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Phytoplankton functional groups as indicators of environmental changes in weir and non-weir sections of the lower Nakdong River, Republic of Korea

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ABSTRACT

The Nakdong River underwent water impoundment after eight weirs were constructed as part of South Korea's Four Major River Restoration Project from 2009 to 2012. In this study, we aimed to confirm whether the assemblage of phytoplankton based on phytoplankton functional groups (PFGs), could indicate environmental changes in the weir section (WS) and non-weir section (NWS) of the lower Nakdong River after the construction of the weir. Thus, we examined the relationships between PFGs and gradients in environmental drivers, such as physicochemical, meteorological, and hydrological variables. Environmental gradients were observed between the WS and NWS in dissolved oxygen (DO), electric conductivity (EC), biochemical oxygen demand (BOD), chemical oxygen demand (COD), total nitrogen (TN), total phosphorus (TP), dissolved total nitrogen (DTN), dissolved total phosphorus (DTP), ammonia nitrogen (NH_3–N), nitrate nitrogen (NO_3–N), and phosphorus (PO_4–P), which were relatively higher in the WS. Seventeen PFGs were identified (A, B, C, D, E, F, G, H1, J, L_M, L_O, MP, P, T, W1, X1, and X2).

Additionally, the L_M and P groups, preferring an enriched lentic system more than other groups, were found to be the dominant PFGs that led the succession of assemblages. Traditional nutrients (N, P) and organic pollutants (BOD, COD) primarily affected the autochthonous growth of the most dominant PFGs in the WS as HRT (hydraulic retention time) increased. Furthermore, the hydrological variables associated with meteorological conditions have a synergistic effect on the composition of the major PFGs and chemical and physical variables in the WS. In other words, the WS may be a new source of inoculum that primarily determines the occurrence and maintenance of phytoplankton in the immediate downstream region (NWS). In particular, group L_M (mainly potentially toxic *Microcystis*) developing in the upper weir impoundment is transported downstream, resulting in a high inoculation effect on further growth in the NWS during the summer monsoon season.

1. Introduction

Freshwater ecosystems provide valuable benefits such as flood control, water resource supply, waste purification, recreation, and habitat for living organisms [1]. Many rivers have been altered by anthropogenic environmental change to meet social and ecological

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demands despite their enormous value as freshwater ecosystems [2]. The decreased natural flow caused by anthropogenic impoundment (e.g., weirs, dams) can deteriorate water quality and adversely affect the ecological processes in rivers [3,4].

Phytoplankton have specific physiological and morphological characteristics that allow it to grow and adapt to different environmental conditions [5]. Therefore, phytoplankton species could be used as an indicator of water environment change. Reynolds [6] proposed the concept of phytoplankton functional groups (PFGs) based on environmental tolerance and sensitivity in a given habitat. PFGs have been widely used as biological indicators to assess water ecology conditions [7–12]. Due to climate change and environmental gradients of the water body in each local or regional habitat, PFGs compositions change significantly, which accurately represents the state of environmental change [12,13]. This indicates that the PFGs that respond directly or indirectly to environmental variables are advantageous for interpreting phytoplankton communities and the state of aquatic ecology. In South Korea, from 2009 to 2012, 16 new weirs were constructed in four rivers (Han, Nakdong, Geum, and Youngsan) as part of the Four Major River Restoration Project. The installation of the weirs has altered environmental gradients due to the decreased water flow caused by water impoundment. The construction of eight weirs on the Nakdong River has caused significant environmental changes, including the acceleration of eutrophication and the accumulation of pollutants [14–16].

The hydrological regime can affect different physicochemical variables, and simultaneously, combinations of these drive the distribution and community structure of potamoplankton in large rivers [17,18]. The composition of phytoplankton assemblages is primarily determined by the combined effects of multiple environmental variables, including physicochemical, hydrological, and meteorological regimes [19,20]. This is primarily attributable to the various responses of species to numerous environmental factors. PFGs are based on niche preferences in relation to their component species ecological and physiological characteristics in a given habitat environment [7,21]. Anthropogenic influences, such as river water impoundment, significantly alter hydrological conditions (e.g., hydraulic retention time) in natural rivers, which can serve as a transitional step in the development of a lotic into a lentic environment [22]. In the upper water impounding section, depending on meteorological conditions, water discharge can transport already proliferating phytoplankton cells downstream, especially during the warm rainy season [23,24]. First noted that artificial water impoundment forms a transitional environment between the existing lotic system and the lentic system in the natural river section, which may result in distinct changes to the phytoplankton assemblage.

In this study, we hypothesized that: i) artificial weir construction will induce an environmental change while generating a lotic to lentic transition in natural rivers, which can lead to distinct differences in environmental characteristics between the weir section (WS) and non-weir sections (NWS) within a given river system; ii) such different unique environmental conditions will be the primary cause of the formation of the differentiated structure of the phytoplankton assemblage in the two sections. although the phytoplankton assemblage composition in the downstream NWS may be influenced directly or indirectly by the upstream WS; iii) PFGs can indicate

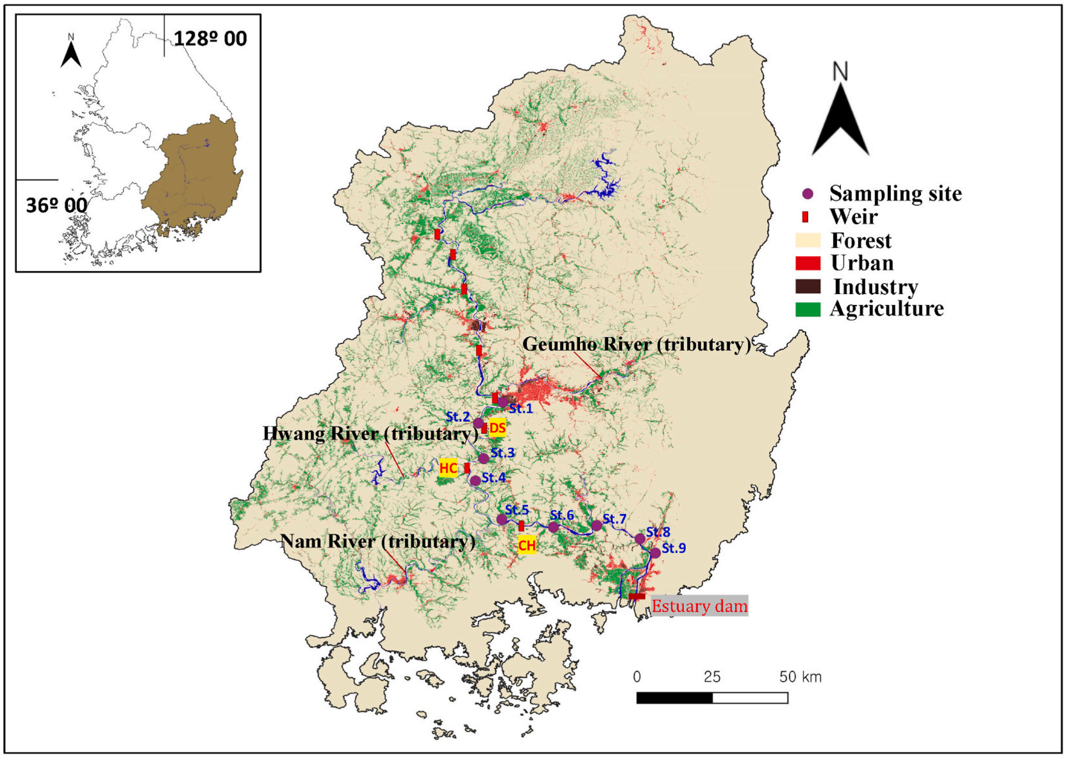

Fig. 1. Map showing monitoring sites in weir and non-weir sections of Nakdong River Basin. Weir section (blue): St.1 Hwawon (HW), St. 2 Goryeong (GR), St. 3 Daeam (DA), St. 4 Hapcheon (HC), St. 5 Namji (NJ). Non-weir section (red): St.6 Buk-myeon (BM), St.7 Samnangjin (SNJ), St.8 Mulgeum (MG), St.9 Geumgok (GG). Weirs: DS (Dalseong), HC (Hapcheon-Changnyeong), CH (Changnyeong-Haman).

the restructuring of phytoplankton assemblages in specific river sections that maintain unique environmental conditions after the construction of weirs. In the present study, we aimed to determine whether the PFG-based phytoplankton assemblage demonstrates spatiotemporal reactivity in response to environmental changes in the WS and NWS of the lower Nakdong River, and to assess its potential as a biological indicator in these river sections.

2. Materials and methods

2.1. Sampling sites

The Nakdong River is the longest river (ca. 525 km) in South Korea, with a total drainage area of approximately 23,690 km^2 [25]. Large-scale industrial complexes and the metropolitan cities of Daegu and Busan are located in the river's basin around its middle and lower reaches [26]. The average annual precipitation in the Nakdong River basin over the past decade (2010–2019) is greater than 1200 mm (www.me.go.kr), and 54 % of total precipitation falls between July and September [26]. In 2012, eight weirs were built on the Nakdong River. Large-scale sediment dredging has been conducted extensively during the construction of the weirs, and the hydrological characteristics of the river have been altered by weir barriers, which may impact the biological communities [16]. We investigated nine sites, including Hwawon (HW: St.1), Goryeong (GR: St.2), Daeam (DA: St.3), Hapcheon (HC: St.4), Namji (NJ: St.5), Buk-myeon (BM: St.6), Samnangjin (SNJ: St.7), Mulgeum (MG: St.8) and Geumgok (GG: St.9) in the Nakdong River (Fig. 1). Sites, sites St.1–St.5 and St.6–St.9 are located in the WS and NWS, respectively (Fig. 1; Table 1). Sampling of these nine sites was conducted weekly from May 2018 through November 2020.

