



Potential influence of the proliferation of sediment-based diatoms on blooms of a harmful dinoflagellate *Cochlodinium polykrikoides*: a microcosm approach

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Abstract

Typhoons cause significant environmental damage in coastal areas and one of their effects is the suspension of the resting stage cells of diatoms from the surface sediment. We performed microcosm experiments in 10-L containers using natural sediments from three different sites of southern Korean coastal waters (Geoje, Goheung, and Tongyeong) to simulate the effect of suspension of sediment-based diatoms by a typhoon on blooms of the harmful dinoflagellate *Cochlodinium polykrikoides*. This dinoflagellate grew well under control conditions and exhibited a maximum abundance of 985 cells mL⁻¹ on day 10, but all treatment groups (Geoje, Goheung, and Tongyeong) had decreased abundances by day 4 and fewer than 50 cells mL⁻¹ on day 10. As *C. polykrikoides* declined, two diatoms (*Skeletonema* spp. and *Chaetoceros* spp.) dominated in the three treatment groups. In particular, these diatoms increased to 2.9 × 10⁴ cells mL⁻¹ on day 5 and 2.3 × 10⁴ cells mL⁻¹ on day 7 in the Geoje group. A multivariate redundancy analysis indicated a negative correlation between the abundances of *C. polykrikoides* and *Chaetoceros* spp., and this corresponded to the sharpest decrease of *C. polykrikoides* in the Geoje group. There were also changes in the bacterial community associated with changes in phytoplankton. During the early phase, when *C. polykrikoides* was dominant, Rhodobacterales prevailed (> 50%) in all treatment groups, and the proportion of these bacteria in the Geoje group decreased earlier than in the other groups. At the end of the experiment, there was a high proportion of Verrucomicrobiales, suggesting that sediment addition led to changes in the bacterial community. Overall, our microcosm experiments suggest that the significant environmental changes following the passage of a typhoon, especially the suspension and proliferation of sediment-based diatoms, directly affects the bacterial community and decreases blooms of *C. polykrikoides*.

Keywords Typhoon · Sediment resuspension · Diatoms competition · Bloom control · *Cochlodinium polykrikoides*

Introduction

Typhoons develop at latitudes 180°E to 100°E in the Northern Hemisphere and then move to higher latitudes where they can cause significant physical and chemical changes in the marine environment due to strong winds and heavy rains

(Chung et al. 2012; Tsuchiya et al. 2014). The strong energy of typhoons can drive mixing of the stratified water column during summer, so that abundant nutrients from the bottom layer move to the nutrient-depleted surface layer (Lin et al. 2003; Zheng and Tang 2007; Baek et al. 2020). Many previous studies indicated that an increase of primary production was closely associated with blooms of diatoms after typhoon passage (Delesalle et al. 1993; Lin et al. 2003; Chen et al. 2009; Tsuchiya et al. 2013, 2014).

Many planktonic diatoms form resting stage cells during their life cycles and these resting stage cells prolong viability in a variety of coastal environments (Itakura et al. 1997; Ishikawa and Furuya 2004; Tsukazaki et al. 2018). Diatom resting stage cells are abundant in the sediments of coastal areas, and light triggers their germination (Hollibaugh et al. 1981; Imai et al. 1996; McQuoid 2002). The suspension of

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resting stage cells to the euphotic layer from the sediment is therefore essential for initiation of the growth of diatoms as vegetative cells (Pitcher et al. 1991; Ishikawa and Furuya 2004). The passage of a typhoon alters the stability of water masses, and this mixing process suspends sediment that has abundant diatom resting stage cells (Ishikawa and Furuya 2004).

The ichthyotoxic dinoflagellate *Cochlodinium polykrikoides* (*Margalefidinium polykrikoides*) can form large blooms during the summer in Korean coastal waters (KCWs), leading to massive fish mortality in the fish farms (Lee et al. 2013a; Park et al. 2013). Our previous study (Lim et al. 2021b) found that blooms of *C. polykrikoides* were affected by typhoons. In particular, the strong winds and waves of a typhoon generated significant turbulence and this had a rapid negative effect on *C. polykrikoides* blooms. However, this previous research did not consider the possibility that the decline of *C. polykrikoides* abundance was due to increases in the abundance of diatoms that occurred after passage of a typhoon. A sudden supply of nutrient into coastal area from river discharge and water mixing related with rainfall and typhoon events can promote diatom growth, particularly in summer season of KCWs (Baek et al., 2015, 2019, 2020). Tang and Gobler (2010) reported that an allelopathic interaction depended on the abundance of cells of the competing species. In addition, a negative effect of vegetative diatom cells and their filtrates on dinoflagellates, including *C. polykrikoides*, can occur (Yamasaki et al. 2010; Lim et al. 2014). In other words, the passage of typhoons during a *C. polykrikoides* bloom may trigger competition between *C. polykrikoides* and sediment-based diatoms. However, to our knowledge, no experimental studies confirmed the effects of sediment-based diatoms on *C. polykrikoides* blooms.

The composition of the bacterial community is an indicator of the ecological dynamics of an aquatic ecosystem (Harnisz 2013; Glasl et al. 2017; Karimi et al. 2017). Changes in bacterial community composition are associated with changes in dissolved organic matter and changes in phytoplankton composition (Pinhassi et al. 2004; Teeling et al. 2012; Klindworth et al. 2014). Several previous studies showed that different diatom species are associated with different bacterial communities (Grossart et al. 2005; Behringer et al. 2018). Although it is likely that bacterial communities undergo unique changes when sediment-based diatoms begin to thrive in the marine environment, few studies have investigated these effects.

These previous studies led to two hypotheses. First, we hypothesized that the suspension and proliferation of sediment-based diatoms inhibit the growth of *C. polykrikoides*. Second, we hypothesized that proliferation of sediment-based diatoms due to typhoon-related nutrient supplementation affects the bacterial community. We tested these two hypotheses by performing microcosm experiments using

natural sediments collected from three different sites in the KCWs that experience frequent blooming. We also used our experimental results and historical data to analyze the effect of environmental changes following the passage of typhoons on the population dynamics of *C. polykrikoides*.

