

Regional disparities of phytoplankton in relation to different water masses in the Northwest Pacific Ocean during the spring and summer of 2017

Gengming Lin¹, Yanghang Chen¹, Jiang Huang¹, Yanguo Wang^{1*}, Youyin Ye¹, Qingliang Yang¹

¹Third Institute of Oceanography, Ministry of Natural Resources, Xiamen 361005, China

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Abstract

The West Pacific Ocean is considered as the provenance center of global marine life and has the highest species diversity of numerous marine taxa. The phytoplankton, as the primary producer at the base of the food chain, effects on climate change, fish resources as well as the entire ecosystem. However, there are few large-scale surveys covering several currents with different hydrographic characteristics. This study aimed to explore the relationships between the spatio-temporal variation in phytoplankton community structure and different water masses. A total of 630 water samples and 90 net samples of phytoplankton were collected at 45 stations in the Northwest Pacific Ocean (21.0°–42.0°N, 118.0°–156.0°E) during spring and summer 2017. A total of 281 phytoplankton taxa (>5 μm) belonging to 61 genera were identified in the study area. The distribution pattern of the phytoplankton community differed significantly both spatially and temporally. The average abundances of phytoplankton in spring and summer were 797.07×10^2 cells/L and 84.94×10^2 cells/L, respectively. Whether in spring or summer, the maximum abundance always appeared in the northern transition region affected by the Oyashio Current, where nutrients were abundant and diatoms dominated the phytoplankton community; whereas the phytoplankton abundance was very low in the oligotrophic Kuroshio region, and the proportion of dinoflagellates in total abundance increased significantly. The horizontal distribution of phytoplankton abundance increased from low to high latitudes, which was consistent with the trend of nutrient distributions, but contrary to that of water temperature and salinity. In the northern area affected by the Oyashio Current, the phytoplankton abundance was mainly concentrated in the upper 30 m of water column, while the maximum abundance often occurred at depths of 50–75 m in the south-central area affected by the Kuroshio Current. Pearson correlation and redundancy analysis (RDA) showed that phytoplankton abundance was significant negatively correlated with temperature and salinity, but positively correlated with nutrient concentration. The phytoplankton community structure was mainly determined by nutrient availability, especially the N:P ratio.

Key words: phytoplankton, regional disparity, species composition, spatial distribution, Northwest Pacific Ocean

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1 Introduction

The West Pacific Ocean is considered as the provenance center of global marine life (Gaston, 2000; Briggs, 2005; Allen, 2007), and the highest species diversity of numerous marine taxa occurs in these waters (Jensen, 2006; Tittensor et al., 2010). The water currents in the Northwest Pacific Ocean (NWPO) are complex, including several different hydrographic waters such as subtropical Kuroshio water, subpolar Oyashio water, upwelling and coastal water. These currents transport large amounts of heat and materials and varies both spatially and temporally, which in turn control the nutrient supply, light environment, primary productivity, climate change and fish resources (Hu et al., 2015; Schlundt et al., 2017). The northwest subarctic Pacific Ocean (especially in the Oyashio region) is known to be one of the regions where the biological drawdown effect of $p\text{CO}_2$ in surface waters is among the highest in the world (Takahashi et al., 2002). The subarctic Oyashio Current with low temperature and salinity and

high nutrients flows south-westward, and the subtropical Kuroshio Current with high temperature and salinity and low nutrients flows north-eastward in the Northwest Pacific, converging in the waters off northern Japan to form the Kuroshio-Oyashio transition region. The interaction between the Oyashio and the Kuroshio can provoke eddies that stir up nutrients from deeper waters, fueling more blooms (Nakata et al., 1995; Nakata, 1988). In addition, modified Kuroshio warm-water rings, which detach from the Kuroshio Extension (KE), are frequently found in the Oyashio region. Intense warm-core rings and cold-core rings occur in this transition region. Eddy-eddy interactions, vortex mergers, and eddy-Kuroshio interactions are also frequently observed (Yasuda et al., 1992). Similarly, the KE and its adjacent regions are important nursery grounds for small pelagic fishes during winter and spring (Watanabe, 2007). Food availability in these regions may be one of the factors that affect fluctuations in the populations of these fishes (Takahashi et al., 2008). Further-

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*Corresponding author, E-mail: wangyanguo@tio.org.cn

more, the transition waters exhibit considerable seasonal and interannual variations of sea surface temperature (SST) in autumn and spring in comparison to the relatively stable SST of the Kuroshio water. SST anomalies were also larger in the transition waters in autumn and spring than in the Kuroshio water (Watanabe et al., 2003). Large variability is also seen in the major oceanographic fronts. The Kuroshio Extension Front had interannual variations in latitudinal anomalies of the first meander crest greater than $\pm 1^\circ$. The subarctic Oyashio Front exhibited interannual variations in latitude anomalies of $\pm 1^\circ$ averaged from 146° – 155° E (Yasuda, 2003).

As primary producers in the ocean, phytoplankton play significant roles in regulating the marine ecosystem, global carbon cycle and climate variability by photosynthesis and thus providing energy for other organisms (Falkowski and Woodhead, 1992). There are many studies on the phytoplankton community in the West Pacific Ocean, which provide abundant historical data. However, most of these researches focus on local or regional scale such as the Kuroshio and the Oyashio regions (Kasai et al., 1997; Saito et al., 2002; Nakata and Hidaka, 2003; Hashihama et al., 2008; Hayakawa et al., 2008; Okamoto et al., 2010; Nakayama et al., 2010; Siswanto et al., 2016). Only a few oceanographic surveys have involved broad-scale latitudinal changes. Moreover, the collection and analysis methods of phytoplankton are inconsistent. The collection of phytoplankton includes net-sampling (Marumo et al., 1961; Yamamoto et al., 1988) and water sampling, and most of the existing studies on phytoplankton species composition were analyzed by size fractionation (Nishibe et al., 2015) and biomarker pigments (Nishibe et al., 2017). The phytoplankton biomass were estimated mainly from the chlorophyll *a* concentrations, cell volume, carbon content, nitrogen content, etc. Therefore, historical data of phytoplankton are dis-

continuous and incomparable, and available data are limited and fragmented. Although identification by light microscopy is time-consuming and requires a high level of taxonomic skills, it is still the most reliable method of microalgal identification (Tomas, 1997). In addition, since copepods and nauplii generally prefer to prey on $>10\ \mu\text{m}$ phytoplankton, the relationship between large phytoplankton and fishery resources often shows a positive correlation (Runge, 1980; Nakata et al., 1995; Nishibe et al., 2017). In this investigate, not only a wide scope with latitude ranging from 21.0° to 42.0° N, longitude ranging from 118.0° to 156.0° E was covered, but also two sampling methods were carried out simultaneously. The present paper analyzed the species composition, horizontal and vertical distributions, seasonal variation, regional disparities, and its relation to different water masses and nutrient structure in the NWPO.