2.2. Sampling and analysis of water quality

Field water quality parameters (water temperature, pH, dissolved oxygen, and electric conductivity) were measured using a multiparameter instrument (Horiba U-50, HORIBA Ltd., Japan). General parameters of water quality, such as biochemical oxygen demand (BOD_5), chemical oxygen demand (COD_{Mn}), total nitrogen (TN), nitrate (NO_3–N), ammonia (NH_3–N), total phosphorus (TP), phosphate (PO_4–P), suspended solids (SS), and Chlorophyll-a (Chl-a), were measured according to South Korean standard methods for water pollutant testing [16]. TN and TP were analyzed using an Integral Futura Autoanalyzer (Alliance Instruments, Frépillon, France). NO_3–N was examined by ion chromatography (850 Professional IC; Metrohm, Herisau, Switzerland). NH_3–N and PO_4–P were analyzed with an ion analyzer (Smartchem 140, Alliance Instruments, Frépillon, France), Chl-a was assessed using U/V visible spectrometry (UV–1900I; Shimadzu, Japan). HRT (hydraulic retention time) was calculated based on discharge rate and water biovolume provided from K-water (http://kwater.or.kr). Automated synoptic observing system data from the Korea Meteorological Administration Open MET Data Portal (http://data.kma.go.kr) were used for precipitation and water discharge. For precipitation, 7-day cumulative data based on the date of phytoplankton collection were utilized, whereas, for water discharge, data corresponding to the date of field sample collection were utilized. For cluster analysis, specific diversity index (H') [27], species evenness index (J') [28], species richness index (RI) [29], and dominance index (DI) [30] were calculated.

2.3. Sampling and analysis of the phytoplankton assemblage

Phytoplankton was sampled at a depth of 0.3–0.5 m at each site. Qualitative and quantitative phytoplankton samples were collected using a plankton net with a 30 μm mesh size and a sterilized 1 L plastic bottle and fixed with formaldehyde (2 % v/v) in situ. Phytoplankton species were identified and enumerated to the species level or the genus level using a light microscope (Axio Imager M2, Carl Zeiss Inc., Germany) under 200 × –1000 × magnification [31–34], and were counted under 200 × using a Sedgwick Rafter counting chamber. The phytoplankton biovolume was calculated using the formula for geometric shapes proposed by Hillebrand et al. [35]. Only phytoplankton species with relative abundance ≥5 % in at least one sample were classified into the dominant functional groups [6,36,37] (Table S4).

Table 1
Location of sampling points.

No.	Sampling site	Longitude	Latitude
St. 1	Hwawon (HW)	128.477503	35.808539
St. 2	Goryeong (GR)	128.389678	35.750056
St. 3	Daeam (DA)	128.391647	35.622475
St. 4	Hapcheon (HC)	128.362250	35.525186
St. 5	Namji (NJ)	128.473664	35.402222
St. 6	Buk-myeon (BM)	128.643111	35.373917
St. 7	Samnangjin (SRJ)	128.799319	35.363094
St. 8	Mulgeum (MG)	128.972189	35.315297
St. 9	Geumgok (GG)	129.010808	35.264217

2.4. GIS (geographical information system) mapping

The array of data types provided by Korea's Ministry of Environment was used to determine land use along the Nakdong River watershed, and the land use map in Fig. 1 was constructed using the buffering function in Arc GIS 9.3 software [16] (ESRI, Redlands, CA, USA). The proportional symbols in each taxonomic group's longitudinal distributions of water discharge and biovolume were represented using QGIS software (3.30.x' s-Hertogenbosch, Netherlands).

2.5. Statistical analysis

Multivariate analysis of variance tests were conducted to compare physicochemical, hydrological, and meteorological variables and assemblage metrics between river sections (weir and non-weir), years (2018, 2019, and 2020), and seasons (spring, summer, and autumn) using SPSS software version 16 (IBM, Armonk, NY). Correlations between environmental factors and phytoplankton taxonomic groups were evaluated based on Pearson's correlation coefficient calculated using the same version of SPSS software. The influence of environmental variables on PFGs was analyzed by redundancy analysis (RDA) using CANOCO 5.0 software. Based on the detrended correspondence analysis, the gradient length was less than three SD units. Thus, the RDA ordination technique was applied to analyze correlations between PFGs and environmental variables [38]. Finally, environmental variables that had a variance inflation factor <20 for eliminating multicollinearity were used to explain the variation of PFGs in the WS and NWS. Only phytoplankton species with relative abundance ≥ 5 % in at least one sample were used for the correlations between PFG distribution and environmental variables in RDA.

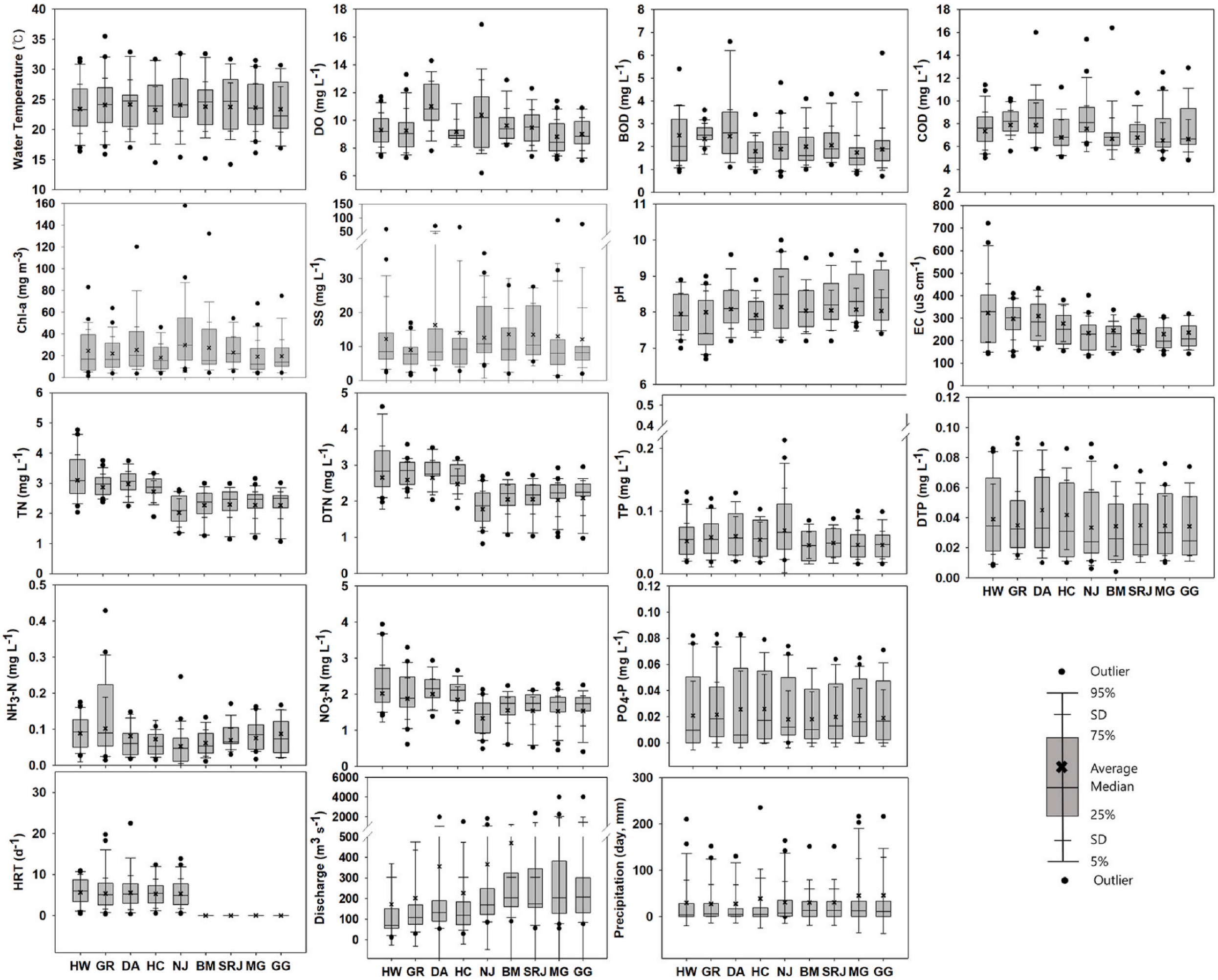

Fig. 2. Box plots showing seasonal and spatial variations in weir and non-weir sections of Nakdong River during period of study. Weir section: Hwawon (HW), Goryeong (GR), Daeam (DA), Hapcheon (HC), Namji (NJ). Non-weir section: Buk-myeon (BM), Samrangjin (SRJ), Mulgeum (MG), Geumgok (GG).

Table 2
Results of multivariate analysis of variance on environmental assemblage metrics measured in all sections of Nakdong River from 2018 to 2020. WT: water temperature, DO: dissolved oxygen, SS: suspended solids, pH: potential hydrogen, EC: electrical conductivity, BOD_5: biochemical oxygen demand, COD_{Mn}: chemical oxygen demand, TN: total nitrogen, DTN: dissolved total nitrogen, TP: total phosphorus, DTP: dissolved total phosphorus, NH_3–N: ammonia nitrate, NO_3–N: nitrate nitrogen, PO_4–P: phosphate phosphorus, Precipitation; 7 day cumulative precipitation, Discharge: water discharge, HRT: hydraulic retention time, Chl. *a*: chlorophyll *a*.

