



Spring phytoplankton community response to an episodic windstorm event in oligotrophic waters offshore from the Ulleungdo and Dokdo islands, Korea

Seung Ho Baek^{a,*}, Minji Lee^a, Yun-Bae Kim^b

^a South Sea Research Institute, KIOST (Korea Institute of Ocean Science and Technology), Geoje 656-830, Republic of Korea

^b Ulleungdo/Dokdo Ocean Science Station, KIOST (Korea Institute of Ocean Science and Technology), Ulleungdo, Republic of Korea

ARTICLE INFO

Keywords:

Japan/East Sea
Ulleungdo and Dokdo
Spring phytoplankton blooms
Episodic windstorm
Algal bioassays

ABSTRACT

We investigated the phytoplankton distribution and its relationship to environmental factors at 40 stations in oligotrophic waters offshore from the Ulleungdo and Dokdo islands (hereafter Ulleungdo or Dokdo) in Japan/East Sea, prior to and following an episodic windstorm event. Nutrient addition bioassay experiments (control, + N, + P, and + NP, in both the presence and absence of added Fe) were also conducted to investigate the growth response of the phytoplankton assemblage and its nutrient consumption, using surface seawater collected from stations 36 and 40, which are in the vicinity of the Dokdo. Field measurements showed that the surface water temperature ranged from 13.33 °C to 16.18 °C and the salinity ranged from 34.03 to 34.55. The nitrate + nitrite, phosphate, and silicate concentrations varied from 0.07 to 2.22 μM, 0.01 μM to 0.19 μM and 0.76 to 6.93 μM, respectively. The Chl-*a* concentration varied from 0.36 to 15.97 μg L⁻¹ (average 2.66 ± 3.26 μM), but was significantly higher in Zone III-*a* (Dokdo) than in Zone I-*b* (between Ulljin and Ulleungdo, prior to the windstorm), Zone I-*a* (between Ulljin and Ulleungdo, following the windstorm), and Zone II-*a* (Ulleungdo) ($F = 17.438$, $p < 0.001$; ANOVA). Diatoms and Raphidophyta were the dominant phytoplankton types. Following episodic windstorm events the abundance of the raphidophyte *Heterosigma akashiwo* was maintained at high levels in the offshore oligotrophic area around the Ulleungdo and Dokdo, particularly in Zone III-*a* ($F = 16.889$, $p < 0.001$; ANOVA). In the algal bioassays conducted with and without added Fe, the *in vivo* fluorescence values in the + N and + NP treatments were higher than in the control and the + P treatments, which suggests that plankton biomass production was stimulated by N availability. In the + N and + NP treatments, *H. akashiwo* typically dominated in the initial, logarithmic, and stationary growth phases. The growth rate of the phytoplankton community in the presence of added Fe was not statistically different ($p > 0.05$) from that in the treatments without added Fe. The results suggest that in this area natural phytoplankton communities, including those dominated by *H. akashiwo*, respond rapidly to pulsed nitrogen loading events. The episodic windstorm event probably resulted in vertical mixing that brought nutrients into the euphotic upper layer. The results suggest that such events are important in triggering spring phytoplankton blooms in potentially oligotrophic waters, such as those in the vicinity of the Dokdo in the Japan/East Sea.

1. Introduction

In temperate seas the spring and fall phytoplankton blooms are related to seasonal changes in the mixed layer depth. Spring blooms develop in response to increased insolation, nutrients, and water column stability, and autumn blooms are associated with the breakdown of summer stratification, which allows nutrient rich deep waters to mix into the euphotic zone (Townsend et al., 1992; Smayda, 1997; Baek et al., 2009b). Sverdrup (1953) explained the timing of spring blooms in relation to the critical depth. The stirring of upper layers by

convective overturn and winds is the major mechanism regulating phytoplankton growth (Evans and Paslow, 1985; Yentsch, 1990; Kim et al., 2007), and nutrients provided by wind stress intensity are positively related to spring phytoplankton blooms (Saitoh et al., 2002; Smayda, 2002; Kim et al., 2007).

In oceanic and coastal regions, the passage of typhoons causes physical disturbances including upwelling and vertical mixing, terrestrial runoff, and sediment resuspension, which result in nutrients being transported to the euphotic layer (Trainer et al., 2002; Chen et al., 2009; Tsuchiya et al., 2013a, b). Episodic windstorm events, resulting

* Corresponding author.

E-mail address: baeksh@kiost.ac.kr (S.H. Baek).

from the passage of low pressure systems over ocean areas, have significantly changed in aquatic ecosystems with their powerful winds (Roegner et al., 2002; Ryan et al., 2002; Zhao et al., 2008; Tsuchiya et al., 2013a, b). Increased nutrient loading causes a significant increase in phytoplankton biomass; based on classic marine ecosystem and food-web responses initiated by episodic nutrient loading, this will result in significant carbon flux (Michaels and Silver, 1988; Townsend et al., 1992; Tsuchiya et al., 2013a, b).

In the western North Pacific region, the total number of typhoons from 1951 to 2016 was estimated to be 1726, with 26 typhoons occurring annually. According to Zheng and Tang (2007), 40% of all typhoons passed through the South China Sea, and the remaining 60% impacted the East China Sea and East Asian countries. Of these, 14% of typhoons impacted the Korean Peninsula (National Typhoon Center in Korea; http://typ.kma.go.kr/TYPHOON/index_eng.jsp). Even though episodic windstorm events by cyclone have sometimes occurred in spring and autumn, major typhoon events have approached during summer monsoons, accounting for 90% of total typhoons seasonally (Zheng and Tang, 2007). For the past 30 years, strength and frequency of typhoons have significantly increased in relation to global climate change and global warming and have had a negative impact on humans (IPCC, 2007). Conversely, strong windstorm events generated by typhoons are a critical factor in enhancing oceanic primary productivity, particularly in oligotrophic ocean waters (McGillicuddy et al., 1998; Ning et al., 2004). Tang et al. (2003) and Zhao et al. (2008) demonstrated phytoplankton blooms caused by nutrient supply to the euphotic zone by wind-driven upwelling in the South China Sea. Kim, et al. (2007) reported the relationship between wind stress data and seasonal dynamics of phytoplankton blooms in the central Japan/East Sea, suggesting that strong wind events in spring and fall delay timing of phytoplankton blooms. Yamada et al. (2004) demonstrated that strong winds may play a key role in breaking down stratification and thereby initiating fall blooms. However, scant attention has been given to the impact of strong windstorm passages on phytoplankton bloom during spring in oligotrophic offshore waters.

Nutrients are generally very important in controlling phytoplankton blooms and succession. Nutrient limitation is largely determined by the mass balance among the elements silicon (Si, as silicate), nitrogen (N), and phosphorus (P), and nutrient concentrations and their stoichiometric ratios in water samples can be used to indicate nutrient loading status and predict productivity (De-Pauw and Naessens, 1991; Justić et al., 1995). Differing phytoplankton species can respond differently to the same nutrient conditions because of their various nutrient requirements, and the half saturation constants among species. Therefore, nutrient addition bioassays are useful in assessing the effects of nutrients on variations in phytoplankton communities, and in identifying nutrient limitations (Holmboe et al., 1999).

The Japan/East Sea (the JES) is a large marginal sea located between the Eurasian continent and Japan. The JES is associated with the warm Tsushima Current and the cold Liman Current, and a well-defined subpolar front at approximately 38–40°N (Isoda and Saitoh, 1993; Isobe and Isoda, 1997). The JES is a semi-closed ecosystem having an average water depth of 1700 m (Fig. 1), and consists of the Yamato Rise in the center and three major basins: the Tsushima Basin/Ulleung Basin to the southwest, the Yamato Basin to the south, and the Japan Basin to the north (Isobe and Isoda, 1997). These basins are all deeper than 2000 m, with the maximum water depth being > 3000 m in the Japan Basin. The continental shelves of the JES are wide on the eastern margin, but narrow on the western margin, particularly along the Korean coast. The JES is connected to the East China Sea, the North Pacific Ocean, and the Sea of Okhotsk through the Korea/Tsushima Strait (hereafter referred to as the Korea Strait; KS), the Tsugaru Strait (TS), the Soya Strait (SS), and the Tartar/Mamiya Strait (T/MS) (Fig. 1). Inflow is primarily in the southwest, associated with the KS, and outflow is primarily through the TS and the SS in the east; weak seasonally variable inflow/outflow

occurs through the shallow T/MS in the north (Oshima, 1994; Martin and Kawase, 1998). As the water depths of these straits are < 150 m, the water exchange between the JES and the North Pacific Ocean is limited. The volume transported through the KS has a major impact on the hydrography and circulation in the JES (Oshima, 1994; Kim and Yoon, 1999).

The objectives of the present study were to: (i) investigate the horizontal distribution of phytoplankton assemblages; (ii) examine the loading of nutrients caused by episodic windstorm events, and the phytoplankton response; and (iii) confirm the phytoplankton community response to nutrient addition in bioassay experiments. The results will help explain the natural spring phytoplankton blooms that occur in waters of the offshore frontal area in the JES, following strong windstorms in the region around the Ulleungdo and Dokdo.

2. Materials and methods

2.1. Field investigation

From 2 to 9 May 2016, water samples from 40 stations (Stns 1–40) in the JES were collected using a bucket aboard the R/V *Jangmok II* (Fig. 1). On 2 May sampling at Stns 1–14 were concluded. As a result of strong winds no sampling occurred on 3 May. Stns 15–20 were sampled on 4 May, while Stns 21–40 were sampled on 6–7 May; the latter are located between the Ulleungdo and Dokdo. After seven days (on 9 May), we surveyed again at Stns 1, 4, 5, 7, and 11 to assess the biological, chemical, and physical effects of strong episodic windstorm events. In addition, we distinguished three zones and four time-series areas. The zones were designated based on whether they were sampled prior to or following the windstorm event in addition to their geography, and for this analysis involved Zone I-b: Stns 1, 4, 5, 7, and 11 (prior to the windstorm event); Zone I-a: Stns 1, 4, 5, 7, and 11 (following the windstorm event); and Zones II-a and III-a: Stns 14–26 around Ulleungdo waters and Stns 32–40 in around water of Dokdo (following the windstorm event).

Time series data for air pressure, maximum wave height, wind gust speed, and wind direction, measured at 30 min intervals, were obtained from the Donghae Ocean Data Buoy (Korea Meteorological Administration), which is located at Stn 6 and 75 km from Ulleungdo (Fig. 1). Water temperature, salinity, pH, and dissolved oxygen were measured at each station using a YSI 6600 data sonde (YSI, USA). Water samples for nutrient analysis aboard the research vessel were immediately filtered (GF/F; 25 mm, pore size 0.45 µm; Whatman, Middlesex, U.K.), placed in acid-cleaned polyethylene bottles, and fixed using HgCl₂. Each filtered water sample was stored in a freezer (−20 °C) for later measurement of nutrient concentrations. Ammonia, nitrate, nitrite, phosphate, and silicate concentrations were determined in the laboratory using a flow injection autoanalyzer (QuikChem 8000; Lachat Instruments, Loveland, CO, USA). The nutrient concentrations were calibrated using standard brine solutions (CSK Standard Solutions; Wako Pure Chemical Industries, Osaka, Japan). For chlorophyll-*a* (Chl-*a*) measurements, 1.0 L of seawater was immediately filtered through a 47-mm diameter GF/F filter (pore size 0.45 µm; Whatman) on board the research vessel, and the filters were stored at −20 °C until further laboratory analysis. Chl-*a* was measured using a Turner-designed fluorometer (Turner BioSystems, Sunnyvale, CA, USA), following extraction of the filtered material in 90% acetone for 24 h in the dark. To identify and enumerate phytoplankton, 0.5 L subsamples were stored in polyethylene bottles and fixed using 0.5% Lugol's solution. These subsamples were then concentrated to approximately 50 mL by decanting the supernatant, as described by Sournia (1978). A Sedgewick-Rafter counting chamber was used to estimate the number of phytoplankton cells, using light microscopy. Most diatoms and dinoflagellates were identified to species level.