Materials and methods

Experimental design

The LIMS-PS-2335 strain of *Cochlodinium polykrikoides* was from the Library of Marine Samples (LIMS; Korea Institute of Ocean Science and Technology, Republic of Korea). This strain was originally isolated from surface water (16 °C) near Tongyeong on 18 December 2013. These cells were incubated at 22 °C under 100 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ cool white fluorescent light with a 12-h light:12-h dark cycle (Photometer HD2101.1, Delta Ohm SrL, Caselle, Italy). The growth medium was f/2 without silicate (Guillard 1975), the temperature was approximately 22 °C, and the salinity was 32 (Fig. 1A). Cultures were established by gradually increasing the volume from 1 to 4 L to 20 L. When the cell density of *C. polykrikoides* in each culture bottle increased to be 200 cells mL^{-1} , it was transferred into large-volume cultural bottles and scaled up. An 80-L sample of *C. polykrikoides* cells was used for the microcosm experiments (four experimental groups with two 10-L replicates per group), in which the initial abundance was approximately 330 cells mL^{-1} . To simulate the effect of heavy rainfall after typhoon passage, the salinity of each experimental group was reduced to 26 using distilled water during the inoculation process. Sediments used in the microcosm experiments were obtained using a Van Veen grab sampler on 5 August 2019 at three sites of the southern KCWs (Fig. 1B): a site in the Geoje (34.99°N, 128.68°E, 10-m depth); a site in the Goheung (34.48°N, 127.64°E, 17-m depth); and a site in the Tongyeong (34.81°N, 128.28°E, 17-m depth). The sediment collected from each site was from the upper 20 mm of the surface. Each sediment sample was stored in refrigerator (4 °C in darkness) and was added at a concentration of 1 g L^{-1} into 10-L polypropylene boxes filled with *C. polykrikoides* culture. Experiments were performed for 14 days starting on 27 August 2019. The four groups were control without sediment, sediment from Geoje, sediment from Goheung, and sediment from Tongyeong.

Sample collection and analysis

Environmental variables (water temperature, salinity, dissolved oxygen: DO, and pH) were measured using a YSI 6600 data sonde (USA). To obtain a homogeneous water sample from the microcosm, each microcosm was mixed

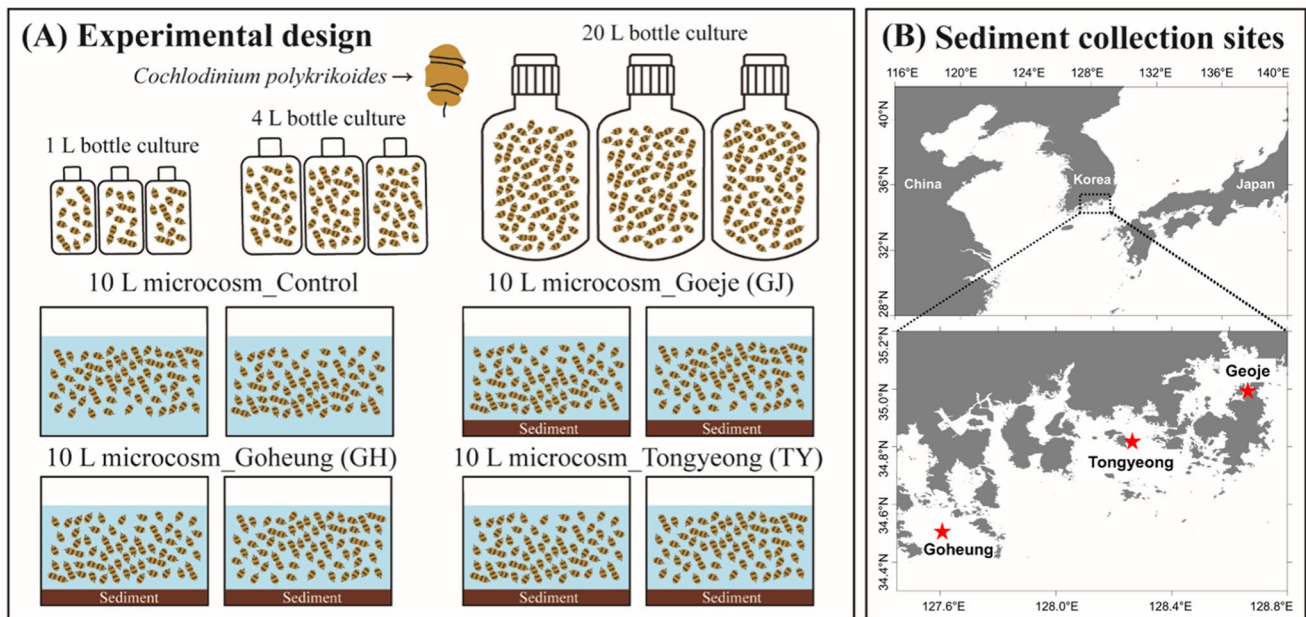


Fig. 1 Experimental design. Scaling up the culture of *Cochlodinium polykrikoides* and culturing after inoculation of the sediments (A). Locations of sediment collection (Goheung, Tongyeong, and Goeje) in the southern Korean coastal waters (B)

gently prior to water sampling using a customized plastic rod. During this process, settled bottom sediment was not completely re-suspended into the water column, and water samples were collected using a 50-mL syringe. For measurement of dissolved inorganic nutrients (nitrate + nitrite, ammonia, phosphorus, and silicate), samples were collected after passing through cellulose-acetate membrane syringe filter with a pore size of 0.45 μm (Advantec, Japan). The filtrates were placed in acid-cleansed 15-mL conical tubes (SPL Life Science, Korea) and HgCl_2 (final concentration: 0.1%) was added to prevent changes due to biological reactions (Kirkwood 1992). The concentrations of dissolved inorganic nutrients were measured using a flow injection autoanalyzer (Quattro 39; Seal Analytical, UK) according to a published protocol (Parsons et al. 1984), and all measurements were calibrated using reference materials for nutrients in seawater (RMNS; KANSO Technos Co., Ltd., Japan). Chlorophyll *a* (Chl. *a*) concentration was measured using a PHYTO-PAM phytoplankton analyzer (Heinz Walz GmbH, Germany). For the identification and enumeration of phytoplankton, water samples were fixed with 3% Lugol's solution and then stored in darkness prior to microscopic analysis. Fixed samples were transferred to Sedgewick-Rafter chambers, and phytoplankton were counted and/or identified at 100 \times , 200 \times , and 400 \times using light microscopy (Axio Scope A1; Carl Zeiss, Germany).