Variables	River section (Weir + Non-weir)		Year		Season		Year × Season		River section × Year		River section × Season		River section × Year × Season	
	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*
WT (°C)	0.539	0.827	6.611	**0.001**	285.977	**< 0.001**	3.542	**0.007**	0.129	1.000	0.295	0.997	0.104	1.000
DO (mg L^{-1})	4.181	**< 0.001**	3.091	**0.046**	9.425	**< 0.001**	2.673	**0.031**	1.622	0.059	0.680	0.815	0.716	0.876
SS	0.436	0.899	0.371	0.690	15.126	**< 0.001**	2.657	**0.032**	0.214	1.000	0.185	1.000	0.288	1.000
pH	0.995	0.439	6.274	**0.002**	31.663	**< 0.001**	20.030	**< 0.001**	2.925	**< 0.001**	0.771	0.719	0.506	0.990
EC (μs cm^{-1})	11.956	**< 0.001**	8.889	**< 0.001**	99.150	**< 0.001**	13.104	**< 0.001**	0.285	0.997	0.443	0.970	0.703	0.889
BOD_5 (mg L^{-1})	6.642	**< 0.001**	0.895	0.409	34.051	**< 0.001**	3.101	**0.015**	1.611	0.062	0.707	0.788	0.526	0.986
COD_{Mn} (mg L^{-1})	7.363	**< 0.001**	12.863	**< 0.001**	46.648	**< 0.001**	3.013	**0.018**	0.995	0.461	0.692	0.803	0.504	0.990
TN (mg L^{-1})	20.822	**< 0.001**	6.509	**0.002**	31.262	**< 0.001**	1.870	0.114	0.695	0.800	0.998	0.458	0.496	0.991
DTN (mg L^{-1})	24.443	**< 0.001**	10.415	**< 0.001**	46.835	**< 0.001**	1.299	0.269	0.780	0.709	0.907	0.561	0.520	0.987
TP (mg L^{-1})	1.641	0.111	5.339	**0.005**	33.904	**< 0.001**	4.463	**< 0.001**	0.451	0.968	0.983	0.474	0.486	0.993
DTP (mg L^{-1})	1.312	0.235	2.267	0.105	47.485	**< 0.001**	7.500	**< 0.001**	0.252	0.999	0.431	0.974	0.188	1.000
NH_3–N (mg L^{-1})	5.099	**< 0.001**	1.219	0.296	9.436	**< 0.001**	0.950	0.435	1.391	0.141	1.417	0.129	0.887	0.647
NO_3–N (mg L^{-1})	17.366	**< 0.001**	16.904	**< 0.001**	74.690	**< 0.001**	1.772	0.133	1.192	0.270	0.882	0.591	0.863	0.685
PO_4–P (mg L^{-1})	0.592	0.785	1.180	0.308	54.327	**< 0.001**	10.178	**< 0.001**	0.201	1.000	0.380	0.987	0.198	1.000
Precipitation (mm)	0.514	0.846	1.889	0.152	5.017	**0.007**	1.167	0.325	0.106	1.000	0.106	1.000	0.194	1.000
Discharge (m^3 s^{-1})	2.184	**0.027**	1.717	0.181	6.413	**0.002**	5.142	**< 0.001**	0.374	0.988	0.364	0.989	0.292	1.000
Chl-*a* (mg m^{-3})	2.173	**0.028**	1.232	0.293	15.000	**< 0.001**	5.942	**< 0.001**	0.350	0.991	0.537	0.928	0.571	0.973
DI	2.621	**0.008**	5.344	**0.005**	23.380	**< 0.001**	36.810	**< 0.001**	1.715	**0.041**	1.315	0.182	0.698	0.893
H'	2.901	**0.004**	3.595	**0.028**	27.840	**< 0.001**	41.995	**< 0.001**	1.725	**0.039**	1.056	0.396	0.533	0.984
RI	5.313	**< 0.001**	11.402	**< 0.001**	35.925	**< 0.001**	60.136	**< 0.001**	5.075	**< 0.001**	1.155	0.301	0.485	0.993
J'	2.077	**0.037**	5.715	**0.004**	35.700	**< 0.001**	25.501	**< 0.001**	1.203	0.261	0.760	0.732	0.679	0.910

3. Results

3.1. Environmental characteristics

In the lower portion of the Nakdong River, the mean concentrations of DO, EC, BOD, COD, TN, TP, DTP, DTN, NH_3–N, NO_3–N, PO_4–P, and Chl-*a* were relatively higher in the WS than in the NWS. The precipitation and water discharge measured in the NWS were greater than those measured in the WS (7-day cumulative data prior to sampling). The mean values for water temperature, pH, and SS were the same as or comparable between the WS and NWS. Fig. 2 depicts spatial differences in longitudinal environmental gradients between the WS and NWS. Similar patterns were observed for yearly changes in environmental variables (Fig. S1).

Table 2 shows the multivariate analysis of variance results for environmental factors measured in different river sections (WS and NWS). DO, EC, BOD, COD, TN, DTN, NH_3–N, NO_3–N, water discharge, and Chl. *a* significantly differed among the river sections. Significant interannual differences occurred in water temperature, DO, pH, EC, COD, TN, TP, DTN, and NO_3–N through the three years. No significant differences were found between years and seasons for nitrogen-based nutrients and water discharge. All environmental variables investigated had significant differences between the three seasons, but no significant differences were found for most variables in the interactions between river sections- and years, river sections- and seasons, and river sections-, years- and seasons (Table 2). Significant differences were observed for DO, EC, BOD, COD, TN, DTN, NH_3–N, and NO_3–N among sites in WS, while the values of all environmental factors except NH_3–N were similar across NWS sites (Tables S1–S3).

3.2. Phytoplankton assemblage

Six hundred eighty-two taxa were identified with nine phyla, 17 classes, 45 orders, 80 families, 164 genera, 588 species, 80 varieties, and 14 forms in all river sites (WS and NWS) during the study period. These species belong to nine taxonomic groups: Chlorophyta (310 taxa), Bacillariophyta (108 taxa), Charophyta (97 taxa), Euglenophyta (91 taxa), Cyanophyta (38 taxa), and others (38 taxa) (see supplementary data for phytoplankton taxa). The concordance rate between the WS and NWS was approximately 68 % among the total observed species, showing 613 species in the WS and 528 species in the NWS. Except for species with less than 5 % biovolume in the total sample, a phytoplankton total of 86 taxa was investigated, belonging to six phyla, nine in classes, 22 orders, 30 families, 34 genera, 74 species, 11 varieties, and one form. The observed species included 34 in Bacillariophyta, 30 in Chlorophyta, nine in Cyanobacteria, and 13 in other groups (see supplementary data for phytoplankton taxa).

In the spatial taxonomic distribution, 86 species belonging to six phyla, nine classes, 22 orders, 30 families, 34 genera, 74 species, 11 varieties, and one form were identified in the WS. Additionally, 82 species were observed with a decrease of two species and two varieties, in the NWS, which belong to six phyla, nine classes, 22 orders, 30 families, 34 genera, 72 species, 9 varieties, and one form

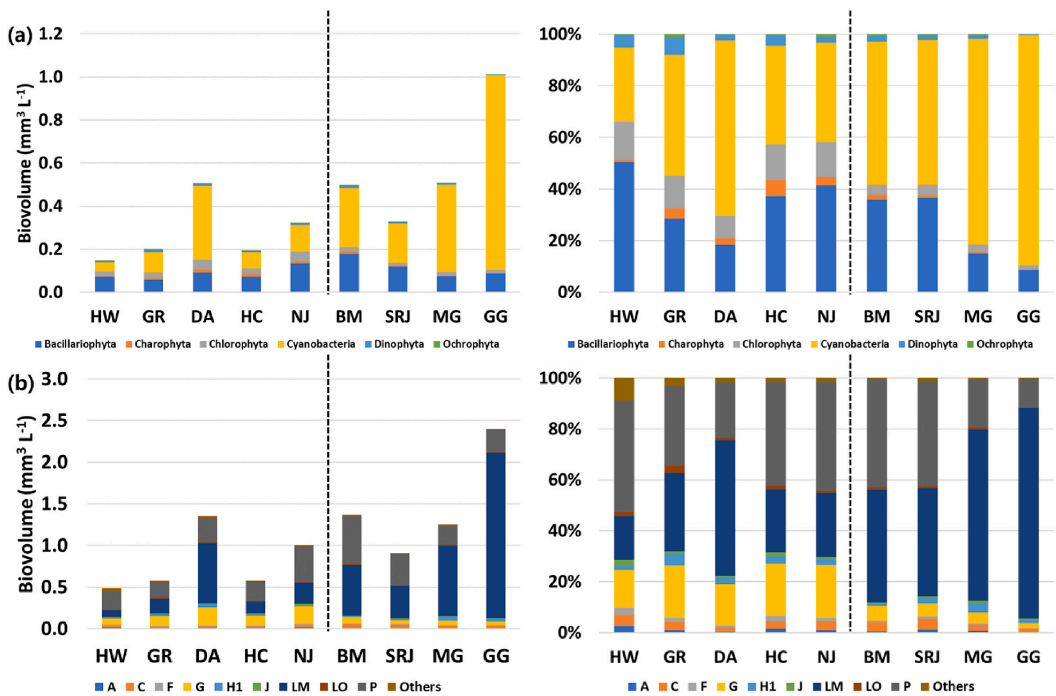

Fig. 3. Spatial variations for mean relative biovolume of (a) phytoplankton taxonomic groups and (b) phytoplankton functional groups in weir and non-weir sections of Nakdong River from 2018 to 2020. Weir section: Hwawon (HW), Goryeong (GR), Daeam (DA), Hapcheon (HC), Namji (NJ). Non-weir section: Buk-myeon (BM), Samrangjin (SRJ), Mulgeum (MG), Geumgok (GG).

(see supplementary data for phytoplankton taxa). Therefore, there was no marked difference in the number of species between the WS and the NWS based on species with more than 5 % biovolume in at least one sample. According to the PFGs criteria suggested [6,36,37], these taxa were classified into a total of 28 PFGs (A, B, C, D, E, F, G, H1, J, K, L_M, L_O, MP, N, P, Q, R, S1, S_N, T, T_C, W1, W2, W_S, X1, X2, $X_{Ph,}$ and Y), and further classified into 17 PFGs (A, B, C, D, E, F, G, H1, J, L_M, L_O, MP, P, T, W1, X1, and X2) based on the species with 5 % or more biovolume per sample. In spatial distributions, the mean total biovolumes in taxonomic groups and PFGs were relatively higher in the NWS than in the WS during the study period (Fig. 3, Figs. S3–S4). At the taxonomic level, the mean relative biovolume of cyanobacteria (WS: 45.6 ± 12.2 %, NWS: 74.4 ± 8.6 %) was relatively higher than other taxonomic groups in two sections (Fig. 3a). Furthermore, in these sections, the mean relative biovolume of cyanobacteria was higher than that of other taxonomic groups in 2018 and 2019, while there was a clear shifting of the dominant taxonomic group from Cyanobacteria to Bacillariophyta in 2020 (Fig. S3).

