The significance of phosphorus in algae growth and the subsequent ecological response of consumers

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ABSTRACT

Human activities have substantially disrupted phosphorus (P) cycles in the ecosystem, affecting producers and consumers along the food chain. To assess the ecological effects of imbalanced P on producers as well as consumer reactions to changes in food quality, the effects of P concentrations (HP, MP, LP) on \textit{Scenedesmus obliquus}, were investigated. To investigate the indirect effects of P levels on consumer feeding behavior and life history strategies, the algae were fed to \textit{Rotaria rotatoria}. The results showed that P concentrations increased population density, environment capacity, cell size, specific growth rate, chlorophyll a, and chlorophyll b substantially. As a result of the P intracellular concentration of algae produced in HP and MP media, the algae were classified as two categories of food quality (P-rich, P-poor). Rotifers' grazing and filtration rates were significantly increased when they were fed P-poor algae. In reaction to a lack of P in their diet, rotifers extended their juvenile and reproductive periods, resulting in a longer life span, generation time, and life expectancy at rotifer hatching. Despite living longer than P-rich groups, rotifers fed P-poor algae produced much fewer offspring and had a significantly lower net reproductive rate, which was linked to the rotifers' longer generation period. According to the findings, phosphorus has a major impact on algal food quality, and herbivorous consumers are subjected to significant food quality variation of algae, which they respond to by modifying their life history strategies and feeding behavior.

1. Introduction

Phosphorus (P), a fundamental element of all life, is essential to aquatic ecosystems (Aversa et al. 2016; Roy 2017). In organisms, P is not only the backbone component of nucleic acids but also the transmission center of chemical energy through ATP (Brembu
et al. 2017). Particularly, P is an essential component of ribosomal RNA, which drives the synthesis of protein, and further influences the growth and reproduction of organisms (Zhou 2019). Studies also have demonstrated that the expression of many genes may be regulated indirectly by phosphate content (excess or limited) at the post-transcriptional or post-translational levels (Anne-Marie et al. 2020; Guo et al. 2016). In ecosystems, P, both inorganic and organic, is requisite nutrients for nearly all photoautotrophs, such as microbes, algae and plants (Elser et al. 2007; Grossman and Aksoy 2015). Therefore, the phosphorus in waters plays a vital role in maintaining the growth and metabolism of organisms and stability of ecosystems.

Phytoplankton biomass and production can be controlled by phosphorus availability, which is one of the classical paradigms in modern limnology (Lewis and Wurtsbaugh 2008). P input excessively in water results in eutrophication, exhibiting by harmful algal blooms, changes in phytoplankton and zooplankton community structure, as well as food chain chaos (Grossman and Aksoy 2015; Schindler et al. 2016; Schmoker et al. 2016; Xu et al. 2010). On the contrary, many freshwater ecosystems are oligotrophic caused by nutrient deficiency (Elser et al. 2009; Stockner et al. 2000). A low level of accessible P often impacts the community composition and limits the growth, biomass (Mousing et al. 2018; Reed et al. 2016; Teufel et al. 2017), the amount of highly unsaturated fatty acids (Anne-Marie et al. 2020; Challagulla et al. 2015) and metabolic activities (Karl 2014) of phytoplankton, resulting in different food quality for the subsequent zooplankton consumers. As a consequence of P limitation, photoautotrophs evolve a series of adaptive strategies to cope with phosphorus deficiency better, and nutrient-sparing reactions of algae were motivated in the environment of insufficient phosphorus (Grossman and Aksoy 2015). For example, the transcription factor inorganic phosphate starvation response1 (PSR1) and lipid remodeling regulator 1 (LRL1) were the global regulators of phosphorus deficiency responses in green algae Chlamydomonas reinhardtii (Bajhaiya et al. 2016; Hidayati et al. 2019). Studies showed that truncated hemoglobins (trHbs) may be implicated in functions other than oxygen delivery, for example, the depletion of some trHb genes (THB1 and THB2) may lead to a reduction in cell size and chlorophyll levels under conditions of P deprivation (Filina et al. 2019). However, little is known if the nutrient level in algae is affected positively by the phosphorus concentration in the culture medium.