2 Materials and methods

2.1 Sampling and analysis methods

The study region encompassed an area between 21.0° – 42.0° N and 118.0° – 156.0° E. The 45 phytoplankton sampling stations included Sections A, B and C in different water currents and Section D along 146.5° E (Fig. 1). Two seasonal cruises were carried out in the NWPO during 11 to 30 May and 27 August to 24 September 2017, representing spring and summer, respectively. A total of 720 phytoplankton samples were collected, including 630 water samples and 90 net samples. The net samples were collected from 0 to 200 m by vertical tows with a conical plankton net (mouth opening $0.1\ \text{m}^2$, mesh size $0.076\ \text{mm}$). The samples were concentrated to 500 mL and preserved with formaldehyde (final concentration of 2%). A total of 0.5 mL subsamples were identified under a Carl Zeiss microscope. The water samples

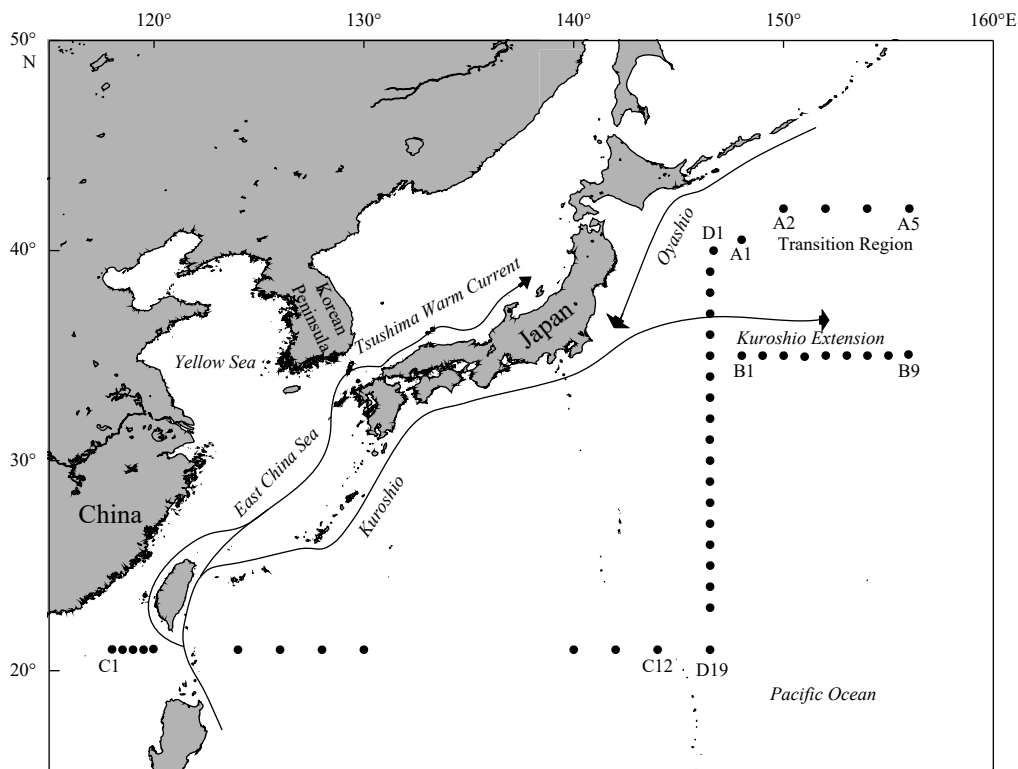


Fig. 1. Locations of sample stations in the Northwest Pacific Ocean in spring and summer 2017. Three cross Sections A, B and C were located in different water currents, and longitudinal Section D along 146.5° E represented different latitudes.

were collected using 10 L Niskin bottles at discrete depths (2, 30, 50, 75, 100, 150 and 200 m). All samples were immediately fixed with Lugol's solution (final concentration of 2%). After 24 h, buffered formaldehyde was added (final concentration 2%). Determinations and counts of 10 mL subsamples were analyzed under an inverted Zeiss-Z1 microscope (Carl Zeiss MicroImaging, Göttingen, Germany) at 200× or 400× magnification using the Utermöhl method (Utermöhl, 1958). Identification of algal species was based on Round et al. (1990), Tomas (1997), Sun and Liu (2002) and Lee (2008). Temperature and salinity data were collected using a Sea-Bird 911 CTD probe (Seabird Electronics, Inc., Bellevue, WA, USA). Nutrient samples were collected using Niskin water bottles and processed using a Model 300 automated nutrient analyzer (Alpkem, Clackamas, OR, USA; Grasshoff et al., 1999). The size limit of resolution for this analysis was ~5 μm.

2.2 Data analysis

Community diversity is described by the Shannon-Wiener diversity index (H'), following the formulation given by Sun and Liu (2004): $H' = -\sum p_i \log_2 p_i$, $J = H' / \log_2 S$, where p_i is defined as n_i / N , n_i is the sum of cell abundance for species i in all samples, N is the sum of cell abundance for all species, and S is the species number in the sample.

Relationships between the phytoplankton community and environmental parameters were analyzed by SPSS 14.0 and CANOCO version 4.5. Only those taxa that were observed in more than 10% of the samples and with more than 1% in the total abundance were included in analyses. Both of the species data and the environmental variables were $\log_{10}(x+1)$ transformed before analyses. Detrended correspondence analysis (DCA) for the species data was used to determine the methods that would be applied. As was suitable for unimodal ordination, redundancy analysis (RDA) was chosen since that the maximum gradient length of the four axes was less than 3.

3 Results

3.1 Physico-chemical parameters

The distribution of temperature, salinity and nutrients in the surface water are shown in Fig. 2 and Table 1. SST was relatively low in spring. The average temperature of the whole region was $(21.46 \pm 6.58)^\circ\text{C}$, varying from 6.62 to 29.37°C . The water temperature increased significantly from north to south, the values of Transect A in the Transition Region was below 10°C , and that of Transect B in the Kuroshio Extension region increased to nearly 20°C . The water temperature of Transect C in the southern region further increased to above 28°C , whereas a small cold eddy appeared at Sta. C4 in the south of Taiwan with water temperature below 27.8°C due to the upwelling. In summer, the water temperature increased markedly, with an average of $(26.70 \pm 3.03)^\circ\text{C}$, ranging from 16.72°C to 30.25°C . The temperature in the Transition Region was still the lowest, with the minimum value (16.72°C) recorded at Sta. A1. The distribution pattern of temperature was consistent with that in spring.

In spring, the average of sea surface salinity (SSS) was 34.46 ± 0.56 , varying from 32.98 to 35.18 . The salinity of Transect A was the lowest, and that at Stas A1 and A2 was below 33 due to the influence of the Oyashio current. While the salinity in the southern area was the highest, with levels at Stas D14–D18 was above 35. In summer, the average salinity of the whole region was 34.35 ± 0.54 , varying between 32.27 and 34.87 . Because the Oyashio current became weaker and retreated northward, only the sa-

linity at Stas A1 (32.27) and D1 (32.40) in the northern area was below 33.0. Similarly, since the influence of coastal current in the south of Taiwan, the salinity from Stas C1 to C5 in Transect C was lower than 34.0, with an average of 33.72 ± 0.15 , whereas that from Stas C6 to C12 in Transect C was higher than 34.0, with an average of 34.56 ± 0.25 .