In the spatial distributions for PFGs, the L_M, P, G, and C 17 PFGs (among the 17 with relative biovolume ≥5 % in at least one sample) showed a marked distribution pattern with a distinct contribution rate to the total phytoplankton biovolume in two sections over the entire survey period (2018–2020) (Fig. 3b). Groups L_M and P occupied the highest relative biovolume in all sites of the WS and the NWS, and group L_M showed a higher contribution rate to the mean total biovolume in the NWS (Fig. 3b). In 2018, group L_M showed the highest contribution rate in most of the sites in both sections, and this group was more prevalent in the NWS (77.0–96.3 %) than in the WS (25.2–46.9 %) (Fig. S4). In 2019, the proportion of group L_M within the two sections showed a relative decrease, while group P started to show a clear increase. L_M group was relative biovolume in 2020 had a significantly higher contribution rate than other PFGs in the WS and NWS (WS: 38.7–77.6 %, NWS: 64.0–84.1 %) (Fig. S4).

The seasonal succession characteristics of phytoplankton in the WS and NWS are shown in Figs. 4–6. The highest values of the total mean phytoplankton biovolume were recorded in August and November throughout the study period (Fig. 4). For each taxon, the highest biovolumes for Cyanobacteria and Bacillariophyta were recorded in August and November, respectively (Fig. 5). In particular, the total phytoplankton biovolume and the cyanobacterial biovolumes increased longitudinally in proportion to the water discharge in the river sections during the monsoon season (Fig. 11). These biovolumes showed significant correlations with water discharge, unlike other taxonomic groups (Table 3). Amongst the PFGs, groups A, B, C, D, F, G, H1, J, L_M, L_O, and P showed a wide distribution by season. Among them, L_M and P showed the most distinct dominance in summer and autumn (Fig. 5).

In the WS, from 2018 to 2020, the diatom functional group P (mainly *Aulacoseira* spp., *Fragilaria* spp., and *Melosira* spp.) showed the highest peaks mainly in spring and autumn, consistent with the seasonal succession of the diatom group. These peaks have continued to increase year by year, reaching a maximum value (35.2 $mm^3\ L^{-1}$ in November) in 2020 (Table S4; Fig. 6a). We observed that seasonal variations in the functional dominant peak of the cyanobacterial group L_M (mainly *Microcystis* spp.) reached a maximum value (36.7 $mm^3\ L^{-1}$) in August 2018, and then decreased sharply (Table S4; Fig. 6a). The green algal functional group G (mainly *Carteria* sp., *Eudorina* spp., *Pandorina morum*, and *Volvox* spp.) dominated intermittently in summer (June) and autumn (September) of each year, while the functional group $L_{O,}$ mainly including Chlorococcales, and the cyanobacterial functional group J (mainly *Chroococcus* species) temporarily dominated in 2018 (May) and 2019 (May, June) (Table S4; Fig. 6a).

In the NWS, the dominant peak patterns in the diatom functional group P (mainly *Aulacoseira* spp., *Fragilaria* spp., and *Melosira* spp.) through 2018–2020 were comparable to those in the WS, with the maximum value (42.1 $mm^3\ L^{-1}$) being reached in October 2020. (Table S4; Fig. 6b). Dominant peaks in the cyanobacterial group L_M (*Microcystis* spp.) were observed in the summers of 2018–2020 (June, July, and August), with the highest peak value in August 2018 (126.2 $mm^3\ L^{-1}$) (Table S4; Fig. 6b). The diatom functional group C (mainly *Asterionella* spp., *Aulacoseira* spp., *Cyclotella meneghiniana*, and *Cyclotella ocellata*) and the filamentous cyanobacterial functional group H1 (*Anabaena* spp., *Anabaenopsis* sp., and *Aphanizomenon flos-aquae*) appeared temporarily in 2018 (October) and 2020 (June), respectively, the dominance of these groups was not observed in the WS. In addition, groups G and J, which included the same species found in the WS, alternately dominated in 2018 and 2019 (Table S4; Fig. 6b).

Based on single biovolume peaks, the order of the dominant PFGs for each year in the WS was 2018 (P, L_M, G, L_O) → 2019 (L_M, P, G, J) → 2020 (P, G), whereas, in the NWS, the order was 2018 (P, L_M, G, C) → 2019 (L_M, P, G, J, L_O) → 2020 (L_M, P, H1). This suggests that WS and NWS are transitioning to a pattern in which a small number of specific PFGs dominate each year. In the WS and NWS, the dominant index was relatively higher at non-weir sites, while the diversity, richness, and evenness indices decreased from WS to NWS. (Table S1; Fig. 7). In the changes in the annual assemblage metric in the WS and NWS, the dominance index continued to increase on average from 2018 to 2020, while the diversity, richness, and evenness indices showed the opposite pattern (Fig. 8). In particular, the values of the dominance index were relatively high in autumn, whereas other indices were low (Fig. 8a and b). There were significant differences in all assemblage metrics through the interactions between years and seasons (Table 2).

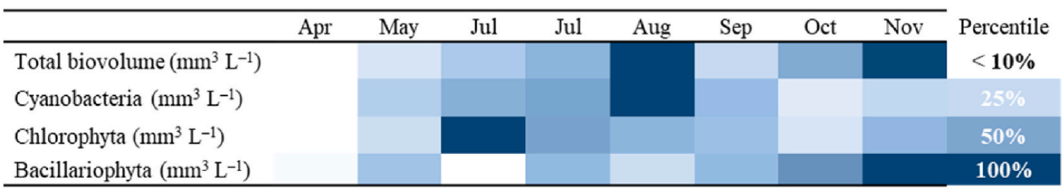

Fig. 4. Heatmap showing seasonal variations of phytoplankton taxonomic groups in river sections (weir and non-weir) during entire study period (2018–2020).

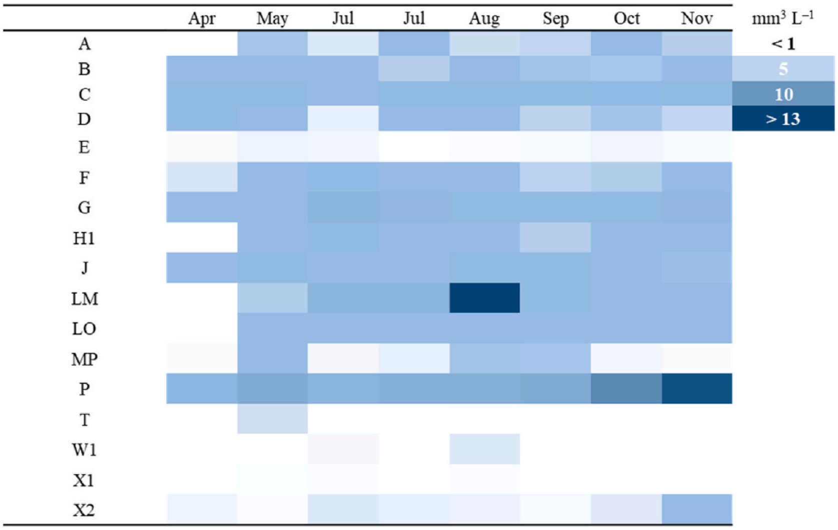

Fig. 5. Heatmap showing seasonal variations of phytoplankton functional groups in river sections (weir and non-weir) during entire study period (2018–2020).

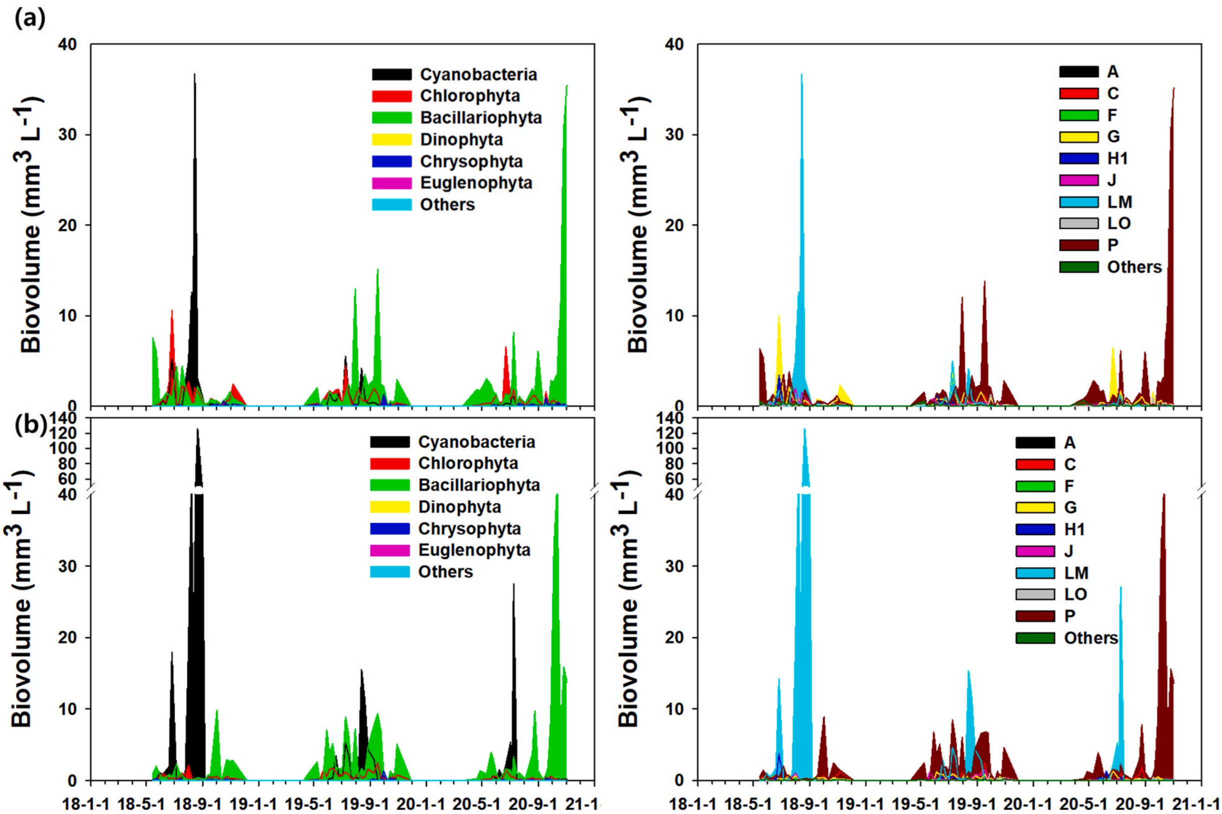

Fig. 6. Seasonal variations of relative biovolume of phytoplankton taxonomic groups and functional groups in weir (a) and non-weir (b) sections of Nakdong River (2018–2020).

