

# Phytoplankton productivity in a pond of brownish-colored water in a Japanese lowland marsh, Naka-ikemi

Kentaro Nozaki · Yukihiro Kohmatsu ·  
Toshiya Yamamoto · Akihiro Tuji

Received: 30 January 2009 / Accepted: 30 March 2009 / Published online: 16 May 2009  
© The Japanese Society of Limnology 2009

**Abstract** To understand the characteristics of the ecosystem in Japanese lowland marsh, we investigated chlorophyll-*a* (Chl. *a*), photosynthesis and respiration of a phytoplankton community in a brownish-colored pond in Naka-ikemi marsh, Tsuruga, Fukui Prefecture. Chl. *a* concentrations and volumetric gross primary production rates ranged between 1.3–57.0  $\mu\text{g Chl. } a \text{ l}^{-1}$  and 148–1619  $\mu\text{g C l}^{-1} \text{ day}^{-1}$  during the study period. Higher values of Chl. *a* and primary production rates were clearly observed from June to September, when the dominant algae were the phytoflagellates, *Peridinium* (Dinophyceae) and *Cryptomonas* (Cryptophyceae), with swimming ability. The trophic status of the pond water of Naka-ikemi marsh was defined as being in eutrophic condition based on the biomass and productivity of phytoplankton. However, depths of  $Z_{1\%}$  showing the productive layer in this study

site were relatively narrower than those observed in the hyper-eutrophic Lake Suwa with frequent cyanobacterial water bloom. Factor-attenuating underwater light intensity in Naka-ikemi marsh was presumed to be colored dissolved organic matter. Thus, not only phytoplankton primary production, but also allochthonous organic matter supplied from the catchment area seems to be the dominant factor in the whole energy budget of the pond. In conclusion, we regarded the pond ecosystem in Naka-ikemi marsh to be in a eutrophic–dystrophic condition.

**Keywords** Phytoplankton productivity · Lowland marsh · Brownish-colored water · Underwater light attenuation · Eutrophic–dystrophic condition

## Introduction

Most Japanese lowland marshes have been replaced by paddy fields since rice production was introduced from China and Korea in 3 B.C. (the *Yayoi* Age). Areas of the original marshes were converted to artificially constructed ponds (*Tame-ike*) and canals to supply water for irrigation. Moriyama (1997) described how the ecosystem of the paddy fields, including *Tame-ike* ponds, canals and forests, significantly contributed to forming Japan's freshwater biota. In recent years, many paddy fields and other connecting aquatic environments have been drained to create the land needed for buildings and housing lots as rice cultivation has drastically declined. Although the Japanese lowland marshes continue to be rapidly reduced by human impact, there is still very little information about their ecosystems (Kawano 1998).

Phytoplankton sometimes plays an important role as primary producers in wetland ecosystems (Goldsborough

---

K. Nozaki (✉)  
School of Education, Sugiyama Jogakuen University,  
Moto-machi 17-3, Hoshigaoka,  
Chikusa, Nagoya 464-8662, Japan  
e-mail: ken@sugiyama-u.ac.jp

Y. Kohmatsu  
Research Institute for Humanity and Nature,  
457-4 Motoyama, Kamigamo,  
Kita-ku, Kyoto 603-8047, Japan  
e-mail: kohmatsu@chikyu.ac.jp

T. Yamamoto  
Toyota Yahagi River Institute, 2-19, Nishimachi,  
Toyota, Aichi 471-0025, Japan  
e-mail: yamamotoshi@yahagigawa.jp

A. Tuji  
Department of Botany, National Museum of Nature and Science,  
Amakubo 4-1-1, Tsukuba 305-0005, Japan  
e-mail: tuji@kahaku.go.jp

and Robinson 1996). However, there have only been a few investigations into the phytoplankton productivity in Japanese wetlands, and a limited number of previous studies have been carried out mainly in highland moors, such as *Ozegahara* (located in Gunma, Fukushima and Niigata Prefecture). Ponds and pools in such moors were generally characterized by brownish-colored, nutrient-poor water (Sakamoto 1982a; Hirata et al. 1995). The biomass of phytoplankton corresponding to chlorophyll-*a* (Chl. *a*) in the water of ponds and pools fell very low, to 0.2–3.0  $\mu\text{g Chl. } a \text{ l}^{-1}$  (Hogetsu et al. 1982; Kurasawa et al. 1982; Taira 1989, 1992). Thus, the trophic status of water bodies in highland moors was regarded as being in an oligotrophic–dystrophic condition, with the role of phytoplankton productivity in their material cycles generally receiving little attention.