In spring, nitrogen and silicon were abundant, while phosphorus was relatively insufficient. The average of dissolved inorganic nitrogen (DIN) concentration was $(2.29 \pm 4.81) \mu\text{mol/L}$, varying from 0.27 to $22.03 \mu\text{mol/L}$. Affected by the nutrient-enriched Oyashio Current, the average DIN concentration of Transect A in the northern area was the highest (mean $14.48 \mu\text{mol/L}$), and the values at Stas A2, A4 and A5 were as high as $16.18 \mu\text{mol/L}$, $22.03 \mu\text{mol/L}$ and $18.56 \mu\text{mol/L}$, respectively. Due to the influence of the oligotrophic Kuroshio, the DIN concentrations in the south-central area declined significantly, and the average of Transects B, C and D were all below $1.0 \mu\text{mol/L}$. The average of phosphate concentration was $(0.19 \pm 0.97) \mu\text{mol/L}$, the levels at several stations were below the detection limit. Whereas, the level of Transect A was also the highest, with maximum value ($1.18 \mu\text{mol/L}$) recorded at Sta. A5. The average of silicate concentration was $(2.91 \pm 3.69) \mu\text{mol/L}$, and level of Transect A was also the highest, with an average of $(12.20 \pm 1.92) \mu\text{mol/L}$, which was 6.35, 6.74 and 7.44 times higher than that of Transect B, C and D, respectively. In summer, the nutrient concentrations decreased drastically. Especially, the phosphate and silicate at about 25% of the stations were lower than the detected value. The distribution pattern of nutrients was similar to that in spring, which the nutrient concentrations of Transect A were the highest. The average of DIN concentration was $(0.30 \pm 0.34) \mu\text{mol/L}$, varying from 0.08 to $1.87 \mu\text{mol/L}$. The average DIN concentration of Transect A was still the highest, with an average of $(0.83 \pm 0.56) \mu\text{mol/L}$, which was 3.95, 2.24 and 3.19 times higher than that of Sections B, C and D, respectively. The average of phosphate concentration was $(0.10 \pm 0.09) \mu\text{mol/L}$, and that at Stas A1, A2 and D1 in the Transition Region were 0.21 , 0.14 and $0.16 \mu\text{mol/L}$, respectively. Whereas, the values of Transect C in the southern area was the lowest, and that at Stas C9–C12 were lower than the detection value. The average of silicate concentration was $(0.61 \pm 0.52) \mu\text{mol/L}$. The concentrations of most stations were less than $1.00 \mu\text{mol/L}$, while the concentration of Transect A was relatively high, and the maximum value ($2.53 \mu\text{mol/L}$) was observed at Sta. A2.

3.2 Species composition

A total of 281 phytoplankton taxa belonging to 5 phyla and 61 genera were identified in the two seasons. The phytoplankton community in the NWPO was mainly composed of diatoms and dinoflagellates, with 165 taxa in 44 genera of diatoms and 110 taxa in 13 genera of dinoflagellates, respectively. Most of the phytoplankton communities were cosmopolitan species and warm-water species, a few warm-temperate species such as *Thalassiosira nordenskiöldii*, *Chaetoceros concaivicornis*, *C. convolutus* and *C. furcellatus* were mainly found in the Transition Region due to the influence of the Oyashio Current. Warm-water species such as *Planktoniella sol*, *Ceratium vultur* var. *sumatranum*, *Ornithocercus splendidus* and *Pyrocystis hamulus* var. *inaequalis* mainly appeared in the south-central area affected by the Kuroshio Current. *Trichodesmium erythraeum*, *T. hildebrandtii* and *T. thiebauti* of Cyanophyta were mainly distributed in the south of Taiwan. The most species-rich genera were *Chaetoceros* spp., *Coscinodiscus* spp. and *Rhizosolenia* spp. for diatoms, and *Ceratium* spp. for dinoflagellates. The number of phytoplankton species in spring was more than that in summer, with 248 spe-

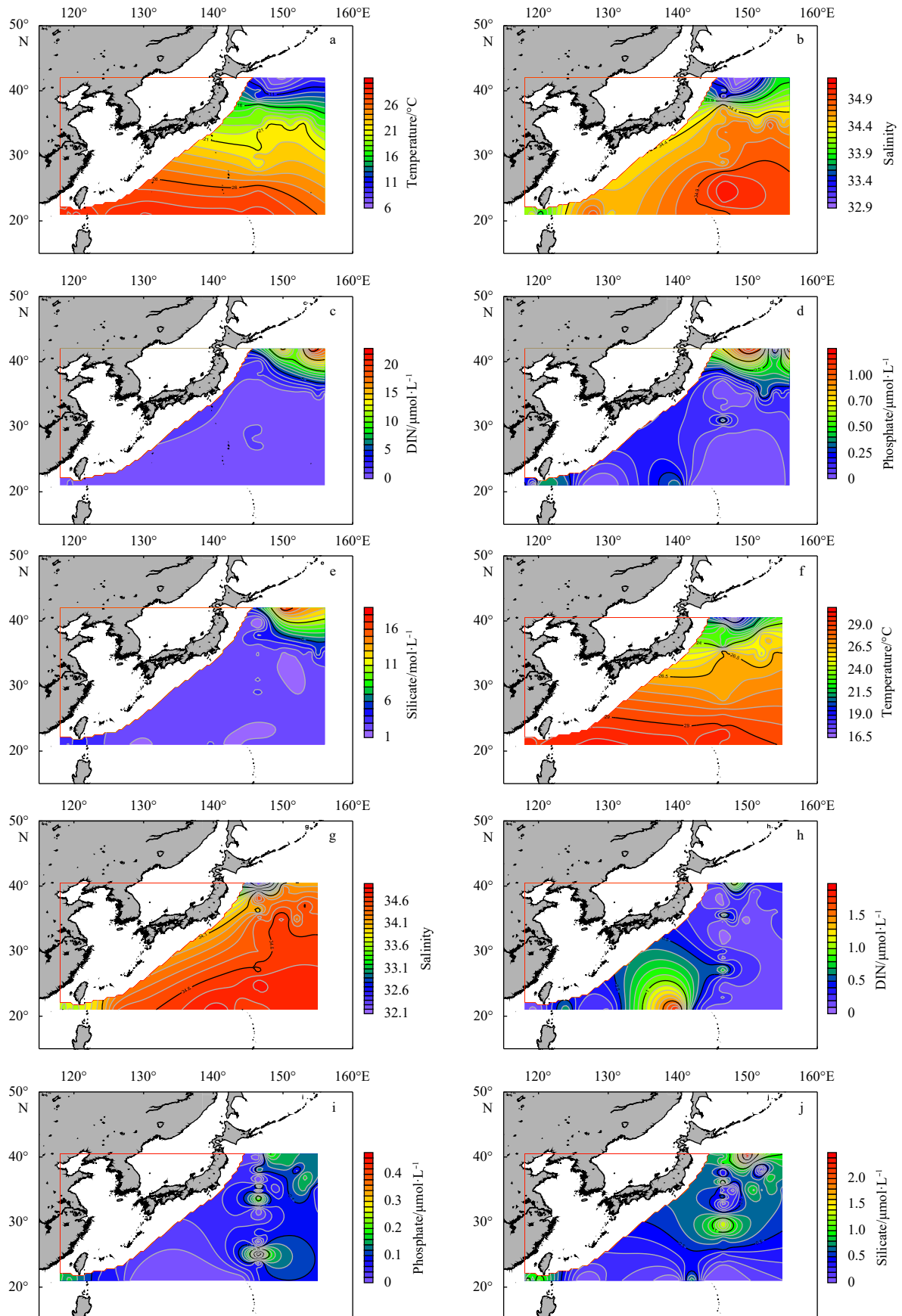


Fig. 2. Distribution of temperature ($^{\circ}\text{C}$), salinity, DIN ($\mu\text{mol/L}$), phosphate ($\mu\text{mol/L}$) and silicate ($\mu\text{mol/L}$) in the surface layer of the Northwest Pacific Ocean in spring (a–e) and summer (f–j).