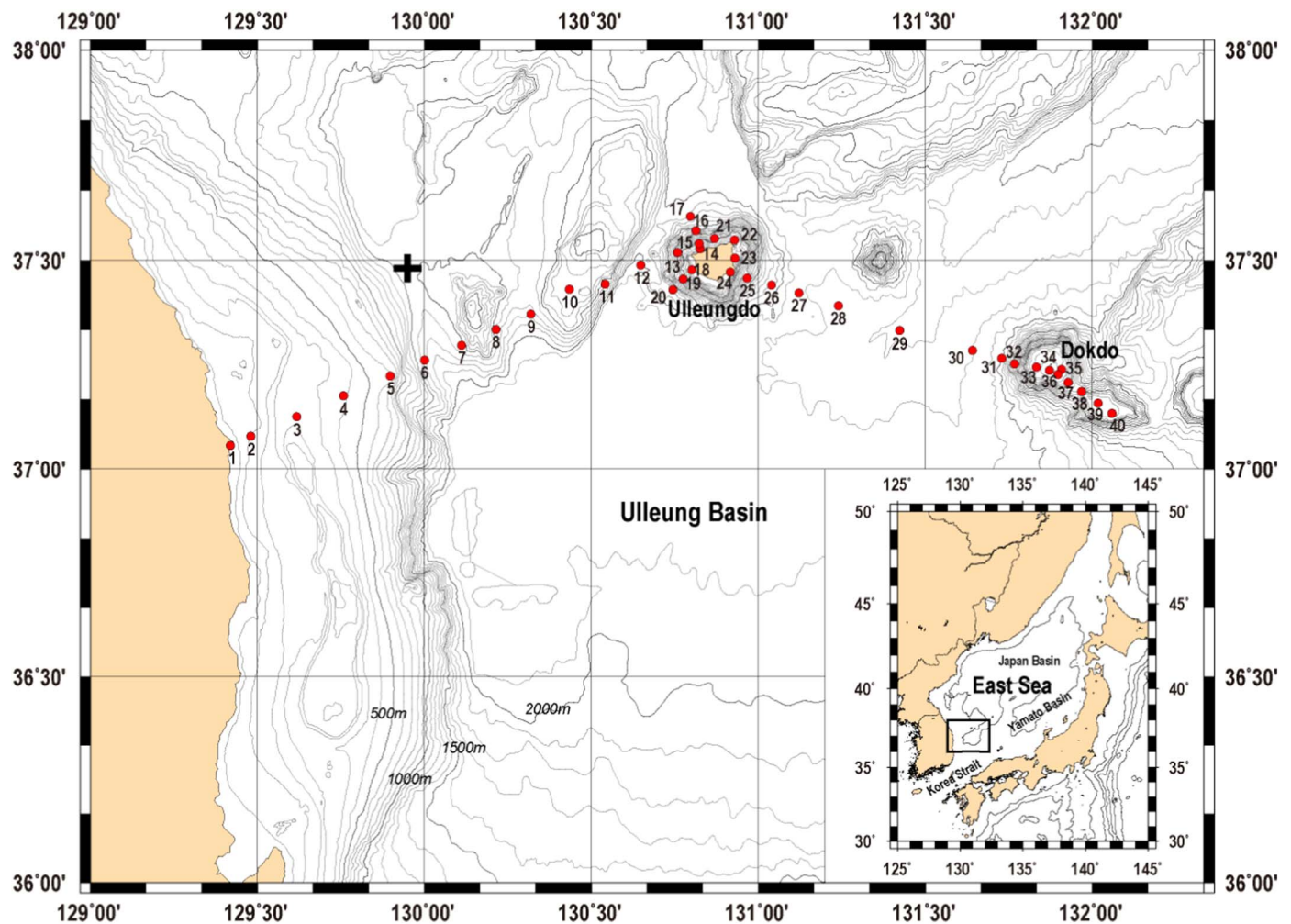


Fig. 1. Locations of sampling sites. The black cross shows the location of the Donghae Ocean Data Buoy (Korea Meteorological Administration). The background contours represent isobaths.

2.2. Nutrient addition bioassays

Bioassay experiments were designed to assess the nutrient requirements of the phytoplankton bloom following strong windstorms in the JES. Phytoplankton samples were collected from two stations (36 and 40) by collecting natural surface layer water using a bucket. Debris and large-sized plankters in the collected waters were removed by filtering through 330 μm mesh on board ship immediately and the collected samples were transferred to 2-L autoclaved bottles. In the laboratory, 50 mL subsamples of the water collected from each station were transferred to two duplicate test tubes (22 \times 200 mm; PYREX®) for the bioassay treatments. The bioassay treatments involved nutrient addition, and were established in duplicate (per treatment or control). The control involved seawater without nutrient addition. The treatments included the addition of: (i) nitrogen (+ N; 20 μM nitrate); (ii) phosphorus (+ P; 2 μM phosphate); (iii) nitrogen and phosphorus (+ NP; added at the same concentrations as for the + N and + P treatments alone). An additional experiment involved the addition of Fe to the control and the + N, + P, and + NP treatments described above, as iron plays a potentially important role in limiting phytoplankton growth in oligotrophic oceans. All experimental tubes were incubated at 15 $^{\circ}\text{C}$ (ambient seawater temperature) and 60 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ illumination (cool white fluorescent light; 12 h:12 h light:dark cycle). Growth of phytoplankton was monitored using *in vivo* fluorescence (10-AU fluorometer; Turner BioSystems) at 1–2 day intervals for 11 days; growth measurements were based on the assumption that Chl-*a* is a

quantitative measure of algal biomass. The specific growth rate (μ day^{-1}) was calculated by linear regression as the slope coefficient (μ) according to the methods of Staehr and Sand-Jensen (2006). The calculation was based on the equation: $\ln(F_t) = \mu \times t + \ln(F_0)$, where F_0 and F_t are the *in vivo* fluorescence of Chl-*a* measured at 685 nm at the start of the experiment and after t days of incubation, respectively. The relative response (%) to enrichment of the phytoplankton community under different nutrient conditions was calculated using the equation: Relative response (%) to enrichment = $(T_f \div C_f - 1) \times 100$, where T_f (treatment) and C_f (control) are the growth rates in the treatment (+ N, + P, or + NP) and the control, respectively (Baek et al., 2015). To determine the relationship between nutrient fate and phytoplankton response, subsamples (10 mL) for nutrient analysis were taken from each treatment during the logarithmic and stationary growth phases. Each subsample was immediately filtered using a disposable syringe filter (pore size 0.45 μm ; ADVANTEC), fixed with HgCl_2 , and placed at -20°C for later measurement of the nutrient and then, ammonia, nitrate, nitrite, phosphate, and silicate concentrations using a flow injection autoanalyzer, as noted above. The dominant phytoplankton species in the initial, logarithmic, and stationary phases were determined by light microscopy examination using a Sedgewick-Rafter counting chamber.

2.3. Data analysis

Differences in measurements of abiotic and biotic factors before and

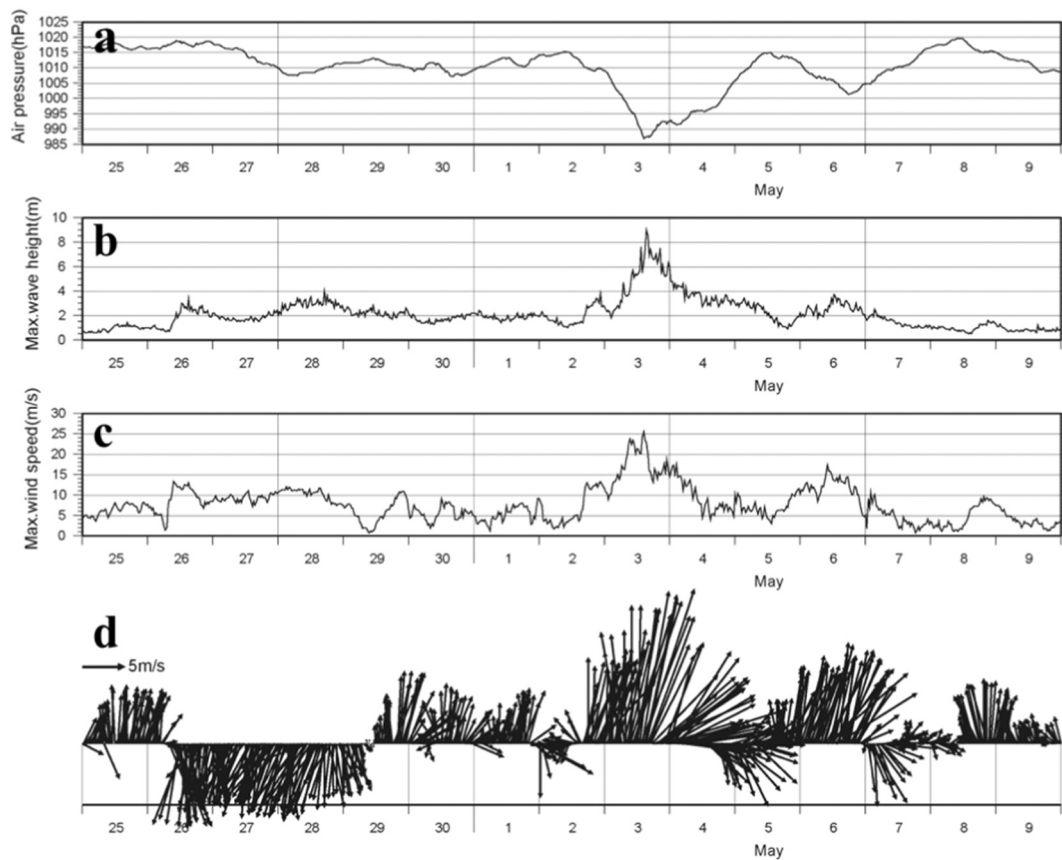


Fig. 2. Time series of: (a) air pressure (hPa); (b) maximum wave height (m); (c) wind gust speed (m s^{-1}); and (d) wind direction between 25 April and 9 May 2016 at the Donghae Ocean Data Buoy (Korea Meteorological Administration).

after passage of a low pressure weather system in the area were assessed using a one-way ANOVA followed by Tukey's HSD test; for this analysis the area was separated into four zones, based on the phytoplankton community structure. Analysis of the phytoplankton community structure involved cluster analysis (group averages) and non-metric multi-dimensional scaling (MDS) ordination of species abundance data, based on the Bray-Curtis similarity index (Field et al., 1982). The bioassay data were analyzed using the *t*-test to compare results of nutrient treatments and control groups. Differences were considered significant at $p < 0.05$. All statistical analyses were performed using the SPSS version 17.0 (SPSS, Inc., Chicago, IL, USA).

3. Results

The time series of air pressure (hPa), maximum wave height (m), wind gust speed, and wind direction measured at the Donghae Ocean Data Buoy are shown in Fig. 2. A strong wind on 3 May was associated with the lowest sea level pressure recorded (986.8 hPa), the maximum wind speed (25.5 m s^{-1}), and the maximum wave height (9.0 m); wave heights exceeding 4.0 m were continuously recorded from 09:00 on 3 May to 05:00 on 4 May. Surface water temperature and water currents in coastal and oceanic waters of the JES are shown Fig. 3, based on satellite-derived sea surface temperature for 9 May 2016. The surface water temperature was 8–13 °C in the northern region and 15–17 °C in the southern region, with a front of water temperature difference located at approximately 38°N latitude. Field measurements showed that the surface temperature ranged from 13.33 °C to 16.18 °C during May 2016 (Fig. 4). The highest temperature was recorded in waters around Ulleungdo, and the lowest was in coastal waters near the eastern part of the Korean peninsula. Surface salinity varied from 34.03 to 34.55. Salinity during the sampling period showed small spatial variation,

with lower values being found at Stn 1, which is located near land, where discharge of fresh water into the coastal waters occurs. Although water surface temperature showed relatively large differences, the salinity did not differ greatly among the stations.

The surface distribution of nutrients is shown in Fig. 5. Large spatial variation was observed in the concentrations of dissolved inorganic nutrients. The nitrate + nitrite concentration varied from 0.07 to $2.22 \mu\text{M}$ (average $0.58 \pm 0.55 \mu\text{M}$), and showed large spatial variation; it was relatively high in water around Ulleungdo Island. The ammonium concentration varied from 0.01 to $2.05 \mu\text{M}$ (average $0.21 \pm 0.43 \mu\text{M}$); it showed great variation among stations, and several stations near the Ulleungdo and Dokdo had particularly high values. The phosphate concentration was low, ranging from the lower limit of detection ($0.01 \mu\text{M}$) to $0.19 \mu\text{M}$ (average $0.09 \pm 0.05 \mu\text{M}$), and showed relatively little variation relative to N and Si. The Si concentrations were relative high, varying from 0.76 to $6.93 \mu\text{M}$ (average concentration $3.78 \pm 1.67 \mu\text{M}$).