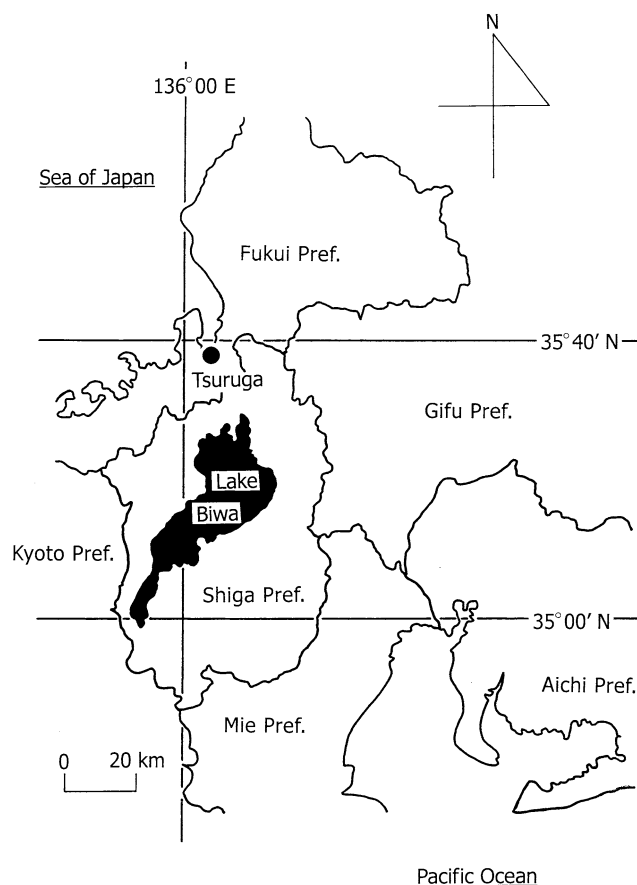
On the other hand, the nutrient concentrations in lowland marshes are usually higher than those of highland moors because the nutrients are supplied from catchment areas via streams and springs (Sakamoto 1982b; Nozaki and Tuji 1999; Tuji et al. 1999). Therefore, trophic conditions in the lowland marshes seem to be more eutrophic than those in the highland moors. However, no studies have addressed the biomass and productivity of phytoplankton in Japanese lowland marshes.

In this study, to better understand the ecosystem of Japanese lowland marshes, we investigated the temporal changes in biomass and productivity of phytoplankton in a brownish-colored water pond in Naka-ikemi marsh.

## Methods

### Study site

This study was carried out on a brownish-colored pond in the Naka-ikemi marsh located at latitude 35°39' N and longitude 136°06' E near the center of Tsuruga City, Fukui Prefecture, Japan (Fig. 1). The marsh is in a hilly district with an elevation of 50–60 m and extends 1.3 km from east to west and 0.5 km from north to south, with a total area of approximately 0.25 km<sup>2</sup>. Although most of the marsh had long been utilized as paddy fields, rice cultivation ended in the late 1990s, and the abandoned fields have been replaced by a reed zone. The bottom of the pond is covered with peat, and the brownish water darkens markedly in summer and autumn. The peat bed of the marsh has become cumulatively about 40 m thick, and analysis of sediment layers and fossil pollen revealed it to contain a continuous record of the past 50,000 years (Miyamoto et al. 1995, 1996). Characteristics of the seasonal succession of phytoplankton composition and water chemistry of the pond have been reported in our previous papers (Nozaki et al. 1998a, b; Nozaki and Tuji 1999).



**Fig. 1** Locations of study site and sampling station, Naka-ikemi marsh

### Sampling and analysis

Surveys were conducted 13 times from 25 April 1996 to 7 November 2004. Water samples were collected at about 5 cm below the water surface, stored in a box with ice and returned to the laboratory within 5 h after sampling. Underwater light intensity was measured vertically at 10–20-cm intervals with a quantum meter (LI-COR, LI-1000) equipped with a light sensor (cosine corrected and with 400–700-nm wavelengths). Water samples were transferred to a glass fiber filter (Whatman GF/C) in preparation for the analysis of chlorophyll-*a* (Chl. *a*) and suspended solid (SS) concentrations. The Chl. *a* concentration expressed as planktonic algal biomass was measured by the method of Lorenzen (1967), while the SS concentration was obtained as the weight after being dried at 60°C for 72 h.

### Photosynthesis and primary production

The photosynthesis and respiration rates of phytoplankton were measured ten times by the light and dark bottle method under laboratory conditions from 25 April 1996 to 5 September 1997. Large zooplankters were removed using

a plankton net with a 150- $\mu\text{m}$  mesh. Fourteen glass bottles each holding 300 ml were filled with water samples. Dissolved oxygen concentrations of two bottles were determined to establish an initial condition by the Winkler method. For a dark condition, two bottles were completely wrapped in aluminum foil. Ten light bottles and two dark bottles were incubated in a water bath at the sampling site water temperature and exposed to a light gradient from an artificial lamp (300 W  $\times$  2, National RF-300 W). The incubation time was 8 h. The dissolved oxygen concentrations of 12 bottles were determined after the incubation period by the Winkler method. The measured oxygen production or consumption in the bottles was converted to a carbon transfer, on the assumption that PQ was 1.

Primary production was estimated using the photosynthesis and irradiance relations ( $P$ – $I$  curves) and Chl.  $a$  concentration. The  $P$ – $I$  curve was approximated to a rectangular hyperbola by the formula  $P = bI/(1 + aI)$  (Tamiya 1951), where  $P$  is the gross photosynthesis rate ( $\mu\text{g C } \mu\text{g Chl. } a^{-1} \text{ h}^{-1}$ );  $I$  is the irradiance ( $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ );  $a$  and  $b$  are constants.

Daily change of light intensity was approximately given by the formula of Ikusima (1967),  $I_0 = I_{\text{max}} \sin^2 wt$ , where  $I_0$  is the photon flux density just below the water surface (0 m depth,  $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ );  $I_{\text{max}}$  is the photon flux density just below the water surface (0 m depth) at noon ( $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ );  $w = \pi D^{-1}$  where  $\pi$  is the circular constant,  $D$  is day length by hour (sunrise to sunset);  $t$  is the time from sunrise (h).