DNA extraction and sequencing analysis of the bacterial community

Bacterial cells were collected by filtering samples through polycarbonate membrane filters (pore size: 0.22 μm , filter diameter: 47 mm; Isopore). For genetic analysis of the bacterial community, the filters were cut into pieces prior to extraction of genomic DNA (gDNA) using the DNeasy Plant Mini Kit (Qiagen, USA). The extracted gDNA was quantified using Quant-IT PicoGreen (Invitrogen, USA). A sequencing library was prepared using the Illumina Metagenomic Sequencing Library protocols to amplify the V3 and V4 hypervariable regions of the bacterial 16S ribosomal RNA (rRNA) gene. The input gDNA (2 ng) was PCR-amplified using 5 \times reaction buffer, 1 mM of dNTP mix, and 500 nM each of the universal Illumina-tagged forward and reverse PCR primers (Herlemann et al. 2011) (341F: 5'-TCG TCGGCAGCGTC-AGATGTGTATAAGAGACAG-CCT ACGGGNGGCWGCAG-3'; 805R: 5'-GTCTCGTGGGCT CGG-AGATGTGTATAAGAGACAG-GACTACHVGGG TATCTAATCC-3'; the underlined sequences indicate the target region primer), and Herculase II fusion DNA polymerase (Agilent Technologies, USA). The first PCR protocol was 3 min at 95 $^{\circ}\text{C}$ for heat activation; 25 cycles of 30 s at 95 $^{\circ}\text{C}$, 30 s at 55 $^{\circ}\text{C}$, and 30 s at 72 $^{\circ}\text{C}$; and a 5-min final extension at 72 $^{\circ}\text{C}$. The first PCR product was purified using AMPure beads (Agencourt Bioscience, USA). Following

purification, 2 μL of this product was amplified for final library construction containing the index using NexteraXT Indexed Primer. The protocol for the second PCR was the same as for the first PCR, except there were 10 (rather than 25) amplification cycles.

The PCR product was purified using AMPure beads and was quantified using qPCR in accordance with the qPCR Quantification Protocol Guide (KAPA Library Quantification kits for Illumina Sequencing platforms). Quality was assessed using the TapeStation D1000 ScreenTape (Agilent Technologies, Germany). Paired-end sequencing (2×300 bp) was performed by Macrogen using the MiSeq platform (Illumina, USA). Sequencing adaptors and barcodes were removed using Cutadapt (Martin 2011). To correct errors in the amplicon sequencing, reads were filtered based on quality scores and trimmed using the DADA2 package version 1.18.0 (Callahan et al. 2016) in R software version 4.0.3. Forward and reverse reads were truncated at 250 bp and 200 bp, respectively; then, they were filtered to remove any reads with an expected error of 2 or more. After merging of paired-end reads and correction of sequencing errors, the PCR chimera sequence was removed using the consensus method of DADA2 to infer amplicon sequence variants (ASVs). Silva database release 138 was used to align and classify the 16S rRNA gene sequences (Quast et al. 2012). All ASVs that were in Archaea, mitochondria, or chloroplasts were removed from the dataset.

Historical records of *C. polykrikoides* blooms

To determine the locations of the first occurrences and geographical distributions of *C. polykrikoides* blooms in Korea from 1995 to 2020, the historical records of these blooms were obtained from “Status of Red Tides in the Korean Coast in 2020” (National Institute of Fishery Science of Korea [NIFS]; <http://www.nifs.go.kr/red/>).

Statistical analysis

Redundancy analysis (RDA) was conducted using CANOCO version 4.5 for Windows (Lepš and Šmilauer 2003) to investigate the relationships of environmental variables and phytoplankton population dynamics. The measured environmental factors (DO, pH, and dissolved inorganic nutrients [nitrate + nitrite, ammonia, phosphorus, and silicate]) were the explanatory variables. The data used for RDA were phytoplankton numbers and environmental data at 0, 3, 5, 7, 10, and 14 days in each treatment group. Data were square-root transformed prior to RDA ordination. Based on the RDA results indicating that phytoplankton numbers had a negative correlation with *C. polykrikoides*, a non-parametric Kruskal–Wallis test was used to compare the abundance of *Chaetoceros* spp. in each treatment group from day 3 to 7,

followed by the non-parametric Mann–Whitney *U*-test with a Bonferroni correction for post hoc pairwise comparisons (significance level: $p < 0.05/3 = 0.0167$). The similarities of bacterial communities in the treatment groups were determined using an unweighted pair-group method with arithmetic mean (UPGMA) with the R pheatmap package (<https://github.com/raivokolde/pheatmap>).

Results

Changes in the levels of *C. polykrikoides*, diatoms, and chlorophyll *a*

The change in abundance of *C. polykrikoides* was clearly different in the control group and the three treatment groups (Fig. 2A). In the control group, the abundance continuously increased until day 10 (maximum: $985 \text{ cells mL}^{-1}$) and was slightly lower on day 14. In each treatment group, the abundance of *C. polykrikoides* increased (with some fluctuations) until day 3. On day 4, the abundance in the Geoje group was slightly greater, but it was lower in the Goheung and Tongyeong groups. After day 4, the abundance in the Geoje group rapidly decreased, and it reached a minimum of 15 cells mL^{-1} on day 7. The abundances decreased more slowly in the Goheung and Tongyeong groups and were less than 50 cells mL^{-1} on day 10. In all three treatment groups, the abundance of *C. polykrikoides* markedly declined from day 4 to day 7. During this period, the abundance decreased from 525 to 15 cells mL^{-1} in the Geoje group, 372 to $115 \text{ cells mL}^{-1}$ in the Goheung group, and 303 to $160 \text{ cells mL}^{-1}$ in the Tongyeong group.

