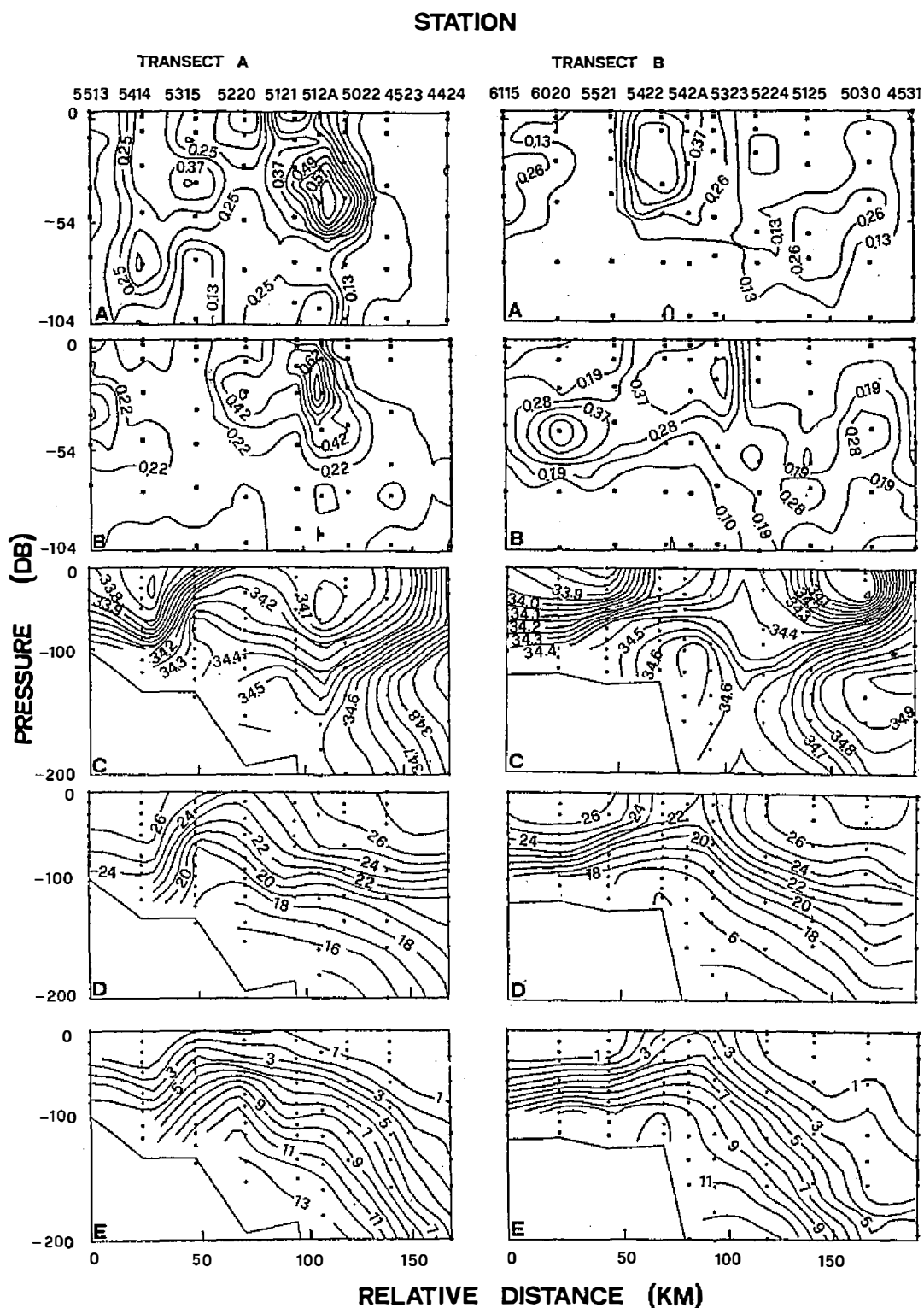


Fig. 3. Cross sections of (A) netplankton chlorophyll a ($\mu\text{g}\cdot\text{l}^{-1}$), (B) nanoplankton chlorophyll a ($\mu\text{g}\cdot\text{l}^{-1}$), (C) salinity (0/00), (D) temperature ($^{\circ}\text{C}$) and (E) nitrate (μM) along Transects A and B, September 1990. Temperature, nitrate and salinity results were adopted from Gong and Liu (1991).

in September. High nitrate content, low temperature and high salinity were observed in both cruises at stations 5422, 542A, 5323 of transect B and stations 5220, 5121, 512A of transect A (Figures 2 and 3). This indicated active upwelling in those stations. High concentrations of chlorophyll *a* were also observed at these stations (Figures 2 and 3). Stations having surface $\text{NO}_3\text{-N}$ concentrations higher than $0.6\mu\text{M}$ had surface chlorophyll *a* concentrations higher than $0.5\text{mg}\cdot\text{m}^{-3}$ (Figure 4) during September.