The surface Chl-*a* concentration varied from 0.36 to $15.97 \mu\text{g L}^{-1}$ (average $2.66 \pm 3.26 \mu\text{M}$) (Fig. 6). The spatial variation in the Chl-*a* concentration was similar at Stns 1–32, and averaged $1.26 \pm 0.73 \mu\text{M}$. However, the Chl-*a* concentration increased significantly from Stn 33 to Stn 40, which is located near the Dokdo. Phytoplankton population abundances showed similar fluctuations to the Chl-*a* concentration. Diatoms and raphidophyta were the dominant phytoplankton groups in the study, accounting for almost 38.4% of the total phytoplankton at all stations. At Stns 1–14, diatoms made a higher relative contribution to the total phytoplankton biomass (Fig. 7). In contrast, the abundance of raphidophytes increased dramatically between Stns 33 and 40, and reached a maximum at Stn 33, when the highest Chl-*a* concentration occurred in seawater near the Dokdo. The abundance of dinoflagellates was generally low compared with that for diatom, raphidophyte and

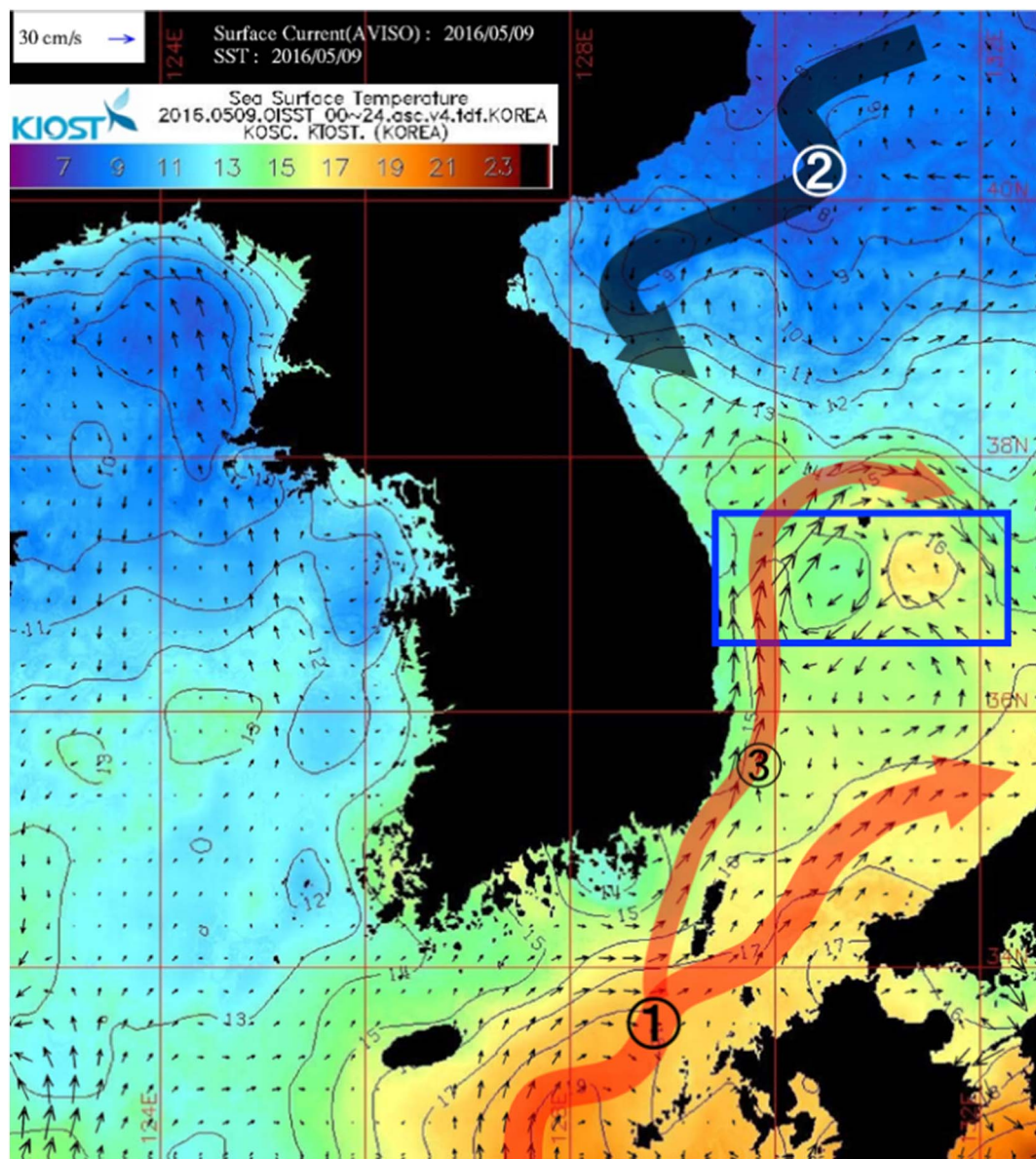


Fig. 3. Satellite-derived sea surface temperature for May 9, 2016. Geostrophic surface velocities are shown overlaid. Major three current indicates as (1): Tsushima Warm Current, (2): North Korean cold water current and (3): East Korean Warm Current. Surface water temperature is a clear transition between cold and warm water at approximately 38°N.

cryptophyte species.

The phytoplankton communities at Stns 1–6 and 9–14 were dominated by the diatoms *L. danicus* (average 50.8%) and *Chaetoceros* spp. (average 72.0%), respectively. The concentration of the raphidophyte *Heterosigma akashiwo* averaged 1.9×10^5 cells L^{-1} at Stns 15–28, accounting for 51.4% of the total phytoplankton. High abundances of *H. akashiwo* were observed at Stns 33–40, where this species accounted for an average of 86.1% of the total phytoplankton; its abundance reached 2.9×10^6 cells L^{-1} at Stn 33, and constituted the highest biomass among the phytoplankton communities.

Based on the MDS and cluster analysis, the phytoplankton community structures were categorized into three major groups (groups I–III; analysis of similarities; Fig. 8). The community in Group I was characterized by high diatom cell abundances (average: 4.0×10^5 cells L^{-1}), and was mainly dominated by *Chaetoceros* spp. Groups II and III were characterized by medium (average: 0.3×10^5 cells L^{-1}) and high (average: 9.8×10^5 cells L^{-1}) cell abundances of *Heterosigma*, respectively; in particular, this species dominated in Group III.

The temporal variation in the bioassay growth of phytoplankton cultured in the controls and the + N, + P, and + NP treatments with (+ Fe) and without (non-Fe) added iron is shown in Fig. 9. Although the *in vivo* fluorescence values in the + Fe experiment were not statistically different from those in the non-Fe experiment ($p > 0.05$), the *in vivo* fluorescence values in the + N and + NP treatments was significantly higher than in the + P treatment ($p < 0.05$). In particular, the specific growth rate of the phytoplankton community in the control was similar to that in the + P treatment, and the growth trend was similar in the water collected from each station for the bioassays (Fig. 10). On the other hand, the specific growth rate in the + NP treatment both with and without added Fe was slightly higher than that in the + N treatments. The dominant phytoplankton species in the initial, logarithmic, and stationary growth phases in treatments with and without added Fe are shown in Tables 1 and 2. *H. akashiwo* dominated these growth phases in the + N and + NP treatments, particularly in treatments without added Fe. However, the abundance of the diatom *L. danicus* was clearly higher in the + Fe treatments than in the non-Fe treatments. Changes in nutrient concentrations measured at initiation of the

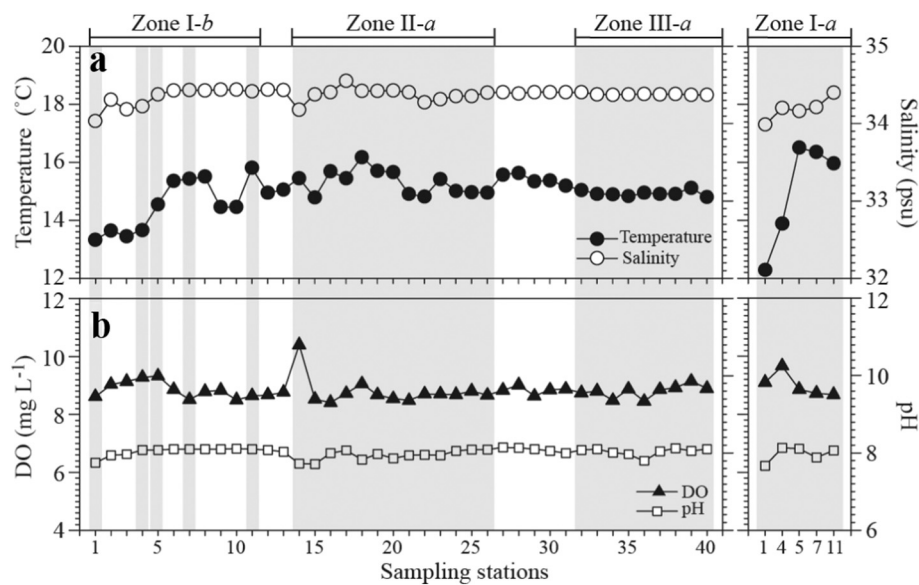


Fig. 4. Horizontal distribution of: (a) temperature (white circles) and salinity (black circles); and (b) pH (black triangles) and DO (white squares) at the sampling stations in the Japan/East Sea. Gray areas indicate various zones within the study area prior to and following the windstorm events. Four zones were designated, including: Zone I-b: Stns 1, 4, 5, 7, and 11, prior to the windstorm event; Zone I-a: Stns 1, 4, 5, 7, and 11, following the windstorm event; zones II-a and III-a: Stns 14–26 and 32–40, following the windstorm event.

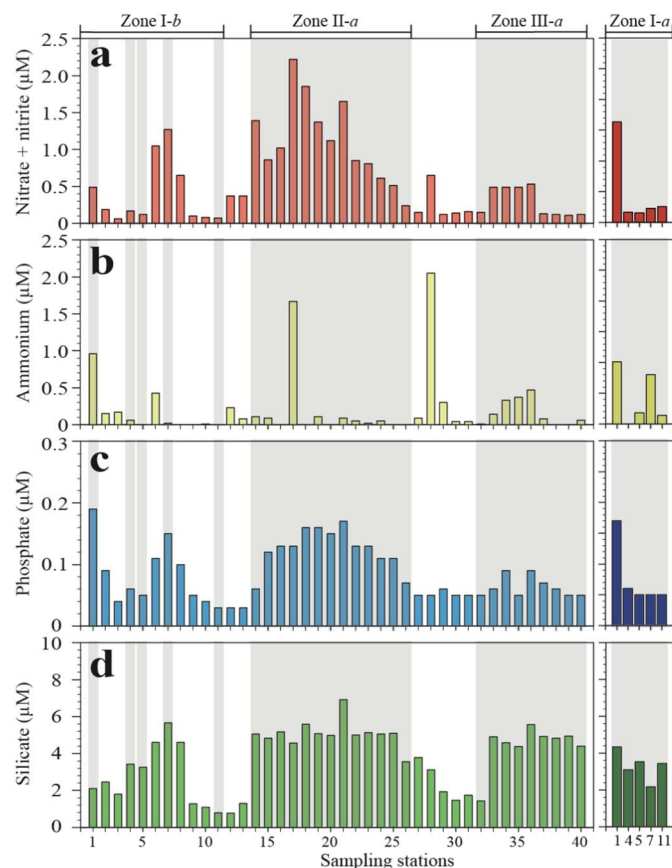


Fig. 5. Horizontal distribution of nutrients at the sampling stations in the Japan/East Sea: (a) nitrate + nitrite; (b) ammonium; (c) phosphate; and (d) silicate.

bioassays and at 7 and 11 days in treatments with and without added Fe are shown in Figs. 11 and 12. The trends in nutrient consumption in the control and the + N, + P, and + NP treatments between Stns 36 and 40 were similar, with and without added Fe. The nitrate and nitrite concentrations had rapidly decreased by Day 7 in the + N and + NP treatments, and remained at approximately 2.0 μM , which is the limiting concentration for phytoplankton growth. In the + P treatments the phosphate concentration on Day 7 in the water from Stns 36 and 40 was 1.0 μM and 1.5 μM , respectively, indicating that phosphate uptake was

limited because of the low nitrite + nitrate concentrations. The silicate concentration in the control without added Fe was higher than that in the + Fe control. There were significant differences in silicate uptake between with and without added Fe treatments.

