Ann. Limnol. - Int. J. Lim. 2021, 57, 3
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https://doi.org/10.1051/limn/2020028

Available online at:
www.limnology-journal.org

RESEARCH ARTICLE

# Bottom-up and top-down effects on phytoplankton functional groups in Hulun Lake, China

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Received: 10 November 2020; Accepted: 14 December 2020

**Abstract –** The debates about the extent to which phytoplankton in freshwater ecosystems are regulated by top-down or bottom-up forces have been ongoing for decades. This study examines the effects of bottom-up and top-down factors on the phytoplankton functional groups in a eutrophic lake. Phytoplankton and zooplankton were sampled and physical-chemical variables measured from May 2019 to October 2019 in Lake Hulun, China. Approximately 43 phytoplankton species were observed and grouped into 23 functional groups. For the zooplankton, about 27 species were observed and classified into 8 functional groups. The study revealed that the bottom-up effects of physical-chemical variables on some phytoplankton functional groups was stronger than the top-down effects of zooplankton. Water temperature (WT), total phosphorus (TP), total nitrogen (TN), conductivity (Cond), water transparency (SD), and dissolved oxygen (DO) significant influence the biomass of the phytoplankton functional groups. The biomass of phytoplankton functional groups was influenced positively by nutrient availability likely because nutrients influence the growth and reproduction of phytoplankton in freshwater. WT and DO had a positive influence on biomass of phytoplankton functional groups. Conversely, phytoplankton biomass revealed a decreasing trend when SD and Cond significantly increased. This study showed that zooplankton functional groups were positively correlated with phytoplankton biomass implying that the top-down control of phytoplankton by the zooplankton in the lake is not strong enough to produce a negative effect. It is evident that the zooplankton functional groups in Lake Hulun are controlled more by bottom-up force than top-down.

**Keywords:** Phytoplankton / zooplankton / bottom-up / top-down / functional group

## 1 Introduction

Phytoplankton and zooplankton are not only among the most important organisms in aquatic systems but also serve as key indicators for water quality assessment (Cadotte *et al.*, 2011; Li *et al.*, 2020; Mwagona *et al.*, 2018). In lakes, phytoplankton are the main primary producer while zooplankton are predators, preying on phytoplankton. Zooplankton also acts as a crucial link in the aquatic food web between the primary producers (phytoplankton) and higher consumers. Studies have revealed season changes in plankton communities (Liu *et al.*, 2010; Ma *et al.*, 2019a), which occur not as a change in plankton communities density, species number, diversity and biomass but also as seasonal changes in plankton community structure (Ke *et al.*, 2008; Vallina *et al.*, 2017). These changes are mainly impelled by physical-chemical (bottom-up effects) and predation (top-down effects) through the biological aquatic food web (Doi *et al.*, 2013; Li *et al.*, 2020).

According to White (1978) and Li *et al.* (2020), the bottom-up effect means that a lower trophic level in the biological food web affects the aquatic community structure of higher trophic levels by means of resource restrictions. On the other hand, top-down effect means a higher trophic level in the aquatic system influences the community structure of a lower trophic level through predation (Carpenter *et al.*, 1985; Li *et al.*, 2020). The effect of predation (top-down effects) has been hypothesized to be strong at the top of the aquatic biological food web and weakens towards the bottom, while the influence of physical-chemical (bottom-up effects) is remarkably stronger at the bottom of aquatic food web and dwindles further up in the trophic level (McQueen *et al.*, 1986). Phytoplankton species composition and density has been

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shown to be influenced by nutrients through bottom-up effects, whereas predation by zooplankton (top-down effect) controls the distribution, abundance and size of phytoplankton (Carignan and Neiff, 1992; Nicolle *et al.*, 2011). For instance, Hongjun *et al.* (2014) revealed that the bottom-up effects of environmental variable had a strong influence on phytoplankton. While analyzing the effects of predation by zooplankton and nutrients on phytoplankton biomass in a eutrophic reservoir in Brazil. dos Santos Severiano *et al.* (2012) showed that (top-down effect) predation by zooplankton had significant influence on phytoplankton. Experiments in microcosm have shown that zooplankton are strongly preyed by fish, whereas phytoplankton has been found to be controlled more by the bottom-up effects of physical-chemical parameters (Sinistro *et al.*, 2007). While modeling top-down and bottom-up effect on the trophic structure of eutrophic and oligotrophic lakes (McQueen *et al.*, 1986) depicted that phytoplankton production is controlled primarily by nutrients and that the effect of predation is dependent on zooplankton size.