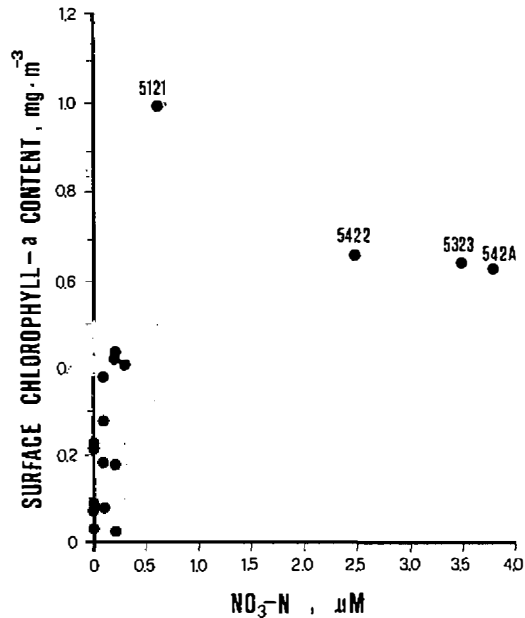


Fig. 4. Relationships of surface nitrate concentrations and surface chlorophyll *a* concentrations measured during September, 1990.

The vertical distribution of chlorophyll *a* in September was characterized by a subsurface maximum between 0-25m in stations associated with the upwelling, and between 50-75m in other stations (Figure 5). The depths of nanophytoplankton chlorophyll *a* maxima always coincided that of netphytoplankton (Figure 5). Comparison of the mean squares and the ranges of the chlorophyll *a* concentrations of nanophytoplankton and netphytoplankton (Table 1) indicated that the variations in netphytoplankton were either higher than or similar to those of nanophytoplankton. The August netphytoplankton and nanophytoplankton chlorophyll *a* concentrations ranged from 0.005 to $0.882\text{mg}\cdot\text{m}^{-3}$ and 0.003 to $0.641\text{mg}\cdot\text{m}^{-3}$ respectively. In September, they were between 0.005 and $0.796\text{mg}\cdot\text{m}^{-3}$ as well as between 0.007 and $0.930\text{mg}\cdot\text{m}^{-3}$, respectively.

Cluster analysis on the surface phytoplankton species compositions between the eight stations on the B transect of the August cruise indicated that the phytoplankton which appeared in stations 5422 and 542A were similar to those found in stations 5521 and 5030 (Figure 6) which were on the shelf and on the main axis of the Kuroshio Current respectively (Figure 1). These stations were grouped as one cluster. The species composition of the surface phytoplankton found in station 5323 was between the cluster mentioned above and the shallowest station of 6020. This indicated the mixing of the Kuroshio Current water and the East China Sea coastal water in the area around stations 542A and 5323. High diatom (5.90×10^3 and 14.80×10^3 cells $\cdot\text{l}^{-1}$, respectively) and low *Trichodesmium*