The abundance of total diatoms in the different groups showed similar overall patterns over time, although the groups differed greatly in magnitude (Fig. 2B). Overall, diatom abundance markedly increased until day 7, and then decreased. In the Geoje group, the abundance increased very rapidly (more than $10^3 \text{ cells mL}^{-1}$ on day 3, $1.3 \times 10^4 \text{ cells mL}^{-1}$ on day 4, and $3.3 \times 10^4 \text{ cells mL}^{-1}$ on day 5). The Goheung group showed slower changes, with a maximum abundance of $2.0 \times 10^4 \text{ cells mL}^{-1}$ on day 7. The maximum abundance in the Tongyeong group was $4.0 \times 10^3 \text{ cells mL}^{-1}$ on day 5, the lowest of all three treatment groups. Comparing the average abundance of total diatoms during the period when *C. polykrikoides* abundance began to decrease (day 4) indicated the average abundance of *Chaetoceros* in the Geoje group (7.6×10^3) was higher than in the Goheung group ($4.4 \times 10^3 \text{ cells mL}^{-1}$) and the Tongyeong group ($7.0 \times 10^2 \text{ cells mL}^{-1}$). The average abundance of the diatom *Skeletonema* exhibited a similar trend (Geoje: $1.2 \times 10^4 \text{ mL}^{-1}$ > Goheung: $1.9 \times 10^3 \text{ mL}^{-1}$ > Tongyeong: $1.5 \times 10^3 \text{ mL}^{-1}$).

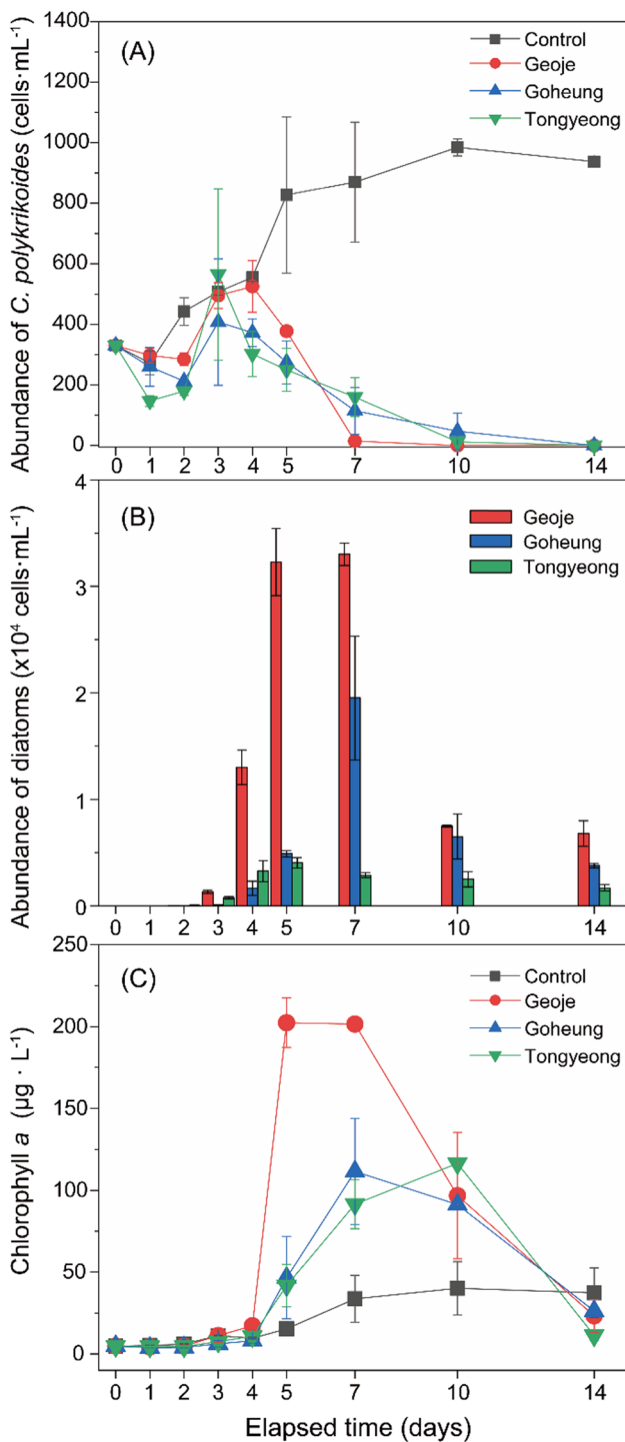


Fig. 2 Changes in the abundance of *Cochlodinium polykrikoides* (A), total diatoms (B), and concentration of chlorophyll *a* (C) in the four experimental groups from day 0 to day 14

The change in the level of Chl. *a* was similar to the change in diatom abundance, in that there was a rapid increase until day 7, followed by a decrease (Fig. 2C). The date of maximum concentration differed among the groups. In the Geoje

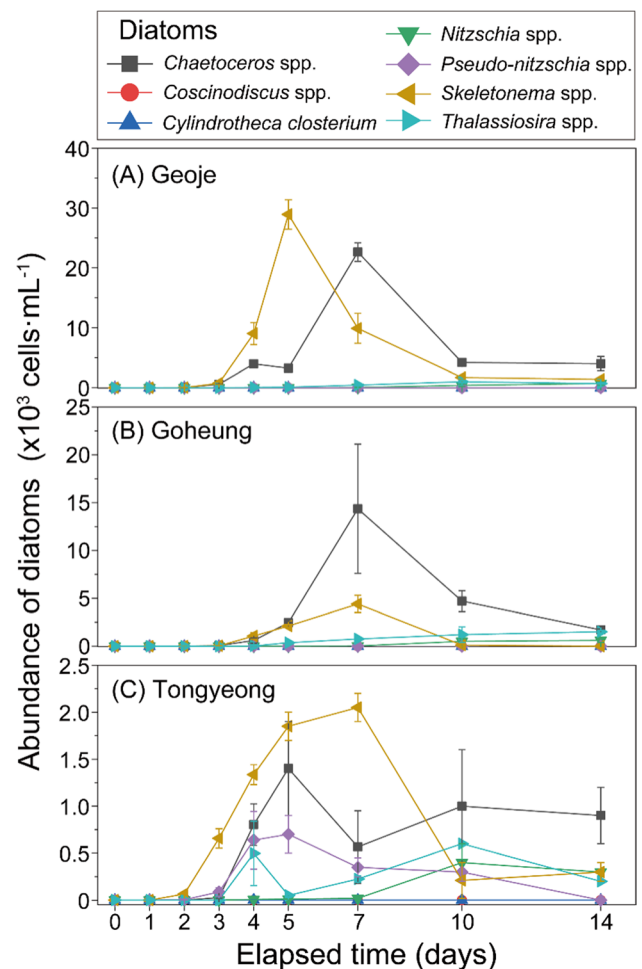


Fig. 3 Changes in abundance of individual diatoms in the three treatment groups from day 0 to day 14

group, the concentration was $202.3 \pm 15.1 \mu\text{g L}^{-1}$ on day 5 but it declined to $96.8 \pm 38.6 \mu\text{g L}^{-1}$ on day 10. On day 7, the maximum Chl. *a* concentration was $111.5 \pm 32.4 \mu\text{g L}^{-1}$ in the Goheung group. In the Tongyeong group, the maximum concentration was $116.5 \pm 1.2 \mu\text{g L}^{-1}$ on day 10. In the control group, the concentration increased slowly until reaching a maximum on day 10 ($40.1 \pm 16.4 \mu\text{g L}^{-1}$).