4. Discussion

4.1. Characteristics of the Ulleung Basin water mass in the JES

The Tsushima Warm Current flows into the JES through the Korea Strait, and exits through the Tsugaru and Soya straits. According to Gong and Son (1982) and Martin and Kawase (1998), the northern region has cold water that has a salinity of approximately 34.0, is nutrient rich, and has a high oxygen content. In contrast, the southern region has warmer water, and is more saline (approximately 34.5) and nutrient poor. In the present study, satellite images for 9 May show a clear transition in surface water temperature at approximately 38°N (Fig. 3), which is consistent with previous findings. Talley et al. (2004) and Min and Warner (2005) reported the presence of meso- and small-scale eddies in the JES. These are important physical features that are located to the south and north of the subpolar front, and play important roles in ventilating intermediate depths and in water mass transformations in the JES (Min and Warner, 2005; Mitchell et al., 2005). In the Ulleung Basin the presence of a quasi-stationary anticyclonic warm eddy, the Ulleung Warm Eddy (UWE; Stns 27–30 in this study), has been reported numerous times (Lee, 1983; Cho et al., 1990; Kim et al., 1991; Mitchell et al., 2005; Lee et al., 2009). The UWE is a recirculating gyre of the East Korean Warm Current (Fig. 3). It may be generated by diffusion of the negative vorticity in the western boundary current (Kim and Yoon, 1999; Mitchell et al., 2005), and is an important pathway for southward flow from the western Japan Basin with the Dokdo Cold Eddy (DCE; Stns 37–40 in this study), which forms to the southwest of the Dokdo (Mitchell et al., 2005). We found that although there was no significant difference in salinity, the water temperature gradually decreased toward the DCE region from the UWE (DCE vs. UWE; t -test; $t = 4.95$, $p < 0.05$). In the vicinity of Stns 29–32 the phytoplankton community structure was significantly different Stns 28 and 33, suggesting that the offshore regions between the Ulleungdo and Dokdo may have been influenced by the UWE water mass. The Chl-*a* concentration and the phytoplankton abundance increased significantly from Stn 33 to Stn 40 (ANOVA test; $p < 0.001$), as described below. Therefore, the characteristics of the water mass between the Ulleungdo and Dokdo is important in determining the phytoplankton biomass and

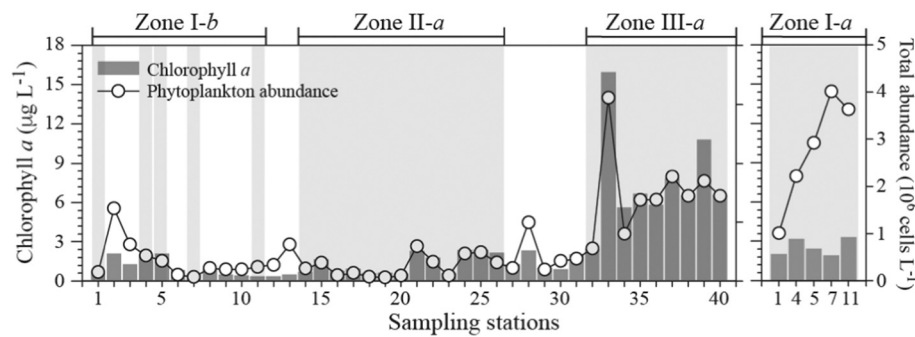


Fig. 6. Horizontal changes in the Chl-*a* concentration and total phytoplankton abundance at the sampling stations in the Japan/East Sea.

community structure in this region of small scale eddies in the Ulleung Basin.

4.2. Physical, chemical and biological factors prior to and following a strong windstorm event

In coastal and offshore waters of temperate seas, wind plays an important role in determining stratification–destratification processes, which facilitate vertical mixing that brings nutrients into the euphotic upper layer. The JES is heavily influenced by monsoon patterns involving strong northwesterly winds in winter and spring (Lie and Cho, 2016). According to Kim et al., (2007), timing of the spring phytoplankton blooms is related to wind speed and duration, and wind events in spring in the JES could delay timing of phytoplankton blooms.

However, in this study, specific phytoplankton bloom occurred soon after the wind event, recorded May 3–4 at Ulleungdo and Dokdo. In offshore waters during this event highest wind speed was 25 m s^{-1} , and largest wave was 9 m. To analyze effects of these episodic windstorm events in the Ulleungdo and Dokdo regions of the JES, we compared physical, chemical, and biological factors in four zones (*i.e.*, Zone I-b, Zone I-a, Zones II-a and III-a) prior to and following the May 3–4 windstorm event in the study area.

For physical factors, water temperature did not differ significantly among Zones I-b, II-a, III-a, and I-a ($F = 1.015$, $p > 0.05$; ANOVA) (Fig. 13). The salinity was slightly lower in Zone I-a than in Zones II-a and Zone III-a ($F = 4.737$, $p < 0.05$; ANOVA), implying that the East Korean Warm Current region was slightly influenced by rainfall discharges from the land and rivers following the windstorm. However, pH

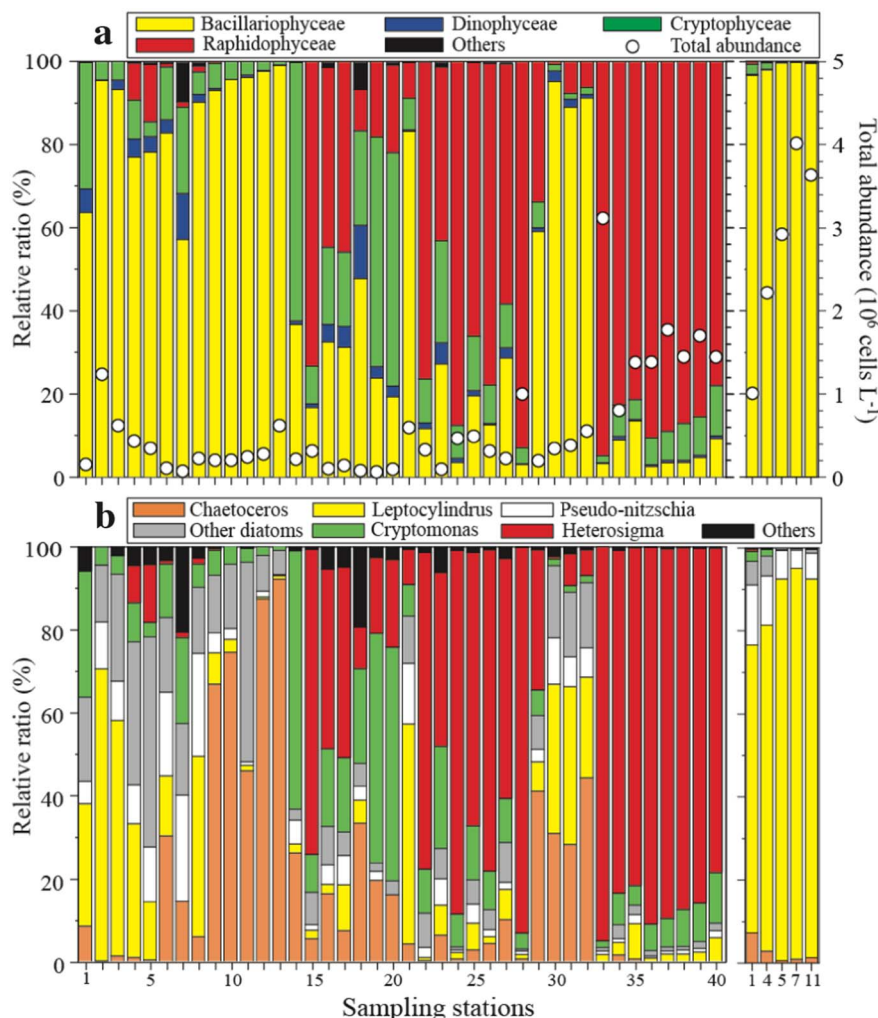


Fig. 7. Spatial differences in: (a) relative phytoplankton abundance; and (b) dominant species at the sampling stations in the Japan/East Sea.

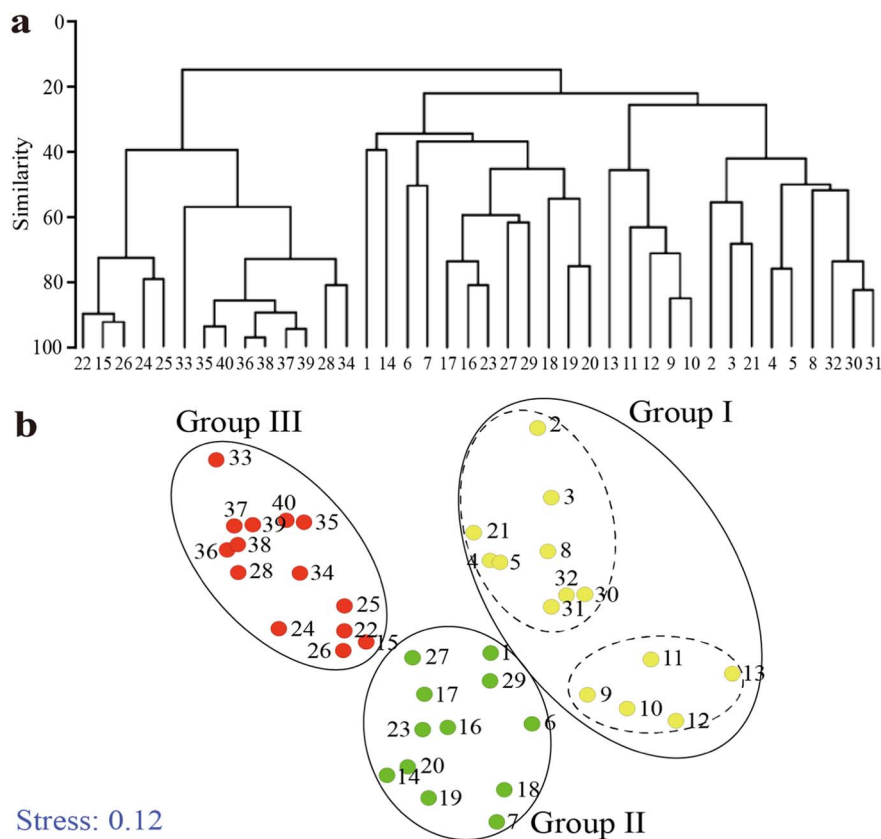


Fig. 8. (a) Similarity of phytoplankton composition between the different stations; (b) Non-metric multidimensional scaling (MDS) plot of phytoplankton composition and each group was categorized based on the similarity.

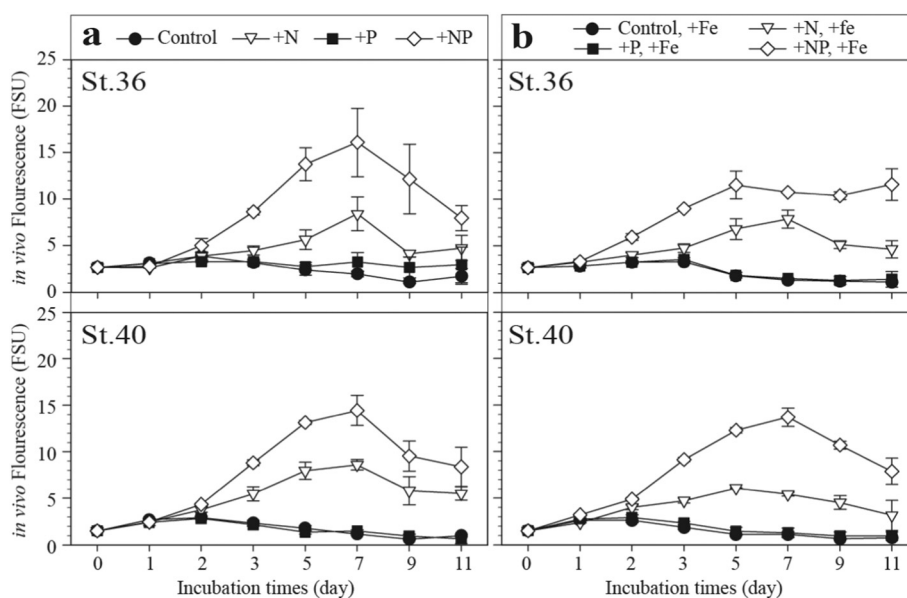


Fig. 9. Change in *in vivo* fluorescence (FSU) values for phytoplankton assemblages during nutrient addition algal bioassays. The experiments involved natural surface water collected from Stns 36 and 40, in the Japan/East Sea. Control: no nutrient addition; + N: nitrate added; + P: phosphate added; + NP: nitrate and phosphate added. Data are presented as the mean \pm standard errors for duplicate samples. a: treatments without added Fe; b: treatments with added Fe.

and the DO concentration did not differ significantly among the zones (pH: $F = 0.908$, $p > 0.05$; DO: $F = 0.365$, $p > 0.05$). With respect to chemical factors, although the nitrate + nitrite concentration did not differ significantly between zones I-b and I-a ($p > 0.05$; ANOVA), it was significantly different between zones II-a and III-a ($p < 0.001$; ANOVA), with Zone III-a having a factor of 2 lower concentration. A similar trend was also observed for the phosphate and silicate concentrations, but not ammonium. With respect to biological factors, the Chl-*a* concentrations in Zone III-a were significantly higher than in zones I-b, I-a, and II-a ($F = 17.438$, $p < 0.001$; ANOVA), and the raphidophyte abundance was significantly higher in Zone III-a

($F = 16.889$, $p < 0.001$; ANOVA). The total phytoplankton and diatom abundance increased significantly in Zone I-a following the windstorm event. The higher abundance of raphidophytes in Zone III-a ($p < 0.001$; ANOVA) made a major contribution to the total phytoplankton abundance. It is likely that water mixing following strong wind events in the vicinity of Ulleungdo Island (Zone II-a) provides nutrients for phytoplankton growth. On the other hand, the supply of nutrients in Zone III-a may be rapidly exhausted by phytoplankton blooms over time. Bleiker and Schanz (1997) and Kim et al. (2005) demonstrated that in lake and ocean conditions (respectively), initiation of growth of phytoplankton following a windstorm event in spring