3.3. Correlation between phytoplankton functional groups and environmental variables

In each WS and NWS, RDA ordinations revealed a correlation between the PFGs and the environmental factors distributed by year, season, and site (Figs. 9 and 10). In the WS, pseudo-canonical correlations between PFGs and environmental variables on the first and

Table 3
Pearson correlations for total phytoplankton biovolume and biovolume of Cyanobacteria, Chlorophyta, and Bacillariophyta related to water discharge in weir and non-weir sections during monsoon season (June–September) through the whole study period.

	Total biovolume ($mm^3 L^{-1}$)	Cyanobacteria ($mm^3 L^{-1}$)	Chlorophyta ($mm^3 L^{-1}$)	Bacillariophyta ($mm^3 L^{-1}$)
Discharge ($m^3 s^{-1}$)	0.762 ($p < 0.05$)	0.756 ($p < 0.05$)	−0.480	0.192

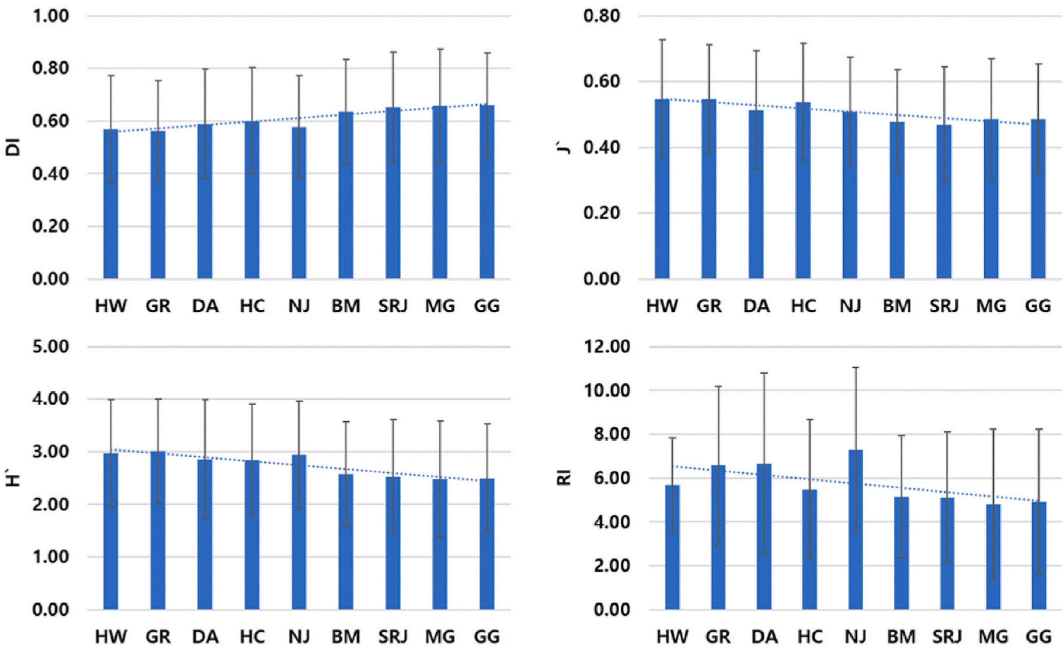

Fig. 7. Spatial variations of assemblage metrics in weir and non-weir sections of Nakdong River from 2018 to 2020. Weir section: Hwawon (HW), Goryeong (GR), Daeam (DA), Hapcheon (HC), Namji (NJ). Non-weir section: Buk-myeon (BM), Samrangjin (SRJ), Mulgeum (MG), Geumgok (GG). DI: dominance index, H': diversity index, RI: richness index, J': evenness index.

the second axis respectively explained 0.720 and 0.530 of the total variation in the phytoplankton assemblage (Table S5). The RDA results in the WS revealed clear seasonality in the fluctuations of environmental factors and PFGs throughout the entire survey period, whereas the RDA ordination did not reveal year- and site-specific distribution patterns (Fig. 9). Additionally, RDA axis 1 clearly distinguished summer sampling sites from other seasons (spring, autumn). Precipitation and discharge were associated with the summer and fall samples (Fig. 9b). During the summer, WS samples were characterized by relatively high water temperature, pH, BOD, COD, EC, and HRT, and these factors correlated with groups L_M, J, G, H1, and F (Fig. 9a).

In NWS, pseudo-canonical correlations between PFGs and environmental variables on the first and second axis respectively explained 0.769 and 0.601 of the total variation in the phytoplankton assemblage (Table S6). The RDA results in the NWS were comparable to those in the WS, and seasonality significantly affected the distributions of environmental factors and PFG throughout the survey period (Fig. 10). Summer samples formed around RDA axis 1, were associated with elevated water temperature, BOD, COD, and EC, whereas summer and autumn samples were affected by relatively elevated precipitation, discharge, TN, TP, NO_3–N, and PO_4–P (Fig. 10b). Group L_M, which predominated in the summer, was positively correlated with water temperature and organic matter (BOD, COD), whereas groups B and E, which predominated in the fall, were associated with nutrients (TN, TP, NO_3–N, and PO_4–P) (Fig. 10a). The RDA results by year are displayed in Figs. S5–S7. In 2018, 2019, and 2020, the RDA results in the WS were characterized by high precipitation, water discharge, and nutrients mainly in summer and autumn, along with high water temperature, organics (BOD, COD), and HRT in summer, showing a clear seasonal distribution of environmental factors in common (Figs. S5–S7). However, different specific correlations were observed between the main PFGs and the environmental factors observed by year. In 2018, group P exhibited a positive correlation with water discharge, precipitation, SS, TP, DTP, PO_4–P, NH_3–N, and NO_3–N. The L_M, G, J, and F were positively correlated with pH, HRT, BOD, and EC (Fig. S5). The groups L_M, H1, and F were positively associated with pH, water temperature, BOD, and COD in 2019. (Fig. S6). In 2020, groups L_M, G, and H1 were positively correlated with water temperature, group P was positively correlated with BOD, and group C was positively correlated with HRT and EC (Fig. S7). In 2018, 2019, and 2020, the RDA results in NWS exhibited seasonal distribution patterns comparable to those of WS in terms of environmental factors (Figs. S8–S10). In 2018, group L_M correlated positively with pH, WT, and BOD, and group H1 correlated positively with NH_3–N. (Fig. S8). In 2019, the L_O and J groups were positively correlated with water discharge and TP, while the L_M and H1 groups were positively correlated with pH, water temperature, and BOD. Groups P, G, and C were correlated positively with COD. (Fig. S9). In 2020, groups L_M, LO, G, and J

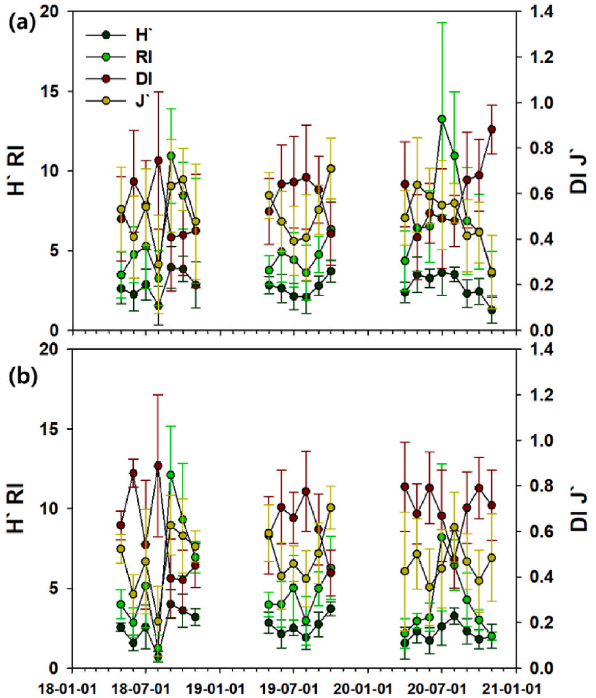

Fig. 8. Seasonal variations of assemblage metrics in weir (a) and non-weir (b) sections of Nakdong River from 2018 to 2020. DI: dominance index, H': diversity index, RI: richness index, J': evenness index.

became extinct. H1, and F were positively correlated with water temperature, BOD, and COD (Fig. S10).

In the WS and NWS, the results in RDA variation partitioning (pRDA) using the main environmental variable groups are shown in Figs. 12 and 13. In the pRDA results for WS, chemical variables (e.g., EC, BOD, COD, TN, TP, NH_3–N, NO_3–N, DTP, and PO_4–P) explained 34.3 % of the total PFG variance, while physical variables (e.g., water temperature, DO, and suspended solids) and hydrological–meteorological variables (water discharge, 7-day cumulative precipitation) accounted for 23.0 % and 11.0 % of total PFG variance, respectively (Fig. 12). The shared variation between the three groups of environmental variables was 1.9 %. The shared variation between the physical and chemical variables was 27.5 %, while shared variation was 0.3 % between the chemical and hydrological–meteorological variables and 1.9 % between the physical and hydrological–meteorological variables (Fig. 12). According to the pRDA results in the NWS, chemical variables (e.g., EC, BOD, COD, TN, TP, NH_3–N, NO_3–N, DTP, and PO_4–P) explained 60.7 % of the total variance of PFG, while physical variables (e.g., water temperature, DO, and suspended solids) and hydrological–meteorological variables (water discharge, 7-day cumulative precipitation) explained 7.6 % and 2.1 %, respectively (Fig. 13). The variance shared between the three environmental variables was 1.1 %. 25.4 % of the variation was shared between physical and chemical variables, 2.3 % was shared between chemical and hydrological–meteorological variables, and 0.8 % was shared between physical and hydrological–meteorological variables (Fig. 13).