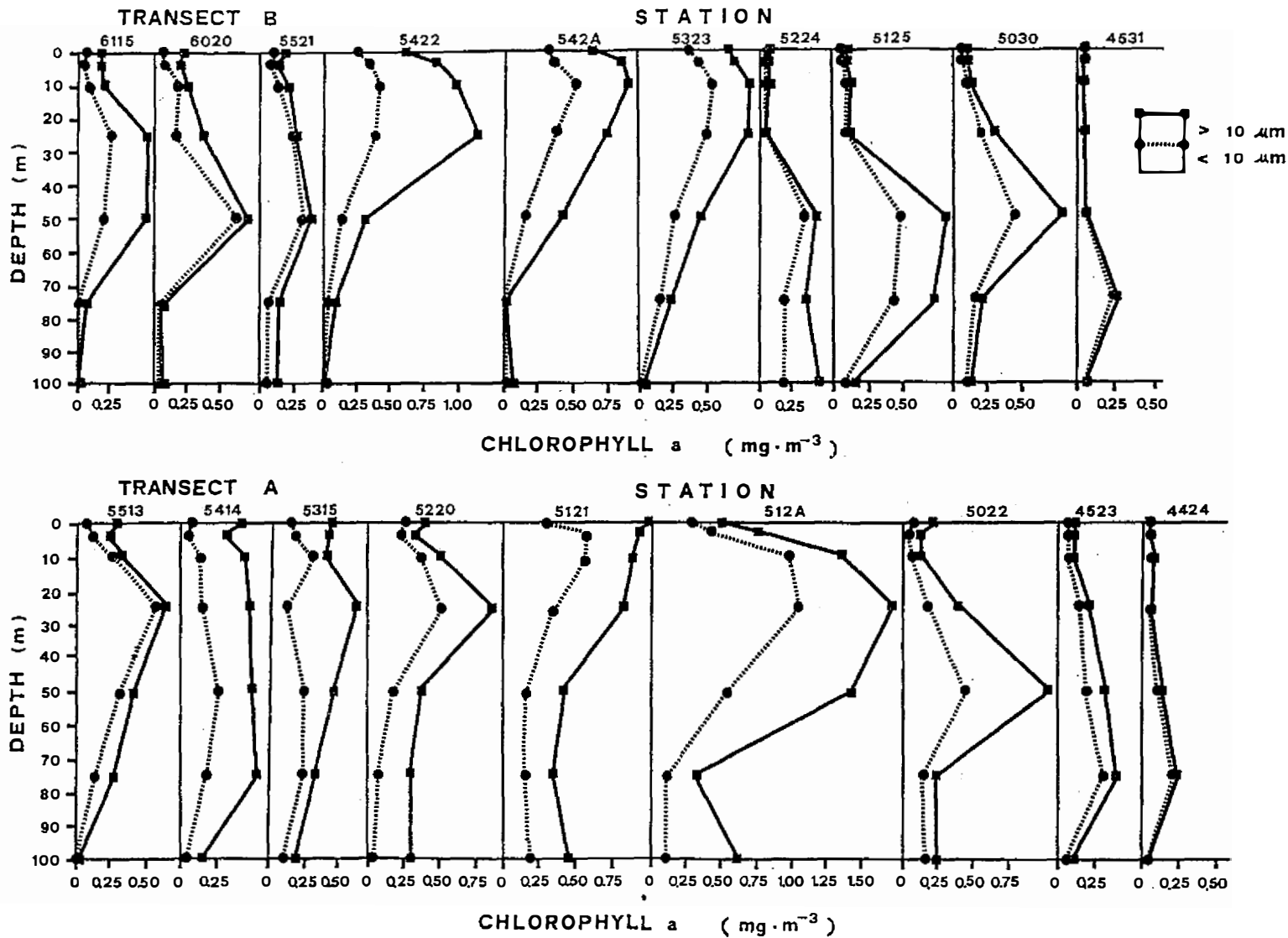


Fig. 5. Vertical distribution of chlorophyll a concentration of netplankton ($>10 \mu\text{m}$; solid) and nanoplankton ($<10 \mu\text{m}$; shaded) on transects A and B, September 1990.

Table 1. Mean squares($\text{mg}\cdot\text{m}^{-3}$, $\text{mg}\cdot\text{m}^{-2}$) and range (minimum-maximum) of chlorophyll a concentrations for nannophytoplankton and netphytoplankton measured in two cruises

Cruise	Fraction	Mean squares		Range	
		$\text{mg}\cdot\text{m}^{-3}$	$\text{mg}\cdot\text{m}^{-2}$	$\text{mg}\cdot\text{m}^{-3}$	$\text{mg}\cdot\text{m}^{-2}$
August, 1990	Nannophytoplankton	0.10	5.37	0.003-0.641	3.41-22.72
	Netphytoplankton	0.12	9.69	0.005-0.882	1.76-34.07
September, 1990	Nannophytoplankton	0.18	9.33	0.007-0.930	7.62-46.71
	Netphytoplankton	0.18	12.24	0.005-0.796	1.00-48.08