Zooplankton dwells in rapidly changing environment, with the instability of abundance and quality of food resources. As unselective filter feeders, zooplankton is highly susceptible to algal food quality (Schälicke et al. 2019), so the food in nature for freshwater zooplankton (cladoceras, copepods and rotifers) are often restricted seriously (Kirk 1997). Previous studies have indicated that the dietary energy from algae is highly retained in the aquatic food webs (Guo et al. 2016). Insufficiency of nutrients such as nitrogen and phosphorus in the water body can cause the growth of algae to stagnate or decrease in reproduction, resulting in high mortality of zooplankton and a decline in the population of zooplankton. Thus, nutrient stoichiometry in the primary producers can affect subsequent consumers’ growth (Burian et al. 2020; Darchambeau 2005; Elser et al. 2001; Malzahn and Boersma 2012), egg size and number (Franco-Santos et al. 2018; Nobili 2013) and feeding behavior (Meunier et al. 2016; Vad et al. 2020). Therefore, the nutrient quality of algae is critical for the subsequent zooplankton consumers. Studying on the life history characteristics of rotifer is of great significance to explain the competition and utilization of food resources by grazing zooplankton.

Rotaria rotatoria is an asexual freshwater bdelloid rotifer, although which has been designated as indicator of heavy pollution, its response strategies to nutrient levels are still
need to be further studied, and little evaluation has been explored to understand the relative importance of direct and indirect effects of nutrient element on producers and consumers. In this study, the main aims are: (1) to assess the relative effects of P limitation and rich on producers; (2) to explore the life history strategy of grazing consumers under different food quality; (3) to make clear how consumers regulate feeding behavior in response to changes in food quality.

2. Materials and methods

2.1. Experimental organisms

In this study, the algae \textit{S. obliquus} was purchased from the Freshwater Algae Culture Collection at the Institute of Hydrobiology (FACHB-collection), then semi-continuously cultured in illumination incubator \((28 \pm 1^\circ C, 3000Lx, \text{Light: Dark} = 12h:12h)\) with the BG-11 medium (Andersen 2005). The \textit{R. rotatoria} was sampled from a pond near Jing village \((31^\circ 73'67'' N, 118^\circ 33'72'' E)\) in Hexian County, Anhui Province, China. After collection, rotifer individuals were clonally cultured at \(28 \pm 1^\circ C\), with the green algae \textit{S. obliquus} as food at the density of \(1.0 \times 10^6 \text{cells}\cdot\text{mL}^{-1}\). The rotifer culture was maintained using an EPA medium, which contained \(96mg \text{NaHCO}_3, 60mg \text{CaSO}_4, 60mg \text{MgSO}_4\cdot7\text{H}_2\text{O}\) and \(4mg \text{KCl}\) per liter of distilled water \((\text{pH} 7.4–7.8)\) (Peltier and Weber 1985).

2.2. Algal growth experiment

In this experiment, semicontinuous cultures of \textit{S. obliquus} were established in BG-11 medium with high P \((2mg\cdot\text{L}^{-1}, \text{HP})\), medium P \((0.2mg\cdot\text{L}^{-1}, \text{MP})\) and low P \((0.02mg\cdot\text{L}^{-1}, \text{LP})\) according to the P concentration classification in the environmental quality standards for surface water, and the medium without P was set as the control. The algae in the exponential growth phase were inoculated in four mediums to a final density of \(1.0 \times 10^5 \text{cells}\cdot\text{mL}^{-1}\). During the experiments, density of algae in each group was determined for every day by counting using a hemocytometer. Seven days later, the experiment was terminated. According to the daily density of algae specific growth rate \((\mu)\) was calculated with Equation (1).

\[
\mu_{i\rightarrow j} = \frac{\ln X_j - \ln X_i}{t_j - t_i} \text{ (day}^{-1})
\]

where \(\mu_{i\rightarrow j}\) is the specific growth rate from time \(i\) to \(j\); \(X_j\) is the density at time \(j\); and \(X_i\) is the density at the time \(i\).