4. Discussion

Sudden environmental changes can induce niche partitioning of organisms with different ecological needs in each habitat, which, in turn, affects the determination of the qualitative and quantitative composition of species within a community [39]. Furthermore, in natural lotic systems, weir impoundments induce hydrological alterations (e.g., increased HRT), which can affect the composition of the phytoplankton community, including potamoplankton species associated with the longitudinal water flow in natural channels. Consequently, species that prefer the lentic environment can form a new community structure. This means that artificial, especially hydrological environmental changes can form new niche differentiation while influencing the shift in the quantitative dominance of species with different ecological niches, which causes high variation in phytoplankton assemblages [40]. In this respect, artificial weir construction in the Nakdong River created a new habitat environment in impounded weir sections, which led to clear differences in the composition of phytoplankton assemblages between the WS and NWS. In the present study, we observed that weir construction can transform the existing lotic environment into lentic conditions [16] and hypothesized that PFGs can be used as biological indicators for the management of new water environments in artificially restructured river systems. We hypothesized that i) the construction of weirs would transform the Nakdong River from a lotic to a lentic system, thereby causing significant changes in the river's physicochemical characteristics, and ii) these environmental changes in the WS would result in a different phytoplankton community structure from that in the lotic system. Additionally, iii) the qualitative and quantitative compositions of specific phytoplankton assemblages based on the composition of PFGs, along with environmental changes in the WS, could also affect the NWS.

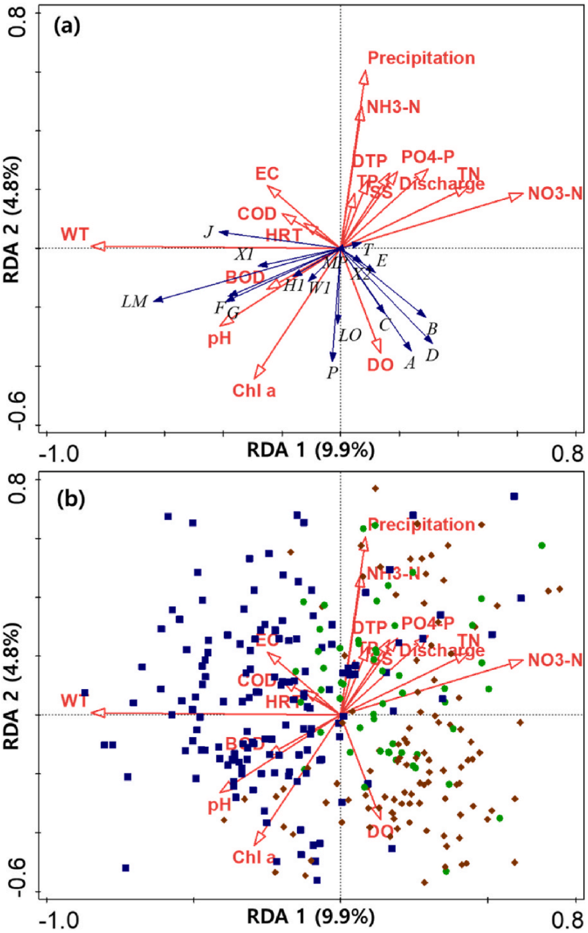

Fig. 9. Redundancy analysis (RDA) ordination diagrams (a) Association between environmental variables with dominant phytoplankton functional groups in weir section of lower Nakdong River from 2018 to 2020. Weir section: Hwawon (HW), Goryeong (GR), Daeam (DA), Hapcheon (HC), Namji (NJ). (b) Spring: circle, Summer: square, Autumn: diamond. WT: water temperature, DO: dissolved oxygen, SS: suspended solids, pH: potential hydrogen, EC: electrical conductivity, BOD_5: biochemical oxygen demand, COD_{Mn}: chemical oxygen demand, TN: total nitrogen, DTN: dissolved total nitrogen, TP: total phosphorus, DTP: dissolved total phosphorus, NH_3–N: ammonia nitrate, NO_3–N: nitrate nitrogen, PO_4–P: phosphate phosphorus, Precipitation; 7 day cumulative precipitation, Discharge: water discharge, HRT: hydraulic retention time, Chl. *a*: chlorophyll *a*.

After the construction of weirs on the Nakdong River, the main environmental change was the increase in HRT. Although there were no measured values of HRT before the weir construction, it has been reported that HRT can be increased up to eight times the natural water velocity (69 days) after weir construction, according to model-based simulation [41]. In the post-weir construction period, the average HRT for the three weirs (Dalseong, Hapcheon-Changnyeong, Changnyeong-Haman) included in the WS was measured from 7.3 to 10.5 days (maximum: 15.9–44.3 days) [42]. These HRT values exceed 7 days, which is the criterion for lentic conditions [43], showing that the Nakdong River is changing status from lotic to lentic after weir construction, and also supporting our first hypothesis. After weir construction, there were also marked differences in DO, EC, BOD, COD, TN, DTN, NH_3–N, NO_3–N, and discharge between the WS and NWS (Table 2). DO, nutrient, and organic matter values were higher in the WS than in the NWS (Table S1; Fig. S2). The water temperature in summer was also relatively higher in the WS (Fig. S2). These are typical environmental variations observed after river impounding, and are demonstrated by quantitative gradients of physicochemical variables between the WS and NWS, also proving our first hypothesis. Furthermore, previous studies suggest that water temperature and organic pollutants (BOD, COD) are the most significantly increased environmental variables, along with the increase in HRT after weir installation, consistent with our findings [42,44]. In connected lentic–lotic systems, seasonal and longitudinal distributions of phytoplankton assemblage composition are known to be influenced by dispersal stochasticity and environmental filtering [45].

In this study, the PFG composition in the WS and NWS showed environmental filtering, specific dispersal patterns, and environmental gradients under the influence of seasonal meteorological conditions and physicochemical variables, supporting our three hypotheses. The interruption of unidirectional flow can confine river phytoplankton introduced from upstream or tributary streams to the WS, resulting in a temporary increase in the number of species in relatively limited and closed local habitats. This was demonstrated by significant differences in alpha diversity metrics of phytoplankton between the WS and NWS. The WS contained 613 species more than the NWS, which contained 528 species (Table 2; Figs. 7 and 8). In particular, the diversity index (H') was higher during the

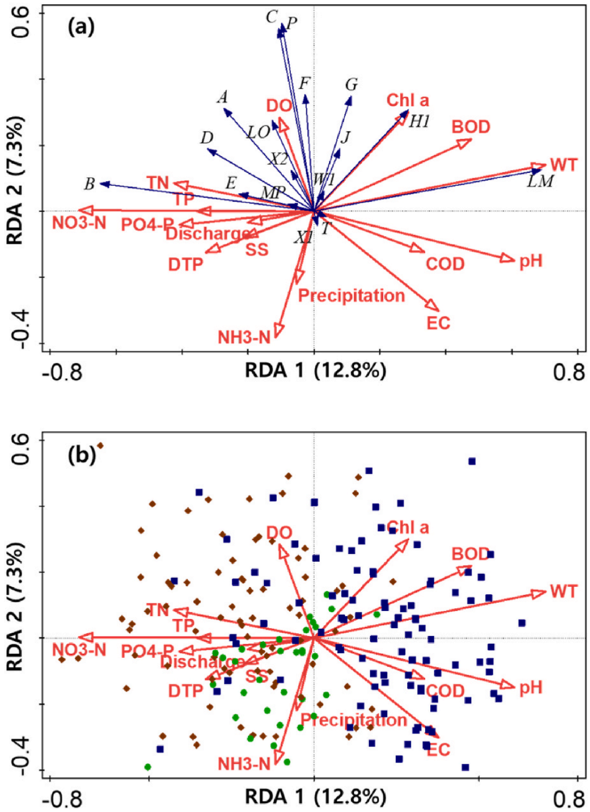

Fig. 10. Redundancy analysis (RDA) ordination diagrams (a) Association between environmental variables with dominant phytoplankton functional groups in non-weir section of lower Nakdong River (2018–2020). Non-weir section: Buk-myeon (BM), Samnangjin (SNJ), Mulgeum (MG), Geumgok (GG). (b) Spring: circle, Summer: square, Autumn: diamond. WT: water temperature, DO: dissolved oxygen, SS: suspended solids, pH: potential hydrogen, EC: electrical conductivity, BOD_5: biochemical oxygen demand, COD_{Mn}: chemical oxygen demand, TN: total nitrogen, DTN: dissolved total nitrogen, TP: total phosphorus, DTP: dissolved total phosphorus, NH_3–N: ammonia nitrate, NO_3–N: nitrate nitrogen, PO_4–P: phosphate phosphorus, Precipitation; 7 day cumulative precipitation, Discharge: water discharge, HRT: hydraulic retention time, Chl. *a*: chlorophyll *a*.

monsoon season (especially in 2020) with high precipitation and discharge, which may have been caused by temporary inflow from neighboring tributaries or floating benthic algae. However, the composition of the phytoplankton community, which consists of limnoplankton and lacustrine or fluvial phytoplankton (potamoplankton), can be reconstructed by the interaction between species classified by altered environmental variables, in particular local sections [46]. Generally, species diversity increases in natural river sections with flowing mixing conditions [47,48]. In contrast, the diversity of the species in the NWS was lower than that in the WS, indicating that the NWS is located at the downstream end of a typical river with slow flow, and also probably due to the increased sedimentation by its own water stability that caused a decrease in the number of species of potamoplankton (mainly diatoms). In other words, the species pools formed transiently in the lentic system exhibit individual differences in their quantitative biovolume through processes of adaptation to modified environments, mainly altered hydrological conditions, and interspecific competition [49,50]. Among the 613 species were identified appearing in the WS, 86 species above a biovolume of 5 %, and the remaining 527 species (86 % of total species) were excluded from the competition through the environmental filtering process in the total phytoplankton biomass, which means a rare species with a low contribution rate. In the NWS, there were 528 species, which is relatively fewer than in the WS. However, 82 species similar to those in the WS were identified as the dominant species, comprising more than 5 % of the biovolume. This can be explained by previous studies reporting that a dam of an upper impounded river has a greater diversity of species composition and that the immediate downstream causes homogenization in phytoplankton species by reducing environmental heterogeneity as a result of water discharge from the dam, which also definitively proves our second hypothesis [46,51]. Therefore, we classified PFG species that comprised more than 5 % of the total biovolume (as suggested by previous research) in two given sections (weir and non-weir) and used them as indicators of environmental change [52–54]. In this regard, the present study identified 17 PFGs (A, B, C, D, E, F, G, H1, J, L_M, L_O, MP, P, T, W1, X1, and X2) as potentially indicative of environmental variation. In the process of phytoplankton succession, L_M and P were the most dominant PFGs, while G, J, C, L_O, and H_1 were also identified as dominant PFGs. In the process of environmental filtering, dominant PFGs comprised species with explicit traits, rather than a few conventional species that quantitatively indicated human-altered environments [55]. This shows that dominant PFGs can indicate modified environmental conditions in the WS and NWS after the installation of a weir, supporting our third hypothesis. The seasonal and longitudinal distributions of these PFGs in the WS and NWS were determined by autochthonous growth and the effect of allochthonous dispersal