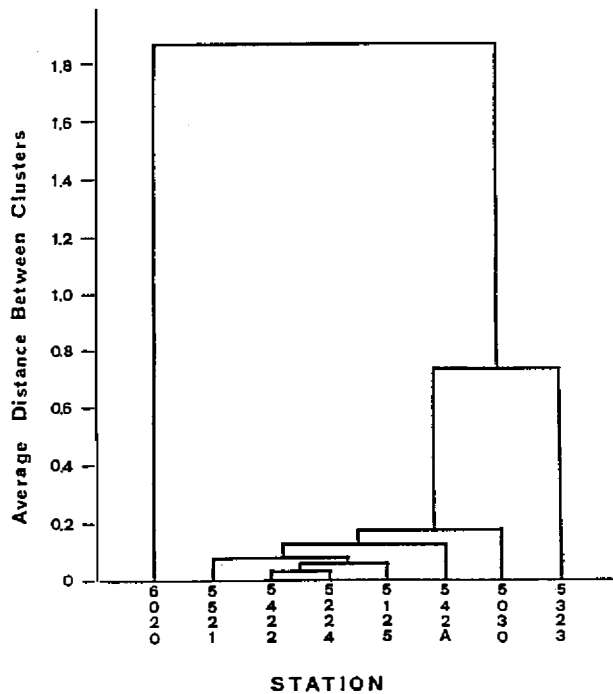


Fig. 6. Dendrograms showing cluster analysis by the average-linkage method of phytoplankton community structure between eight surface samples collected in August, 1990.

concentrations (0.17 and 0 filaments $\cdot\text{l}^{-1}$ respectively) were also observed at these two stations (Table 2). The remaining stations, in contrast, had diatom concentrations of between 0.37×10^{-3} and 1.01×10^{-3} cells $\cdot\text{l}^{-1}$ and *Trichodesmium* concentrations of between 0.24 and 36.44 filaments $\cdot\text{l}^{-1}$, with the exception of station 6020. A high diatom concentration of 16.32×10^{-3} cells $\cdot\text{l}^{-1}$ was observed in that station (Table 2).

Table 2. Comparisons of densities of diatom ($\times 10^3$ cells $\cdot l^{-1}$), dinoflagellate ($\times 10^3$ cells $\cdot l^{-1}$) and filamentous blue-green algae ($\times 10^3$ filaments $\cdot l^{-1}$) among various stations

Cruise	Phytoplankton groups	Station (Transect B)							
		6020	5521	5422	542A	5323	5224	5125	5030
August (248)	Diatom	16.32	0.37	1.00	5.91	14.80	0.92	1.01	0.44
	Dinoflagellate	0.16	0.07	0.03	0.08	0.06	0.01	0.01	0.01
	Blue-green algae	36.52	0.24	0.64	0.17	0	0.78	2.30	4.94
September (254)	Diatom	0.04	1.37	36.60	12.76	13.20	1.49	2.36	1.86
	Dinoflagellate	0.05	0.12	0.25	0.09	0.07	0.01	0.08	0.08
	Blue-green algae	0.04	0.07	0.15	3.07	0.07	0.05	0.07	0.15

Diversity indices of the August surface phytoplankton showed the lowest values of H' (1.3), N_1 (3.9), and N_2 (1.7) at station 5323 (Table 3). *Skeletonema costatum* with a density of 11.22×10^3 cells $\cdot l^{-1}$ (about 76% of total cells) dominated the phytoplankton community in the station. In contrast, its neighbor station 542A showed a high diatom concentration but had the highest values of H' (3.3), N_1 (28.3) and N_2 (14.3). *S. costatum* also occurred in station 542A but with a lower density (0.89×10^{-3} cells $\cdot l^{-1}$) than that in station 5323. *Trichodesmium thiebautii*, which was reported to occur in mass quantities in summer in the Kuroshio Current waters (Marumo, 1957a; 1957b), was observed in the present study in relatively large quantities in stations 6020 (36.52×10^{-3} filaments $\cdot l^{-1}$) and 5030 (4.94×10^3 filaments $\cdot l^{-1}$), but none in station 5323.