At the end of the experiments, cell sizes of algae were determined by picture which photographed in a microscope (Leica DM2000), and cell volumes \((V)\) were calculated with Equation (2). Besides, algae were collected by centrifugation \((12000\text{rpm, }5\text{min})\) to remove the excrecent medium. Centrifugal algae with 5ml 80% acetone were dipped in a water bath \((55^\circ C)\) for 60min to extract chlorophyll. The absorptivity at 663nm and 645nm were determined by spectrophotometer, and the chlorophyll content was calculated with Equations (3) and (4).

\[
V = \frac{2}{3} \pi a^2 b
\]

Chlorophyll a \((\text{Ca, mg/L}) = 12.7 \times A_{663} - 2.69 \times A_{645}
\]
Chlorophyll b \((\text{Cb}, \text{ mg/L}) = 22.9 \times A_{645} - 4.68 \times A_{663}\) \((4)\)

where \(a\) is the half of algae cell width, \(b\) is the half of algae cell length, \(A_{663}\) is the value of absorptivity at 663 nm, and \(A_{645}\) is the value of absorptivity at 645 nm.

Moreover, centrifuged algae were dried at bake oven (30°C, 24 h) for C, N and P element detection by the Science Spectrum R&D Center (Qingdao, China). C and N were detected by an elemental analyzer (Elementar vario MICRO cube\textsuperscript{MT}) and P was detected by ICP-OES (iCAP7400).

### 2.3. Feeding experiments

The algae cultured in different (Control, HP, MP and LP) mediums were collected by centrifugation at 4000 rpm for 5 min on the seventh day. After collection, \(S. \text{obliquus}\) was washed three times with bicarbonate solution (15 mg·L\(^{-1}\)) to remove trace of dissolved P in the algal medium. In the feeding experiment, ten neonates (less than 6 h old) were transferred to 8-mL glass beakers containing 5 mL EPA medium with the washed algae at the density of \(1.0 \times 10^6\) cells·mL\(^{-1}\). Subsequently, a plastic board was used to cover on beaker for preventing the evaporation of water from EPA medium, and then the container was put in an incubator with natural illumination at 28 ± 1°C. Each treatment was repeated three times. According to the previous results of life table experiment, the time at the first offspring of \(R. \text{rotatoria}\) appeared was about 60–80 h. Therefore, all experiments were sustained for 60 hours for avoiding the disturbance of neonatal offsprings to the filtration and grazing rates, during the process no extra algae food was supplied to rotifers. In addition, for preventing the algal deposition in the experiment, we suspended the algae culture every 8 h. After that, the density of unconsumed algae cells was measured using a hemocytometer. The EPA medium, containing algae at \(1.0 \times 10^6\) cells·mL\(^{-1}\) without rotifers, was set as reference.

The grazing rate refers to the amount of food that an individual ingests in a specific period of time, and the filtration rate is expressed as the volume of swept the filter-feeder to collect food. In other words, the filtration rate \((F)\) is the average volume of liquid filtered by each rotifer per unit time (ml·ind.\(^{-1}\)·h\(^{-1}\)), and the grazing rate \((G)\) is the average number of algae cells taken by each rotifer per unit time (cells·ind.\(^{-1}\)·h\(^{-1}\)), which can be calculated based on the Equations (5) and (6) (Frost 1972):

\[
F = \frac{V}{n} \times \frac{(\ln C_t - \ln C_{tf})}{t} \quad (5)
\]

\[
G = F \times \frac{C_{gf} - C_0}{\ln C_t - \ln C_0} \quad (6)
\]

where \(V\) is the medium volume (ml); \(t\) is the experimental time (h); \(n\) is the number of rotifers in each replicate; \(C_0\) and \(C_{gf}\) are the initial and final densities of a given algae; and \(C_t\) is the final algal density of the reference group in which no rotifer is present and the algae \(S. \text{obliquus}\) is cultured synchronously with the test groups.