Daily gross production ( $P_{\text{g day}}$ ), respiration ( $R$ ) and net production ( $P_{\text{n day}}$ ) rates were calculated using the formulae of Nozaki (2001).

$$P_{\text{g day}} (\mu\text{g C l}^{-1} \text{ d}^{-1}) = (\rho bD/a) (1 - (1/\sqrt{1 + aI_{\text{max}} \exp(-kz)}))$$

$$R (\mu\text{g C l}^{-1} \text{ d}^{-1}) = 24r\rho$$

$$P_{\text{n day}} (\mu\text{g C l}^{-1} \text{ d}^{-1}) = P_{\text{g day}} - R$$

where  $\rho$  is the chlorophyll- $a$  concentration ( $\mu\text{g Chl. } a \text{ l}^{-1}$ );  $k$  is the underwater light attenuation coefficient ( $\text{m}^{-1}$ );  $z$  is the depth (m);  $r$  is the hourly respiration rate ( $\mu\text{g C } \mu\text{g Chl. } a^{-1} \text{ h}^{-1}$ ).

$I_{\text{max}}$  and day length ( $D$ ) in this study are shown in Table 1.  $I_{\text{max}}$  was calculated using the monthly average value of solar radiation at noon measured by the Fukui Local Meteorological Observatory located in Fukui City (latitude 36°03.2' N, longitude 136°13.5' E).  $I_{\text{max}}$  values were regarded as 40% of the solar radiation, because the photon flux density in air attenuated approximately 40% just below the water surface in this study site. Solar radiation ( $\text{MJ m}^{-2}$ ) was converted to photon flux density ( $\text{mol m}^{-2}$ ) by the formulae of Parsons et al. (1984).

**Table 1**  $I_{\text{max}}$  and day length used to calculate primary production in the study

Month	Year		Day length (h)
	1996	1997	
	$I_{\text{max}}$ ( $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ )		
January	440	400	11
February	610	740	11
March	850	990	12
April	1,240	1,050	13
May	1,230	1,090	14
June	960	1,100	14
July	1,270	890	14
August	1,280	1,210	14
September	980	910	13
October	970	990	12
November	480	670	11
December	460	530	10

$$1 \text{ g cal} = 4.185 \text{ J}$$

$$1 \text{ mol photon} = 52 \times 10^3 \text{ g cal}$$

Day lengths ( $D$ ) in each month were cited from the URL of the National Astronomical Observatory of Japan.

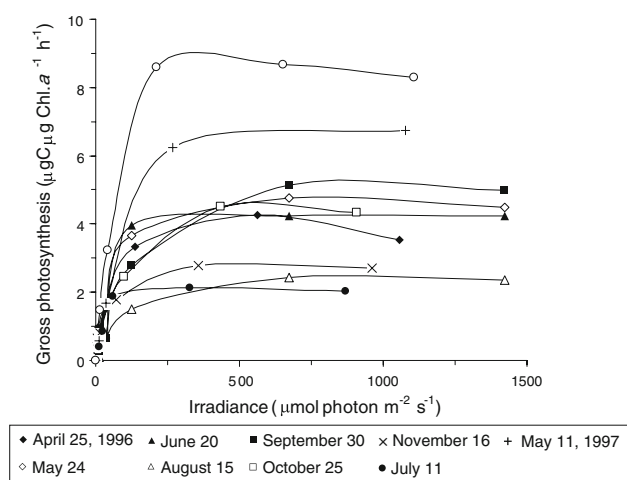
## Results

Chl.  $a$  and SS concentrations and  $k$  values at this study site were shown in Table 2. Higher concentrations of Chl.  $a$  exceeding 10  $\mu\text{g Chl. } a \text{ l}^{-1}$  were clearly observed from June to September in 1996 and in July of 1997, when the dominant algae were phytoflagellates *Peridinium* (Dinophyceae) and *Cryptomonas* (Cryptophyceae) (Nozaki et al. 1998b). There was a positive linear correlation between SS and Chl.  $a$  ( $r^2 = 0.558$ ,  $p = 0.008$ ). However, unknown factors affecting the SS concentrations contributed more than 40% to determine the seasonal change of SS.  $k$  values positively correlated to Chl.  $a$  concentrations in a linear regression ( $r^2 = 0.620$ ,  $p = 0.007$ ), whereas no correlation was found between  $k$  values and SS concentrations ( $r^2 = 0.163$ ,  $p = 0.247$ ). On October 25, 1996 and September 5, 1997, the  $k$  values were relatively high despite a decrease in the Chl.  $a$  and SS concentration. Thus, we assumed that the underwater light intensity was attenuated by the phytoplankton biomass and/or colored dissolved organic matter (CDOM = humic substances).

The  $P$ – $I$  curves of phytoplankton are shown in Fig. 2. No remarkable photo-inhibition was observed in this study. Therefore, we confirmed that the  $P$ – $I$  curve was approximated by a rectangular hyperbola.  $P_{\text{g max}}$ ,  $r$ ,  $a$  and  $b$

**Table 2** Suspended solid and chlorophyll-*a* concentrations and underwater light attenuation coefficient (*k*) on each sampling day

Date	Chlorophyll- <i>a</i> ( $\mu\text{g l}^{-1}$ )	Suspended solid ( $\text{mg l}^{-1}$ )	<i>k</i> ( $\text{m}^{-1}$ )
25 April 1996	7.0	11.6	1.65
24 May	7.6	7.8	2.27
20 June	12.8	8.3	2.92
16 August	36.1	20.7	3.95
30 September	30.7	9.3	3.14
25 October	7.1	6.4	3.45
16 November	7.1	8.8	1.43
6 February 1997	1.3	4.3	No data
11 May	6.9	8.4	2.13
11 July	57.0	15.1	5.11
5 September	5.6	4.3	3.48
24 February 2003	3.1	No data	No data
20 December	1.8	No data	No data
7 November 2004	8.9	No data	No data