The importance of bottom-up and top-down effects on phytoplankton abundance and community structure is well documented in marine systems (Metaxas and Scheibling, 1996; Smith and Lancelot, 2004), and some freshwater lakes in China (Li *et al.*, 2020). However, no study has been conducted in Lake Hulun in China to assess the relative importance of bottom-up and top-down effects in regulating phytoplankton functional groups. Lake Hulun is the largest lake in northern China forming an important ecological corridor in northeast China. The lake plays a key role in climate regulation, water resources conservation, averting desertification and maintaining the balance of the grassland ecosystem. However, Lake Hulun has been suffering from eutrophication since 1980s due to high levels of nutrients in the aquatic environment (Li *et al.*, 2008). Studies have revealed that the most important nutrient source in the lake is from the hay which is being flowed by wind from the vast Hunlunbier Grassland (Chuai *et al.*, 2012; Wang, 2006). Eutrophication of lakes such as Hulun put critical challenges to the lake managers and limnologists who are trying to treat and remediate the water body. These challenges arise mainly from how to formulate the criteria and standard of nutrients for the lake based on factors such as the nutrients and biological variable (*e.g.* phytoplankton). Therefore, being a component of biological variable, it is important to explore the buttom-up and top-down effects in phytoplankton functional groups within Lake Hulun, as the dynamics and structure of phytoplankton communities play a crucial role in the lake. Understanding the influence of bottom-up and top-down effects in freshwater lakes would provide meaningful evidence for better management. This study examines the effects of bottom-up (physical-chemical) and top-down (predation) factors on the phytoplankton functional groups in the eutrophic Hulun Lake; testing the hypothesis that bottom-up effects has a more significant influence on the phytoplankton functional groups than the top-down effects of zooplankton.

## 2 Materials and methods

### 2.1 Study area and sampling sites

The study was conducted in Lake Hulun also known as Hulun Pond or Dalai Lake. Lake Hulun is the largest lake in northern China and fourth largest freshwater lake in China (Li *et al.*, 2008). It is located in the west of the Hulun Buir Grassland (48°31′−49°20′N, 116°58′−117°48′E), between New Barag Left Banner, New Barag Right Banner, and Manzhouli City (Fig. 1). The lake covers an area of about 2339 km$^2$ with an average width of 32 km. The maximum water depth of Lake Hulun is about 8 m and the water storage capacity is 13.2 billion m$^3$. The lake receives water from direct precipitation and direct surface runoff. The main rivers flowing into Lake Hulun include Kherlen River and Urson River between Baikal Lake and Lake Hulun. Xinkai River located in the northeast of Lake Hulun also drains its water into the lake. Hailar River which is a man-made river created by diversion of rivers into the lake also is an important source of water to the lake. The mean annual precipitation received in this area is between 247 and 319 mm, and approximately 80–86% of the annual precipitation falls in June-September (Li *et al.*, 2019).

A total of 10 sampling sites were selecting taking into consideration the ecological environment characteristics of Lake Hulun. The sites included four located at the discharge points of the rivers into the lake (S1-Xinkai River Estuary, S4-Kherlen River Estuary, S6-Urson River Estuary and S7-Hailar River Estuary); two sites, S2 and S3 were located on the western side of Lake Hulun; sites S5 and S6 were located on the eastern side of the lake; and sites S8 and S10 were located in the central regions of the lake (Fig. 1).

### 2.2 Sampling collection and analysis

At every sampling site, physical-chemical variables including water temperature (WT), pH, conductivity (Cond), and dissolved oxygen (DO) were measured directly in the field using a portable multi-probe (YSI 6600, YSI Inc., USA). Secchi disk was used to measure water transparency (SD) in the field. Water samples for nutrients analysis were collected, placed in a cooler box and transported to the laboratory for analysis. Total nitrogen (TN), total phosphorus (TP) and chemical oxygen demand (COD) were analyzed according to the standard methods for China (MEP Ministry of Environmental Protection, 2002).

Replicates of phytoplankton samples (1 L at each site) were collected, put in a labeled bottle and immediately fixed with Lugol's solution. The phytoplankton samples were allowed to sediment for 48 h and then concentrated to 30 mL. Phytoplankton were identified by referring to the identification key of Hu (2006) and counted using an inverted microscope at 400× magnification. Phytoplankton species were classified into functional groups (FGs) according to (Padisák *et al.*, 2009) and (Reynolds *et al.*, 2002). Biovolume (mm$^3$/L) of phytoplankton was estimated according to the solid geometric shape, and cell volumes of at least 40 algal units were estimated by approximation to the nearest solid geometric solid. Conversion of biovolume into biomass was done as 1 mm$^3$/L = 1 mg/L as described by (Ma *et al.*, 2019a).

For the zooplankton samples, 20 L of water were filtered through plankton net (mesh size 64 mm) and the samples were transferred into specimen bottles (pre filed with 4% formaldehyde solution). The concentrated zooplankton samples were allowed to settle in a 1 L jar for 24 h before identification and enumeration. The zooplankton were identified by referring to species keys (Chen *et al.*, 1974;