Changes in the abundances of different diatoms

The species of diatoms also differed among the three treatment groups. In the Geoje group, *Skeletonema* spp. exceeded $2.9 \times 10^4 \text{ cells mL}^{-1}$ on day 5, and *Chaetoceros* spp. rapidly increased to $2.3 \times 10^4 \text{ cells mL}^{-1}$ on day 7 (Fig. 3A). In the Goheung group, the abundance of *Chaetoceros* spp. and *Skeletonema* spp. was similar until day 5, then the abundance of *Chaetoceros* spp. increased remarkably to $1.4 \times 10^4 \text{ cells mL}^{-1}$; *Skeletonema* spp. only increased slightly to $4.4 \times 10^3 \text{ cells mL}^{-1}$ on day 7 (Fig. 3B). Relative

to the two other groups, there was a greater diversity of diatoms in the Tongyeong group (Fig. 3C). The abundance of *Skeletonema* spp. increased first, and this was followed by increases of *Chaetoceros* spp., *Pseudo-nitzschia* spp., and *Thalassiosira* spp. Notably, the abundance of each diatom in the Tongyeong group was about 10-times lower than in the other groups.

Changes in bacterial communities

Analysis of the changes in the different orders of bacteria indicated the community composition in each of the three treatment groups was dominated by Rhodobacterales (18.5–78.1%) until day 4, and by Flavobacteriales (10.4–42.7%) from day 7 to day 14 (Fig. 4). On days 1 and 3, the relative abundance of Opitutales was high only in the Goheung and Tongyeong groups (average: 29.5%). At the time when the number of diatoms increased rapidly (days 4–7), the abundance of Caulobacteriales was high in all treatment groups; the maximum was 46.1% in the Geoje group, 53.1% in the Goheung group, and 52.0% in the Tongyeong group. Among the bacterial orders with relative abundance more than 10%, the abundance of Verrucomicrobiales and Sphingobacteriales differed among the treatment groups. In particular, the

abundance of Verrucomicrobiales was high only in the Geoje and Tongyeong groups on day 14 (average: 27.4%), and the abundance of Sphingobacteriales was high only in the Geoje and Goheung groups on day 14 (average: 23.3%).

Changes in environmental variables

The four groups showed generally similar changes in pH and DO (Fig. 5A and 5B), but there were some differences in the timing of maximum pH. The maximum pH was 9.2 ± 0.1 in the Geoje group on day 5, 8.9 ± 0.1 in the Goheung group on day 10, and 9.1 ± 0.2 in the Tongyeong group on day 10. In the control group, the pH gradually increased until day 7 (maximum: 9.7 ± 0.1), and then remained steady. The concentration of DO indicated the maximum concentration was on day 5 in the Geoje group (18.2 ± 0.9 mg L⁻¹) and on day 7 in the Goheung group (12.7 ± 0.9 mg L⁻¹) and in the Tongyeong group (12.3 ± 1.3 mg L⁻¹). In the Geoje group, the pH and DO had large increases on day 5, after which the pH slowly declined and the DO rapidly declined. The other groups differed in the days when the pH was maximal (day 10) and when the DO was maximal (day 7).

The initial concentrations of nutrients were high due to the influence of the *f/2* medium used for the *C. polykrikoides* stock culture (Fig. 5C–F). The initial average concentration of nitrate + nitrite was 330.0 ± 3.1 μM (Fig. 5C), and a sharp decrease began on day 7. From day 10, there were differences in the nitrate + nitrite concentration among the experimental groups. In particular, the nitrate + nitrite level in the Geoje group had a rapid decrease that corresponded to the remarkable increase of diatom abundance. On day 14, the nitrate + nitrite level in the Geoje group was the lowest of all groups (284.4 μM). The average concentration of phosphorus was 22.9 ± 1.6 μM on day 0, and it showed gradual decline over time (Fig. 5D). The ammonia concentration remained at an average of 1.8 ± 1.6 μM until day 10, and then increased rapidly to an average of 30.0 ± 10.4 μM on day 14 (Fig. 5E), although the level in the control group remained low (1.5 μM on day 14). The initial concentration of silicate differed among the treatment groups; it was 20.1 μM in the control group, 25.7 μM in the Geoje group, 33.3 μM in the Goheung group, and 33.0 μM in the Tongyeong group (Fig. 5F). From day 3 to 7, the concentration of silicate declined in the three treatment groups (from 23.1 ± 0.7 to 0.7 ± 0.4 μM), but the concentration remained relatively constant at about 20 μM in the control group.