### 2.4. Life history traits experiments

The life history experiment of \(R. \text{rotatoria}\) was also performed with four treated algae (Control, LP, MP and HP). For each treatment, 48 neonates, born within 6 h, were transferred into two 24-well tissue culture plates by introducing one neonate into each well which contained 0.5 mL EPA medium with \(1.0 \times 10^6\) cells·mL\(^{-1}\) of \(S. \text{obliquus}\). The eight
plates (two plates for each group) were put in a nature illumination incubator at 28 °C. During the initial several days, all rotifers were inspected every 6 h until all neonates produced offspring. Here, we recorded the time of the first offspring produced. Afterwards, the number of original alive individuals and neonates were recorded every 12 h and the neonates were removed. Besides, the rotifer medium was renewed every 24 h, and simultaneously the fresh food was supplied before the whole cohort died.

Based on the data collected, the juvenile period \((P_1)\), reproductive period \((P_2)\), post-reproductive period \((P_3)\), the number of offspring \((NO)\) and mean lifespan \((ML)\) of rotifers fed with different treated algae were calculated. The age-specific survival \((l_x)\) and age-specific fecundity \((m_x)\) were constructed for each experiment group using conventional life-table techniques (Poole, 1974). Life expectancy at hatching \((e_0)\), generation time \((T)\) and net reproductive rate \((R_0)\) were calculated with Equations (7)–(9). The intrinsic rate of increase \((r_m)\) was first approximated using: 

\[
  r_{\text{rough}} = \ln R_0 / T
\]

For final calculation, we solved with Equation (10).

\[
  e_x = \frac{T_x}{n_x}
\]

\[
  R_0 = \sum_{0}^{\infty} l_x m_x
\]

\[
  T = \frac{\sum x l_x m_x}{R_0}
\]

\[
  \sum_{x=0}^{n} e^{-rx} l_x m_x = 1
\]

2.5. Data analysis

All data were analyzed by using SPSS 25.0 and expressed as Mean ± SE (standard error). The one-sample Kolmogorov-Smirnov procedure and Levene’s test were used to test the data for normality and homogeneity of variances, respectively. Kaplan-Meier analyses were performed to test for the differences in the age-specific survivorships of rotifers fed with different quality algae. One-way analysis of variance (ANOVA) was conducted to identify the significant effect of phosphorus on each of the population variables of algae. The life-history traits of rotifers also performed by one-way ANOVA. Multiple comparisons were conducted using Student-Newman-Keuls (SNK) to identify which groups were significantly different among treatments. The statistically significant level \((p)\) was set as less than 0.05.

3. Results

3.1. Algal growth

In different experimental groups, the density of \(S.\ obliquus\) increased daily, and each group achieved maximum population density at day 7 (Figure 1). The population density of treatment groups was higher and increased faster than that in control group. The relevant parameters were analyzed among different groups and the results showed in Table 1. The \(P\) concentration in the medium significantly increased the specific growth rate \((\mu)\) \((p < 0.05)\). The cell volumes of algae were significantly bigger in the MP and HP treatments than the control group \((p < 0.05)\). Moreover, the chlorophyll a \((Ca)\) in groups of
MP and HP were significantly much higher compared with the control and LP (p < 0.05). However, no significant difference was found in chlorophyll b (Cb) among all groups (p > 0.05). In this experiment, the result showed that the C, N and P content in algae were 343.4–388.7 mg/g, 82.2–97.2 mg/g and 0.6–11.5 mg/g, respectively. The nitrogen content in different experimental groups was nonsignificant (p > 0.05). However, the content of P in groups of MP and HP increased significantly compared with the control and LP, and the contents of C in three treatments were higher significantly than the control. We also analyzed the ratio of different elements (Figure 2), and the results showed that the values of C:P ratio and N:P ratio in control and LP were significantly higher than MP and HP (p < 0.05), corresponding to two different food quality (P-poor at LP and control, P-rich at MP and HP). Additionally, significant differences were not found in C:N ratio (p > 0.05).

3.2. The feeding experiment of R. rotatoria

Alterations in feeding behaviors of zooplankton can be an indicator of food quality. The results of one-way ANOVA with SNK-q method indicated that food quality had a significant effect on feeding behaviors of rotifers, both the grazing and the filtration rates (p < 0.05, Figure 3). Compared with P-rich food (MP and HP), rotifers had higher grazing and filtration rates by feeding the P-poor algae (Control and LP). In other words, the P concentration in environment indirectly affected the feeding behavior of rotifers by adjusting the essential element components and ratio in algae (food quality).
3.3. Life history strategy

The results of the one-way ANOVA investigating the life history strategy on the development duration, offspring production and population growth are presented in Figure 4. It was indicated that the life history demographic parameters were strongly correlated with food quality. The age at which the first offspring appeared ($P_1$) was younger significantly with the enriching phosphorus in the algae ($p < 0.05$). In addition to earlier maturation, rotifers fed with the P-insufficient food (Control, LP and MP) reproduced for a longer duration ($P_2$) than those fed with P-sufficient food (HP) ($p < 0.05$). There was no significant effect of food quality on the duration of post-reproductive period ($P_3$) except for the significantly longer $P_3$ in the HP group than that in MP ($p > 0.05$) (Figure 4-I). Correspondingly, the mean lifespan ($ML$), the life expectancy at hatching ($e_0$) and the generation time ($T$) of rotifers fed with P-poor food were significantly longer than those fed with P-rich food ($p < 0.05$) (Figure 4-II). On the other hand, rotifers in the P-rich
The groups had high fecundity, as evidenced by a significant increase in the number of offspring (NO), the net reproductive rate \((R_0)\) and the intrinsic rate of increase \((r_m)\) with raising of P content in food \((p < 0.05)\) (Figures 4-III and 4-IV).

We compared the survivorship and fecundity of rotifers fed with different food quality of algae using standard life table methods (Figure 5). The Kaplan-Meier survival analysis showed that no matter what the food quality was, food quality had no significant influence on the survivorship of \(R.\ rotatoria\) \((p > 0.05)\). However, the age-specific survivorship \((l_x)\) of treatment groups tended to decrease earlier compared with the control. As for the age-specific fecundity \((m_x)\), the maximum values in control, LP, MP and HP groups were 0.50, 0.67, 1.13 and 1.14 ind. respectively, and their reproduction periods lasted 25, 25, 21 and 20 days, moreover, the peaks of all treatments appeared earlier compared with control.

4. Discussion

Compared with terrestrial organic matter, algae are generally recognized as high-quality food for the growth and reproduction of subsequent consumers (Guo et al. 2016). However, environmental change-induced fluctuation of P element could cause an alternation of algal food quality directly, which may further lead to significant influence on the
subsequent consumers. Previously it was reported that P is the limiting factor for the phytoplankton growth, and its excessive content in the environment leads to the massive growth of algae (Song et al. 2018; Young and Beardall 2003). While severe P limitation caused algae to develop high C:P and N:P ratio in biomass and that imbalanced stoichiometric components provide poor-quality food for consumers (Souza et al. 2012; Sterner and Elser 2002). What’s more, the minimum law of Liebig also states that under any circumstances, there is only one factor that can restrict the growth and reproduction of organisms, which shows that the increase in growth rate should stabilize with the increase of P concentration if P is a restrictive element (Becker and Boersma 2003). In the present study, population density, environmental capacity, specific growth rate, chlorophyll a, cell sizes and P content in algal cells increased with the gradual enhancement of P in the medium. No matter what the population parameter is, significantly difference was not found between group MP and HP. The experimental results are consistent with the previous theories and supplied more ecological characteristics for algal culture under the fluctuant environment.