Table 1. Temperature, salinity, nutrients and phytoplankton of the surface layer for different transects in the Northwest Pacific Ocean

Parameter	Season	Transect A	Transect B	Transect C	Transect D	The whole region
Water temperature/°C	spring	8.44±1.16	19.84±1.43	28.40±0.49	21.28±4.89	21.46±6.58
	summer	18.54±2.59	26.04±0.60	29.83±0.28	26.29±2.53	26.70±3.03
Salinity	spring	33.39±0.41	34.65±0.16	34.47±0.35	34.65±0.52	34.46±0.56
	summer	33.38±1.39	34.54±0.15	34.21±0.48	34.44±0.53	34.35±0.54
DIN/μmol·L ⁻¹	spring	14.48±5.24	0.73±0.86	0.66±0.51	0.88±0.50	2.29±4.81
	summer	0.83±0.56	0.21±0.12	0.37±0.51	0.26±0.24	0.30±0.34
Phosphate/μmol·L ⁻¹	spring	0.82±0.49	0.14±0.12	0.14±0.15	0.09±0.14	0.19±0.97
	summer	0.18±0.05	0.09±0.04	0.08±0.07	0.09±0.13	0.10±0.09
Silicate/μmol·L ⁻¹	spring	12.20±1.92	1.92±1.33	1.81±0.93	1.64±1.03	2.91±3.69
	summer	1.82±1.00	0.61±0.28	0.52±0.50	0.54±0.47	0.61±0.52
Phytoplankton abundance/10 ² cells·L ⁻¹	spring	1 090.40±518.40	126.0±68.13	92.83±48.80	134.21±180.27	227.78±366.86
	summer	226.60±196.74	59.11±23.17	49.67±26.99	79.05±115.62	83.62±109.71
<i>H'</i>	spring	2.16±0.45	2.56±0.75	2.44±1.03	2.55±0.73	2.46±0.78
	summer	3.10±0.46	3.19±0.22	3.07±0.99	3.13±0.56	3.12±0.46
<i>J</i>	spring	0.66±0.11	0.65±0.17	0.64±0.27	0.65±0.17	0.64±0.19
	summer	0.77±0.06	0.78±0.03	0.75±0.17	0.75±0.09	0.76±0.11

cies and 235 species, respectively. In spring, diatom was the largest group, accounting for 58.47% of the total number of species and 97.45% of the total phytoplankton abundance. The dominant species were *C. compressus*, *R. alata* and *T. subtilis*, accounting for 14.52%, 12.86% and 11.1% of the total phytoplankton abundance, respectively. Dinoflagellate was the second most common group, accounting for only 39.11% of the total number of species and 0.44% of the total phytoplankton abundance. The frequently encountered species were *C. fusus* var. *seta*, *C. fusus* and *C. trichoceros*, which accounted for less than 0.10% of the total phytoplankton abundance. In summer, the species composition of phytoplankton community diversified, the dominant species were not prominent, with individual distribution among species was relatively uniform. The dominant genera of diatom was *Chaetoceros* spp., accounting for 41.10% of the total phytoplankton abundance, and the dominant species were *Thalassionema frauenfeldii*, *Pseudo-nitzschia delicatissima*, *C. messanensis* and *C. lorenzianus*, which accounted for 13.68%, 7.40%, 7.02% and 5.69% of the total phytoplankton abundance, respectively. The dominant genera of dinoflagellate was still *Ceratium* spp., and the dominant species were *C. trichoceros*, *C. tripos*, *C. fusus* and *C. fusus* var. *seta*, which accounted for 0.27%, 0.23%, 0.19% and 0.17% of the total phytoplankton abundance, respectively.

3.3 Horizontal distribution of phytoplankton

The horizontal distributions of surface phytoplankton abundance are shown in Fig. 3a, b. In spring, the average of surface phytoplankton abundance was (227.78±366.86)×10² cells/L, ranging from 38.0×10² to 1 860.0×10² cells/L. Phytoplankton abundance was mainly concentrated in the northeastern area affected by the Oyashio Current, and high phytoplankton abundances were observed at Stas A1 to A5 of Transect A as well as Stas D1 and D2 of Transect B. The maximum abundance appeared at Sta. A2, and the predominant genera were *Chaetoceros* spp., *Rhizosolenia* spp. and *Thalassiosira* spp., accounting for 63.90%, 27.18% and 2.40% of the station abundance, respectively. The predominant species mainly consisted of *T. nordenskioldii* (17.52%), *C. concavicornis* (17.07%), *P. delicatissima* (15.42%), *R. alata* (7.49%), *C. diadema* (4.87%) and *R. hebetata* f. *semispina* (3.24%). Elevated abundances (100.0×10² cells/L) were observed at Stas B1–B4 in Transect B, with dominant species being chain-forming diatoms such as *Pseudoeunotia doliolus* and *T. nitzschioides*. Along Tran-

sect C, patches of high abundance (225.0×10² cells/L) occurred at Sta. C4 in the south of Taiwan, and the predominant species was *T. subtilis* being clump-forming diatoms, which was brought to the surface by upwelling and contributed more than 67.76% of cell abundance at this station.

In summer, phytoplankton abundance declined significantly, with average of (83.62±109.71)×10² cells/L, ranging from 15.0×10² to 560.0×10² cells/L. High abundances (>500.0×10² cells/L) still appeared in the northern part of the survey area, but the range was reduced to Stas A1 and D1. The maximum abundance appeared at Sta. A1, which mainly consisted of *T. subtilis* (12.28%), *C. affinis* (9.70%), *T. nitzschioides* (6.48%), *P. delicatissima* (5.51%), *Leptocylindrus mediterraneus* (2.37%), *C. lorenzianus* (1.52%). A relatively high abundance was observed at Stas D6 and B1 in the Kuroshio Extension region, which were mainly composed of cosmopolitan species and warm-water species. Phytoplankton abundance in Transect C was the lowest. However, due to the influence of coastal current, the abundance at Stas C1–C5 in the south of Taiwan was significantly higher than other stations in this transect. Some neritic species such as *Skeletonema costatum*, *P. delicatissima* and *Paralia sulcata* were relatively abundant in the adjacent water of Taiwan.

For comparison of the two sampling methods, the horizontal distributions of net-sampling phytoplankton were shown in Figs 3c, d. In spring, the mean phytoplankton abundance of net-sampling was (959.06±1 539.22)×10³ cells/m³, ranging from 60.0×10³ to 8 600.0×10³ cells/m³. The abundance at Stas A1 to A5 in Transect A and D1 to D3 in Transect D were all above 1 000.0×10³ cells/m³, and the maximum occurred at Sta. A2, up to 8 600.0×10³ cells/m³. In summer, the mean phytoplankton abundance of net-sampling was (143.77±269.91)×10³ cells/m³, ranging from 3.07×10³ to 1 767.0×10³ cells/m³. The high value areas with abundance more than 1 000×10³ cells/m³ only appeared at Stas A2, A3 and D3 in the northern Transition Region. The maximum abundance appeared at Sta. A3, but decreased to 1 767.0×10³ cells/m³. Distribution of phytoplankton abundance of net-sampling was similar to that in the surface layer. In summary, in both water-sampling and net-sampling, the maximum phytoplankton abundance in the NWPO always appeared in the northern transition region affected by the nutrient-rich Oyashio Current, while the minimum always appeared in the southern area affected by oligotrophic Kuroshio Current. The horizontal distri-