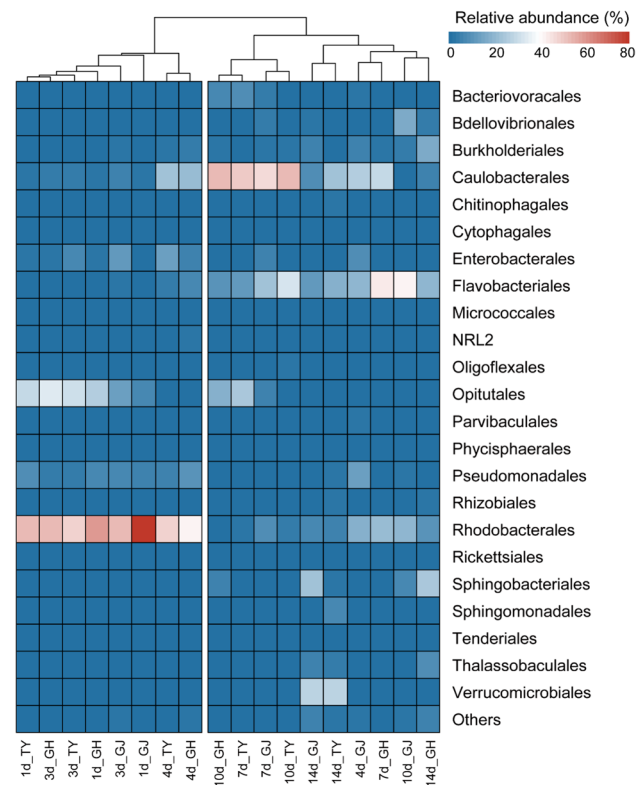


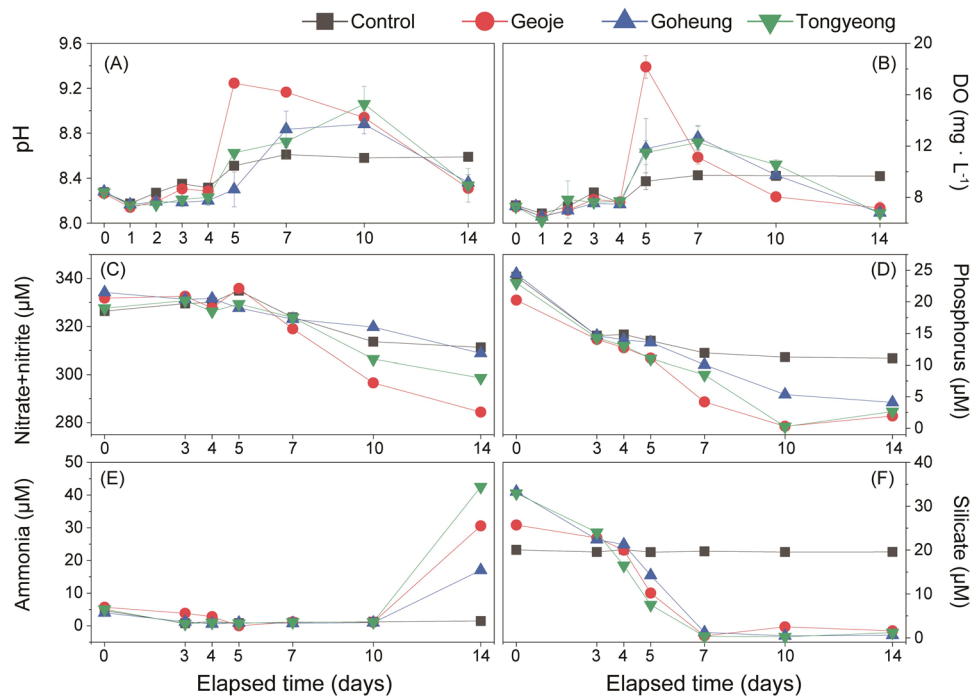
Fig. 4 Relative abundances (%) of bacteria in taxonomic orders in the three treatment groups (Geoje, GJ; Goheung, GH; Tongyeong, TY). Communities were clustered using the unweighted pair-group method with arithmetic mean (UPGMA) in the R pheatmap package

Discussion

Hypothesis of slow effect of typhoon on *C. polykrikoides* bloom

The NIFS reported that red tides due to *C. polykrikoides* occurred every year in the KCWs from 1995 to 2020,

Fig. 5 Changes in environmental variables in the four experimental groups from day 0 to day 14



except 2011 and 2017 (Supplementary Table 1). Most of these blooms began in the southern KCWs, and these huge blooms formed and remained there. Among these blooms, 42% expanded to the eastern KCWs (East/Japan Sea) due to the east-flowing Tsushima Warm Current. However, *C. polykrikoides* blooms in the western KCWs (Yellow Sea) only occurred during 2012. The Yellow Sea has a macrotidal environment and a change between 6 and 10 m in the spring tidal range, depending on location (Kang 1984). These strong tidal currents cause resuspension of sediment (Lee et al. 2013b), similar to the water mixing effects of typhoons. Yoon (2014) estimated that the relatively high nutrient concentration of seaweed (“nori” or “gim”) farms around the southwestern KCWs was mainly due to resuspension of surface sediments, with nutrient inflow due to tidal mixing. Unlike motile dinoflagellates, which can migrate up and down the water column to utilize nutrients at different layers, non-motile diatoms require water mixing to supply nutrients or else they sink to the sediment (Watanabe et al. 1991; Baek et al. 2009). In addition, the strong tidal current of the western KCWs causes constant turbulence. Under these dynamic conditions, diatoms can gain a competitive advantage over dinoflagellates because of their greater tolerance to turbulence and their potentially rapid growth rate (Thomas and Gibson 1990; Estrada and Berdalet 1997; Baek et al. 2008). There is evidence of direct physical damage of dinoflagellates caused by intense turbulence, including cellular disorientation, damage of flagella, and growth inhibition (White 1976; Thomas and Gibson 1990; Thomas et al. 1995). Our previous study (Lim

et al. 2021b) described this direct physical effect as a “fast effect” of typhoons on *C. polykrikoides* blooms that occurs immediately after typhoon passage. Indeed, numerous studies reported that diatoms have mainly dominated in the western KCWs in all seasons, even in summer (Choi and Shim 1986; Shim and Yeo 1988; Yeo and Kang 1998; Yoon 2020). In particular, the dominant diatoms during summer in this region are *Chaetoceros curvisetus*, *Skeletonema costatum*, *Leptocylindrus danicus*. On the other hand, unlike western KCWs of dynamic environment, the southern KCWs has stable stratification during summer due to a relatively low tidal range (2–3 m), leading the dominance of motile dinoflagellates (Lim et al. 2019; Baek et al. 2020; Seo et al. 2020). As an episodic event, when a typhoon passes this region during summer, the conditions are similar to those that occur during the spring tidal events of the western KCWs. The similarity of the environment leads to the similar changes in the phytoplankton community. Recent field studies of the southern KCWs indicated that after the passage of typhoons, the abundance of two diatoms (*Pseudo-nitzschia* and *Chaetoceros*) exceeded the abundance of dinoflagellates, including *C. polykrikoides* (Baek et al. 2020; Lim et al. 2021b). In addition, this phenomenon has been also reported in other regions of temperate coastal waters during summer. For example, after passage of a typhoon in southern East China Sea, the dominant phytoplankton community shifted from the dinoflagellate *Gymnodinium* to the diatom *Chaetoceros* (Chung et al. 2012). Based on these previous findings, we therefore propose there is also a “slow effect” of typhoons

on *C. polykrikoides* blooms, in which strong turbulence from a passing typhoon creates an environment more favorable for diatoms by mixing of the water column, and this can lead to termination of the *C. polykrikoides* bloom because of the competitive advantages of diatoms. To verify this hypothesis, we used a microcosm experimental approach in which sediment with diatoms resting stage cells were inoculated into highly dense cultures of *C. polykrikoides* under conditions of low-salinity and high-nutrients. The results supported our hypothesis, in that the abundance of diatoms in three different treatment groups increased as the abundance of *C. polykrikoides* decreased.