The feeding behaviors of zooplankton can be changed over time, depending on endogenous rhythms and exogenous variables (Gustav-Adolf 1988). Previous studies have

Figure 5. Age-specific survivorship ($l_x$ filled square) and fecundity ($m_x$ unfilled square) of $R$. rotatoria fed with different food quality of algae (Mean ± SE).
shown that zooplankton can amplify their feeding ability in response to low stoichiometric food to make up for deficiencies in essential elements (Hillebrand et al. 2009). Mandal et al. (2018) also found that phytoplankton with high cellular C:N and C:P ratio was grazed more intensely by Daphnia, and fatty acid unsaturation and short average chain length were more important than any aspect of algal stoichiometry in feeding conversion efficiencies of Daphnia. Because of the interdependency among the grazing rate, growth and reproduction, high grazing rates of zooplankton will benefit the growth and reproduction of filter feeders (without limitation of food quantity) and result in rapid growth of zooplankton (Ashforth and Yan 2008; Rinke and Vijverberg 2005). In this study, the results showed that S. obliquus cultured in BG-11 medium with low P concentration (0–0.02 mg/L) had higher C:P ratios, which resulted in the grazing and filtration rates of R. rotatoria fed with P-poor food were significantly higher than those fed with P-rich food. Our results indicate that rotifers increase their food consumption rate in order to compensate for low stoichiometric food quality. However, the offspring productions of rotifers with high feeding rates (Control and LP) were significantly lower than those with low feeding rates (MP and HP), which may attribute to the interpretation that the increasing food quantity does not offset the restriction of low food quality on the reproduction of rotifers. The effect of S. obliquus on R. rotatoria reproduction is likely a combined influence of grazing resistance and poor food quality (element composition).

Rotifera is one of the oldest model organisms in ecology, evolution and environmental science because of its sensitivity to environmental changes. Many studies have shown that the difference in life-history strategies of zooplankton induced by varied food quality (Lürling et al. 1997; Vanni and Lampert 1992). Jensen and Verschoor (2004) found that the duration of juvenile period, reproductive period and post-reproductive period of Brachionus calyciflorus differed significantly among food types. Moreover, Vanni (1987) suggested that the age at first reproduction of Daphnia was earlier in eutrophic lake water. In this study, the duration of juvenile period and reproductive period were significantly shortened with the increase of P content in food. Our results are consistent with this conclusion. Due to the difference in age structure, the mean lifespan, generation time and the life expectancy at hatching of rotifers fed with P-poor algae are significantly longer than those with P-rich food, which could be attributed to the faster metabolic rate under sufficient phosphorus supply.

The intrinsic rate of population growth, a good indicator of a specific population response to environment changes, can sensitively reflect subtle changes in the environment. In the study on the effect of different nutritional limitations on the growth rate, Kilham et al. (1997) found that population growth rates of Daphnia pulicaria reduced significantly under conditions of P-poor algae. In addition, the P-poor diet may bring the population density and biomass down compared with the P-rich food (Pulkkinen et al. 2014). In our study, the highest intrinsic rates of population growth occurred when R. rotatoria fed with P-rich algae. At the same time, the intrinsic rates of population growth increased significantly with the raise of P content in food in a certain range.

**Conclusion**

This study indicated that the chlorophyta S. obliquus, which is one of the most widespread and dominant mixotrophic flagellate genus in freshwater, generated the P-poor and P-rich food quality and altered the life history strategy in rotifers. Briefly, the P concentration in environment directly affected the growth of algae, including the population density, specific growth rate, photosynthetic pigment and food quality (element ratio and
cells sizes). Furthermore, P-rich algae significantly shortened the duration of development and reproductive period by accelerating the metabolic rate, but with the compensation of increasing offspring reproduction and net reproductive rate. We compared the feeding behaviors of *R. rotatoria* by providing four types of algae cultured under different P concentrations, not only grazing rate but also filtration rate enhanced significantly as rotifers fed with P-poor food. Consequently, it was concluded that the P content not only affected the growth of primary producer directly, but also affected the subsequent consumers indirectly via alteration in the stoichiometric food quality. This study may improve our understanding of the underlying role of phosphorus in affecting aquatic food chain in complex natural environment.

**Disclosure statement**

The authors declare that they have no conflict interest.

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