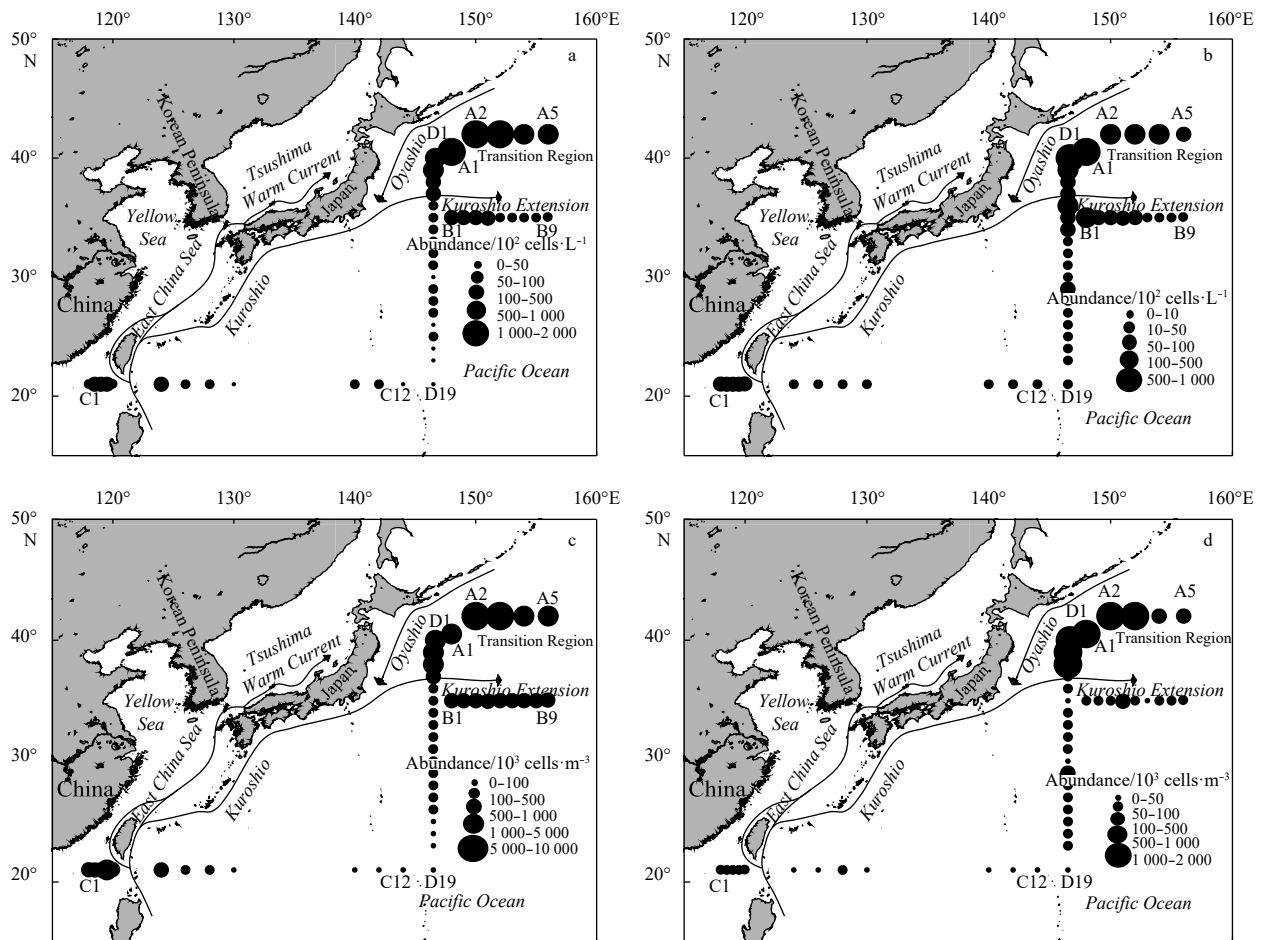


Fig. 3. Horizontal distribution of phytoplankton abundance in the Northwest Pacific Ocean. a. Spring, surface layer; b. summer, surface layer; c. spring, net sampling; and d. summer, net sampling.

bution of phytoplankton abundance increased from low to high latitudes, which was consistent with the trend of nutrient distributions, but contrary to that of water temperature and salinity.

3.4 Vertical distribution of phytoplankton

The vertical distribution of phytoplankton in the NWPO showed regional differences and seasonal variations. The vertical distribution of phytoplankton varied significantly in spring. The phytoplankton abundance at depths of 2, 30, 50, 75, 100, 150 and 200 m were 227.78, 231.22, 138.36, 57.83, 18.96, 8.79 and 5.08×10^2 cells/L, respectively. However, the vertical variation of phytoplankton abundance was not obvious in summer. The phytoplankton abundance at depths of 2, 30, 50, 75, 100, 150 and 200 m were 83.62, 64.36, 35.33, 12.89, 5.12, 2.95 and 1.54×10^2 cells/L, respectively. Because the stations in Transect D were distributed from low latitude to high latitude, the distribution pattern of phytoplankton in Transect D was basically consistent with that in the whole survey area, which could reflect the distribution trend of phytoplankton in the NWPO. Therefore, this study only took Transect D as an example to analyze the regional differences of vertical distribution of phytoplankton. The vertical distributions of temperature, salinity, nutrients and phytoplankton abundance along Transect D are shown in Fig. 4. The vertical distribution of phytoplankton abundance was notably different among regions. In the northern area affected by the Oyashio Current, the phytoplankton abundance was mainly concentrated in

the upper 30 m of water column, and was mainly composed of diatoms. In the south-central area affected by the Kuroshio Current, the maximum abundance often occurred at depths of 50–75 m, which was mainly composed of dinoflagellates. For example, at Stas D1 and D2 affected by the Oyashio Current in spring, the phytoplankton abundance was mainly concentrated in the surface layer. While the phytoplankton abundance at Stas D3–D7 peaked at depth of 30 m. The maximum abundance at Stas D8–D14 appeared at depths of 30–50 m and decreased rapidly with increased depth. At Stas D15–D19 in the southern Kuroshio region, the maximum abundance was observed at depths of 50–75 m. In summer, the water column was homogeneously mixed except for the northern region. At Sta. D1 affected by the Oyashio Current, the phytoplankton abundance was mainly concentrated in the super layer, while the phytoplankton abundance at Stas D2–D5 peaked at depth of 30 m. At Stas D6–D14 in the central region, the maximum abundance were recorded at depths of 50–75 m and decreased gradually with increased depth. At Stas D15–D19 in southern region, the phytoplankton abundance was distributed homogeneously throughout the water column.