**Fig. 2** Photosynthesis and irradiation relations (*P*–*I* curves) of phytoplankton community collected from surface water of sampling station

obtained from the *P*–*I* curve and water temperature during the incubation period are shown in Table 3.  $P_{g \max}$  values were higher in May and September to October, whereas lower values were observed on 16 August, 16 November 1996 and 11 July 1997.  $P_{g \max}$  and *r* values were tending toward negative correlations with the increase in Chl. *a* concentration (Fig. 3), and higher values were obtained at about 20°C, except on 5 September 1997 (Fig. 4). Thus, the photosynthetic activity of phytoplankton in this pond seems to be increasing in early summer and autumn, and decreasing in mid-summer when the biomass has increased and temperature is high.

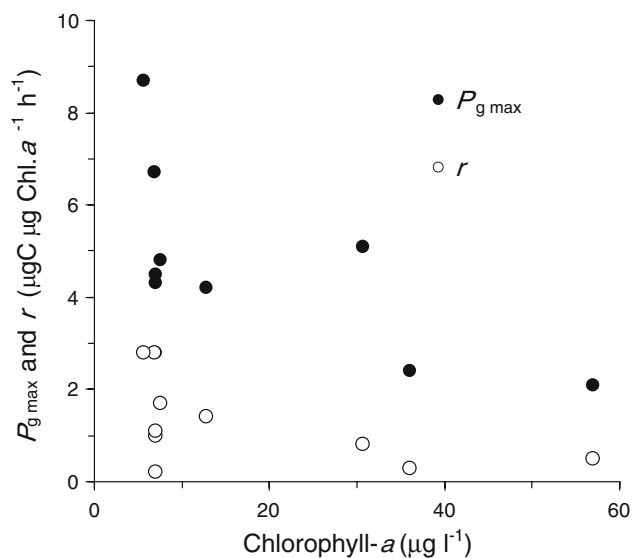
The volumetric daily gross and net production and respiration of phytoplankton in surface water on each sampling day are shown in Table 4. Remarkably higher net production rates were obtained on 16 August and 30 September 1996 and 11 July 1997 when the Chl. *a* concentrations were also higher than those of other sampling days. Volumetric primary production rates in this study site were one or two orders higher than those in Swedish humic (dystrophic) and nutrient-poor lakes measured in summer (Jansson et al. 2000; Drakare et al. 2002) and were equal to the higher rates reported from 83 colored water lakes (Nurnberg and Shaw 1998).

## Discussion

To define the ecosystem of Naka-ikemi in terms of Japanese freshwater environments, the phytoplankton biomass and productivity of this study site were compared to those of some Japanese lakes. The relationships between Chl. *a* concentrations and volumetric daily net production ( $P_{n \text{ day}}$ ) rates in surface water of the pond in Naka-ikemi are shown in Fig. 5 in comparison to three other Japanese lakes having different trophic conditions. Methods of productivity measurement on each study were the DO method in the present study and Lake Suwa (Okino and Hanazato 1997), and the  $^{13}\text{C}$  technique in Lake Biwa (Nakanishi et al. 1992; Tsuda and Nakanishi 1992) and Lake Towada (Takamura and Katano 1991; Makino et al. 2003). Primary production rates measured by  $^{13}\text{C}$  technique were regarded as  $P_n$ . The Chl. *a* concentrations and  $P_{n \text{ day}}$  rates of Naka-ikemi were higher than those of oligotrophic Lake Towada and mesotrophic Lake Biwa, and lower than those of hypereutrophic Lake Suwa. Therefore, the trophic status of our study site was evaluated as eutrophic. Nozaki et al. (1998b) and Nozaki and Tuji (1999) reported that the  $\text{NH}_4^+\text{-N}$ ,  $\text{NO}_2^-\text{-N}$ ,  $\text{NO}_3^-\text{-N}$  and  $\text{PO}_4^{3-}\text{-P}$  concentrations in surface water of the pond were  $53.8 \pm 46.7$ ,  $5.1 \pm 3.5$ ,  $273.6 \pm 137.9$  and  $7.3 \pm 8.0 \mu\text{g l}^{-1}$  (average  $\pm$  SD,  $n = 8$ ), respectively, from April to November 1996. These concentrations were clearly higher than those in the water of a typical Japanese highland moor (Sakamoto 1982a; Hirata et al. 1995; Hayashi and Nohara 1997). For example,  $\text{NH}_4^+\text{-N}$ ,  $\text{NO}_2^-\text{-N}$ ,  $\text{NO}_3^-\text{-N}$  and  $\text{PO}_4^{3-}\text{-P}$  concentrations in surface water of the ponds and pools of the *Ozegahara* moor were  $23.2 \pm 20.8$ ,  $1.6 \pm 1.8$ ,  $90.3 \pm 35.0$  and  $1.8 \pm 0.6 \mu\text{g l}^{-1}$  (average  $\pm$  SD,  $n = 6$ ), respectively, in June 1995 (Hayashi and Nohara 1997). The nutrients in highland moors were mainly supplied from rainfall (e.g., Sakamoto 1982b). Thus, the nutrient concentrations were usually poor, and the growth of phytoplankton seemed to be regulated by such a nutrient limitation. In contrast, the nutrient-rich spring and stream water flow into the Naka-ikemi marsh (Nozaki and Tuji