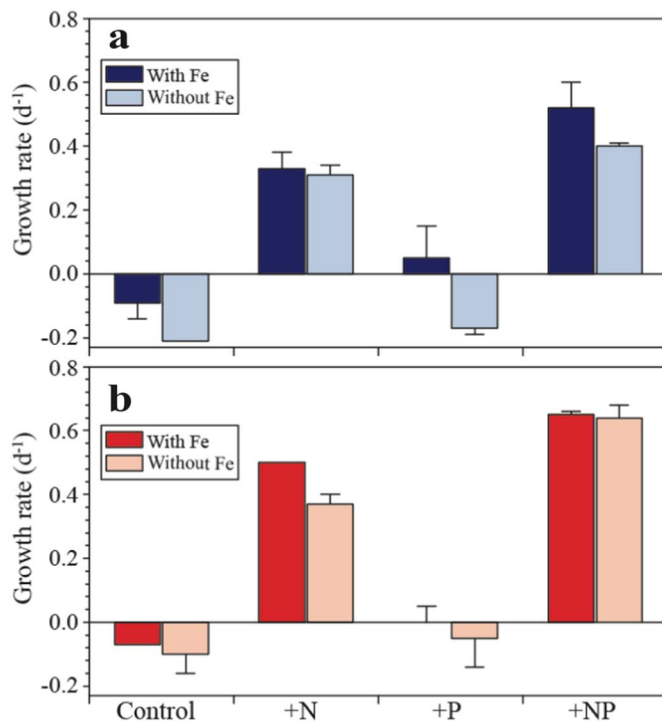


Fig. 10. Specific growth rate of phytoplankton assemblages with and without added Fe, based on water collected from: (a) Stn 36; and (b) Stn 40. Data are presented as the mean \pm standard error for duplicate samples.

required at least 7–10 days without wind-driven vertical mixing. In contrast, Yin et al. (1997) reported that phytoplankton rapidly responded to the nutrient increase that occurred concurrently with wind-driven mixing of the water column, and that blooms occurred soon after the wind events. In the present study, a phytoplankton bloom (described below) occurred in Zone III-a (near Dokdo) over several days following the wind event, which is a similar finding to that reported by Yin et al. (1997). Therefore, phytoplankton in spring responded soon after the wind events and specific windstorm events are likely to be vital in regulating the fate of nutrients and biomass of phytoplankton assemblages in offshore areas of Ulleungdo and Dokdo in the JES.

4.3. Spatial variation in phytoplankton community structure

The regions having intermediate Chl-*a* concentrations (Stns 1–5) were dominated by the diatoms *L. danicus* and *Eucampia zodiacus*, which are species that are associated with the East Korean Coastal Water. These diatom species are able to adapt to low water temperature, and *E. zodiacus* is known as an indicator of cold water. In regions having low Chl-*a* concentrations (Stns 6–12), the diatoms *Chaetoceros socialis* and *E. zodiacus* dominated. High abundances of *C. socialis* extended to coastal waters of Ulleungdo (Stns 13–21), together with cryptomonad species. The region was directly affected by episodic wind events, and was characterized by relative high nitrate + nitrite and phosphate concentrations. However, the Chl-*a* concentration was relatively low because the date of sampling was only one day following the episodic wind event, and it is feasible that there was a time lag prior to the development of a phytoplankton bloom following nutrient inputs (Kim et al., 2005). *H. akashiwo* mainly dominated in samples from Stns 22–28 (Ulleungdo coastal waters). This area is located in an inshore area, and *H. akashiwo* cells may have accumulated in the southeastern inshore area of the island following the strong southerly wind. At Stns 29–33, the nitrate + nitrite and phosphate concentrations remained at relatively low levels and then, the phytoplankton community structure and dominant species was greatly different at the regions, which may

Table 1

Dominant species at initiation and in the logarithmic and stationary phases of the nutrient bioassay experiment involving no added Fe for the control and the +N, +P, and +NP treatments, based on natural seawater collected from two sites in the Japan/East Sea.

| Station | Types | Dominant species | | |
|---------|---------|---|--|--|
| | | 0 days | 7 days | 11 days |
| St.36 | Control | <i>H. akashiwo</i> ⁺⁺⁺ <i>Cryptomonad</i> spp. ⁺ <i>L. danicus</i> ⁺ | <i>H. akashiwo</i> ⁺⁺⁺ <i>Cryptomonad</i> spp. ⁺⁺ | <i>H. akashiwo</i> ⁺⁺ |
| | + N | | <i>H. akashiwo</i> ⁺⁺⁺⁺⁺ <i>L. danicus</i> ⁺⁺ | <i>H. akashiwo</i> ⁺⁺⁺⁺⁺ <i>L. danicus</i> ⁺⁺⁺⁺ <i>Pseudo-nitzschia</i> spp. ⁺⁺ |
| | + P | | <i>Pseudo-nitzschia</i> spp. ⁺ <i>H. akashiwo</i> ⁺⁺⁺ | <i>H. akashiwo</i> ⁺⁺⁺⁺⁺ |
| | + NP | | <i>H. akashiwo</i> ⁺⁺⁺⁺⁺ <i>Cryptomonad</i> spp. ⁺⁺⁺⁺ | <i>H. akashiwo</i> ⁺⁺⁺ <i>Pseudo-nitzschia</i> spp. ⁺⁺ |
| St.40 | Control | <i>H. akashiwo</i> ⁺⁺⁺ <i>Cryptomonad</i> spp. ⁺⁺ <i>L. danicus</i> ⁺ <i>Pseudo-nitzschia</i> spp. ⁺ | <i>H. akashiwo</i> ⁺⁺⁺⁺⁺ | <i>H. akashiwo</i> ⁺ <i>Cryptomonad</i> spp. ⁺ <i>Pseudo-nitzschia</i> spp. ⁺ |
| | + N | | <i>H. akashiwo</i> ⁺⁺⁺⁺⁺ <i>L. danicus</i> ⁺⁺⁺ <i>Pseudo-nitzschia</i> spp. ⁺⁺ <i>Cryptomonad</i> spp. ⁺⁺ | <i>H. akashiwo</i> ⁺⁺⁺⁺⁺ <i>L. danicus</i> ⁺⁺⁺ <i>Pseudo-nitzschia</i> spp. ⁺ |
| | + P | | <i>H. akashiwo</i> ⁺ <i>Cryptomonad</i> spp. ⁺ | <i>Cryptomonad</i> spp. ⁺ <i>Pseudo-nitzschia</i> spp. ⁺ |
| | + NP | | <i>Cryptomonad</i> spp. ⁺⁺ <i>Pseudo-nitzschia</i> spp. ⁺⁺ | <i>H. akashiwo</i> ⁺⁺⁺⁺⁺ <i>L. danicus</i> ⁺⁺ <i>Pseudo-nitzschia</i> spp. ⁺⁺ <i>Cryptomonad</i> spp. ⁺ |

Phytoplankton abundances; +: > 10 to < 10²; ++: > 10² to < 10³; +++: > 10³ to < 10⁴; ++++: > 10⁴ (cells ml⁻¹).

have been influenced by eddying surface water currents, as noted in Fig. 3. High abundances of *H. akashiwo* were found between Stns 33 and 40. As a result, variations in phytoplankton community structure and biomass were clearly evident in the JES study area. The MDS and cluster analyses suggested that prior to and following the passage of the strong windstorm event the phytoplankton assemblages could be categorized into one of three groups. Diatom species dominated Group I, which mainly occurred prior to the windstorm. Following the windstorm the raphidophyte *H. akashiwo* was abundant in groups II and III (particularly the latter), indicating that the windstorm event introduced a large biomass of this species. Thus, we showed that the spring phytoplankton bloom in waters in the vicinity of Ulleungdo and Dokdo was probably an example of a ‘small island effect’, whereby rapid proliferation of autotrophic algae followed nutrient input to the euphotic layer through water mixing following a strong wind event, and that such events constantly affect the carbon flux and trophic structures in central parts of the JES.

4.4. *Heterosigma akashiwo* blooms in the vicinity of Dokdo

H. akashiwo comprised > 85% of the total phytoplankton assemblage in ocean waters in the vicinity of Ulleungdo (Stns 22–28) and Dokdo (Stns 33–40). *H. akashiwo* is a relatively small (approximately 10 μ m) and rapidly growing species, and is considered a cause of harmful algal blooms. It produces resting cysts, the growth and germination of which are strongly affected by water temperature. The optimum growth temperature for *H. akashiwo* is approximately 15 $^{\circ}$ C,

Table 2

Dominant species at initiation and in the logarithmic and stationary phases of the nutrient bioassay experiment involving added Fe for the control and the + N, + P, and + NP treatments, based on natural seawater collected from two sites in the Japan/East Sea.

| Station | Types | Dominant species | | |
|---------|---------|--|--|--|
| | | 0 days | 7 days | 11 days |
| St.36 | Control | <i>H. akashiwo</i> ⁺⁺ <i>Cryptomonad</i> spp. ⁺ <i>L. danicus</i> ⁺ | <i>Pseudo-nitzschia</i> spp. ⁺⁺ | <i>H. akashiwo</i> ⁺⁺ <i>Cryptomonad</i> spp. ⁺ |
| | + N | | <i>H. akashiwo</i> ⁺⁺⁺⁺ <i>L. danicus</i> ⁺⁺⁺⁺ <i>Cryptomonad</i> spp. ⁺⁺⁺⁺ <i>Pseudo-nitzschia</i> spp. ⁺⁺ <i>H. akashiwo</i> ⁺⁺⁺⁺ | <i>H. akashiwo</i> ⁺⁺⁺⁺ <i>L. danicus</i> ⁺⁺⁺⁺ <i>Pseudo-nitzschia</i> spp. ⁺ |
| | + P | | | <i>H. akashiwo</i> ⁺⁺ <i>Pseudo-nitzschia</i> spp. ⁺ <i>Cryptomonad</i> spp. ⁺ |
| | + NP | | <i>H. akashiwo</i> ⁺⁺⁺⁺ <i>L. danicus</i> ⁺⁺ <i>Pseudo-nitzschia</i> spp. ⁺⁺ | <i>H. akashiwo</i> ⁺⁺⁺⁺ <i>L. danicus</i> ⁺⁺ <i>Pseudo-nitzschia</i> spp. ⁺⁺ |
| St.40 | Control | <i>H. akashiwo</i> ⁺⁺⁺⁺ <i>Cryptomonad</i> spp. ⁺⁺ <i>L. danicus</i> ⁺ <i>Pseudo-nitzschia</i> spp. ⁺ | <i>L. danicus</i> ⁺⁺⁺⁺ <i>Pseudo-nitzschia</i> spp. ⁺⁺ <i>H. akashiwo</i> ⁺⁺ <i>Cryptomonad</i> spp. ⁺⁺ | <i>Cryptomonad</i> spp. ⁺⁺ <i>L. danicus</i> ⁺⁺ <i>Pseudo-nitzschia</i> spp. ⁺ |
| | + N | | <i>L. danicus</i> ⁺⁺⁺⁺ <i>Cryptomonad</i> spp. ⁺⁺ <i>H. akashiwo</i> ⁺ | <i>L. danicus</i> ⁺⁺⁺⁺ <i>H. akashiwo</i> ⁺⁺⁺ <i>Pseudo-nitzschia</i> spp. + |
| | + P | | <i>H. akashiwo</i> ⁺⁺ <i>Cryptomonad</i> spp. ⁺⁺ | <i>Cryptomonad</i> spp. ⁺⁺ <i>L. danicus</i> ⁺⁺ <i>Pseudo-nitzschia</i> spp. ⁺ |
| | + NP | | <i>L. danicus</i> ⁺⁺ <i>Pseudo-nitzschia</i> spp. ⁺⁺ <i>Cryptomonad</i> spp. ⁺⁺ | <i>H. akashiwo</i> ⁺⁺⁺⁺ <i>L. danicus</i> ⁺⁺⁺ <i>Pseudo-nitzschia</i> spp. ⁺⁺⁺ <i>Cryptomonad</i> spp. ⁺ |

Phytoplankton abundances; +: > 10 to < 10²; ++: > 10² to < 10³; +++: > 10³ to < 10⁴; ++++: > 10⁴ (cells ml⁻¹).

although the growth response at different temperatures depends on the strain (Smayda, 1998). *H. akashiwo* is considered to be a euryhaline species that grows well at salinities of 9–31 psu (Watanabe and Nakamura, 1984); consequently, *H. akashiwo* can proliferate without any lag time between salinity changes and commencement of growth (Mahoney and McLaughlin, 1979). In the present study, the water temperature and salinity ranged from 14.9 to 15.1 °C and from 34.0 to 34.4 psu, respectively, which is in the optimum range for rapid proliferation of *H. akashiwo*. Honjo (1993) demonstrated that *H. akashiwo* blooms are closely related to eutrophication in semi-enclosed bays. Park et al. (1989) and Jeong et al. (2014) investigated fluctuations in the abundance of *H. akashiwo* in southern bays of Korea, and reported that *H. akashiwo* blooms occur annually in Masan Bay, which is eutrophic, but not in the oligotrophic Gajodo Bay. However, we found that *H. akashiwo* proliferated in the oligotrophic waters around Ulleungdo and Dokdo. Several explanations are possible for the maintenance of high abundances of *H. akashiwo* in the oligotrophic waters offshore from Ulleungdo and Dokdo. Firstly, prior to the strong windstorm event *H. akashiwo* cells may have been present at low densities following germination from benthic resting cysts in sediments in the vicinity of Dokdo. In addition, many cysts of *H. akashiwo* may have been resuspended from the sediment by water mixing during strong windstorm events, and rapidly germinated under the stable conditions in the water

column. As a result of the *H. akashiwo* bloom the nitrate + nitrite and phosphate concentrations would be exhausted, and thereafter these nutrients would become limiting. Secondly, *H. akashiwo* cells could actively migrate to overcome the limitations of low surface nutrient concentrations. The maintenance of continuous blooms of phytoflagellates including *H. akashiwo* is primarily associated with their diel vertical migration (DVM) (Wada et al., 1985; Watanabe et al., 1988; Baek et al., 2009a). This ecological phenomenon could explain the presence of *H. akashiwo* in conditions of low surface nutrient concentrations, and may be a control factor in bloom development. The ecological advantage of DVM is also likely to play a role in maintaining high population densities, enabling population growth even in low nutrient conditions. Thirdly, the phytoplankton community (mainly *H. akashiwo*) was dramatically concentrated in the DCE water mass, as noted above. Future research focusing on the resting cysts and DVM behavior of *H. akashiwo* will be needed to explain bloom outbreaks in waters in the vicinity of the Dokdo.

4.5. Phytoplankton response in nutrient addition bioassays

As noted above, an episodic windstorm induced strong upwelling and vertical mixing in waters in the region around the Ulleungdo and Dokdo, leading to elevated nutrient concentrations in surface waters, which fueled a phytoplankton bloom. Our bioassay experiments were based on seawater collected from two station (Stns 36 and 40) near the Dokdo, and were designed to investigate changes in biochemical factors and the phytoplankton response following the addition of nutrients (+ N, + P, and + NP) in the presence and absence of added Fe. The experiments were also to assess the pattern of succession of dominant phytoplankton species, and the fate of nutrients from initiation of growth to the logarithmic and stationary phases. In the algal bioassays conducted with added Fe, the *in vivo* fluorescence values in the + N treatment were higher than in the control and the + P treatments, which suggests that the plankton biomass was stimulated by N availability (Fig. 8; $p < 0.001$), and that this nutrient may be a major factor controlling phytoplankton blooms in waters in the vicinity of the Dokdo during spring. The N:P ratio at Stns 36 and 40 were 11.09 and 3.86, respectively. These ratios are significantly lower than the Redfield ratio (16:1), indicating that N was potentially a limiting factor for phytoplankton development. In the bioassay, *H. akashiwo* dominated in the initial, logarithmic, and stationary phases mainly in the + N and + NP treatments, particularly in the absence of Fe addition. According to Shikata et al. (2008), *H. akashiwo* growth in a + NP treatment was significantly greater than that in a + P treatment. They also reported that there was no significant difference in growth between the control and the + P treatment in their bioassay, which is a similar finding to the results reported here. Smayda (1998) demonstrated that *H. akashiwo* has a relatively high nutrient requirement because it has a high nutrient half-saturation constant (K_s), and also has a marked ability for luxury phosphate uptake and storage of polyphosphate for subsequent use, and to overcome low nutrient conditions. Watanabe et al. (1989) reported that luxury phosphate uptake is an important survival strategy for *H. akashiwo* in the bloom process. In the present study, *H. akashiwo* was initially dominant in the + P treatment, and it maintained high levels beyond the final sampling period (Day 11) compared with other members of the phytoplankton community. This indicates that *H. akashiwo* has an advantage over other phytoplankton species, even under low nitrogen conditions. According to Örnólfsson et al. (2004) and Baek et al. (2015), phytoplankton growth is influenced by differences in the N and P requirements of each species, suggesting that differences in nutrient availability can cause a shift in the plankton community structure. We found that naturally occurring phytoplankton, including *H. akashiwo*, can rapidly respond to pulsed nitrogen loading events. *H. akashiwo* also has an advantage over other algal species under potentially N limiting conditions in areas such as the Dokdo. However, our bioassay results do not explain the relatively low growth ability of *H. akashiwo* in the + P treatment relative to the + N treatment. Hodgkiss and Ho (1997) reported a relationship exists between red tides and the N and P

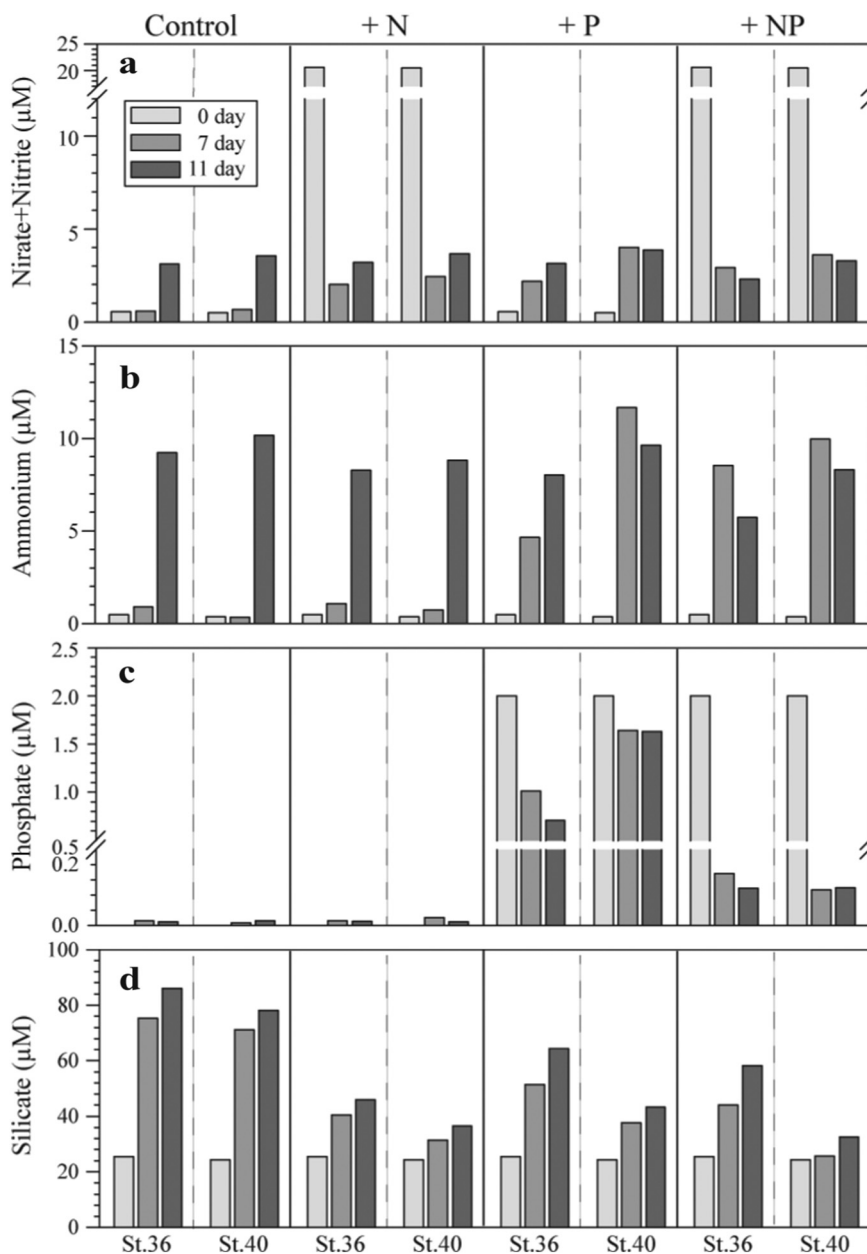


Fig. 11. Changes in: (a) nitrate + nitrite; (b) ammonium; (c) phosphate; and (d) silicate concentrations in a bioassay experiment involving no Fe addition. Analyses occurred at initiation of the experiment and at 7 days and 11 days, and were based on natural water samples collected from Stns 36 and 40 in the Japan/East Sea. The bioassay experiment involved a control (no added nutrients), and treatments with added N, P, and N + P. Subsamples (10 mL) collected for nutrient analysis were filtered using a disposable syringe filter.

load of coastal waters, suggesting that growth of most red tide causative organisms in Hong Kong coastal waters is optimized at low N:P ratio of between 6 and 15. Conversely, Baek et al. (2008) found that densities of two *Ceartium* species peaked during low phosphate concentration and high N:P ratios in Sagami Bay, Japan, and were optimized under phosphorus-limited conditions in laboratory experiments. In addition, optimal N:P ratio was affected by source of nitrogen and optimal N:P ratio for *H. akashiwo* growth was higher than 25:1 (Jiang et al., 2006; Zhang and Hu, 2011). Therefore, *H. akashiwo*, dominant in the field, have an advantage over other algal species under high N:P ratio, especially in nitrate-rich environments.

The growth stimulating effect of the addition of trace metals and nutrients has been reported in numerous studies, and it is known that some trace metals are required for growth of *H. akashiwo* (Yamochi, 1983; Watanabe et al., 1989; Brand, 1991; Baek et al., 2008). Brand (1991) demonstrated that the Fe requirement of *H. akashiwo* is higher than that for other flagellates, and Honjo (1993) and Shikata et al. (2008) observed that the addition of Fe to seawater promoted the growth of *H. akashiwo* in field and bioassay experiments. In our

bioassay experiments, the *in vivo* fluorescence values in the +Fe treatments was not statistically ($p > 0.05$) different from that in the non-Fe treatments, indicating that the growth response of the phytoplankton community was not significant, even where *H. akashiwo* dominated. However, the species composition and pattern of phytoplankton succession was slightly different between the non-Fe and the +Fe treatments. In particular, in the +Fe treatments the abundance of the centric diatom *L. danicus* was clearly higher than in the non-Fe treatments, implying that the trace metal requirements of phytoplankton species differ, and may be involved in determining species successions. In the control group, more silicate was consumed more in the +Fe treatment compared with the non-Fe treatment, which is consistent with diatoms such as *Pseudo-nitzschia* spp. dominating in the +Fe treatments, while non-diatoms such as *H. akashiwo* dominated in the absence of Fe. Although we did not investigate the interaction of Fe with *H. akashiwo*, some diatom species, including *L. danicus*, are positively affected by the presence of Fe under pulsed N and P nutrient conditions.

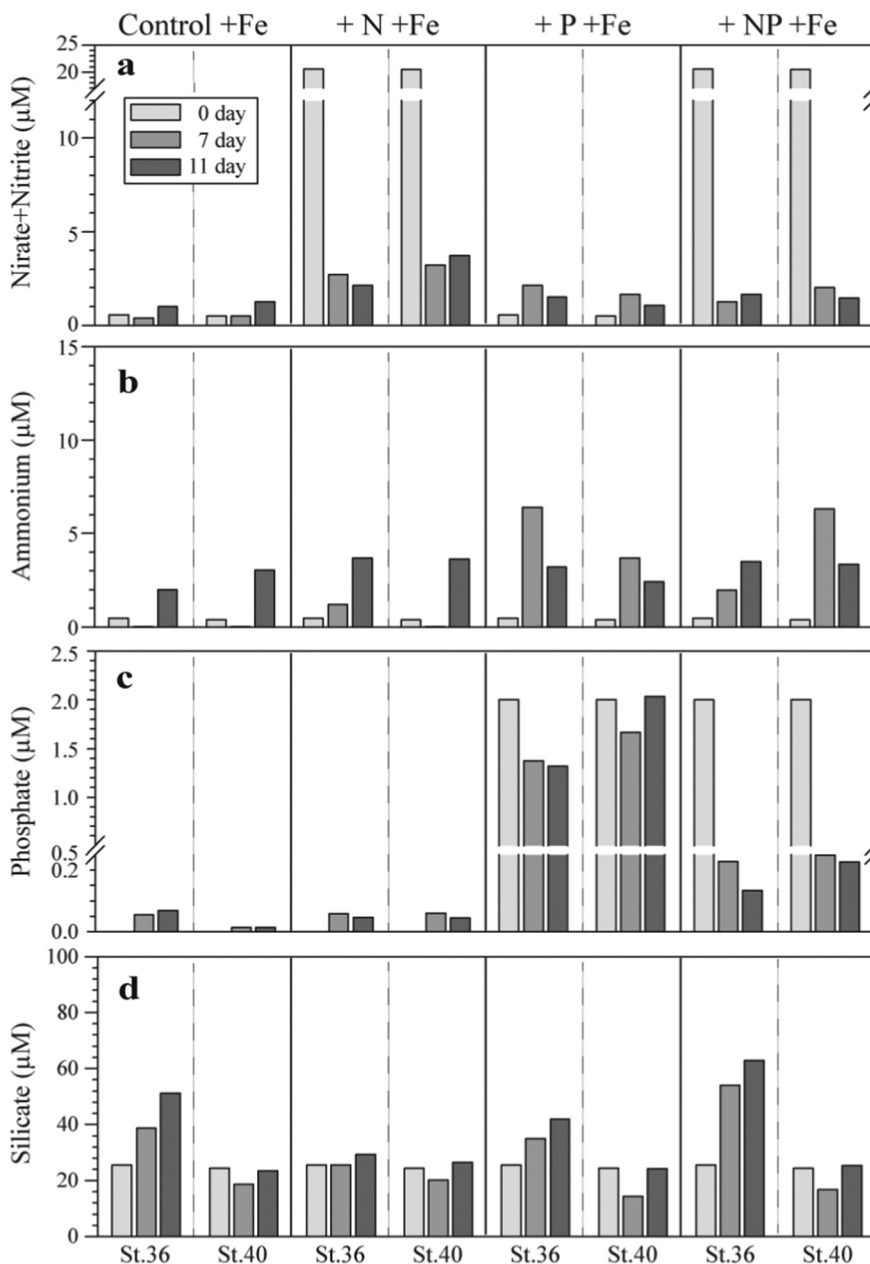


Fig. 12. Changes in: (a) nitrate + nitrite; (b) ammonium; (c) phosphate; and (d) silicate concentrations in a bioassay experiment involving Fe addition. Analyses occurred at initiation of the experiment and at 7 days and 11 days, and were based on natural water samples collected from Stns 36 and 40 in the Japan/East Sea. The bioassay experiment involved a control (Fe added, but no addition of other nutrients), and treatments with added N, P, and N + P. Subsamples (10 mL) collected for nutrient analysis were filtered using a disposable syringe filter.

5. Summary and conclusion

The time-course response of natural plankton communities to a spring episodic windstorm event is summarized schematically in Fig. 14. From field observations we showed that: (1) Zone I-b had low phytoplankton biomass and Chl. *a* concentrations prior to the windstorm event; (2) nutrient concentrations were elevated in surface waters following the windstorm event, which is associated with vertical mixing. This resulted in nutrients acting as a cue for initiation of a phytoplankton bloom, (particularly *H. akashiwo*) in the oligotrophic area offshore from the Ulleungdo and Dokdo; (3) differences in the horizontal distribution of nutrients in offshore oceanic waters played a key role in species shifts and the patterns of phytoplankton distribution. In the algal bioassay experiments, the growth of several diatom species and *H. akashiwo* was significantly increased in treatments involving the addition of N and N + P, whereas phytoplankton growth was not significantly changed by enrichment with P only. According to Zheng and Tang (2007), an offshore phytoplankton bloom has responded rapidly

to pulsed nitrogen loading after a previous typhoon in South China Sea. Similarly, the nutrient distribution after hurricane *Katrina* played a dominant role in the development of the phytoplankton bloom in the Gulf of Mexico (Liu et al., 2009). In addition, satellite-derived water temperature and Chl. *a* measurements after hurricane and tropical cyclone clearly revealed rapid upwelling and phytoplankton bloom in the oligotrophic waters of Gulf of Mexico (Walker et al., 2005) and Arabian Sea (Subrahmanyam et al., 2002). Consequently, pulsed N inputs resulting from episodic windstorm events result in high phytoplankton biomass in waters near Dokdo and can be considered essential to facilitate food-web responses in marine ecosystems of the JES. Further study is needed to generalize carbon flux of classic food-web associated with high phytoplankton biomass.

Acknowledgement

This research was supported by the Basic Core Technology Development Program for the Oceans and the Polar Regions of the

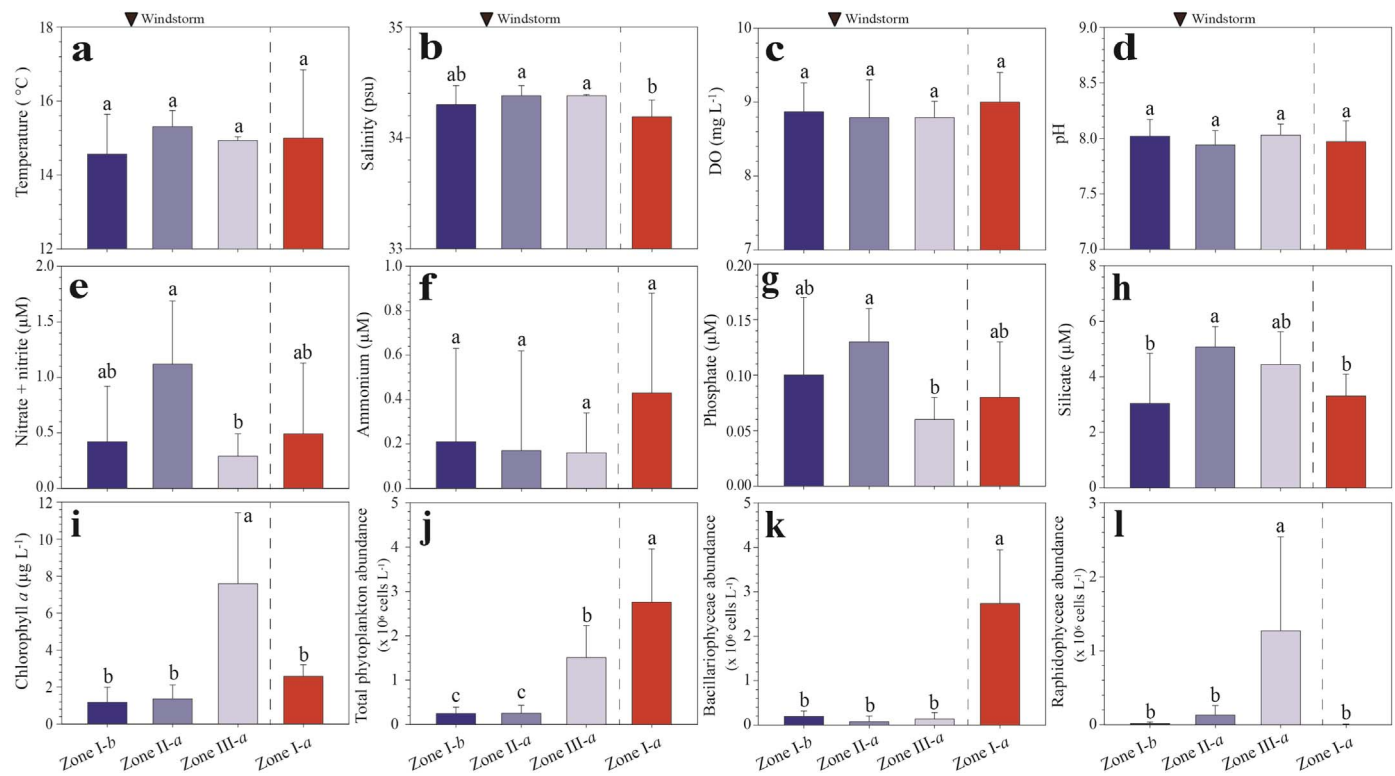


Fig. 13. Comparison of abiotic (a–h) and biotic (i–l) factors in four designated zones in the study area in the Japan/East Sea, prior to and following the windstorm event. The data are presented as the mean ± standard errors of the sampling data for each zone. The results were analyzed using one-way ANOVA and Tukey's *post hoc* test. Letters (a, b, c, and d) represent significant differences ($p < 0.05$).

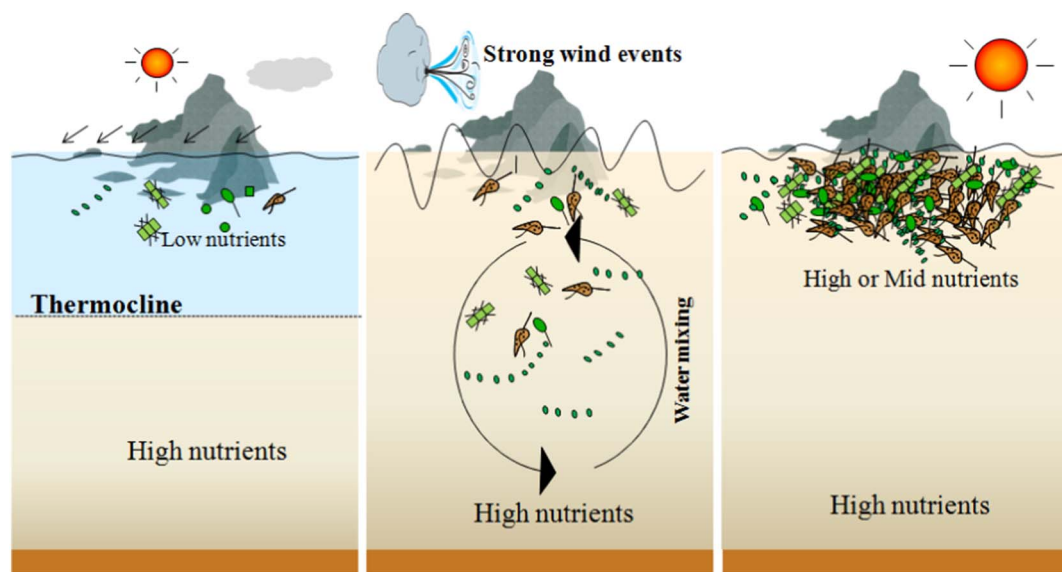


Fig. 14. A schematic illustration of the time course response of the natural plankton community prior to and following the windstorm event.

National Research Foundation (NRF) funded by the Ministry of Science, ICT & Future Planning (grant number NRF-2016M1A5A1027456), and a project of Ministry of Ocean and Fisheries (PG49260).

References

- Baek, S.H., Shimode, S., Han, M.-S., Kikuchi, T., 2008. Growth of dinoflagellate, *Ceratium furca* and *Ceratium fusus* in Sagami Bay, Japan: the role of nutrients. *Harmful Algae* 7, 729–739.
- Baek, S.H., Shimode, S., Shin, K.S., Han, M.S., Kikuchi, T., 2009a. Growth of dinoflagellate, *Ceratium furca* and *Ceratium fusus* in Sagami Bay, Japan: the role of vertical migration and cell division. *Harmful Algae* 8, 843–856.
- Baek, S.H., Shimode, S., Kim, H.C., Han, M.S., Kikuchi, T., 2009b. Strong bottom-up effects on phytoplankton community caused by a rainfall during spring and summer in Sagami Bay, Japan. *J. Mar. Syst.* 75, 253–264.
- Baek, S.H., Kim, D.S., Son, M.H., Yun, S.M., Kim, Y.O., 2015. Seasonal distribution of phytoplankton assemblages and nutrient enriched bioassays as indicators of nutrient limitation of phytoplankton growth in Gwangyang Bay, Korea. *Estuar. Coast. Shelf Sci.* 163, 265–278.
- Bleiker, W., Schanz, F., 1997. Light climate as the key factor controlling the spring dynamics of phytoplankton in Lake Zuerich. *Aquat. Sci.* 59, 135–157.
- Brand, L.E., 1991. Minimum iron requirements of marine phytoplankton and the implications for the biogeochemical control of new production. *Limnol. Oceanogr.* 36, 1756–1771.
- Chen, Y.L., Chen, H., Jan, S., et al., 2009. Phytoplankton productivity enhancement and assemblage change in the upstream Kuroshio after typhoons. *Mar. Ecol. Prog. Ser.*

- 385, 111–126.
- Cho, K.D., Bang, T.J., Shim, T.B., Yu, H.S., 1990. Three dimensional structure of the Ulleung warm lens. *Bull. Korean Fish. Soc.* 23, 323–333.
- De-Pauw, N., Naessens, F.E., 1991. Nutrient-induced competition between species of marine diatoms. *Hydrobiol. Bull.* 25, 23–28.
- Evans, G.T., Paslow, J.S., 1985. A model of annual plankton cycles. *Biological Oceanogr.* 3, 327–347.
- Field, J.G., Clarke, K.R., Warwick, R.M., 1982. A practical strategy for analyzing multi-species distribution patterns. *Mar. Ecol. Prog. Ser.* 8, 37–52.
- Gong, Y., Son, S.J., 1982. A study of oceanic thermal fronts in the southern Japan Sea. *Bull. Fish. Res. Dev.* 28, 25–54.
- Hodgkiss, I.J., Ho, K.C., 1997. Are changes in N: P ratios in coastal waters the key to increased red tide blooms? *Hydrobiologia* 352, 141–147.
- Holmboe, N., Jensen, H.S., Andersen, F.Ø., 1999. Nutrient addition bioassays as indicators of nutrient limitation of phytoplankton in an eutrophic estuary. *Mar. Ecol. Prog. Ser.* 186, 95–104.
- Honjo, T., 1993. Overview on bloom dynamics and physiological ecology of *Heterosigma akashiwo*. In: Smayda, T.J., Shimizu, Y. (Eds.), *Toxic phytoplankton blooms in the sea*. Elsevier, pp. 33–41.
- Summary for policymakers. In: IPCC, Solomon, S., Qin, D., Manning, M. (Eds.), *Climate Change 2007: The Physical Science Basis. Working Group I Contribution to the Fourth Assessment Report of the IPCC*. Cambridge University Press, Cambridge, pp. 1–18.
- Isobe, A., Isoda, Y., 1997. Circulation in the Japan Basin, the northern part of the Japan Sea. *J. Oceanogr.* 55, 373–381.
- Isoda, Y., Saitoh, S.I., 1993. The northward intruding eddy along the east coast of Korea. *J. Oceanogr.* 49, 443–458.
- Jeong, H.J., Yoo, Y.D., Lim, A.S., Kim, T.W., Lee, K., Kang, C.K., 2014. Raphidophyte red tides in Korean waters. *Harmful Algae* 30, S41–S52.
- Jiang, Y., Gan, X.H., Tang, Y.X., Chen, X.L., Chen, Y.R., 2006. Effects of nutrients nitrogen and phosphorus on *Heterosigma akashiwo* growth. *Chin. J. Appl. Ecol.* 17, 557–559.
- Justić, D., Rabalais, N.N., Turner, R.E., Dortch, Q., 1995. Changes in nutrient structure of river-dominated coastal waters: Stoichiometric nutrient balance and its consequences. *Estuar. Coast. Shelf Sci.* 40, 339–356.
- Kim, C.H., Yoon, J.H., 1999. A numerical modeling of the upper and the intermediate layer circulation in the East Sea. *J. Oceanogr.* 55, 327–345.
- Kim, K., Kim, K.R., Chung, J.Y., Yoo, H.S., Park, S.G., 1991. Characteristics of physical properties in the Ulleung Basin. *J. Korean Soc. Oceanogr.* 31, 155–163.
- Kim, H.C., Yoo, S.J., Oh, I.S., 2005. Relationship between phytoplankton bloom and wind stress in the sub-polar frontal area of the Japan/East Sea. *J. Mar. Syst.* 67, 205–216.
- Lee, J.C., 1983. Variation of sea level and sea surface temperature associated with wind induced upwelling in the southeast coast of Korea in summer. *J. Oceanol. Soc. Korea* 18, 149–160.
- Lee, J.Y., Kang, J.H., Kim, I.N., Rho, T.K., Lee, T.S., Kang, C.K., Kim, K.R., 2009. Spatial and temporal variability in the pelagic ecosystem of the East Sea (Sea of Japan): a review. *J. Mar. Syst.* 78, 288–300.
- Lie, H.J., Cho, C.H., 2016. Seasonal circulation patterns of the Yellow and East China Seas derived from satellite-tracked drifter trajectories and hydrographic observations. *Prog. Oceanogr.* 146, 121–141.
- Liu, X., Wang, M., Shi, W., 2009. A study of a Hurricane Katrina-induced phytoplankton bloom using satellite observations and model simulations. *J. Geophys. Res.* 114 (C03023).
- Mahoney, J.B., McLaughlin, J.J.A., 1979. Salinity influence on the ecology of phtop-flagellate bloom in lower New York Bay and adjacent waters. *J. Exp. Mar. Biol. Ecol.* 37, 213–223.
- Martin, S., Kawase, M., 1998. The role of the southern flux of sea ice in the Tatarskiy Strait of the Japan Sea in the generation of the Liman Current. *J. Mar. Res.* 56, 141–155.
- McGillicuddy, D.J., Robinson, A.R., Siegel, D.A., Jannasch, H.W., et al., 1998. Influence of mesoscale eddies on new production in the Sargasso Sea. *Nature* 394, 263–266.
- Michaels, A.F., Silver, M.W., 1988. Primary production, sinking fluxes and the microbial food web. *Deep-Sea Res.* 4, 473–490.
- Min, D.H., Warner, M.J., 2005. Basin-wide circulation and ventilation study in the East Sea (Sea of Japan) using chlorofluorocarbon tracers. *Deep-Sea Res.* II 52, 1580–1616.
- Mitchell, D.A., Watts, D.R., Wimbush, M., Teague, W.J., Tracey, K.L., Book, J.W., Chang, K.I., Suk, M.S., Yoon, J.H., 2005. Upper circulation patterns in the Ulleung Basin. *Deep-Sea Res.* II 52, 1617–1638.
- Ning, X., Chai, F., Xue, H., Cai, Y., Liu, C., Shi, J., 2004. Physical-biological oceanographic coupling influencing phytoplankton and primary production in the South China Sea. *J. Geophys. Res.* 109 (C10005).
- Örnólfsson, E.B., Lumsden, S.E., Pinckney, J.L., 2004. Nutrient pulsing as a regulator of phytoplankton abundance and community composition in Galveston Bay, Texas. *J. Exp. Mar. Biol. Ecol.* 303, 197–220.
- Oshima, K.I., 1994. The flow system in the Japan Sea caused by a sea level difference through shallow straits. *J. Geophys. Res.* 99, 9925–9940.
- Park, J.S., Kim, H.G., Lee, S.G., 1989. Studies on red tide phenomena in Korean coastal waters. In: Okaichi, T., Anderson, D.M., Nemoto, T. (Eds.), *Red Tides*. Elsevier, pp. 34–40.
- Roegner, G.C., Hickey, B.M., Newton, J.A., Shanks, A.L., Armstrong, D.A., 2002. Wind-introduced plumn and bloom intrusions into Willapa Bay, Washington. *Limnol. Oceanogr.* 47, 1033–1042.
- Ryan, J.P., Polito, P.S., Strutton, P.G., Chavez, F.P., 2002. Unusual large-scale phytoplankton blooms in the Equatorial Pacific. *Prog. Oceanogr.* 55, 263–285.
- Saitoh, S.I., Iida, T., Sasaoka, K., 2002. A description of temporal and spatial variability in the Bering Sea spring phytoplankton blooms (1997–1999) using satellite multi-detector remote sensing. *Prog. Oceanogr.* 55, 131–146.
- Shikata, T., Yoshikawa, S., Matsubara, T., Tanoue, W., Yamasaki, Y., Shimasaki, Y., Matsuyama, Y., Oshima, Y., Jenkison, I.R., Honjo, T., 2008. Growth dynamics of *Heterosigma akashiwo* (Raphidophyceae) in Hakata Bay, Japan. *Eur. J. Phycol.* 43, 395–411.
- Smayda, T.J., 1997. Harmful algal blooms: their ecophysiology and general relevance to phytoplankton blooms in the sea. *Limnol. Oceanogr.* 42, 1137–1153.
- Smayda, T.J., 1998. Ecophysiology and bloom dynamics of *Heterosigma akashiwo* (Raphidophyceae). In: Anderson, D.M., Cembella, A.D., Hallegraeff, G.F. (Eds.), *Physiological ecology of harmful algal blooms*. Springer-Verlag, pp. 113–131.
- Smayda, T.J., 2002. Turbulence, watermass stratification and harmful algal blooms: an alternative view and frontal zones as ‘pelagic seed banks. *Harmful Algae* 1, 95–112.
- Sournia, A., 1978. *Phytoplankton Manual*. UNESCO, Paris, pp. 337.
- Staehr, P.A., Sand-Jensen, K., 2006. Seasonal changes in temperature and nutrient control of photosynthesis, respiration and growth of natural phytoplankton community. *Freshw. Biol.* 51, 249–262.
- Subrahmanyam, B., Rao, K.H., Srinivasa Rao, N., Murty, V.S.N., Sharp, R.J., 2002. Influence of a tropical cyclone on chlorophyll-a concentration in the Arabian Sea. *Geophys. Res. Lett.* 29, 2065.
- Sverdrup, H.U., 1953. On conditions for the vernal blooming of phytoplankton. *J. du Conseil - Conseil Permanent International Pour L'exploration de la Mer* 18, 287–295.
- Talley, L.D., Tishchenko, P., Luchin, V., Nedashkovskiy, A., Sagalaev, S., Kang, D.J., Warner, M., Min, D.H., 2004. *Atlas of Japan (East) Sea hydrographic properties in summer, 1999*. *Prog. Oceanogr.* 61, 277–348.
- Tang, D., Kester, D.R., Ni, I.H., Qi, Y., Kawamura, H., 2003. *In situ* and satellite observation of a harmful algal bloom and water condition at the Pearl River estuary in late autumn 1998. *Harmful Algae* 2, 89–99.
- Townsend, D.W., Keller, M.D., Sieracki, M.E., Ackleson, S.G., 1992. Spring phytoplankton blooms in the absence of vertical water column stratification. *Nature* 360, 59–62.
- Trainer, V.L., Hickey, B.M., Horner, R.A., 2002. Biological and physical dynamics of domoic acid production off the Washington Coast. *Limnol. Oceanogr.* 47, 1438–1446.
- Tsuchiya, K., Kuwahara, V.S., Yoshiki, T., Nakajima, R., Miyaguchi, H., Kumekawa, N., Kikuchi, T., Toda, T., 2013a. Phytoplankton community response and succession in relation to typhoon passages in the coastal waters of Japan. *J. Plankton Res.* 36, 424–438.
- Tsuchiya, K., Yoshiki, T., Nakajima, R., Miyaguchi, H., Kuwahara, V.S., Taguchi, S., Kikuchi, T., Toda, T., 2013b. Typhoon-driven variations in primary production and phytoplankton assemblages in Sagami Bay, Japan: a case study of typhoon Mawar (T0511). *Plankton Benthos Res.* 8, 74–87.
- Wada, M., Miyazaki, A., Fujii, T., 1985. On the mechanisms of diurnal vertical migration behavior of *Heterosigma akashiwo* (Raphidophyceae). *Plant Cell Physiol.* 26, 431–436.
- Walker, N.D., Leben, R.R., Balasubramanian, S., 2005. Hurricane-forced upwelling and chlorophyll a enhancement within cold-core cyclones in the Gulf of Mexico. *Geophys. Res. Lett.* 32 (L18610).
- Watanabe, M., Kohata, K., Kunugi, M., 1988. Phosphate accumulation and metabolism by *Heterosigma akashiwo* (Raphidophyceae) during diel vertical migration in a stratified microcosm. *J. Phycol.* 24, 22–28.
- Watanabe, M., Takamatsu, T., Kohata, K., Kunugi, M., Kawashima, M., Koyama, M., 1989. Luxury phosphate uptake and variation of intracellular metal concentration in *Heterosigma akashiwo* (Raphidophyceae). *J. Phycol.* 25, 428–436.
- Watanabe, M.M., Nakamura, Y., 1984. Growth characteristics of a red tide flagellate, *Heterosigma akashiwo* (Hada). 2. The utilization of nutrients. *Res. Rep. Natl. Inst. Environ. Stud. Jpn.* 63, 59–67 (in Japanese with English abstract).
- Yamada, K., Ishizak, J., Yoo, S., Kim, H., Chiba, S., 2004. Seasonal and interannual variability of sea surface chlorophyll a concentration in the Japan/East Sea (JES). *Prog. Oceanogr.* 61, 193–211.
- Yamochi, S., 1983. Mechanism for outbreak of *Heterosigma akashiwo* red tide in Osaka Bay, Japan. Part I. Nutrient factors involved in controlling the growth of *Heterosigma akashiwo* Hada. *J. Oceanogr. Soc. Jpn.* 31, 97–106.
- Yentsch, C.S., 1990. Estimates of ‘new production’ in the Mid-North Atlantic. *J. Plankton Res.* 12, 717–734.
- Yin, K., Harrison, P.J., Goldblatt, R.H., St. John, M.A., Beamish, R.J., 1997. Factors controlling the timing of the spring bloom in the Strait of Georgia estuary, British Columbia, Canada. *Can. J. Fish. Aquat. Sci.* 54, 1985–1995.
- Zhang, Q., Hu, G., 2011. Effect of nitrogen to phosphorus ratios on cell proliferation in marine micro algae. *Chin. J. Oceanol. Limnol.* 29, 739–745.
- Zhao, H., Tang, D., Wang, Y., 2008. Comparison of phytoplankton blooms triggered by two typhoons with different intensities and translation speeds in the South China Sea. *Mar. Ecol. Prog. Ser.* 365, 57–65.
- Zheng, G.M., Tang, D., 2007. Offshore and nearshore chlorophyll increases induced by typhoon winds and subsequent terrestrial rainwater runoff. *Mar. Ecol. Prog. Ser.* 333, 61–74.