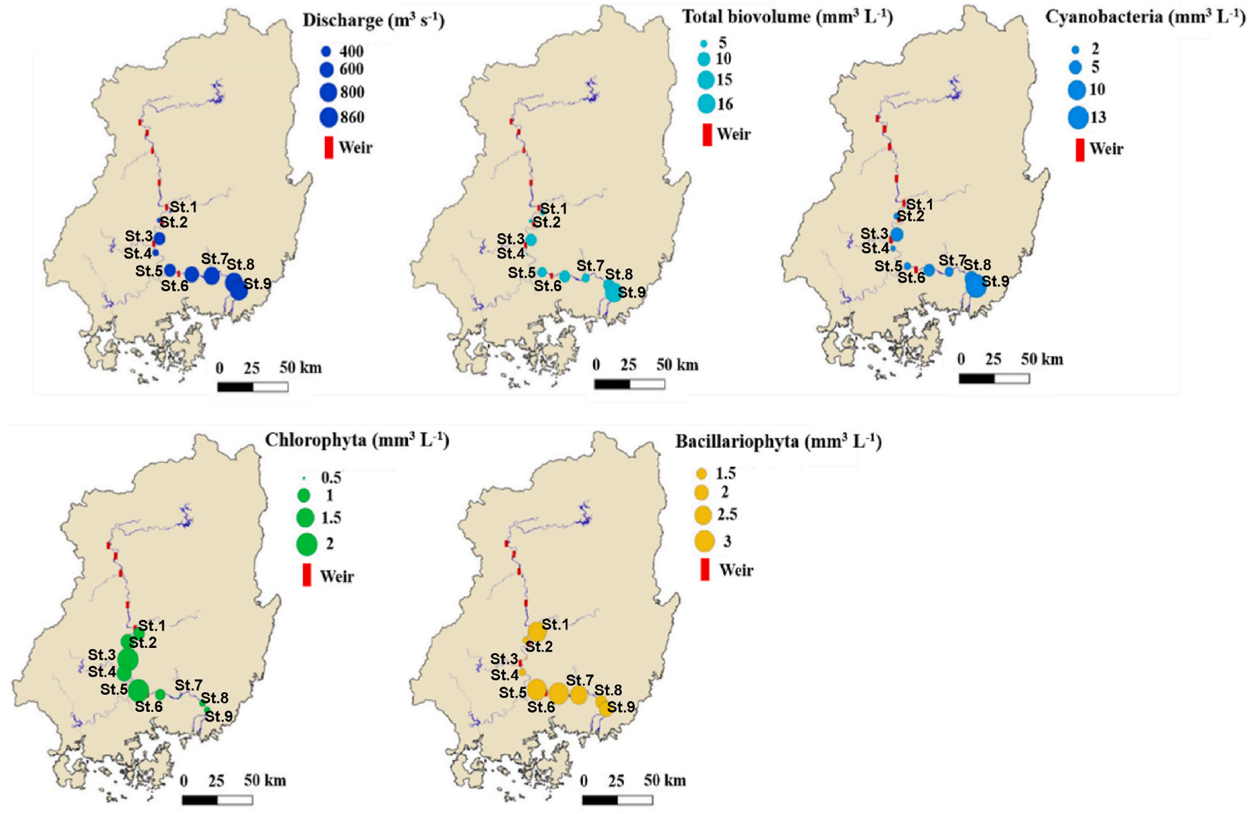

Fig. 11. Symbol proportions illustrating longitudinal distributions for water discharge ($m^3 s^{-1}$), total phytoplankton biovolume ($mm^3 L^{-1}$), Cyanobacteria biovolume ($mm^3 L^{-1}$), Chlorophyata biovolume ($mm^3 L^{-1}$) and Bacillariophyta biovolume ($mm^3 L^{-1}$) in all sections (weir and non-weir) of Nakdong River during monsoon season from 2018 to 2020. Each symbol proportion size indicates mean value at each site during Korean monsoon season (June–September 2018–2020). Weir section: St.1 Hwawon (HW), St.2 Goryeong (GR), St.3 Daeam (DA), St.4 Hapcheon (HC), St.5 Namji (NJ). Non-weir section: St.6 Buk-myeon (BM), St.7 Samnangjin (SNJ), St.8 Mulgeum (MG), St.9 Geumgok (GG).

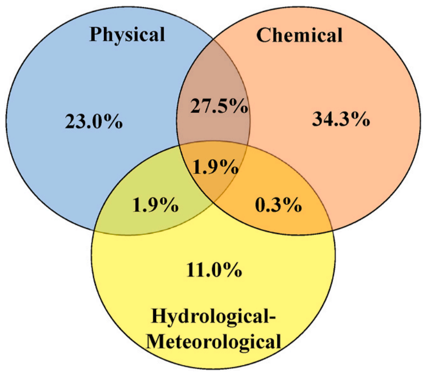

Fig. 12. Venn diagram illustrating relative fractions described by physical, chemical, and hydrological–meteorological variables according to variation partitioning of dominant phytoplankton functional groups in weir section of lower Nakdong River (2018–2020).

(transport) [49,56,57].

In the WS, HRT could be calculated based on quantitative inflow and outflow due to weirs, whereas, the exact HRT could not be derived in the NWS. However, the results of the RDA showed markedly seasonal variations in phytoplankton assemblages through the autochthonous growth response process of PFGs given meteorological, hydrological, and physicochemical variables in the WS and NWS (Figs. 9 and 10). In natural rivers, phytoplankton is destined to achieve maximum growth through cell division within a limited time (before reaching the sea), according to different ecological adaptations in the unidirectional downstream travel process [17].

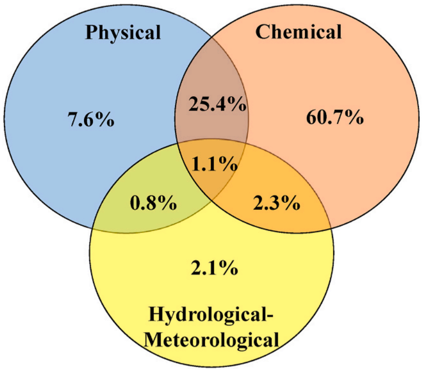

Fig. 13. Venn diagram illustrating relative fractions described by physical, chemical, and hydrological–meteorological variables according to variation partitioning of dominant phytoplankton functional groups in non-weir section of lower Nakdong River (2018–2020).

However, the impoundment of water by weir construction provides sufficient time for cell division of phytoplankton to maintain and grow, due to blocking barriers and creating new environmental conditions, leading to changes in the structure of the phytoplankton assemblage. Consequently, the identification of the adaptation and response characteristics of the main PFGs to changing environmental variables in the WS is the starting point for the management of modified river ecosystems.

In the WS, the RDA ordination plot clearly showed a clear separation between the dry summer monsoon season and the wet summer–autumn monsoon season, demonstrating the effect of seasonal environmental gradients on the structure of the variation in the phytoplankton assemblage (Fig. 9b, Figs. S5–S7). Our findings suggest that precipitation is a critical primary factor that distinguishes the seasonal effects of hydrological and physicochemical variables on the phytoplankton assemblage. Precipitation causes higher water discharge by increasing runoff discharge in river watersheds [58]. River discharge, that is, the volume of water flowing within a river channel is highly dependent on precipitation, which is clearly confirmed during the monsoon season in temperate region [59]. This means that these two variables can have similar or combined effects in determining the distribution of PFGs. The dry monsoon season samples were characterized by a significant increase in organic matter (BOD, COD) and HRT after weir installation, which was the main determinant of the dominance of groups L_M, G, J, C, and H1, along with high temperature during the non-rainy monsoon season. On the other hand, rainy monsoon season samples were associated with increased nutrients, high water discharge, and short HRT related to high precipitation. The levels of nutrients (N, P) in the WS were higher than those in the NWS and increased rapidly in proportion to precipitation during the monsoon season (Table S1, Fig. S2), which is closely related to the land use types of watershed areas around the WS. During the wet season, diffuse water pollutants from the main tributaries of the watershed enter the Nakdong River, which is associated with nutrient surface runoff and combined sewer overflows in agriculture and urban areas [16]. The Geumho River is the largest tributary of the Nakdong River, passing through Daegu Metropolitan City and industrial complex areas, and it joins at the upper reaches of the Dalseong weir, greatly contributing to the increase in nutrients in the WS (Fig. 1), which continuously maintains the prerequisite conditions for phytoplankton growth [60]. A rise in the proportion of urban and industrial land use in the surrounding watershed, as well as an increase in residence time, can exacerbate eutrophication in river-impounded areas [61]. This can result in the dominance of nutrient-tolerant PFG species that favor lentic habitats in the WS.