4 Discussion

4.1 Phytoplankton abundance in different water systems

The survey area is strongly influenced by two currents with

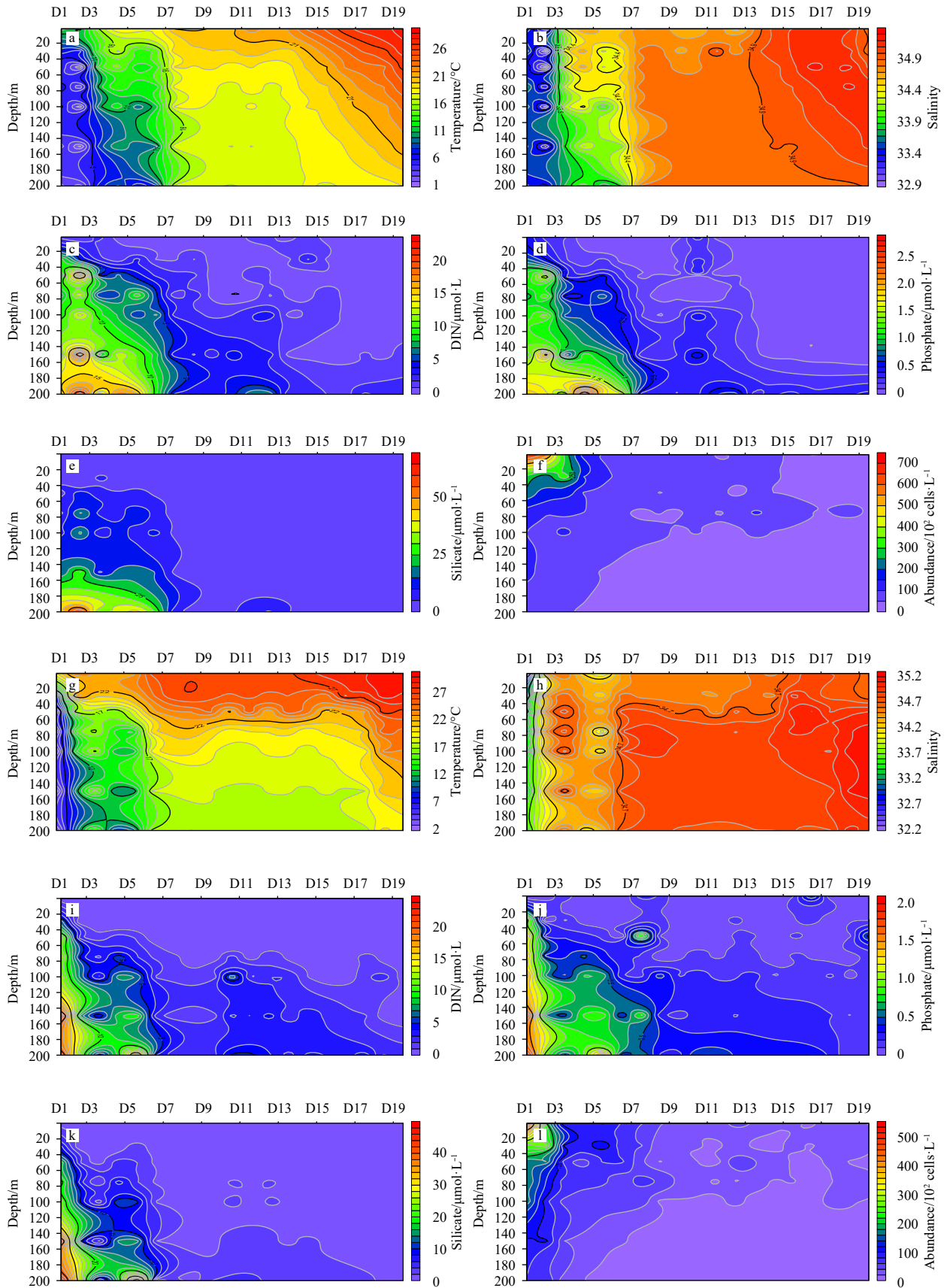


Fig. 4. Vertical distribution of temperature ($^{\circ}\text{C}$), salinity, nutrient concentrations ($\mu\text{mol/L}$) and phytoplankton abundance (10^2 cells/L) along Transect D in the Northwest Pacific Ocean in spring (a-f) and summer (g-l).

different hydrographic properties, and their influence ranges and degrees vary with seasons. The hydrography in the Oyashio region is often complex, with two or three dominant water masses with different chemical and physical properties moving through during spring (Kono and Sato, 2010). The Oyashio Current and coastal waters are both enriched with iron, a critical nutrient for phytoplankton growth. Blooms off the coast of Hokkaido are a yearly spring-time occurrence (Liu et al., 2004; Nakayama et al., 2010). The high productivity of higher trophic levels, including fisheries production, in the Oyashio region is often related to this conspicuous event (spring phytoplankton bloom) (Taniguchi and Kawamura, 1972; Taniguchi, 1999). In spring, the Oyashio Current flowing south-westward was relatively strong and had a wide range of influence, covering five stations of Transect A and two stations of Transect D. Since the Oyashio Current was characterized by low temperature and salinity and high nutrient and chlorophyll *a* concentrations, the temperature and salinity at these stations were obviously lower than that at other stations, with temperature and salinity lower than 12.5°C and 34.0, respectively. Whereas the nutrient concentrations of Transect A were the highest, with the concentrations of DIN, phosphate and silicate were 6.32, 4.32 and 4.19 times as high as that of the whole region, respectively. Although consumed by phytoplankton, the concentrations of DIN, phosphate and silicate were still as high as 14.48 $\mu\text{mol/L}$, 0.83 $\mu\text{mol/L}$ and 0.82 $\mu\text{mol/L}$, respectively. Therefore, the phytoplankton abundance in spring was 2.72 times higher than that in summer. In addition, the phytoplankton abundance of Transect A was the highest in the four transects, which was 8.65, 11.75, 8.12 and 4.79 times higher than that of Transects B, C, D and the whole area, respectively (Figs 3a, c). In summer, the Oyashio Current weakened, and the influence range retreated northward. The Oyashio Current only affected Stas A1 and D1. The water temperature and salinity of these two stations were obviously lower than those of other stations, with the water temperature below 20°C and the salinity below 33.48. Conversely, the Kuroshio Current flowing north-eastward was stronger and the scope of influence expanded northward. For example, the surface water temperature increased markedly from 19.88°C at Sta. D1 to 23.66°C at Sta. D2 and salinity increased significantly from 32.27 to 34.45. Because of the low nutrient and chlorophyll *a* concentrations of Kuroshio Current, the nutrient concentrations decreased greatly, and the decrease of Transect A was the largest. The concentrations of phosphate and silicate at many stations were below the detection values. The average concentration of DIN decreased from 2.29 $\mu\text{mol/L}$ in spring to 0.30 $\mu\text{mol/L}$ in summer. Similarly, the concentration of phosphate decreased from 0.19 $\mu\text{mol/L}$ to 0.10 $\mu\text{mol/L}$, and that of silicate decreased from 2.91 $\mu\text{mol/L}$ to 0.61 $\mu\text{mol/L}$. Thus the average abundance of phytoplankton declined sharply from 227.78×10^2 cells/L in spring to 83.62×10^2 cells/L in summer, and the relatively high abundance appeared only at Stas A1 and D1 (Figs 3b, d). Furthermore, the seasonal variation of phytoplankton abundance in Transect A was the largest among the four transects, and the decrease magnitude of Transects A, B, C and D were 4.81, 2.13, 1.87 and 1.70 times, respectively. In contrast, the nutrients in the south-central area directly affected by the Kuroshio were quite low throughout the year, especially phosphate, the concentrations at many stations was below the detection value. Both nitrogen and phosphorus could limit phytoplankton growth in this area. Therefore, phytoplankton abundance was correspondingly the lowest in the whole region.

