Assimilation Number and Primary Productivity of Phytoplankton in the South Basin of Lake Biwa*

Masami NAKANISHI, Tetsuya NARITA, Norio SUZUKI and Osamu MITAMURA

Abstract

Seasonal changes in assimilation numbers and daily primary production rates of total phytoplankton and nannoplankton were studied in connection with some environmental variables at littoral and pelagic sites in the south basin of Lake Biwa. The assimilation number was not so different with seasonal variation between both sites and within the range of 0.2 to 5.8 mg C \cdot mg Chl. a\(^{-1}\) \cdot hr\(^{-1}\). As a result of multiple regression analysis, water temperature proved to be the most significant contributor in the variation of assimilation numbers of the total and nannoplankton at any site, accounting for 59-73%, while DIN and DIP were not significant. The daily gross primary production rate of the total phytoplankton also was not so very different with seasonal change between both sites, ranging from 0.07 in January to 1.93-2.74 g C \cdot m\(^{-2}\) \cdot d\(^{-1}\) in late August or early September. Nannoplankton contribution to the total daily production rate was very high, averaging 77% during January-July with relatively high DIN stock, against a low 39% of the total during August-December, with low DIN stock mostly below 1 \(\mu\)g at. N \cdot l\(^{-1}\).

Key words: assimilation number, primary productivity, Lake Biwa, nannoplankton

1. Introduction

In an attempt to understand the dynamic status of natural phytoplankton, intensive analytical studies on photosynthesis in relation to primary production processes have been carried out by many investigators (cf. Ichimura, 1968; Harris, 1978; Parsons et al., 1984). In these studies, photosynthesis-light curve has been widely used to assess the effect of physico-chemical variables on photosynthesis and the eco-physiological properties of natural phytoplankton, or to make predictive models of phytoplankton production. One of the important parameters of the curve is the maximum specific photosynthetic rate or assimilation number. The assimilation number, light-saturated photosynthetic rate seems to be a useful index in comparative studies on phytoplankton photosynthesis (Dunstan, 1973; Harrison and Platt, 1980). The effects of light, temperature and nutrients on the assimilation number have been analyzed (Platt and Jassby, 1976; Lastein and Garlan, 1978; Williams, 1978; Harrison and Platt, 1980).

As a part of studies on phytoplankton dynamics in the south basin of Lake Biwa (Nakanishi et al., 1986), the present paper dealt with the assimilation number and productivity of phytoplankton. The objectives are (1) to compare seasonal variations in the assimilation numbers and in simulated daily primary production rates of total phytoplankton and nannoplankton between littoral and pelagic sites in the south basin of Lake Biwa, and (2) to analyze some environmental effects on the assimilation number.

2. Material and methods

The south basin investigated is very shallow (average depth, 2.8 m), small (57 km\(^2\) in surface area) and eutrophic. The surveys were conducted approximately at weekly intervals during April-mid-December 1978 and at biweekly intervals thereafter until April 1979. Water samples for measurement of photosynthesis and for determinations of chlorophyll \(a\) (Chl.\(a\)), dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphorus (DIP) concentrations were collected with a Van-Dorn water sampler from upper and lower layers.
(0.5 m below the surface and above the bottom) at littoral Stas. 1 (2.0-2.5 m deep) adjacent to Otsu City and 2 (2.0-2.5 m) located on the east side with high nutrient level and at a pelagic Sta. 3 (3.5-4.0 m) located on the center of the south basin (Fig. 1). At the same time, water temperature and light attenuation in water were measured with a thermister (Tohodentan, RB-2) and an underwater quanta meter (LI-COL, LI-192s), respectively. Phytoplankton fraction in the filtrate through a screen with 25μm aperture was defined as nannoplankton. Netplankton were obtained by subtracting nannoplankton fraction from total one. