Distribution and population dynamics of cryptomonads in a Chinese lake with three basins varying in their trophic state

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SUMMARY

Cryptomonads are unicellular algae that are important primary producers in various aquatic ecosystems. However, their ecological importance was often neglected owing to their brittleness. Their population in freshwater was thought to be regulated mainly by grazing pressure, and the effects of lake trophy were less important. In this study, the cryptomonad species in three basins of Lake Donghu, a shallow lake in China were identified, and their distribution, seasonal dynamics, and relationships with several environmental factors were investigated. Eight cryptomonads were identified at species level by morphological examination; species belonging to the genera Komma and Cryptomonas were most common. Cryptomonads displayed inconsistent distribution and population dynamics among the three basins of different trophic status. They were the dominant species in the eutrophic basin, while their proportion was lower in the hypertrophic basin and in the mesotrophic basin. The biomass of cryptomonads was highest in the hypertrophic region. As a whole, cryptomonads kept low biomass during winter, while rapid waxing and waning of their population was observed in the other seasons. Cryptomonads species exhibit distinct seasonal trends. Canonical correspondence analysis revealed water temperature and dissolved total nitrogen were the most important factors that affected the composition of the cryptomonads community. Spearman correlation analysis demonstrated that the biomass of cryptomonads was positively correlated with pH value, dissolved total nitrogen and dissolved organic carbon. In conclusion, lake trophy is a crucial factor affecting the total cryptomonads population.

Key words: dissolved organic carbon, dissolved total nitrogen, environmental factors, phytoplankton, seasonal trend.

INTRODUCTION

Cryptomonads comprise autotrophic and heterotrophic flagellates with unique morphological features (Menezes & Novarino 2003). These microalgae are important primary producers in both fresh water and marine habitats. They contribute greatly to the aquatic food web and many species are cosmopolitan in their distribution (Reynolds 1978; Kleneness 1988a,b; Gillot 1990; Barlow & Kugrens 2002). However, cryptomonads may be underrepresented in preserved samples due to their brittleness, and their ecological importance was often neglected. Moreover, by virtue of their unicellularity and small size, proper identification cannot be accomplished by light microscopy, and they were assumed to be a small and obscure taxonomic group of protists (Barlow & Kugrens 2002; Novarino 2003). Recent research modified the taxonomic system of cryptophyta by combined datasets of light and electron microscopical and molecular data, and provided several morphological characters to distinguish some cryptomonad species under light microscopy, which made the identification more rational (e.g. Hoef-Emden & Melkonian 2003; Hoef-Emden 2007). Thus, ecological investigation of cryptomonads at species level is now feasible.

Previous ecological studies on cryptomonads have mainly focused on the identification, distribution and seasonal dynamics (e.g. Barlow & Kugrens 2002; Barone & Naselli-Flores 2003; Menezes & Novarino 2003; Tolotti et al. 2003; Cerino & Zingone 2006). These algae may form blooms in marine (Andreoli et al. 1986; Dame et al. 2000), freshwater (Nishijima 1990), and brackish (Laza-Martinez 2012) ecosystems. In freshwater environments, cryptomonads are often present in constant but relatively low populations throughout the year, and sudden increases in population are common (Novarino 2003). However, the underlying factors that affect their populations remain obscure. Previous studies revealed they were optimal or near-optimal food organisms for zooplankton (Stemberger & Gilbert 1985; Sarnelle 1993; Tirot & Gaedke 2007), and their population was mainly regulated by grazing pressure (Willén 1992; Barone & Naselli-Flores 2003) in freshwater habitats. But undoubtedly, the effects of lake trophy need to be investigated.

In the current study, cryptomonads species in three basins of different trophic status of Lake Donghu, a shallow lake in China were identified. Their distribution, seasonal dynamics, and relationships with environmental factors were also examined. The effects of lake trophy on cryptomonads population were discussed.

MATERIALS AND METHODS

Study site and sample collection

Limnological investigations were performed in Lake Donghu, which is a shallow lake with an average depth of 2.2 m. It is located on the alluvial plain of the middle basin of Yangtze River, City of Wuhan, Hubei province, China. The lake has a
total surface area of 32 km² and is composed of several basins separated by artificial dykes. The main basin of Lake Donghu (the Guozhenghu Basin) is eutrophic, while the Shuiguohu Basin is hypertrophic and the Niuchaohu Basin is mesotrophic (Qiu et al. 2001; Zhou et al. 2002; Zhao et al. 2003).

In the present study, seven sampling sites were set in three basins of the lake. Five sites were in the main basin (the Guozhenghu Basin), and one site each in the Shuiguohu Basin and the Niuchaohu Basin. The locations of sampling sites were as follows: 1# (30°33′ 13.73″ N, 114°20′ 53.81″ E); 2# (30°32′ 46.77″ N, 114°21′ 57.58″ E); 3# (30°32′ 46.86″ N, 114°23′ 42.84″ E); 4# (30°33′ 42.45″ N, 114°24′ 14.57″ E); 5# (30°34′ 05.86″ N, 114°23′ 23.61″ E); 6# (30°34′ 34.88″ N, 114°22′ 37.71″ E); 7# (30°35′ 05.35″ N, 114°22′ 46.07″ E). The map of Lake Donghu and sampling sites are shown in Appendix S1 in supporting information. Phytoplankton samples for qualitative identification were collected by plankton nets (10 μm mesh size), and brought back to the lab alive. For quantitative analysis, phytoplankton samples of surface water (0–50 cm deep) and bottom water (0–50 cm above the sediment surface) were collected monthly from July 2010 to June 2012 using 600 mL plastic bottles. Surface and bottom water samples from the same site were mixed and fixed with Lugol’s iodine solution to obtain a final concentration of 1%. In addition, 100 mL water samples were obtained for environmental parameter measurements.

Measurements of environmental parameters

Water temperature was measured directly using a mercury thermometer, and pH value was recorded using a pH sensor (HI98103, Hanna Instruments, TX, USA).

Water samples were filtered through precleaned 0.45 μm pore size Whatman GF/F glass-fiber filters. Dissolved total nitrogen (DTN) and dissolved total phosphorus (DTP) were measured using potassium peroxodisulfate oxidation and degradation methods (State Environmental Protection Bureau 2002), respectively. A spectrometer (UV-1700 PharmaSpec, Shimadzu, Kyoto, Japan) was used to record the optical density (OD) value. Dissolved inorganic carbon (DIC) and dissolved organic carbon (DOC) were measured using a catalytic combustion analyzer (Multi-N/C 2100TOC, Analytic Jena AG, Eisfeld, Germany). These environmental parameters were measured within 24 h after sampling.

Species identification and calculation

Living cells and cells fixed with Lugol’s solution were observed using differential interference contrast and phase contrast under a light microscope (Leica DM5000B). Micrographs were captured using a digital camera (Leica DFC320, Wetzlar, Germany). When observing live cells, low-melting agarose was added to prevent cells from swimming. In particular, we considered six principal characteristics used in the taxonomy of these species, namely, cell size, cell shape, cell colour, presence and direction of a furrow, number and shape of chloroplast, and arrangement of large euctosomes. Identification mainly followed the procedure of Huber-Pestalozzi (1968), Hill (1991), Novarino et al. (1994), Clay et al. (1999), Hoef-Emden and Melkonian (2003), Javornický (2003), and Kugrens and Clay (2003). At least 30 live cells were observed to identify each cryptomonad species.

The 1.2 L water samples were allowed to settle for 24 h, siphoned, and concentrated to 30 mL. Then, 0.1 mL of the concentrated water samples was placed in a counting chamber, and the cells were counted under an optical microscope (CX21, OLYMPUS, Tokyo, Japan) at 400 × magnification. At least 30 phytoplankton cells were counted. Mean cell volume (μm³/cell) was calculated using appropriate geometric configurations after measuring 50 cells of each taxon with a calibrated ocular micrometer (Hillebrand et al. 1999; Domingues et al. 2005). Volume values were converted to biomass assuming that 1 μm³ is equivalent to 1 pg (Eker & Kideys 2003).

Statistical analysis

Data of biomass, cell density, DTN and DTP were log₂ (x+1) transformed. Spearman correlation analysis was performed using the SPSS 16.0 package (SPSS, Chicago, IL, USA). Canonical correspondence analysis (CCA), a multivariate direct gradient analysis technique, was used to elucidate the relationships between biological assemblages of species and their environment. Ordination analysis was performed using CANOCO 4.5 (Ter Braak & Šmilauer 2002). The significance of environmental variables to explain the variance of cryptomonad data in the CCA was tested using Monte Carlo simulations with 499 permutations (Ter Braak & Šmilauer 2002).

RESULTS

Environmental parameters

The annual average values of the environmental parameters and phytoplankton biomass of the three investigated basins of Lake Donghu are shown in Figure 1. Annual average values of phytoplankton biomass, DTN and DTP in the Shuiguohu Basin were highest, while the above three values were lowest in the Niuchaohu Basin (Fig. 1a,c). Annual average values of DOC and DIC did not display obvious spatial trends among the three basins (Fig. 1b). Monthly variation of the abiotic variables for the three basins is shown in Figure 2. Water temperature ranged from 1.5 to 34.5°C, and pH values were above 7.0 during the whole monitoring period. DTP and DTN had dramatic change in the Shuiguohu Basin, and DIC and DOC showed similar trends in the three basins (Fig. 2).

Cryptomonads identification and population dynamics

The cryptomonads, as a group, were present in all the samples examined. The identified species were: Komma caudata Hill (Fig. 3a,b), Cryptomonas marssonii (Skuja) emend. Hoef-Emden & Melkonian (Fig. 3c,d), C. obovata Skuja (Fig. 3e), C. pyrenoidifera (Geitler) emend. Hoef-Emden & Melkonian (Fig. 3f), C. platyuris Skuja (Fig. 3g,h), C. curvata (Ehrenberg) emend. Hoef-Emden & Melkonian (Fig. 3i,j), C. tenuis Pascher (Fig. 3k) and Plagioselmis nanoplanctica
During the monitoring period of 2 years, the cryptomonad population showed distinct seasonality in the three basins examined; the biomass of cryptomonads was minimal during winter in the three basins, and rapid population changes were observed in the other seasons (Figs 4, 5). In the Shuiguohu Basin, cryptomonads contributed to the phytoplankton biomass most in summer. In the Guozhenghu Basin, cryptomonads became the dominant species of the phytoplankton community in warm and hot months, and they appeared most significant in spring. In the Niuchaohu Basin, cryptomonads were present in constant but relatively low population throughout the year. Rapid growth in the cryptomonads population was observed once in the Niuchaohu Basin (May 2011).

In the Shuiguohu Basin, Cryptomonas always accounted for more than 90% of the biomass of cryptomonads (Fig. 6a). Except for that in May 2011, when Pandorina sp. bloomed there, K. caudata was the only observed Cryptomonad. In the Guozhenghu Basin, where the cryptomonads had the highest contribution to the phytoplankton biomass, Komma was the richest in cell density among the cryptomonads genera, and Cryptomonas accounted for the highest proportion of the biomass of cryptomonads. Komma was observed throughout the year, and dominated the cryptomonads community during winter. By contrast, Cryptomonas was dominant during spring and autumn. Chroomonas spp. and Plagioselmis spp. mostly proliferated during summer and autumn (Fig. 6b).

In the Shuiguohu Basin, different seasonal dynamics were observed. Cryptomonas marssonii peaked in spring and autumn, and K. caudata mostly proliferated in summer and spring; C. curvata bloomed twice during summer (July 2010 and June 2011). Other cryptomonad species were occasionally observed. The monthly cell density of cryptomonad species in the Shuiguohu Basin are shown in Appendix S2 in supporting information. While in the Guozhenghu Basin, the more common species, K. caudata, C. marssonii, C. obovata and C. pyrenoidifera had similar seasonal dynamics, and they mostly proliferated in spring and autumn. Cryptomonas marssonii bloomed twice in site 2# (September 2011 and May 2012) and once in site 7# (February 2012) in the Guozhenghu Basin. The monthly cell density of cryptomonad species in the Guozhenghu Basin are shown in Appendix S3 in supporting information.

Cryptomonads and environmental factors

The influence of environmental variables on the cryptomonads species is illustrated in Figure 7. In the ordination biplots, arrows represent environmental variables and triangles depict cryptomonads species. The eigen value ($\lambda$) for CCA axis 1 ($\lambda$: 0.132) and CCA axis 2 ($\lambda$: 0.039) explained 84.4% of the variance in the species data. The summary statistics for the first four axes of Canonical correspondence analysis are shown in Appendix S4 in supporting information. CCA axis 1 was mainly negatively correlated with T ($r = -0.881$, $P = 0.001$), and DTP ($r = -0.3205$, $P = 0.041$), and positively correlated with DIC ($r = 0.4215$, $P = 0.023$). CCA axis 2 was mainly positively correlated with DTN ($r = 0.5455$, $P = 0.009$), and negatively correlated with pH ($r = -0.4200$, $P = 0.015$). All the selected environmental variables explained 99.0% of the total variability in species data.
Cryptomonads species were scattered sparsely on the ordination biplot. The two significant environmental variables screened by automatic forward selection of CCA were T ($F = 18.46, P = 0.002$) and DTN ($F = 5.69, P = 0.004$). The test for significance of all canonical axes by Monte Carlo simulation showed that all canonical axes were significant ($F = 6.201, P = 0.002$, 499 permutations under the reduced model, three replicates for each parameter).

Tendencies revealed by CCA indicated that nutrients were decisive factors that influence the temporal and spatial dynamics of the cryptomonads species. DOC promoted *C. marssonii*, which contributed greatly to the phytoplankton biomass in the Guozhenghu Basin; DTP promoted *P. nannoplanctica*; and *C. curvata* have large demands for DTP and DTN.

During the monitoring period, the biomass of cryptomonads was correlated significantly positively with pH value, DTN and DOC ($P < 0.01$) (Table 2). Correlation analysis also showed that phytoplankton biomass had significant positive correlations with the biomass of cryptomonads.

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Fig. 3. Differential interference contrast micrographs of cryptomonads. (a,b) Vento-lateral view of Komma caudata, showing the typical comma shaped cell, a refractive body (R), a blue-green chloroplast (C), a prominent pyrenoid (P) and a ventrally curved tail (arrow). (c,d) Vento-lateral view of Cryptomonas marssonii, showing the sigmoid cell shape, a large number of starch grains (S), two unequal flagella (F) and a dorsally curved tail (arrow). (e) Vento-lateral view of C. obovata, showing the typical obovoid cell shape, a lobed appearance at the cell subapex (arrow) and rows of ejectoisomes (E) located near the furrow. (f) Dorsal view of C. pyrenoidifera, showing the ellipse cell shape and two prominent pyrenoids (P). (g) Ventral view of C. platyuris, showing the slightly twisted cell shape, two Corps de Maupas (M) and rows of ejectosomes (E). (h) Lateral view of C. platyuris, showing the dorsal-ventrally compressed cell shape. (i) Vento-lateral view of C. curvata, showing the rostrate antetior (arrow), and large ejectosomes (E) located near the furrow. (j) Vental view of C. curvata, showing the numerous pyrenoids (P). (k) Vental view of C. tenuis, showing the ellipsoid cell shape, and the arrangement of starch grains near the edge of chloroplast. (l) Lateral view of Plagioselmis nanoplanctica, showing the brownish chloroplast and the acute tail (arrow). (a,c,e,f,g,h,l,k,l) living cells. (b,d,j) cells preserved with Lugol’s solution. Scale bars = 10 μm.
DISCUSSION

At least 12 cryptomonad morphotypes were observed in our samples collected from Lake Donghu, but only eight species were identified by light microscopy by virtue of their distinct morphological characters. There are still many cryptomonad species that cannot be properly identified under light microscopy. In order to get a more comprehensive understanding of the ecological habits of these flagellated microalgae, a combined means including light and electron microscopical and molecular data urgently need to be developed. In addition, the identified cryptomonads in the present study are all common species reported in other parts of the world, which highlighted their eurytopicity.

Previous studies revealed that cryptomonads often dominate the phytoplankton community in cool and under-ice water (Barlow & Kugrens 2002; Vance et al. 2013). The present study showed they were also dominant in a shallow lake in the subtropical region of China. It is widely believed that resource availability, water motion and temperature largely contribute to set the specific composition of the phytoplankton assemblages, the shape and size of the organisms involved and their seasonal succession (Naselli-Flores et al. 2007; Naselli-Flores & Barone 2011). Hence, we inferred two main abiotic factors for the domination of cryptomonads in the Guozhenghu Basin. On one hand, in eutrophic and hyper-trophic environments, light availability is a major force shaping phytoplankton assemblages (Naselli-Flores et al. 2007). The water body in the Guozhenghu Basin was very turbid, with a secchi depth of approximately 40 cm (Yan et al.

Table 1. Morphological characteristics used to identify cryptomonad species

<table>
<thead>
<tr>
<th>Species</th>
<th>Cell length (μm)</th>
<th>Cell shape</th>
<th>Colour</th>
<th>Furrow</th>
<th>Chloroplast number</th>
<th>Ejectosomes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kom</td>
<td>8–12</td>
<td>Comma shaped</td>
<td>Blue-green</td>
<td>Narrow, straight, short</td>
<td>1, with a prominent pyrenoid</td>
<td>2 rows</td>
</tr>
<tr>
<td>Cma</td>
<td>16–33</td>
<td>Sigmoid</td>
<td>Olive green</td>
<td>Wide, straight, long</td>
<td>2, without pyrenoids</td>
<td>2 rows</td>
</tr>
<tr>
<td>Cob</td>
<td>18–26</td>
<td>Obovate</td>
<td>Olive green</td>
<td>Wide, straight, long</td>
<td>2, without pyrenoids</td>
<td>4–5 rows</td>
</tr>
<tr>
<td>Cpy</td>
<td>15–27</td>
<td>Ellipsoid</td>
<td>Olive green</td>
<td>Narrow, straight, short</td>
<td>2, with a prominent pyrenoid each</td>
<td>2 rows</td>
</tr>
<tr>
<td>Cpl</td>
<td>33–55</td>
<td>Flattened, twisted</td>
<td>Olive green</td>
<td>Wide, curved, long</td>
<td>2, without pyrenoids</td>
<td>6–8 rows</td>
</tr>
<tr>
<td>Ccu</td>
<td>35–48</td>
<td>Sigmoid</td>
<td>Olive green</td>
<td>Wide, curved, long</td>
<td>2, with 3–4 pyrenoids each</td>
<td>8–10 rows</td>
</tr>
<tr>
<td>Cte</td>
<td>8–14</td>
<td>Oblong</td>
<td>Olive green</td>
<td>Narrow, straight, short</td>
<td>2, without pyrenoids</td>
<td>2 rows</td>
</tr>
<tr>
<td>Pla</td>
<td>8–15</td>
<td>Comma shaped</td>
<td>Brownish red</td>
<td>Narrow, straight, short</td>
<td>1, with a prominent pyrenoid</td>
<td>2 rows</td>
</tr>
</tbody>
</table>

Fig. 4. Monthly trends of the biomass of cryptomonads (CB; shading) and percentage of cryptomonads in total phytoplankton biomass (PCB; line) in three basins of Lake Donghu.

Fig. 5. Seasonal trends CB and PCB in three basins of Lake Donghu. See Figure 2 for other information.
Cryptomonads and lake trophy

1997; Mei et al. 2007), and cryptomonads could tolerate low irradiance (Morgan & Kalff 1975; 1979; Pithart 1999). On the other hand, cryptomonads were reported to favour alkaline conditions and most prominent in lakes with pH values above

![Graph 1](image1)

**Fig. 6.** Monthly trends of the biomass of cryptomonads in the Shuiguohu Basin and the Guozhenghu Basin of Lake Donghu. Cry = Cryptomonas; Chr = Chroomonas; Kom = Komma; Pla = Plagioselmis; (a) the Shuiguohu Basin; (b) the Guozhenghu Basin.

![Graph 2](image2)

**Fig. 7.** Ordination biplot of cryptomonads species assemblages and environmental variables obtained by Canonical correspondence analysis in Lake Donghu. Ccu: Cryptomonas curvata; Chr: Chroomonas sp.; Cma: Cryptomonas marssonii; Cpy: Cryptomonas pyrenoidifera; Cob: Cryptomonas obovata; Kom: komma caudata; Pla: Plagioselmis nannoplanctica.

|   | T  | pH  | DTN | DTP | DOC | DIC | PB  | Kom | Chr | Cma | Cpy | Ccu | Cob | Pla | CB  |
|---|----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
|   |    |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
| T | 1.000 | 0.316** | 0.215** | 0.185* | 0.211** | 0.175* | 0.190* | 0.221** | 0.156** | 0.190* | 0.215** | 0.185* | 0.221** | 0.156** | 0.190* | 0.215** |
| pH | 1.000 | 0.316** | 0.215** | 0.185* | 0.211** | 0.175* | 0.190* | 0.221** | 0.156** | 0.190* | 0.215** | 0.185* | 0.221** | 0.156** | 0.190* | 0.215** |
| DTN | 1.000 | 0.316** | 0.215** | 0.185* | 0.211** | 0.175* | 0.190* | 0.221** | 0.156** | 0.190* | 0.215** | 0.185* | 0.221** | 0.156** | 0.190* | 0.215** |
| DTP | 1.000 | 0.316** | 0.215** | 0.185* | 0.211** | 0.175* | 0.190* | 0.221** | 0.156** | 0.190* | 0.215** | 0.185* | 0.221** | 0.156** | 0.190* | 0.215** |
| DOC | 1.000 | 0.316** | 0.215** | 0.185* | 0.211** | 0.175* | 0.190* | 0.221** | 0.156** | 0.190* | 0.215** | 0.185* | 0.221** | 0.156** | 0.190* | 0.215** |
| DIC | 1.000 | 0.316** | 0.215** | 0.185* | 0.211** | 0.175* | 0.190* | 0.221** | 0.156** | 0.190* | 0.215** | 0.185* | 0.221** | 0.156** | 0.190* | 0.215** |
| PB  | 1.000 | 0.316** | 0.215** | 0.185* | 0.211** | 0.175* | 0.190* | 0.221** | 0.156** | 0.190* | 0.215** | 0.185* | 0.221** | 0.156** | 0.190* | 0.215** |
| Kom | 1.000 | 0.316** | 0.215** | 0.185* | 0.211** | 0.175* | 0.190* | 0.221** | 0.156** | 0.190* | 0.215** | 0.185* | 0.221** | 0.156** | 0.190* | 0.215** |
| Chr | 1.000 | 0.316** | 0.215** | 0.185* | 0.211** | 0.175* | 0.190* | 0.221** | 0.156** | 0.190* | 0.215** | 0.185* | 0.221** | 0.156** | 0.190* | 0.215** |
| Cma | 1.000 | 0.316** | 0.215** | 0.185* | 0.211** | 0.175* | 0.190* | 0.221** | 0.156** | 0.190* | 0.215** | 0.185* | 0.221** | 0.156** | 0.190* | 0.215** |
| Cpy | 1.000 | 0.316** | 0.215** | 0.185* | 0.211** | 0.175* | 0.190* | 0.221** | 0.156** | 0.190* | 0.215** | 0.185* | 0.221** | 0.156** | 0.190* | 0.215** |
| Ccu | 1.000 | 0.316** | 0.215** | 0.185* | 0.211** | 0.175* | 0.190* | 0.221** | 0.156** | 0.190* | 0.215** | 0.185* | 0.221** | 0.156** | 0.190* | 0.215** |
| Cob | 1.000 | 0.316** | 0.215** | 0.185* | 0.211** | 0.175* | 0.190* | 0.221** | 0.156** | 0.190* | 0.215** | 0.185* | 0.221** | 0.156** | 0.190* | 0.215** |
| Pla | 1.000 | 0.316** | 0.215** | 0.185* | 0.211** | 0.175* | 0.190* | 0.221** | 0.156** | 0.190* | 0.215** | 0.185* | 0.221** | 0.156** | 0.190* | 0.215** |
| CB  | 1.000 | 0.316** | 0.215** | 0.185* | 0.211** | 0.175* | 0.190* | 0.221** | 0.156** | 0.190* | 0.215** | 0.185* | 0.221** | 0.156** | 0.190* | 0.215** |

*P < 0.05; **P < 0.01. T, water temperature (°C); DTN, dissolved total nitrogen (mg L⁻¹); DTP, dissolved total phosphorus (mg L⁻¹); DIC, dissolved inorganic carbon (mg L⁻¹); DOC, dissolved organic carbon (mg L⁻¹); PB, total biomass of cryptomonads (mg L⁻¹); C, total biomass of Chroomonas sp. (mg L⁻¹); CB, total biomass of cryptomonads (mg L⁻¹).
7.5 (Kugrens & Clay 2003). In the Guozhenghu Basin of Lake Donghu, the pH values were always above 7.0.

The proportions of the cryptomonads in phytoplankton in the Shiguohu Basin and the Niuchao Basin of Lake Donghu were lower than that in the Guozhenghu Basin. We infer this was due to the fact that the Niuchao Basin is in a sparsely populated district, and the pollution from human activities is relatively low. In the Niuchao Basin, the phytoplankton community was mainly dominated by diatoms and chrysophytes. The mesotrophic habitat was not favourable for cryptomonads (Reynolds et al. 2002). By contrast, the Shiguohu Basin was located in a densely populated district, and the pollution from human activities is the most severe among all basins of Lake Donghu. In addition, the water region is narrow, almost static and semi-enclosed. This hypotrophic water body promoted several pollution-resistant species, such as Microcystis, Oscillatoria, Pandorina, Lepocinclis, and Phacus. Cryptomonads were not dominant species because of their relatively small size, although their population was also large.

Different opinions exist about the abiotic factors that regulate the population of cryptomonads. Several studies assumed that cryptomonads were not affected by the nutrient condition because they were ubiquitous, and the cryptomonads population was mainly regulated by grazing pressure (Ilmavirta 1983; Willén 1992; Barone & Naselli-Flores 2003). In the Guozhenghu basin of Lake Donghu, the biomass of zooplankton was highest in summer (Huang et al. 1984; Chen et al. 1991), and the relatively low population of cryptomonads in summer was probably caused by grazing.

Other studies have reported that the variation in pH causes differences in cryptomonads populations (Pringsheim 1968; Klaveness 1988a; Kugrens & Clay 2003). In the present study, the biomass of cryptomonads was significantly correlated with pH values ($P<0.01$). However, determining the primary factor responsible for these differences is difficult, because other environmental factors are coupled with pH under natural conditions. DIC was considered to be an important factor, which was coupled with pH closely (Stumm & Morgan 1995). However, in the current study, DIC was not significantly related to the biomass of cryptomonads as revealed in the Spearman correlation ($P>0.05$).

Dissolved organic carbon and DTN were significantly correlated with the total biomass of cryptomonads ($P<0.01$) in the present study. Several studies have indicated that dissolved organic matter does not enhance the growth of photoautotrophic cryptomonads in lab cultures (Lewitus & Caron 1991; Arvola & Tulonen 1998). The enlarged population in Lake Donghu when DOC increased was probably caused by bacterial respiration, during which the bacteria oxidized the organic molecules and released CO$_2$ (Arvola & Tulonen 1998; Lee & Kugrens 1998), or by bacterial ingestion of some cryptomonads (Tranvik et al. 1989; Kugrens & Lee 1991).

Previous studies reported that nitrate promoted growth of marine cryptomonads (Antia & Chorney 1968; Antia et al. 1975). Nevertheless, in freshwater, nitrogen had not been considered as a critical factor that affects the cryptomonads population. We assumed this is because in many freshwater habitats investigated in the previous studies, the cryptomonads population was mainly regulated by grazing pressure and the influence of lake trophy was overlooked. In the examined lake in this study, however, the grazing pressure on cryptomonads was most significant in summer. And nutrients played a relatively more important role in regulating the cryptomonads population in the other seasons.

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REFERENCES


SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher’s web-site:

Appendix S1. Sampling map.


Appendix S4. Summary statistics of Canonical correspondence analysis.

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