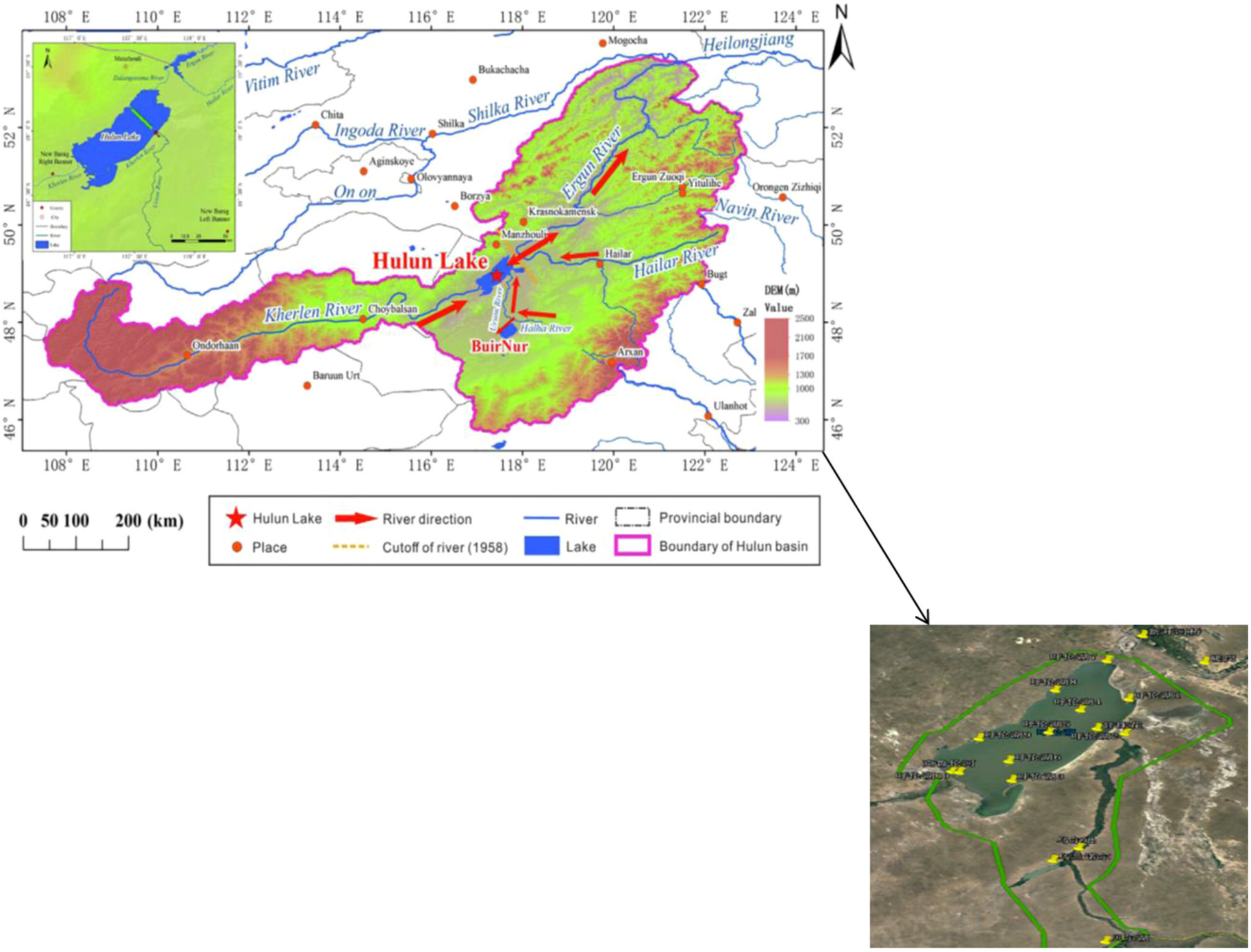

**Fig. 1.** (Top) Map of Hulun Lake drainage basin; (bottom) ten sampling locations within Lake Hulun and surrounding drainage area in Heilongjiang, China.

Haney *et al.*, 2013; Kotov *et al.*, 2013) using an inverted microscope (INVERSO 3000 (TC-100) CETI) at 400× magnification. Using a wide-mouthed pipette, a 1 ml of zooplankton sample was taken and poured into the counting cell of the Sedgewick Rafter and allowed to settle, followed by count. The counting process was made in triplicate for each sample of the plankton. The zooplankton species were classified into functional groups based on their body size/length and mode of feeding (Benedetti *et al.*, 2015; Benedetti *et al.*, 2018; Ma *et al.*, 2019b; Mwagona *et al.*, 2018). Biomass of the zooplankton was computed by dividing wet weight (mg) obtained from length–weight relation of the species to the volume of water (L) filtered (Sun *et al.*, 2010).

### 2.3 Statistical analysis

The significance of the changes in physical chemical variables, the biomass of phytoplankton and zooplankton functional groups in water was tested with post hoc tests: Tukey's HSD (honestly significant difference) test for comparing groups with uneven lot sizes (Statsoft, 1995). It was assumed that the significance level was 0.05. To test the significant bottom-up or top-down influence on phytoplankton functional groups in Lake Hulun, redundancy analysis (RDA) was used after the detrended corresponding analysis (DCA) revealed that the gradient length of the respond data was less than three. Pearson correlation analysis among phytoplankton functional groups biomass, zooplankton functional groups biomass and physical-chemical variables was also conducted.

## 3 Results and discussion

### 3.1 Physical-chemical variables

Physical-chemical variables of lake water play a significant role in the distribution patterns and species composition of plankton (Mahar *et al.*, 2000; Toma, 2011). In aquatic habitats, environmental variables such as dissolved gases, water temperature, pH, phosphates, nitrates, conductivity among many others including various physical properties (gases and solids solubility) are very important for growth and dispersal of phytoplankton on which zooplankton depend for their existence. In this study, all the physical-chemical variables measured in the Lake during the study period differed temporal (with the exception of pH). Water temperature (WT) which is one of the essential factors that regulates growth of plankton

**Table 1.** Mean and standard error (number in brackets) for the physical–chemical variables in recorded during the study period in Lake Hulun.

| | 2019 | | | | | | *p*-value |
|---|---|---|---|---|---|---|---|
| | May | June | July | August | September | October | |
| WT (°C) | 14.88 (2.56) | 20.53 (1.45) | 24.44 (0.99) | 23.61 (1.13) | 13.66 (0.77) | 5.79 (0.78) | $0.000^{**}$ |
| pH | 8.90 (0.03) | 8.84 (0.11) | 8.90 (0.10) | 8.99 (0.22) | 8.98 (0.31) | 8.98 (0.14) | 0.370 |
| Cond (μS/cm) | 1724.75 (29.14) | 1706.7 (77.52) | 1695.7 (89.49) | 1403 (419.01) | 1448.8 (449.49) | 1463.3 (306.85) | $0.045^{*}$ |
| DO (mg/L) | 10.41 (0.80) | 8.72 (0.27) | 7.07 (0.98) | 9.41 (1.40) | 10.02 (0.38) | 12.03 (0.50) | $0.000^{**}$ |
| COD (mg/L) | 106.75 (30.25) | 105.8 (17.97) | 89.3 (15.54) | 113.8 (17.99) | 92.1 (19.62) | 74.8 (14.74) | $0.000^{**}$ |
| SD (cm) | 33.63 (6.48) | 34 (5.77) | 42.4 (7.90) | 29.3 (6.24) | 27.6 (10.75) | 32.9 (4.51) | $0.001^{**}$ |
| TP (mg/L) | 0.15 (0.13) | 0.17 (0.05) | 0.18 (0.03) | 0.20 (0.04) | 0.25 (0.08) | 0.16 (0.02) | $0.000^{**}$ |
| TN (mg/L) | 1.93 (0.31) | 2.05 (0.41) | 2.00 (0.3) | 2.57 (0.70) | 1.97 (0.34) | 1.10 (0.28) | $0.000^{**}$ |
| N:P | 16.78 | 12.74 | 11.46 | 12.97 | 8.43 | 7.06 | $0.000^{**}$ |

communities in aquatic system ranged between 5.79 ± 0.78 °C to 24.44 ± 0.99 °C. The minimum and maximum WT was recorded during October and July, respectively (Tab. 1). Water temperature not only influences the growth and distribution of flora and fauna in aquatic ecosystems, but also influences solubility of gases, water stratification, conductivity and pH (Sharm and Michael, 1987). A possible increase in solar radiation and concomitant evaporation due to comparatively longer day length may explain higher water temperatures in the months of June, July and August. The recorded pH of lake varied between 8.84 ± 0.11 to 9.99 ± 0.22 during the study period (Tab. 1). The values showed that the water of Lake Hulun was alkaline in nature. Although the pH did not differ significantly temporal, relative high values were observed in July and August corresponding with high WT. This is in agreement with other studies that has observed elevated level of pH in the months of June, July and August (summer) likely because of high rate of photosynthesis in aquatic systems (Jakher and Rawat, 2003). The DO measured during the study period ranged from 7.07 ± 0.98 mg/L to 12.03 ± 0.50 mg/L. Unlike the WT, the minimum and maximum DO was observed in July and October. The minimum DO observed in July could be likely due to the utilization DO and decomposition of organic matter and respiration of micro and macro-organisms (Manickam *et al.*, 2018). Water transparency (SD) values varied temporally with the lowest value observed in September (27.6 ± 10.75 cm) and the highest in July (42.4 ± 7.90 cm). The measured values of TP were in the range of 0.15 ± 0.13 mg/L to 0.20 ± 0.04 mg/L while those of TN varied between 1.10 ± 0.28 mg/L to 2.57 ± 0.07 mg/L. The measured TP and TN values in this study were lower than those reported by (Chuai *et al.*, 2012) in 2009 and (Li *et al.*, 2008) in 2008. Hay being flowed by wind to the lake from the Hunlunbier Grassland has been attributed as the most important source of these nutrients (Wang, 2006; Zhao *et al.*, 2007).

### 3.2 Phytoplankton and zooplankton dynamics

During the study period, a total of 43 phytoplankton species were found belonging to seven taxonomic classes: Chlorophyceae, Bacillariophyceae, Cyanophyceae, Euglenophyceae, Chrysophyceae, Cryptophyceae, and Dinophyceae (Tab. 2). The phytoplankton species were categorized in 23 functional groups as described by (Padisák *et al.*, 2009; Reynolds, 2006; Reynolds *et al.*, 2002). Four groups (H1, X2, J, and C) were categorized as dominant groups defined by contributing a minimum of 10% of the total biomass as recommended in literature (Reynolds *et al.*, 2002). The remaining functional groups were clustered together as ‘others’. The four dominant groups accounted for about 81.33% of the total phytoplankton biomass hence used to analyze the composition and dynamics of phytoplankton community in Lake Hulun (Tab. 2). Temporal, the biomass of phytoplankton functional group C ranges from 0.05 mg/L to 0.16 mg/L. The highest mean biomass value was measured in June, followed by May and the least was observed in July (Fig. 2). Higher biomass values of group H1 was measured in July (11.29 mg/L) and August (11.85mg/L) corresponding to higher WT. On the other hand, the biomass of group H1 was very low in May and October (Fig. 2) when WT was low. A post hock test showed that the biomass of group X2 was statistically significant higher biomass in August compared to that of other months.