Several previous studies have shown that small changes in the nutrient supply can have profound impacts on the plankton

communities in oligotrophic regions (Richardson, 2008). The magnitude and duration of the spring bloom are different between the coastal and offshore regions because they can have different strengths of stratification and nutrient concentrations (Kasai et al., 1997). Primary productivity was strongly affected by advection, which causes upward and downward transport of nutrients and phytoplankton blooms resulted from the cross-frontal flow along the meander of the Kuroshio Extension (Ito et al., 2000). The present study found that relatively high phytoplankton abundance was observed in the Kuroshio Extension. The common dominant species were mainly composed of cosmopolitan species such as *T. nitzschoides*, *T. frauenfeldii*, *C. lorenzianus*, *R. styliformis*, *P. seriata*, and warm-water species such as *C. denticulatus*, *R. castracanei*, *P. sol*, *O. splendidus*. The species richness and community diversity of phytoplankton in this region were relatively higher than those in the adjacent regions, implying significant frontal effect on phytoplankton community structure. Numerous studies have found that primary productivity is often high in estuaries and upwelling regions around the world. Large amounts of nutrients are supplied into the East China Sea (ECS) by runoff from the Changjiang River (Yangtze River) (Edmond et al., 1985; Shen et al., 2008) and upwelling of Taiwan Warm Current along the Chinese coast (Lee-Chen, 2000), and a significant amount of nutrients is supplied by the persistent upwelling of Kuroshio subsurface water in the southern ECS northeast of Taiwan (Gong et al., 1996). With such fertile hydrographic conditions, the ECS is famous for its high biological productivity (Chen and Wang, 1999). Similarly, due to the superimposing influence of coastal current and upwelling, the nutrient concentrations in the south of Taiwan were higher than that of other stations in Transect C. In spring, from Stas C1 to C5, the concentrations of DIN, phosphate and silicate in surface layer were 0.80, 0.19 and 2.55 $\mu\text{mol/L}$, respectively. However, from Stas C6 to C12, the average concentrations of DIN, phosphate and silicate in surface layer decreased to 0.55, 0.11 and 1.27 $\mu\text{mol/L}$, respectively. Thus the average abundance of Stas C1–C5 was nearly twice as high as that of Stas C6–C12. In summer, the distribution patterns of phytoplankton abundance and nutrient concentrations in Transect C was similar to that in spring.

In a word, the Oyashio Current flowing south-westward was characterized by low temperature and salinity and high nutrients. Conversely, the Kuroshio Current flowing north-eastward was characterized by high temperature and salinity and low nutrients. As a result, significant negative correlations were observed between phytoplankton abundance and temperature and salinity in all water layers both in spring and summer ($p < 0.01$). Whereas, phytoplankton abundances were positively correlated with DIN, phosphate and silicate concentrations, especially the surface layer in spring ($p < 0.01$, Table 2).

4.2 Phytoplankton community and environmental factors

The relationship between phytoplankton and environmental factors was analyzed by RDA. We obtained a two-dimensional distribution figure of species, sample distribution and environmental factors (Fig. 5). The result showed that there were three distinct communities of phytoplankton in the NWPO in spring: community I distributed in the northern Transition Region which was directly affected by nutrient-enriched Oyashio current, and encompassed samples collected at Stas A1–A5 in Transect A as well as D1 and D2 in Transect D. The community was characteristic of high abundance, and primarily dominated by warm-temperate species such as *R. alata*, *P. delicatissima*, *C. concavicornis* and *T. nordenskioldii*, which were positively correlated with high

Table 2. Correlation analysis (R values) between phytoplankton abundances and environmental parameters in the Northwest Pacific Ocean

Season	Samples	Temperature	Salinity	DIN	Phosphate	Silicate
Spring	surface	-0.76**	-0.83**	0.71**	0.76**	0.77**
	all water layers	-0.34**	-0.52**	0.04	0.11	-0.04
Summer	surface	-0.76**	-0.82**	0.24	0.06	0.34*
	all water layers	-0.24**	-0.73**	0.12	0.15	0.13

Note: * $p < 0.05$; ** $p < 0.01$.

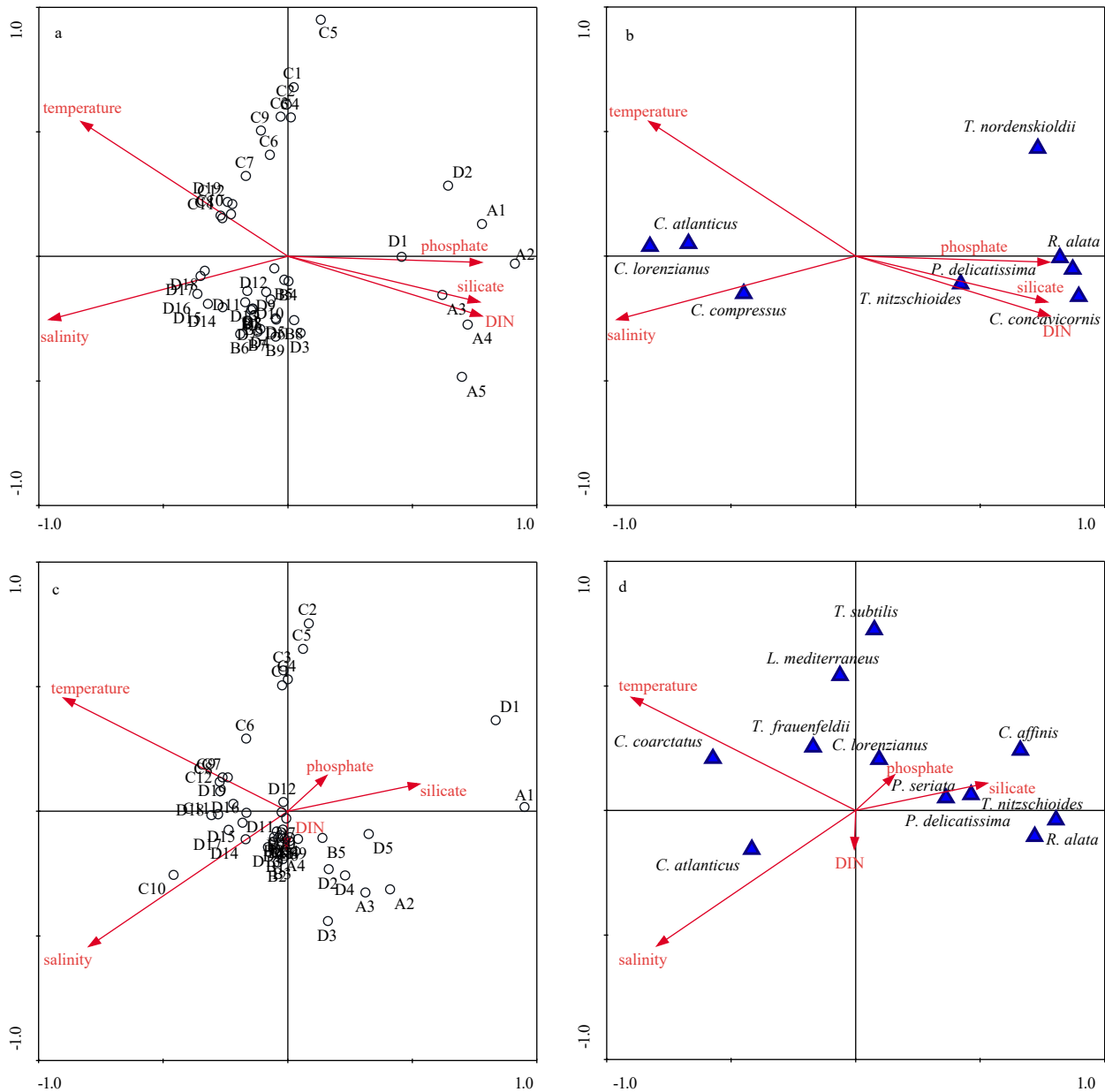


Fig. 5. Redundancy analysis of the dominant phytoplankton species and environmental parameters of the surface layer in the Northwest Pacific Ocean in spring (a, b) and summer (c, d). Circle represents sampling sites, triangle phytoplankton species, and arrows environmental factors.