Groups L_M and P led the seasonal succession in the WS, whereas group G displayed transient peaks. These groups demonstrate that a eutrophic lentic environment is formed in the Nakdong River weir areas. In the spring and fall, group P (mainly *Aulacoseira*, *Fragilaria*, and *Melosira*) was more prevalent than in the summer (Fig. 9a, Figs. S5–S7). This is because it is more competitive at lower water temperatures than other dominant groups, particularly the L_M group [10]. This group's biovolume was proportional to the discharge of water and nutrients (Fig. 5, Figs. S2–S4), and the maximum biovolume correlated with increased HRT and organics when the water column was stable. This indicates that group P prefers relatively high nutrient and organic matter concentrations and is insensitive to discharge variability, allowing for wide spatial and temporal distribution. Reynolds et al. [6] and Padisák et al. [36] report that group P prefers an enriched lentic system with a stable, stagnant water column. Group P also has a high biomass when water discharge decreases rapidly [62]. This is due to the fact that low water discharge creates a more favorable turbulence (physical mixing) condition for the growth of this group [63], and it also indicates that hydrological fluctuations are a necessary driving factor for the growth of group P. In addition, group P prefers eutrophic, turbulent mixing, and short HRT (high water discharge) for growth in the lentic system, whereas group R (ruderal) strategies are tolerant of physical disturbance [5,64]. This is in agreement with our findings that the biovolume of group P increased more in proportion to annual water discharge. Group L_M was correlated with high water temperature and organics, along with increased HRT (Fig. 9a, Figs. S5–S7). Nutrient levels in the water body can further increase the surface nutrient load originating from the surrounding watershed during precipitation [65], which can further extend the magnitude, frequency of occurrence, and duration period of *Microcystis* blooms, combined with other favorable growth conditions such as high water temperature and increased HRT. Therefore, the rapid increase in the L_M group in the WS is strongly related to the environmental conditions during the dry summer–autumn monsoon season (Fig. 9a, Figs. S5–S7). Additionally, the low correlation between *Microcystis* favoring enrichment conditions and nutrients means that the nutrient concentration is already sufficient for this species growth [42] (Fig. 9b, Figs. S5–S7). This is well explained by the results that TP concentrations showed levels of eutrophication (>0.035 mg

L^{-1}) [66] in each section (Table S1). Generally, the concentration of nutrients in rivers is higher than that required for phytoplankton growth, suggesting that nutrients do not limit phytoplankton growth [67]. Furthermore, the high temperature of the water accelerates the conversion of inorganic nutrients from organic nutrients to the water column in the lentic system, which in turn can be a major driving factor for the growth of cyanobacterial growth [68]. This means that high water temperature and organic nutrients exert a synergistic effect that favors cyanobacterial growth more than other phytoplankton in the warm season, consistent with our results. Previous studies have reported that stagnant conditions caused by weir construction led to an increase in HRT, water temperature, nutrients, and organic matter, which in turn caused phytoplankton blooms [60,69]. Additionally, according to Sinokrot and Gulliver [70], a decrease in water velocity causes an increase in water temperature. Park et al. [60] reported that the biovolume peaks of *Microcystis* occurred in the Nakdong River's WS during the non-rainy period of the summer monsoon season (July, August, and September). Stable thermal stratification and organics favor the formation of group L_M (primarily *Microcystis*) blooms in the water column of lentic environments with extended HRT [44,65,71,72]. In particular, the biovolume of group L_M, which accounts for most of the total biovolume of cyanobacteria, decreased in proportion to precipitation and water discharge in 2019 and 2020 in the WS, while it increased in proportion to higher discharge during the same period in the NWS (Fig. S4). This is well confirmed by our results showing that cyanobacteria (L_M) increased in proportion to discharge as they went downstream during the rainy monsoon season and that there was a significant correlation with the discharge along with the total biovolume (Table 3; Fig. 11). The threshold discharge can be the main critical level for disrupting phytoplankton blooms [73]. The high water storage capacity and gentle slope in the NWS probably led to a decrease in the impact of flushing despite high water discharge from the upstream WS [74]. This also suggests that water impoundment may serve as a stock culture and nutrient pool to directly or indirectly induce an increase in *Microcystis* biomass in the downstream section of the river, which is strongly supported by the present result that the biovolume of the cyanobacteria (primarily group L_M) was relatively higher in the NWS than in the WS (WS: 45.6 ± 12.2 %, NWS: 74.4 ± 8.6 %). The pattern in which cyanobacterial peaks decline in the WS but persist (2018) or rise (2019, 2020) in the NWS provides additional support for the aforementioned claims (Fig. 6). Our findings demonstrate not only that weir sections provide adequate time for growth, but also that the overflow of high water discharges can induce a synergistic effect in the accumulation or growth of more biomass during the monsoon season. Previous results have amply demonstrated these findings. According to Qu et al. [56], *Microcystis*, a typical lacustrine species in the lentic–lotic system, is transported from the impounded system to the river downstream in proportion to high water discharge (flushing) and is observed with greater dominance downstream during the high water-level period. This is consistent with previous findings that *Microcystis* developing in the upper impoundment is transported downstream, causing a high inoculation effect for further growth, which influences the compositional changes of phytoplankton assemblages [23,75]. Similar to the WS, RDA results for the NWS showed that group L_M increased under conditions favorable to autochthonous growth (e.g., increased HRT, high water temperature, and organic pollutants) after the mass inoculum from the upper WS (Fig. 10a, Figs. S8–S10). These results suggest that the NWS environment maintains a stagnant condition similar to that of the WS, which can be explained by the concept of a 'dead zone', defined as a stalled area below the surface region of the river that provides optimal conditions for sufficient cell replication and growth for phytoplankton [76]. Moreover, a stagnant zone at the end of a river's course can result in continuously increased recruitment of phytoplankton cells and moderate water storage capacity, allowing the survival of species that are susceptible to mixed and fast-flowing conditions, such as *Microcystis* [76]. Evidently, the presence of the Nakdong River Estuary barrage contributes to the occurrence and maintenance of a phytoplankton peak that conflicts with the fate of the NWS's downstream passage to the sea (Fig. 1). Consequently, the mass inoculum (transporting) effect of the WS and the additional autochthonous growth under optimal conditions in the NWS produced more *Microcystis* biomass in the NWS than in the WS, as stated previously (Figs. 6 and 10b, Figs. S8–S10), supporting our third hypothesis that the composition of the assemblage formed in the WS may influence the NWS. *Microcystis* is a genus of cyanobacteria that produces microcystin hepatotoxin, which can have negative effects on drinking water supplies, recreational activities, fishing, etc. [77,78]. Recently, Zhang et al. [79] reported that toxic cyanobacterial effects on aquatic microorganisms can negatively affect human health by promoting the production of antibiotic-resistance genes. One concern in this regard is that there are six water intakes in the NWS. Related to this, our findings also suggest the importance of water quality and water resource management, considering the connectivity between the WS and NWS for a safe drinking water supply. In this study, groups G, J, and H1 were also occasionally dominant in stagnant and organic-rich environments, indicating that they have the potential to be the dominant phytoplankton that leads succession according to competition or environmental adaptability. Previous studies have also reported that these groups adapt well and dominate in stagnant or highly polluted systems [21,54,57,80].

The variation partition analysis (pRDA) further demonstrated that chemistry variables were the most important determinants in explaining the variation of the structure of the PFG assemblage, showing the highest percentage of total variation compared to those of physical and hydrological–meteorological variables in the WS and NWS (Figs. 12 and 13). However, hydrological and meteorological variables showed a higher contribution to the structure of the phytoplankton assemblage based on PFGs in the WS than those in the NWS. A properly divided ratio among the three environmental variable groups explained the variation for PFGs assemblage in the WS (Fig. 12). In contrast, chemical variables had a more pronounced effect on the variation of PFG assemblages in the NWS (Fig. 13). This is due to a relative decrease in physical and meteorological-hydrological variables compared to that in the WS, and simultaneously proves that NWS is a natural river section that more affected by conventional chemical variables (i.e., nutrients) than WS, although it is adjacent to the lower Nakdong River [81]. These results also show that chemical variables, including nutrients, are the main factors determining phytoplankton assemblages in the Nakdong River, as in general natural river, regardless of the presence of the weir [15,82]. However, our findings suggest that hydrological–meteorological drivers (e.g., discharge (HRT) linked to precipitation) have low independent effects on autochthonous growth and composition in PFGs, but can play a synergistic role in increasing interactive and combined effects with chemical and physical variables under the barrier effect in the WS. In contrast, apart from stagnant conditions, the growth and composition of PFGs within barrier-free survey sites in the NWS were influenced by the conventional group of chemical variables. This clearly suggests that the influence of groups of environmental variables on the structure of local phytoplankton assemblages compared between the WS and NWS is markedly different. Furthermore, our findings demonstrate that the transport (dispersal) of phytoplankton, mainly cyanobacteria from WS to NWS, can be further increased autochthonously by conventional nutrients in WS.

The intensity and frequency of meteorological events, such as floods, droughts, and typhoons, are gradually increasing worldwide, including in South Korea [83]. In this situation, while weir construction in the Nakdong River is effective in mitigating drought and preventing flooding, it can cause deterioration in water quality due to nutrient deposition and increased water residence time [83,84], which means that water resources and environmental management are more necessary for stable water supply after weir construction in the Nakdong River. Therefore, our findings can be used as important basic information for stable water management of artificial systems impounded by weirs in temperate countries, including South Korea.

5. Conclusions

1. The construction of weirs on the Nakdong River resulted in environmental differences between the WS and NWS, which influenced the successional patterns of PFGs in local sections (WS, NWS).
2. Environmental gradients between the WS and NWS were observed in DO, EC, BOD, COD, TN, TP, DTP, DTN, NH_3–N, NO_3–N, and PO_4–P, with the WS exhibiting relatively higher concentrations.
3. 17 PFGs (A, B, C, D, E, F, G, H1, J, L_M, L_O, MP, P, T, W1, X1, and X2) with ≥5 % biovolume were identified; groups L_M and P groups were the dominant PFGs driving the succession of assemblages as an indicator of environmental change.
4. Among environmental variables, nutrients (e.g., N, P) and organics (e.g., BOD, COD), along with increased HRT (hydraulic retention time), affected autochthonous growth of major PFGs in the WS. In particular, cyanobacteria (mainly the potentially toxic group L_M) were transported downstream during the monsoon season, leading to additional proliferation in the NWS. The hydrological variables associated with the meteorological conditions contributed to a synergistic effect in increasing the combined effects on the major components of PFG with chemical and physical variables in the period after weir construction.
5. Our findings can be used for water resources and environmental management of weir-impounded rivers in temperate countries, including, South Korea.

Data availability statement

All data generated or analyzed during this study are included in this published article.

CRediT authorship contribution statement

Jae Hak Lee: Formal analysis, Investigation, Methodology, Project administration, Software, Writing - original draft, Writing - review & editing. **Kyung-Lak Lee:** Conceptualization, Formal analysis, Methodology, Validation, Visualization, Writing - original draft, Writing - review & editing. **Han Soon Kim:** Funding acquisition, Project administration, Supervision, Validation, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.heliyon.2023.e22966.

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