For the zooplankton community dynamics, 27 species belonging to four taxonomic categories: protozoans, rotifers, copepods and cladocerans were observed in Lake Hulun (Tab. 3). Rotifers had the highest number of species (11 species) followed by cladocerans with 6 species, whereas protozoans and copepods had 5 species each. The taxonomic categories were almost similar to those reported in Small Xingkai Wetland Lake by (Ma *et al.*, 2019b) and by (Mwagona *et al.*, 2018) in Xiquanyan Reservoir, Northeast China. The zooplankton species were classified into eight functional groups (Tab. 3). Approximately 40.02% of the total zooplankton functional group biomass contribution was of LCF while 21.60% was of RF group. SCF and MCC were the third and fourth most contributors of the total biomass with, 14.23% and 11.23%, respectively. The percentage biomass contribution for each of the other functional groups PF, RC, MCF, and LCC was less than 5%. The mean biomass of all zooplankton functional group differed significantly temporal as determined by one-way ANOVA ($p < 0.05$). Group LCF accounted for about 37.89%, 51.46%, 54.87% and 42.68% of the total biomass in June, July, September and October, respectively. In July, August and September, group RF accounted the second highest mean biomass (Fig. 3) Group

**Table 2.** List of phytoplankton species with their taxonomic, functional groups, and percentage contribution to their total biomass in Lake Hulun.

| Class | Genus | Representative species | Phytoplnakton functional groups | % biomass |
|---|---|---|---|---|
| Bacillariophyceae | Asterionella | *Asterionella formosa* | C | 10.25 |
| | Cyclotella | *Cyclotella meneghiniana* | | |
| Bacillariophyceae | Synedra | *Synedra acus* | D | 1.9 |
| | | *Synedra ulna* | | |
| Chlorophyceae | Westella | *Westella botryoides* | F | 3.87 |
| | Oocystis | *Oocystis elliptica* | | |
| Cyanophyceae | Anabaena | *Anabaena circinalis* | H1 | 23.07 |
| | | *Anabaena variabilis* | | |
| | Aphanizomenon | *Aphanizomenon flos-aquae* | | |
| Chlorophyceae | Chodatella | *Chodatella quadriseta* | J | 24.00 |
| | Tetrastrum | *Tetrastrum elegans* | | |
| | Tetraëdron | *Tetraëdron trigonum* | | |
| Cyanophyceae | Merismopedia | *Merismopedia minima* | L0 | 3.10 |
| | Synechocystis | *Synechocystis minuscula* | | |
| | Chroococcus | *Chroococcus minutus* | | |
| Cyanophyceae | Microcystis | *Microcystis wesenbergii* | M | 0.35 |
| | | *Microcystis firma* | | |
| Bacillariophyceae | Navicula | *Navicula exigua* | MP | 8.16 |
| | Meridion | *Meridion circulare* | | |
| | Cymbella | *Cymbella ventricosa* | | |
| Chlorophyceae | Cosmarium | *Cosmarium obtusatum* | N | 7.11 |
| | Staurastrum | *Staurastrum gracile* | | |
| Chlorophyceae | Closterium | *Closterium gracile* | P | 0.76 |
| | | *Closterium acerosum* | | |
| Cyanophyceae | Phormidium | *Phormidium allorgei* | S1 | 0.36 |
| Cyanophyceae | Raphidiopsis | *Raphidiopsis curvata* | S2 | 0.04 |
| Euglenophyceae | Euglena | *Euglena oxyuris* | W1 | 1.31 |
| Euglenophyceae | Trachelomonas | *Trachelomonas granulosa* | W2 | 0.01 |
| Chrysophyceae | Synura | *Synura Ehrenberg* | WS | 0.03 |
| Chlorophyceae | Ankistrodesmus | *Ankistrodesmus angustus* | X1 | 0.87 |
| | | *Ankistrodesmus acicularis* | | |
| Chlorophyceae | Chlamydomonas | *Chlamydomonas ovalis* | X2 | 24.01 |
| | | *Chlamydomonas globosa* | | |
| Chrysophyceae | Chromulina | *Chromulina elegans* | X3 | 0.39 |
| | | *Chromulina globosa* | | |
| | | *Kephyrion planctonicum* | | |
| Dinophyceae | Glenodinium | *Glenodinium pulvisculus* | Y | 2.77 |
| Cryptophyceae | Cryptomonas | *Cryptomonas ovata* | | |

SCF had recoded higher biomass values of 1.75 mg/L and 2.54 mg/L in July and August. For the other months, the mean biomass contribution by group SCF was less than 0.05 mg/L. In August, group MCC had higher biomass mean value compared to the other months (Fig. 3).

### 3.3 Response of phytoplankton functional group variables to bottom-up and top-down effects

The relative importance of bottom-up versus top-down effects in aquatic ecosystems remains a longstanding and ongoing controversy. This question of whether the food webs are exerted by bottom-up or top-down trophic levels on lower ones and vice versa has long been the subject of scientific debate (Carpenter *et al.*, 1985; Sinistro, 2010). Although both bottom-up or top-down forces are known to occur in aquatic systems, they may differ in magnitude. This study allowed the investigation of bottom-up and top-down effects on phytoplankton functional groups communities in freshwater lakes. Some studies carried out in lake has acknowledged that community biomass and productivity are controlled by the next higher trophic level (Shapiro *et al.*, 1975). On the other hand, several authors revealed that nutrient loading explained a great amount of variation in phytoplankton biomass and production (Li *et al.*, 2020; McCauley *et al.*, 1989).