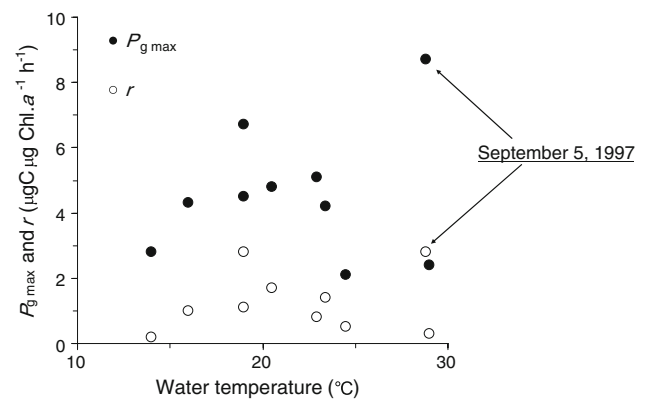
**Table 3** Maximum gross photosynthetic rate ( $P_{g \max}$ ), respiration rate ( $r$ ) and constants ( $a$  and  $b$ ) of  $P$ – $I$  curves of planktonic algal communities and water temperature during the incubation period

Date	$P_{g \max}$ ( $\mu\text{g C } \mu\text{g Chl. } a^{-1} \text{ h}^{-1}$ )	$r$ ( $\mu\text{g C } \mu\text{g Chl. } a^{-1} \text{ h}^{-1}$ )	$a$	$b$	WT ( $^{\circ}\text{C}$ )
25 April 1996	4.3	1.0	0.042	0.165	16.0
24 May	4.8	1.7	0.013	0.070	20.5
20 June	4.2	1.4	0.005	0.031	23.4
16 August	2.4	0.3	0.011	0.028	29.0
30 September	5.1	0.8	0.007	0.043	22.9
25 October	4.5	1.1	0.009	0.049	19.0
16 November	2.8	0.2	0.021	0.063	14.0
11 May 1997	6.7	2.8	0.006	0.056	19.0
11 July	2.1	0.5	0.021	0.055	24.5
5 September	8.7	2.8	0.011	0.114	28.8

**Fig. 3** Relationships between Chl.  $a$  concentrations and  $P_{g \max}$  (closed circle) and  $r$  (open circle) values of phytoplankton community collected from sampling station surface water

1999; Tuji et al. 1999), making nutrient limitations on phytoplankton growth in this study site far less severe than in a highland moor.

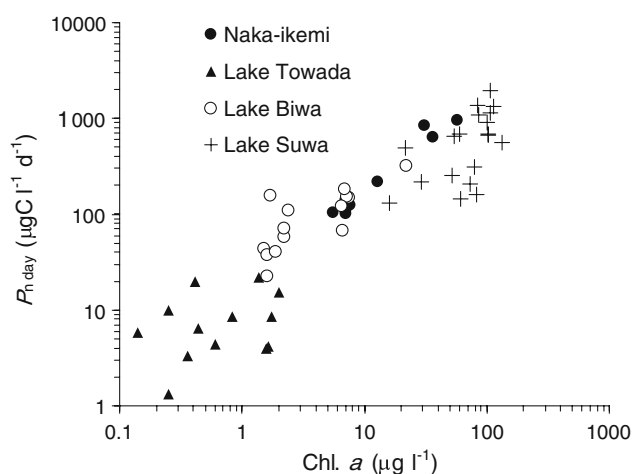
There is, however, a possibility of phosphorus limitation on phytoplankton growth in this study site because the dissolved inorganic phosphorus concentrations were two orders lower than the nitrogen. Humic substances are well known as a bio-available phosphorus source (Jones 1992). To evaluate the nutrient limitation of phytoplankton in a humic lake, Jansson et al. (2001) carried out a fertilization experiment to enrich dissolved inorganic phosphorus (P) and nitrogen (N) in some Swedish lakes. Their result showed that P fertilization had no effects on phytoplankton, whereas phytoplankton were significantly

**Fig. 4** Relationships between water temperature during incubation period and  $P_{g \max}$  (closed circle) and  $r$  (open circle) values of phytoplankton community collected from sampling station surface water**Table 4** Daily gross ( $P_g$ ) and net ( $P_n$ ) production and respiration ( $R$ ) rates of planktonic algal community at the study site

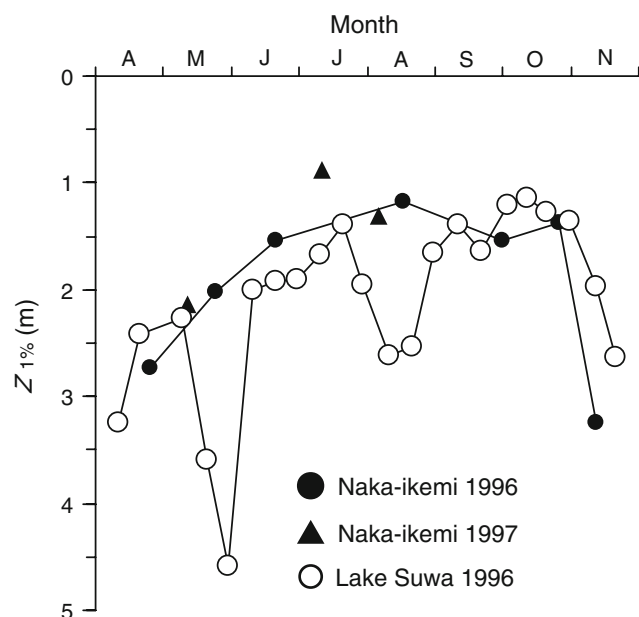
Date	$P_{g \text{ day}}$ ( $\mu\text{g C l}^{-1} \text{ day}^{-1}$ )	$P_{n \text{ day}}$ ( $\mu\text{g C l}^{-1} \text{ day}^{-1}$ )	$R_{\text{day}}$ ( $\mu\text{g C l}^{-1} \text{ day}^{-1}$ )
25 April 1996	308	140	168
24 May	434	124	310
20 June	648	219	429
16 August	887	635	252
30 September	1,456	833	623
25 October	289	100	189
16 November	148	110	38
11 May 1997	576	119	457
11 July	1,619	961	658
5 September	489	105	385

stimulated by N fertilization. This led us to conclude that there was also no P limitation on phytoplankton growth in this study site.