concentrations of DIN, phosphate and silicate. Community II situated in the southern region, including Stas C1–C12 in Transect C as well as D19. The assemblages of phytoplankton were represented by warm-water species such as *C. atlanticus* which was positively correlated with water temperature. Community III mainly distributed in the south-central area, encompassing samples collected at Stas D3–D19 in Transect D and B1–B9 in the

Kuroshio Extension, where was directly affected by the Kuroshio Current. The assemblages of phytoplankton were represented by cosmopolitan species such as *C. compressus* and *C. lorenzianus* which was positively correlated with salinity. In summer, community I included only Stas A1 and D1 which were still affected by the Oyashio, and represented the coastal water with high nutrient concentrations. The phytoplankton assemblage was mainly

composed of neritic species such as *C. affinis* and *P. seriata* and cosmopolitan species such as *T. nitzschioides*, which were positively correlated with silicate concentration. Community II situated in the south of Taiwan Island and included samples collected at Stas C1–C5 in Transect C. The main dominant species were *T. subtilis*, *C. lorenzianus* and *L. mediterraneus*, which were brought by upwelling and coastal water and correlated with phosphate concentration. Community III was distributed in the Transition Region and Kuroshio Extension. The phytoplankton community was mainly composed of *P. delicatissima* and *R. alata*, which was correlated with DIN concentrations. Community IV situated in the south-central area, affected by the offshore Kuroshio water with low nutrient concentrations and high temperature and salinity. The community was characteristic of high species diversity and low abundance. The phytoplankton assemblage was represented by warm-water species such as *C. coarctatus* and *C. atlanticus*, which were positively correlated with water temperature and salinity.

In a word, the availability of nutrients, water temperature and salinity differed among water types. The northern Transition Region was always nutrient-enriched, while southern Kuroshio water was characterized by high temperature, high salinity and low nutrients. The seasonal variation in environmental parameters mentioned above should greatly influence the phytoplankton community. In the south-central area, the phytoplankton abundance was significantly correlated with temperature and salinity regardless of spring and summer, while no obvious correlation was observed between phytoplankton abundances and any nutrient concentration. In the northern Transition Region, the phytoplankton abundances were positively correlated with nutrient concentrations, especially in spring. It embodied the unification between ecological characterization of phytoplankton and its inhabiting environment.

4.3 The ratio of diatoms to dinoflagellates and nutrient structure

Studies of the factors regulating phytoplankton communities have been carried out for several decades, but the role of nutrient limitation and the resource–ratio hypothesis in influencing the phytoplankton community is still not fully understood. As diatoms and dinoflagellates show great differences in cell morphology, structure, and nutrition mode, they differ greatly in their acquisition of nutrients strategy. Many studies have revealed that dinoflagellates have the ability of mixotrophy, and the mixotrophic modes of dinoflagellates include direct engulfment of prey, peduncle feeding, and pallium feeding (Smayda, 1997; Huang et al., 2005). Stoecker (1999) found that phosphorus limit-

ation was a common factor stimulating dinoflagellates to ingest particulate nutrients, which may be another reason for the dominance of dinoflagellates in phosphorus-limited conditions. The variation of phytoplankton community structure was always correlated with the fluctuation of physico-chemical environmental parameters. The nutrients in the NWPO were deficient except the Transition Region in the northern area. The nutrient concentrations in Transect A were the highest in the whole region, and the N:P ratio was 17.66, which was nearly to the Redfield ratio of 16:1 (Redfield et al., 1963). Moreover, the concentration of silicate was still as high as 12.20 $\mu\text{mol/L}$ despite absorbed largely by phytoplankton (Table 1). Smayda (1997) and Egge (1998) considered that when silicate concentration in the environment was $>2 \mu\text{mol/L}$, diatoms could dominate the phytoplankton community if other nutrients were sufficient. Therefore, the growth of diatom in Transect A was not limited by nutrient limitation, the phytoplankton abundance was the highest in the whole region, and diatom dominated the phytoplankton community. However, the nutrient concentrations were very low in the offshore KW. The N:P ratios in Transects B, C and D were all less than 10, which implied nitrogen limitation (Justic et al., 1995). In addition, the phosphate concentrations of almost a quarter of stations were below the detection values (24.44% in spring and 26.67% in summer), and that of nearly two-thirds of the stations were below 0.1 $\mu\text{mol/L}$ (62.22% in spring and 64.44% in summer), which indicated a serious lack of phosphate (Fisher et al., 1992). Egge (1998) found that diatoms are more easily affected than dinoflagellates when nutrients are limited, especially under phosphorus limitation. Thus the growth of diatom in the offshore KW was inhibited by both nitrogen and phosphorus limitation, and the phytoplankton abundance declined sharply. However, due to dinoflagellates possessing a survival advantage over diatoms by utilizing dissolved organic phosphate, the proportion of dinoflagellates in total abundance increased significantly. Whether in spring or summer, the abundance ratio of dinoflagellates to total phytoplankton increased, while that of diatoms to total phytoplankton decreased with N:P ratio decreased. On the other hand, the Si:N ratios were more than 1.0 except for Transect A in spring, which indicates that silicate was relatively abundant in the investigated sea. Therefore, no obvious correlation was observed between phytoplankton composition and Si:N ratio (Table 3). Further analysis revealed that the relative abundance of diatoms to dinoflagellates was significantly positive correlated with the N:P ratio ($R=0.942^{**}$, $^{**}p<0.01$), and negatively correlated with the Si:N ratios ($R=-0.693^{*}$, $^{*}p<0.05$). The present study indicates that N:P ratio rather than Si:N ratio played a significant role in regu-

Table 3. The relationship between the abundance ratio of diatoms to dinoflagellates and the structure of nutrients in different transects

Season	Parameter	Transect A	Transect B	Transect C	Transect D
Spring	ratio of N:P	17.66	5.21	4.71	9.78
	ratio of dinoflagellates to total abundance/%	0.56	1.28	1.62	1.26
	ratio of diatoms to total abundance/%	99.18	98.41	96.66	98.52
Summer	ratio of N:P	4.61	2.33	4.63	2.89
	ratio of dinoflagellates to total abundance/%	8.77	3.05	11.76	7.41
	ratio of diatoms to total abundance/%	90.16	96.73	87.50	92.02
Spring	ratio of Si:N	0.84	2.63	2.74	1.86
	ratio of dinoflagellates to total abundance/%	0.56	1.28	1.62	1.26
	ratio of diatoms to total abundance/%	99.18	98.41	96.66	98.52
Summer	ratio of Si:N	2.19	2.90	1.41	2.08
	ratio of dinoflagellates to total abundance/%	8.77	3.05	11.76	7.41
	ratio of diatoms to total abundance/%	90.16	96.73	87.50	92.02

lating the phytoplankton community structure in the NWPO. Yin et al. (2000) reported a similar phenomenon in the Zhujiang River (Pearl River) Estuary, where phosphorus limitation favored the dominance of dinoflagellates. Hashihama et al. (2008) also reported that the dominance of flagellates was related to the influence of Kuroshio water on the Sagami Bay. Guo et al. (2014) revealed a relatively good correlation between the relative abundance of diatoms and dinoflagellates with N:P ratios in the East China Sea. In contrast, diatom dominance was mainly controlled by the horizontal advection of coastal water.

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