In this study we found that the effect of the bottom-up effects of physical-chemical variables on some phytoplankton functional groups was stronger than the top-down effects of zooplankton. This is in agreement with other studies in the literature. For example, while exploring the bottom-up and top-down effects on phytoplankton communities in two freshwater lakes (Li *et al.*, 2020) observed that the effect of bottom-up (physical-chemical variables) on phytoplankton were stronger that the effects of top-down (predation by zooplankton). Phytoplankton functional group X2 which constitutes about 21.06% of the total biomass of the phytoplankton represented by *Chlamydomonas ovalis* and *Chlamydomonas globosa* species was mainly influenced by TP, Cond, SD and WT (Fig. 4 and Tab. 4). Similarly, as shown in RDA and Pearson correlation analysis (Fig. 4 and Tab. 4), *Anabaena circinalis, Anabaena variabilis,* and *Aphanizomenon flos-Aquae* which composed group H1 and also known to

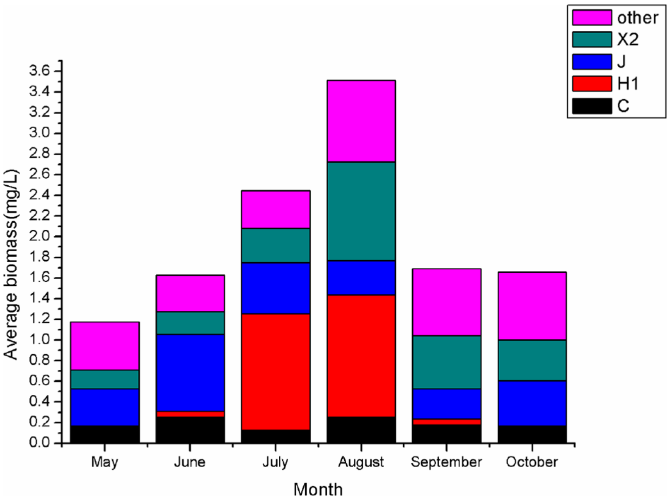

**Fig. 2.** Temporal variation of the biomass of phytoplankton functional groups in Lake Hulun.

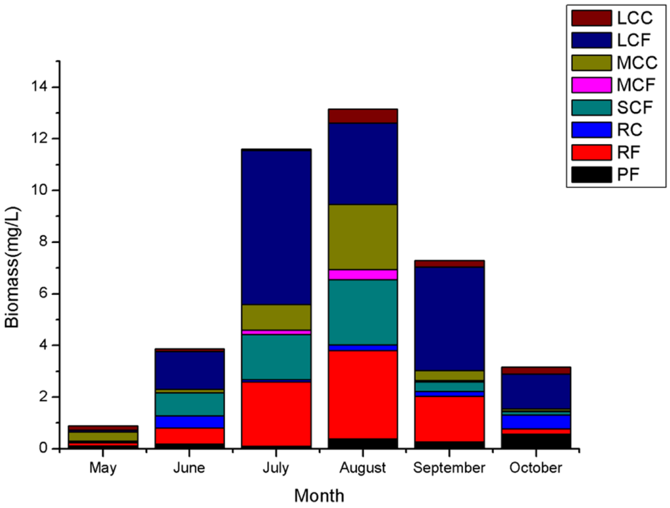

**Fig. 3.** Temporal variation of the biomass of zooplankton functional groups in Lake Hulun.

**Table 3.** List of zooplankton species with their taxonomic, functional groups, and percentage contribution to their total biomass in Lake Hulun.

| Class | Genus | Representative species | Zooplnakton functional groups | % biomass |
|---|---|---|---|---|
| Protozoa | Vorticella | *Vorticella campanula* | PF | 4.05 |
| | Difflugia | *Difflugia globulosa* | PF | |
| | | *Difflugia avellana* | PF | |
| | Tintinnopsis | *Tintinnopsis wangi* | PF | |
| | Stormbidinopsis | *Strombidium viride* | PF | |
| Rotifer | Brachionus | *Brachionus angularis* | RF | 21.60 |
| | Brachionus | *Brachionus calyciflorus* | RF | |
| | Brachionus | *Brachionus forficula* | RF | |
| | Brachionus | *Brachionus diversicornis* | RF | |
| | Keratella | *Keratella cochlearis* | RF | |
| | Keratella | *Keratella quadrata* | RF | |
| | Keratella | *Keratella valga* | RF | |
| | Pompholyx | *Pompholyx sulcata* | RF | |
| | Filinia | *Filinia longiseta* | RF | |
| | Polyarthra | *Polyarthra minor* | RC | 3.80 |
| | Trichocerca | *Trichocerca.sp* | RC | |
| Cladocera | Bosmina | *Bosmina longirostris* | SCF | 14.23 |
| Copepods | Microcyclops | *Microcyclops javanus* | SCF | |
| Cladocera | Diaphanosoma | *Diaphanosoma leuchtenbergianum* | MCF | 1.61 |
| Cladocera | Moina | *Moina rectirostris* | MCF | |
| Copepods | Mesocyclops | *Mesocyclops leuckarti* | MCC | 11.23 |
| Copepods | Thermocyclops.sp | *Thermocyclops.sp* | MCC | |
| Cladocera | Daphnia | *Daphnia magna* | LCF | 40.02 |
| Cladocera | Simocephalus | *Simocephalus vetulus* | LCF | |
| Cladocera | Daphnia | *Daphnia cucullata* | LCF | |
| Copepods | Arctodiaptomus | *Arctodiaptomus rectispinosus* | LCF | |
| Copepods | Cyclops | *Cyclops strenuuss* | LCC | 3.47 |