Similar results of dense diatom concentrations were also observed at stations 5422, 542A and 5323 in the B transect during the September cruise (Table 2). The densities were 36.6×10^3 cells $\cdot l^{-1}$, 12.76×10^3 cells $\cdot l^{-1}$, and 13.2×10^3 cells $\cdot l^{-1}$ respectively. In contrast, densities of between 0.04×10^3 and 2.36×10^3 cells $\cdot l^{-1}$ were observed at their neighboring stations (Table 2). During August pennate diatom *Thalassionema nitzschioids* became dominant instead of the centric diatom *S. costatum*. *T. thiebautii* was more abundant in station 542A with a density of 3.07×10^3 filaments $\cdot l^{-1}$, while its densities in the remaining stations ranged between 0.04×10^3 and 0.15×10^3 filaments $\cdot l^{-1}$.

Table 3. Values of Hill's diversity numbers of the phytoplankton assemblages collected on surface water of the B transect in August

Index	Stations							
	6020	5521	5422	542A	5323	5224	5125	5030
H'	2.2	2.7	2.6	3.3	1.3	2.1	1.9	1.4
N_0	92	52	63	73	50	36	28	25
N_1	8.8	15.4	13.1	28.3	3.9	8.3	6.4	4.0
N_2	3.3	8.4	5.4	14.3	1.7	4.1	3.5	2.7

AIU was smaller at the station 542A than its surrounding stations in both cruises (Table 4). Smaller *AIU* values of 0.11-0.16 were observed in September than in August (0.35- 0.56) at stations 5422, 542A and 5323 (Table 4). This indicated a younger upwelled water mass occurred in September than in August. Markedly higher concentrations of nitrate plus nitrite (2.71-4.06 μM) and chlorophyll *a* (0.66-0.72 $\text{mg}\cdot\text{m}^{-3}$) were also observed in the upwelling stations in September than in August (0.09-0.30 μM and 0.13-0.23 $\text{mg}\cdot\text{m}^{-3}$ respectively) (Table 4).

Table 4. Comparisons of aging index of upwelling (*AIU*), nitrate plus nitrite concentration ($[\text{NO}_3^-]+[\text{NO}_2^-]$, μM), and the total chlorophyll *a* concentration (*Chl.a*, $\text{mg}\cdot\text{m}^{-3}$) between two cruises

	CRUISE	STATION (TRANSECT B)							
		6020	5521	5422	542A	5323	5224	5125	5030
<i>AIU</i>	August	0.79	0.87	0.35	0.56	0.47	0.34	0.54	1.00
	September	0.85	0.48	0.16	0.11	0.11	0.72	0.07	0.78
[NO_3^-] + [NO_2^-]	August	0.02	0.02	0.30	0.09	0.10	0.16	0.11	0
	September	0.03	0.16	2.71	4.06	3.70	0.02	0.03	0.02
[<i>Chl. a</i>]	August	0.11	0.19	0.23	0.16	0.13	0.12	0.18	0.17
	September	0.03	0.21	0.72	0.69	0.66	0.07	0.09	0.07

4. DISCUSSION

Waters along the 200-m isopleth of the study area showed high phytoplankton standing crops in terms of chlorophyll *a* concentrations. High nitrate concentration, high salinity and low temperature were also observed. The chlorophyll *a* maximum was shallower in these areas than in the neighboring waters. These findings agreed with the previous upwelling studies in these waters. The high standing crop and shallow subsurface chlorophyll *a* maximum likely were induced by the increased nutrient supply to the photic zone through vertical mixing. Lohrenz *et al.* (1988) studied the interrelationship among primary production, chlorophyll *a* and environmental conditions in frontal regions of the western Mediterranean Sea, and reported similar results to the present study. They found that the integrated primary production was inversely related to the depth of chlorophyll *a* maximum and further suggested that the inverse relationship is regulated by the rate of nutrient supply.

In the present study, while a high density of the blue-green algae *Trichodesmium thiebautii* (4.94×10^3 filaments $\cdot\text{l}^{-1}$) was found in station 5030 on the Kuroshio Current, the highest density (36.52×10^3 filaments $\cdot\text{l}^{-1}$) among all stations was observed in station 6020 which was far away from the Kuroshio Current. *Trichodesmium* is an oceanic species and is abundant (10^2 - 10^3 filaments $\cdot\text{l}^{-1}$) in summer throughout the Kuroshio Current water and almost absent in winter (Marumo and Nagasawa, 1976). Large blooms of *Trichodesmium* are usually found in oligotrophic oceanic waters. Due to its buoyant nature,

surface water with dense *Trichodesmium* may be transported to a nutrient-rich region, such as station 6020, by storms or meander and ring formation of the Kuroshio Current.