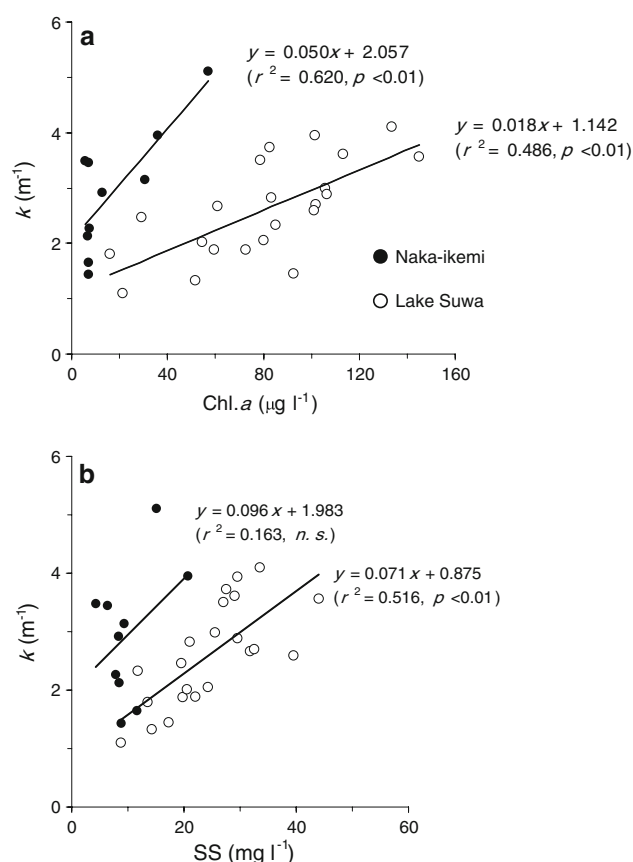


**Fig. 5** Relationships between Chl. *a* concentrations and volumetric daily net production rates ( $P_n$ ) of phytoplankton community collected from sampling station surface water (closed circle this study), oligotrophic Lake Towada (closed triangle May–October 1998 and 1999 after Takamura and Katano 1991; Makino et al. 2003), mesotrophic Lake Biwa (open circle May–October 1983 after Tsuda and Nakanishi 1992; May–September 1989 after Nakanishi et al. 1992) and hyper-eutrophic Lake Suwa (plus symbol April–November 1996 after Okino and Hanazato 1997)



**Fig. 6** Seasonal changes of  $Z_{1\%}$  calculated from  $k$  values in sampling station in this study (closed circle and closed triangle) and Lake Suwa (open circle, after Okino and Hanazato 1997)

Figure 6 shows seasonal variations in the depth of the euphotic layer ( $Z_{1\%}$ ) estimated by the light attenuation coefficient ( $k$ ) in the waters of Naka-ikemi and Lake Suwa. Although the Chl. *a* concentrations as a main factor in the attenuation of underwater light intensity were relatively lower in Naka-ikemi, the depths of  $Z_{1\%}$  in summer were



**Fig. 7** Relationships among underwater light attenuation coefficients ( $k$ ) and Chl. *a* concentrations (a), and suspended solid (SS) concentrations (b) in sampling station in this study site (closed circle) and Lake Suwa (open circle, after Okino and Hanazato 1997). Solid lines show single correlation (*n.s.* not significant)

shallower than those in Lake Suwa. The relationships among  $k$  values, and Chl. *a* and SS concentrations in Naka-ikemi and Lake Suwa are shown in Fig. 7a and b. Values of slope and intercept in regression lines were higher in Naka-ikemi than those in Lake Suwa. Thus, the underwater light intensity in Naka-ikemi was more attenuated in comparison with that in Lake Suwa.  $k$  values were not significantly different between Naka-ikemi and Lake Suwa (Student's *t*-test,  $p = 0.641$ ), whereas Chl. *a* and SS concentrations were clearly higher in Lake Suwa (Student's *t*-test,  $p = 0.020$  in Chl. *a*,  $p = 0.037$  in SS). These results suggested that not only phytoplankton and SS but also colored dissolved organic matter (CDOM) attenuated the underwater light intensity in Naka-ikemi. Many studies have reported that CDOM readily attenuates photosynthetically available radiation (PAR, 400–700 nm), thereby affecting primary production in freshwater ecosystems (e.g., Jones 1992; Carpenter et al. 1998; Marlager and Vincent 2000). In light of those studies, we estimated that CDOM strongly regulated the vertical primary productive structure at our

site, and the pond water condition was defined as dystrophic.

The dystrophic condition of this study site was also supported by the phytoplankton species composition. The dominant phytoplankton in Naka-ikemi were the two phytoflagellates, *Peridinium* and *Cryptomonas*, in summer when the algal biomass was high (Nozaki et al. 1998b). Similar observations were reported in some dystrophic and turbid lakes (Yasuda et al. 1978; Nozaki et al. 1995; Bergstrom et al. 2003). These algae were characterized by their swimming ability that always allowed them to readily move to a more suitable place for their growth. For example, the freshwater red tide of *Peridinium* in a reservoir was well situated at the entrance to catch the nutrients supplied from the watershed (Nakamoto 1975). On the other hand, a dense algal biomass in hypereutrophic Lake Suwa has been formed by the water blooms of non-motile diatoms, green algae and especially cyanobacteria (Sakamoto and Okino 2000). In our study site, motile algae seemed to be much better suited to obtaining solar radiation than non-motile algae, because they had the swimming ability to remain within the narrow euphotic zone regulated by CDOM (Jones 1991; Drakare et al. 2003).

Our study concluded that the trophic status of the pond water of Naka-ikemi marsh could be defined as a eutrophic-dystrophic condition based on its biomass and productivity of phytoplankton as well as its underwater light attenuation. In particular, the eutrophic condition of the pond water was significantly different from that in the Japanese highland moor reported in previous studies. Organic matter production in the surface water of the pond was regarded as an autochthonous condition since the gross primary production of phytoplankton exceeded their respiration on all sampling days. However, the depths of  $Z_{1\%}$  showing the productive layer at this study site was relatively narrower than those in the hypereutrophic Lake Suwa due to the light attenuation by CDOM. Nurnberg and Shaw (1998) found that areal phytoplankton productivity in humic lakes was lower than in clear lakes. However, volumetric productivity in humic lakes was similar or perhaps even slightly higher for the same amount of Chl. *a*, because colored lakes have a smaller euphotic zone (Jones 1992). Thus, not only phytoplankton primary production, but also allochthonous organic matter supplied from catchment area seems to be the major factor underlying the entire energy budget of the pond ecosystem in Naka-ikemi marsh.

**Acknowledgments** We would like to extend our sincere thanks to Drs. Chikage Yoshimizu, Riyo Hirasawa, Toshiyuki Ishikawa, Professors Sho-ichi Kawano, Yasuro Kadono, Makoto Kato and members of the NPO Wetland Naka-ikemi for their valuable help during this study.

## References

- Bergstrom A-K, Jansson M, Drakare S, Blomqvist P (2003) Occurrence of mixotrophic flagellates in relation to bacterioplankton production, light regime and availability of inorganic nutrients in unproductive lakes with differing humic contents. *Freshw Biol* 48:868–877
- Carpenter SR, Cole JJ, Kitchell JF, Pace ML (1998) Impact of dissolved organic carbon, phosphorus and grazing on phytoplankton biomass and production in experimental lakes. *Limnol Oceanogr* 43:73–80
- Drakare S, Blomqvist P, Bergstrom A-K, Jansson M (2002) Primary production and phytoplankton composition in relation to DOC input and bacterioplankton production in humic lake Ortrasket. *Freshw Biol* 47:41–52
- Drakare S, Blomqvist P, Bergstrom A-K, Jansson M (2003) Relationships between picophytoplankton and environmental variables in lakes along a gradient of water color and nutrient content. *Freshw Biol* 48:729–740
- Fukui Local Meteorological Observatory. <http://www.tokyo-jma.go.jp/home/fukui/>. Accessed 20 Dec 2007
- Goldsborough LG, Robinson GCC (1996) Patterns in wetlands. In: Stevenson RJ, Bothwell ML, Lowe RL (eds) *Algal ecology—freshwater benthic ecosystems*. Academic Press, San Diego, pp 77–117
- Hayashi H, Nohara S (1997) Characteristics of water quality of pool waters on the Ozegahara moor (in Japanese). *Jpn J Limnol* 58:107–108
- Hirata T, Nohara S, Iwakuma T, Tang C (1995) Chemical change of ground and surface waters in Miyatoko mire (in Japanese with English abstract). *Res Rep Natl Inst Environ Stud Jpn* 134:23–33
- Hogetsu K, Oshima Y, Sakamoto M (1982) Nitrogen metabolism of the vegetation and pool in the Ozegahara moor. In: *Ozegahara: scientific researches of the High Moor in Central Japan*. Japan Society for the Promotion of Science, Tokyo, pp 263–276
- Ikusima I (1967) Ecological studies on the productivity of aquatic plant communities III. effect of depth on daily photosynthesis in submerged macrophytes. *Bot Mag Tokyo* 80:57–67
- Jansson M, Bergstrom A-K, Blomqvist P, Drakare S (2000) Allochthonous organic carbon and phytoplankton/bacterioplankton production relationships in Lakes. *Ecology* 81:3250–3255
- Jansson M, Bergstrom A-K, Drakare S, Blomqvist P (2001) Nutrient limitation of bacterioplankton and phytoplankton in humic lakes in northern Sweden. *Freshw Biol* 46:653–666
- Jones RI (1991) Advantages of diurnal vertical migration to phytoplankton in sharply stratified, humic forest lakes. *Arch Hydrobiol* 120:257–266
- Jones RI (1992) The influence of humic substances on lacustrine planktonic food chains. *Hydrobiologia* 229:73–91
- Kawano S (1998) Biodiversity of the Naka-ikemi wetland (Tsuruga, Fukui Prefecture) and its significance for conservation (in Japanese). *Jpn J Ecol* 48:159–161
- Kurasawa H, Hayashi H, Okino T, Watanabe Y, Ogawa M, Morita T, Isobe Y, Fukuhara H, Ootaka A (1982) Ecological studies on zooplankton and zoobenthos in the pools of Ozegahara moor. In: *Ozegahara: scientific researches of the High Moor in Central Japan*. Japan Society for the Promotion of Science, Tokyo, pp 277–298
- Lorenzen CJ (1967) Determination of chlorophyll and pheo-pigments: spectrophotometric equations. *Limnol Oceanogr* 12:343–346
- Makino W, Mikami H, Katano N, Nakagawa M, Takamura N (2003) Biological productivity of Lake Towada, a north temperate, oligotrophic, kokanee fishery lake. *Limnology* 4:79–90