**Table 4.** The Pearson correlations between physical chemical variables and phytoplankton functional groups in Lake Hulun.

| | WT | pH | DO | Cond | TP | TN | COD | SD | TN/TP |
|---|---|---|---|---|---|---|---|---|---|
| C | −0.019 | −0.036 | 0.102 | $-0.321^{**}$ | −0.123 | −0.018 | 0.141 | −0.012 | $0.195^{*}$ |
| H1 | $0.291^{**}$ | 0.077 | −0.024 | $-0.182^{*}$ | 0.03 | $0.378^{**}$ | −0.128 | $-0.159^{*}$ | 0.117 |
| J | −0.052 | −0.155 | 0.106 | $-0.167^{*}$ | $-0.212^{*}$ | 0.027 | 0.167 | −0.093 | $0.199^{*}$ |
| X2 | 0.025 | −0.021 | $0.248^{**}$ | −0.155 | $0.205^{*}$ | 0.064 | 0.135 | −0.087 | 0.102 |
| other | 0.06 | 0.128 | −0.184 | −0.146 | −0.016 | 0.183 | $-0.198^{*}$ | −0.161 | 0.179 |

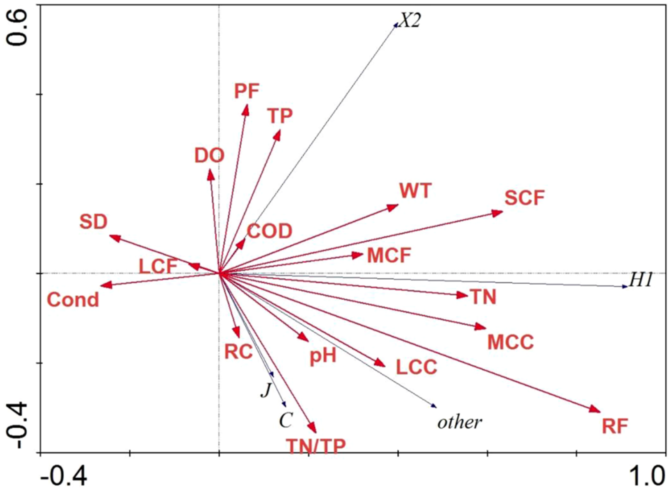

**Fig. 4.** Redundancy analysis (RDA) plots for different phytoplankton functional group biomass, zooplankton functional group biomass and water physical chemical variable parameters in Lake Hulun.

cause bloom in Lake Hulun were also strongly influenced by physical-chemical variables (WT, TN, Cond, and SD). Studies have shown that chemical variables such as N and P influence the growth and reproduction of phytoplankton in water (Elliott *et al.*, 2006; Xu *et al.*, 2010). While using the phytoplankton community model, PROTECH, to examine the effects of elevated temperature and nutrients loading on phytoplankton productivity and succession (Elliott *et al.*, 2006) observed phytoplankton biomass increase with increase in temperature and nutrients loading. These authors further noted that the increased phytoplankton biomass was largely dominated by the cyanobacterium Anabaena. This is in agreement with our finding since the group H1 composed by the Anabaena species was positive influenced by WT and TN. The fact that the biomass of group H1 and X2 were higher in July and August when the WT was high also signifies the importance of temperature. The rate of photosynthesis of phytoplankton is probably promoted by the rising WT, which accelerates the accumulation of biomass. Nutrients such as N and P are important for the growth of phytoplankton, and at particular concentrations can influence the growth of phytoplankton (Elmgren and Larsson, 2001). Sun *et al.* (2008) note that increase concentrations of N and P at a given range can promote the growth of phytoplankton. This, therefore implies that nutrients factors in lakes can effectively control the biomass of phytoplankton functional groups through bottom-up effects.

A significant positive correlation between DO and some phytoplankton biomass in this study was observed (Tab. 4). This observation could be due to the fact that oxygen is produced during photosynthesis. Therefore an increase in phytoplankton biomass comes with a resultant increase in DO concentration. On the other hand, a significant negative correlation between SD and the biomass of some phytoplankton functional group was observed. This is very strange because increased SD increases the intensity of solar radiation that can be captured by phytoplankton, hence increased photosynthesis and other metabolic activities with a subsequent increase in population density and biomass of phytoplankton (Ma *et al.*, 2019a; Yusuf, 2020). Napiórkowska-Krzebietke *et al.* (2013) also observed that phytoplankton biomass and chlorophyll concentration in water were relatively low (typical of mesotrophic lakes), with a decreasing tendency when the water transparency significantly increased.