Skeletonema costatum, a cosmopolitan centric diatom, was most dominant at the upwelling station 5323 in August. The water temperature was lower and the nutrients were higher at this station than its neighboring stations. The abundance of *S. costatum* had been suggested to be influenced by the terrestrial materials brought into the sea by rivers (Huang, 1986). Abundant occurrences have also been observed in many estuaries or coastal waters of Taiwan (Huang and Chiang, 1974; Huang, 1986). On the other hand, *Thalassionema nitzschioides*, a pennate diatom occurred abundantly in the upwelled surface water during the September cruise, is also a cosmopolitan species. It is extremely eurythermal, euryhaline and circum-global in distribution and exists mainly in neritic areas.

The dominance of diatoms has been reported in many other upwelled waters. Tont (1976) observed continuously occurring diatom blooms in large-scale upwelling waters over a long period of time. Even for a short duration of upwelling water, from days to a few weeks, active growth of diatom populations has been recorded (Yoder *et al.*, 1981; Takahashi and Kishi, 1984). Diatoms became dominant when significant amounts of nutrients are supplied to surface or near-surface waters (Ishizaka *et al.*, 1986).

Dominance of diatoms in nutrient-rich water has also been demonstrated in laboratory tests. In a controlled experimental ecosystem where macro-nutrients (nitrate, phosphate and ammonia) were frequently introduced, phytoplankton communities subjected to high nutrients and strong solar radiation were dominated by chain-forming centric diatoms (Takahashi *et al.*, 1982). The effects of these macro-nutrients on the growth of different species of algae were also evaluated by a dialysis bag culture study by Takahashi and Fukazawa (1982). They found that chain-forming *S. costatum* showed a greatly enhanced growth by the additions of nitrate, phosphate or ammonia. In contrast, growth of the algae was extremely poor at low concentrations of the macro-nutrients. Likewise, Turpin and Harrison (1979) described the dominance of centric diatoms under nutrient-rich conditions. *S. costatum* was one of the five diatom species dominated in the upwelled water off Peru (Guillen *et al.*, 1971). In the present study the dominance of *S. costatum* in stations 5323 and 542A reflected the eutrophic condition resulting from upwelling.

Turpin and Harrison (1979) reported that in contrast to the dominance of centric diatoms under nutrient-rich conditions, flagellates are most abundant when nutrients are scarce, and pennate diatoms are favored under intermediate-nutrient conditions. However, in the present study, centric diatom *S. costatum* dominated when the ambient nitrate concentrations were low, while pennate diatom *Thalassionema nitzschioides* dominated when nutrient concentrations were high. In a simulated culture experiment of local upwelling in Japan pennates were often found to grow faster than centric diatoms (Ishizaka *et al.*, 1986). However, the pennate diatoms settle to the bottom of the culture flasks in a much faster rate than do the centric diatoms. The reason diatoms are favored under high nutrient conditions could also be associated with the fact that strong turbulence slows the rate of sinking of the large cells from the photic zone (Longhurst and Harrison, 1989). Sinking rate of algae and the upwelling speed of the water mass, thus, may also influence the dominance of pennate or centric diatoms in an upwelled water.

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台灣東北部黑潮湧升流海域 夏季浮游植物族群結構

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摘要

本研究於1990年夏季在台灣東北部海域，探討橫越黑潮鋒面之十九測站其葉綠素 *a* 濃度及浮游植物種類組成分布。水表至100公尺水深累計之葉綠素 *a* 濃度，8月為8.63至41.80 mg·m⁻²，9月為8.88至94.70 mg·m⁻²。鋒面附近測站呈現低水溫、高鹽度、高硝酸鹽濃度及高葉綠素 *a* 濃度之現象。葉綠素 *a* 濃度之垂直分布，在湧升流附近測站，呈現濃度最大處較淺，約在0-25m水深，其它測站則為50-75m。湧升流附近測站，矽藻顯著量多，八月份主要為 *Skeletonema costatum*，九月份為 *Thalassionema nitzschioides*，此等現象與多量營養鹽之提供有關。