- Marlager S, Vincent WF (2000) Spectral light attenuation and the absorption of UV and blue light in natural waters. *Limnol Oceanogr* 36:642–650
- Miyamoto S, Yasuda Y, Kitagawa H (1995) Sedimentary faces and chronology of core samples from the Naka-ikemi moor, Fukui Prefecture, Central Japan: sedimentary environment for the past 50 ks (in Japanese with English abstract). *J Geogr* 104:865–873
- Miyamoto S, Yasuda Y, Kitagawa H (1996) Paleoenvironments in the last glacial maximum around the Naka-ikemi moor, Fukui Prefecture, Central Japan. *Geogr Rep Tokyo Metrop Univ* 31:131–147
- Moriyama H (1997) Suiden wo mamorutowa douiukotoka (How do we preserve paddy fields?) (in Japanese). *Nou-san-gyoson Bunka Kyokai* (Rural Culture Association), Tokyo
- Nakamoto N (1975) A freshwater red tide on a water reservoir. *Jpn J Limnol* 36:55–64
- Nakanishi M, Tezuka Y, Narita T, Mitamura O, Kawabata K, Nakano S (1992) Phytoplankton primary production and its fate in a pelagic area of Lake Biwa. *Arch Hydrobiol Beih Ergebn Limnol* 35:47–67
- National Astronomical Observatory of Japan. <http://www.nao.ac.jp/>
- Nozaki K (2001) Abrupt change in primary productivity in a littoral zone of Lake Biwa with the development of a filamentous green-algal community. *Freshw Biol* 46:587–602
- Nozaki K, Tuji A (1999) Preliminary survey on water quality of Naka-ikemi marsh, Tsuruga, Fukui, Japan (in Japanese with English abstract). *Biol Inland Water* 14:1–8
- Nozaki K, Takahashi T, Sakai M, Watanabe Y, Nakamoto N (1995) Vertical distributions of nutrient and phytoplankters on Lake Waku-ike in summer (in Japanese with English abstract). *Ann Environ Sci Shinshu Univ* 17:63–68
- Nozaki K, Tuji A, Kohmatsu Y, Yamamoto T, Hirasawa R, Ishikawa T (1998a) Relationship between freshwater biota and water environment (in Japanese). *Jpn J Ecol* 48:187–192
- Nozaki K, Tuji A, Kohmatsu Y, Ishikawa T, Yamamoto T (1998b) Seasonal succession of a planktonic algal community and its characteristics in a small pond of Naka-ikemi marsh, Tsuruga, Fukui, Japan (in Japanese with English abstract). *Jpn J Limnol* 59:329–339
- Nurnberg GK, Shaw M (1998) Productivity of clear and humic lakes: nutrients, phytoplankton, bacteria. *Hydrobiologia* 382:97–112
- Okino T, Hanazato T (1997) A result of the 20-year-monitoring of water quality in Lake Suwa (in Japanese). Report of the Suwa Hydrobiological Station, Shinshu University 10: 7–249
- Parsons TR, Takahashi M, Hargrave B (1984) Biological oceanographic processes. Pergamon Press, New York
- Sakamoto M (1982a) The chemical composition of pool waters on the Ozegahara moor and its ecological significance. In: Ozegahara: scientific researches of the High Moor in Central Japan. Japan Society for the Promotion of Science, Tokyo, pp 243–261
- Sakamoto M (1982b) Ecological characteristics of pool waters on the Ozegahara moor (in Japanese). *Seibutsu Kagaku* 34:22–31
- Sakamoto M, Okino T (2000) Self-regulation of cyanobacterial blooms in a eutrophic lake. *Verh Int Verein Limnol* 27:1243–1249
- Taira M (1989) Species composition and feeding habits of Crustacean plankters in the pools of high moor (in Japanese with English abstract). *Jpn J Limnol* 50:333–339
- Taira M (1992) Faunal characteristics of Crustacean plankters in the Japanese high moor (in Japanese with English abstract). *Biol Inland Water* 7:24–28
- Takamura N, Katano N (1991) Chlorophyll a concentrations in Lake Towada during 1998–1999 (in Japanese). *Res Rep Natl Inst Environ Stud Jpn* 167:150–152
- Tamiya H (1951) Some theoretical notes on the kinetics of algal growth. *Bot Mag Tokyo* 64:167–173
- Tsuda R, Nakanishi M (1992) Light utilization by phytoplankton in the north basin of Lake Biwa. *Arch Hydrobiol* 125:97–107
- Tuji A, Karasaki C, Kohmatsu Y, Yamamoto T, Murayama K, Nozaki K (1999) Water quality and vegetation of Naka-ikemi marsh, Tsuruga, Fukui, Japan: importance of water quality on the conservation of marsh vegetation (in Japanese with English abstract). *Jpn J Limnol* 60: 201–213
- Yasuda I, Arai Y, Iyama Y (1978) Plankton and primary production of the dystrophic lakes in Shiga Heights (in Japanese with English abstract). *Jpn J Water Treat Biol* 14(2):30–40