Conversely, our results showed that the biomass of most phytoplankton functional groups was negatively affected by conductivity (Tab. 4). Conductivity, a measure of a solution's conductive abilities and thus the total dissolved solids within the solution, can affect the ecological viability of freshwater lakes such as Lake Hulun. Conductivity may also affect P availability in the water column by allowing anion binding to P in the form of phosphate, resulting in a decreased concentration of total available P. Since P is a critical nutrient for phytoplankton growth, it is possible that this chemical interaction would prevent phytoplankton from accessing P, resulting in decreased phytoplankton biomass (Chouyyok *et al.*, 2010). This could explain the negative effect of conductivity on phytoplankton biomass observed in this study.

Some experimental and modeling studies have shown that top-down factors are most important in determining phytoplankton biomass, concentration of chlorophyll a, and phytoplankton size-distribution, either directly through grazing or indirectly through increased nutrient supply by excretion (Hansson, 1992; Mao *et al.*, 2020; Metaxas and Scheibling, 1996). McQueen *et al.* (1986) showed that although phytoplankton production is determined mainly by nutrients, the effect of predation by zooplankton is dependent on the size of the zooplankton. In this study, zooplankton functional group RF (Rotifer passive filter feeders feeding on organic detritus and bacteria) (Mwagona *et al.*, 2018) was positively correlated with phytoplankton group C and H1 (Tab. 5). This observation could be attributed by the fact that RF grazed predominantly on heterotrophic components of the microbial food-web, such as bacteria, fungus and detritus which have been documented to be favored by occurrence of higher concentrations of nutrients (TP and TN) (Duggan *et al.*, 2001; Holst *et al.*, 1998).

**Table 5.** The Pearson correlations between phytoplankton functional groups and zooplankton functional groups in Lake Hulun.

| | *PF* | *RF* | *RC* | *SCF* | *MCF* | *MCC* | *LCF* | *LCC* |
|---|---|---|---|---|---|---|---|---|
| C | −0.039 | 0.208$^{*}$ | 0.012 | −0.002 | −0.17 | 0.05 | −0.06 | 0.098 |
| H1 | 0.02 | 0.721$^{**}$ | 0.046 | 0.354$^{**}$ | 0.022 | 0.309$^{**}$ | −0.121$^{*}$ | 0.164 |
| J | 0.116 | 0.215 | 0.07 | −0.061 | −0.265$^{**}$ | −0.025 | −0.119 | −0.04 |
| X2 | 0.256$^{**}$ | 0.155 | 0.006 | 0.144 | −0.173 | 0.007 | −0.061 | −0.034 |
| other | 0.088 | 0.047 | 0.357$^{**}$ | −0.076 | −0.051 | −0.011 | −0.13 | −0.002 |

Zooplankton may also enhance the biomass and abundance of some phytoplankton groups by selectively feeding on their potential competitors (Vanni and Findlay, 1990). Moreover, the fact that most zooplankton functional groups were positively related with the phytoplankton biomass in this study could imply that the top-down control of phytoplankton by the zooplankton in Lake Hulun is not strong enough to produce negative effect. Another possible explanation could be that the grazers (zooplanktons) may have beneficial effects for certain phytoplankton functional groups by increasing nutrients concentration through excretion (Metaxas and Scheibling, 1996; Smith and Lancelot, 2004).

## 4 Conclusions

In this study we found that the effect of the bottom-up effects of physical-chemical variables on some phytoplankton functional groups was stronger than the top-down effects of zooplankton. Of the physical-chemical variables measured in this study, WT, TP, TN, Cond, SD, and DO had significant influence on the biomass of phytoplankton functional groups. Phytoplankton functional group X2 and H1 which constitutes about 47.08% of the total biomass of the phytoplankton were mainly influenced positively by nutrients availability (TP and TN). This is because variables such as N and P influence the growth and reproduction of phytoplankton in water. Moreover, WT and DO had a positive influence on the biomass of phytoplankton functional groups. Also, in this study, phytoplankton biomass revealed a decreasing tendency when the SD and Cond significantly increased.

While the bottom-up effects of physical-chemical variables on phytoplankton are clear, the top-down effects of zooplankton on phytoplankton, which may have been regulated indirectly by fish, are more difficult to predict in aquatic management. This study showed that zooplankton functional groups were positively correlated with phytoplankton biomass implying that the top-down control of phytoplankton by the zooplankton in Lake Hulun is not strong enough to produce a negative effect. Even though our study may not be conclusive as such, it is quite clear that the zooplankton functional groups in Lake Hulun are controlled more by bottom-up force than top-down force. However, these conclusions should be drawn cautiously because more data is needed for a thorough analysis of the two effects. These results can serve as a basis for identifying how phytoplankton dynamics are influenced, which have implications for developing sustainable management strategies and conserving services of Lake Hulun and other eutrophic fresh water lakes.

## Conflict of interest

The authors declare no conflict of interest.

*Acknowledgements.* We wish to acknowledge the financial support from the Fundamental Research Funds for the Central Universities (2572018BE03) and National Key Research and Development Program of China (Grant No.2016YFC0500406).

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**Cite this article as**: Ma C, Zhao C, Mwagona PC, Li Z, Liu Z, Dou H, Zhou X, Bhadha JH. 2021. Bottom-up and top-down effects on phytoplankton functional groups in Hulun Lake, China. *Ann. Limnol. - Int. J. Lim.* 57: 3