Confirmation of “slow effect” hypothesis through microcosm experiments

It is well known that typhoons cause major environmental changes in coastal areas due to reductions in salinity and increases in nutrients from the large amounts of freshwater introduced by heavy rainfall. In order to confirm the possible negative effects of environmental changes after typhoon on *C. polykrikoides*, we performed a microcosm experiment under lower salinity and higher nutrient conditions, compared to natural levels after typhoon event in the southern KCWs. The control group exhibited no suppression of *C. polykrikoides* growth, even in the presence of low salinity. The specific growth rate of *C. polykrikoides* in the control group was 0.27 day^{-1} at a water temperature of $22 \text{ }^\circ\text{C}$ and a salinity of 26, similar to our previous study (Lim et al. 2019). Optimal growth of *C. polykrikoides* in Northeast Asia occurs at a water temperature of 22 to $27 \text{ }^\circ\text{C}$ and a salinity greater than 20 (Kim et al. 2004; Lim et al. 2019, 2021c). The salinity in the surface layer may decrease by 5 or more after passage of a typhoon, but salinity generally stabilizes to the background level within 3 days (Tsuchiya et al. 2014). Actually, a significant decline in salinity of the KCWs occurred after the passage of three recent typhoons, Typhoon Talim in 2017, Typhoon Soulik in 2018, and Typhoon Tapah in 2019 (Kang et al. 2020; Son et al. 2020; Lim et al. 2021b). These salinity shocks apparently did not greatly influence the growth of *C. polykrikoides*. Therefore, even though the passage of a typhoon can lead to a sudden decline in salinity, salinity ranges exceeding 26 are not significant for the growth of *C. polykrikoides* in the southern KCWs.

Our microcosm experiments indicated that diatom abundance was high when dinoflagellate abundance was low, and vice versa. In particular, the abundance of diatoms in the Geoje group increased the fastest and to the highest level, and this was accompanied by a drastic decline in the abundance of *C. polykrikoides*. Several previous studies demonstrated an allelopathic effect of diatoms on growth of some dinoflagellates (Nagasoe et al. 2006; Yamasaki et al. 2010). Lim et al. (2014) examined the effects of competing

diatoms on the dynamics of *C. polykrikoides* and found that the three tested diatoms (*Chaetoceros danicus*, *Skeletonema costatum*, and *Thalassiosira decipiens*) negatively affected the growth and swimming speed of *C. polykrikoides* due to physical contact and chemical stress once the abundance of the tested diatoms exceeded a critical level. In addition, they observed morphological inflation and decomposition of some *C. polykrikoides* cells that were co-cultured with *C. danicus*. We performed a multivariate RDA to characterize the relationships of biotic and abiotic factors with the decline of *C. polykrikoides* in our microcosm experiments (Fig. 6). These results indicated that *C. polykrikoides* had positive correlations with nitrate + nitrite and phosphorus, and negative correlations with the diatom *Chaetoceros* spp. On the other hand, the most dominant diatom—*Skeletonema* spp.—had a significant positive correlation with DO, but not with *C. polykrikoides*. There were also differences in the characteristics of the diatoms in the different treatment groups; there were only two diatom species in the Geoje and Goheung groups (*Chaetoceros* spp. and *Skeletonema* spp.), but the Tongyeong group exhibited multiple diatom species. Among these treatment groups, the sharpest decrease of *C. polykrikoides* abundance was in the Geoje group; during this period (days 3–7), the abundance of *Chaetoceros* spp. was significantly higher in the Geoje group than in the Tongyeong group ($p < 0.05$, chi-square = 8.696, Kruskal–Wallis test, Supplementary Tables 2 and 3). This suggests that the higher abundance of *Chaetoceros* spp. may have been responsible for the sharp decline of *C.*

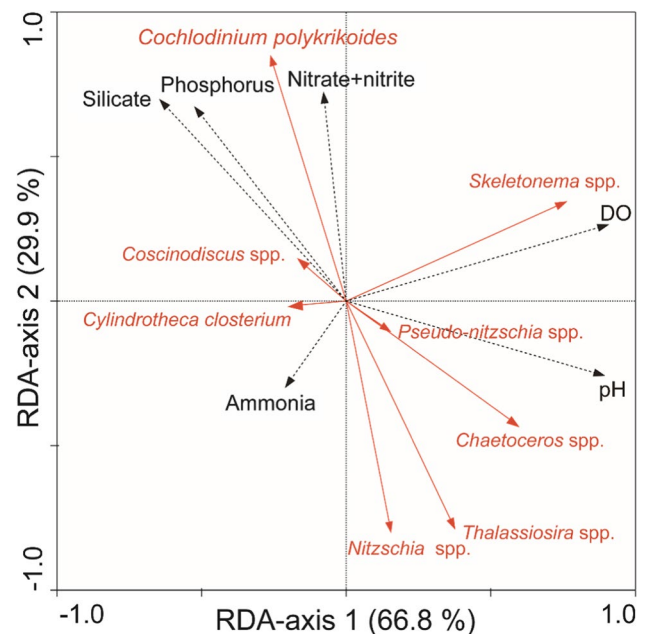


Fig. 6 Redundancy analysis of the relationship between environmental variables (black dashed arrows) and population dynamics of phytoplankton (red arrows) in the treatment groups

polykrikoides. However, the abundance of *C. polykrikoides* declined after diatoms flourished in the Geoje group and the Tongyeong group. This inhibitory effect in both groups may be because the diatom abundance simply exceeded a critical threshold, as proposed by Lim et al. (2014). These findings suggest that the proliferation of sediment-based diatom resting stage cells, in particular *Chaetoceros* spp., negatively affected the growth *C. polykrikoides*, similar to the effect of water-based vegetative diatom cells.

Changes in bacterial communities associated with phytoplankton responses

Historical and our experimental evidence confirmed our first hypothesis that the suspension and proliferation of sediment-based diatoms inhibit the growth of *C. polykrikoides*. Furthermore, during this change, we also characterized changes in the bacterial communities. On the first day when *C. polykrikoides* was dominant, Rhodobacterales were predominant (> 50%) in all treatment groups. Most bacteria in this order have a complete vitamin B12 synthesis pathway (Sañudo-Wilhelmy et al. 2014). According to Tang et al. (2010), most dinoflagellates responsible for harmful algal blooms (HABs), including *C. polykrikoides*, are vitamin B12 auxotrophs. Park et al. (2015) demonstrated that the portions of Rhodobacterales increased during *C. polykrikoides* blooms at multiple regions in southern KCWs. In addition, Cui et al. (2020) suggested that the increased abundance of Rhodobacterales could be causally related to the initiation of *C. polykrikoides* blooms because these bacteria can supply necessary nutrients to this species. The present study showed that the proportion of Rhodobacterales and the abundance of *C. polykrikoides* decreased together after day 4 (Figs. 2 and 4). In particular, the proportion of Rhodobacterales in the Geoje group decreased to 18.5%, significantly lower than in the Goheung and Tongyeong groups (> 40%) at that time. The bacterial community of the Geoje group on day 4 clustered with that of the Goheung group on day 7 (Fig. 4). Given the function of this bacterial group, this may be related to the rapid decline of *C. polykrikoides* in the Geoje group rather than the other groups. On the other hand, the similar decline of this bacterial order in all groups also supports the presence of a positive interaction between *C. polykrikoides* and Rhodobacterales. After a decline in the proportion of Rhodobacterales, there were increases in the bacterial orders Flavobacteriales and Caulobacteriales. The Flavobacteriales are well known for their ability to metabolize high molecular weight substances, including phytoplankton-derived detritus, using polymer-degrading enzymes (Teeling et al. 2012). Similarly, Caulobacteriales can decompose cellulose, and the subset of Caulobacter is exclusive to aquatic and sediment or soil environments (Verastegui et al. 2014; Wilhelm 2018). Because the increase in these bacterial

orders coincided with a decrease of *C. polykrikoides* and an explosive increase of sediment-derived diatoms, we believe this change in bacterial community composition was closely related to phytoplankton succession. In addition, based on previous studies, it has been reported that strains belonging to various bacterial genera, such as *Bacillus*, *Micrococcus*, *Alteromonas*, and *Pseudoalteromonas*, have an algicidal effect on *C. polykrikoides* (Kim et al., 2008; Oh et al., 2011). However, these bacterial genera did not appear or were significantly lower in our microcosm results, suggesting that possibility of an algicidal effect on *C. polykrikoides* population may be relatively low.

The predominately heterotrophic bacterial phylum Verrucomicrobia has carbohydrate-degrading metabolism and a widespread distribution throughout the marine water column (Bano and Hollibaugh 2002; Zaikova et al. 2010) and sediment (Urakawa et al. 1999). Studies of the global distribution of Verrucomicrobia by Freitas et al. (2012) reported that this bacterial group constituted 2.0% of the total bacterial community in the water column and 1.4% in the sediment based on whole PCR libraries. Among the identified subdivisions of Verrucomicrobia in their results, Opitutales and Verrucomicrobiales were dominant, with high proportions in the water column (73%) and sediments (85%). These subdivisions also had different overall composition in the water column and sediment; Opitutales were significantly more common in the water column (especially in the euphotic zone), whereas Verrucomicrobiales were more common in the sediment. In the present study, we found a high proportion of Opitutales at the beginning experimental period (Fig. 4), in agreement with a previous study which reported that the bacterial class Opitutae accounted for about 10% of the bacterial community during a *C. polykrikoides* bloom (Park et al. 2015). On the other hand, we found a high proportion of Verrucomicrobiales at the end of experimental period, when sediment-derived diatoms declined (Fig. 4), in contrast to the results of these previous field observations (Park et al. 2015). At the end our experiments, Sphingobacteriales, which is known to be abundant in the surface layer of sediment (Sørensen et al. 2007), was abundant only in the Geoje and Goheung groups (Fig. 4). Our previous microcosm study (Lim et al. 2021a) investigated changes in pelagic planktonic communities, including phytoplankton and bacteria, and identified an increased proportion of the SAR11 clade of bacteria as a result of the decline of diatoms. Another study also reported an increase in the proportion of the SAR11 clade at the termination of the *C. polykrikoides* blooming period (Park et al. 2015), indicating an association between the decline of pelagic phytoplankton and this clade of bacteria. However, the results of the present study differed from these previous studies, in that different bacterial communities were dominant; we found that Caulobacteriales dominated at the decline of *C.*

polykrikoides, and sediment-related bacterial communities (including Verrucomicrobiales and Sphingobacteriales) dominated at the end of experiment. These findings suggest that bacterial communities changed in response to the introduction of diatoms from the sediment during the termination of a *C. polykrikoides* blooming period. To confirm these changes, additional field research should determine whether sediment-derived bacteria dominate after the end of a *C. polykrikoides* blooming period and the passage of a typhoon.

Conclusion

Blooms of *C. polykrikoides* in Korea mainly occur during summer and they greatly cause fish mortality in fish farm. Typhoons also occur during the summer in KCWs. Although these typhoons cause many environmental changes, few studies have examined their effect on the suspension of sediment-based diatoms on blooms of *C. polykrikoides*. We performed microcosm experiments to determine the relationships of the abundance of *C. polykrikoides*, diatoms, and bacterial community composition. Our results suggest that the proliferation of sediment-based diatoms negatively affected *C. polykrikoides*, and this was accompanied by changes in the bacterial community into a sediment-specific community structure. Our analysis of historical records of red tides and the aquatic biota in the western KCWs indicated similar relationships. Our previous study examined the “fast effect” of typhoons, in which the strong physical energy leads to immediate termination of *C. polykrikoides* blooms (Lim et al. 2021b). The present study indicated that typhoons also had a “slow effect,” in which *C. polykrikoides* blooms ended due to increased abundances of sediment-based diatoms. Together, these studies suggest that the passage of typhoon has a negative effect on *C. polykrikoides* blooms. The intensity and frequency of typhoons are expected to increase in the future due to global warming and climate change (Elsner et al. 2008). Therefore, our studies suggest that the increasing strength and frequency of typhoons may lead to reduced damage from red tides caused by *C. polykrikoides* in the southern KCWs.

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Data availability The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation, to any qualified researcher.

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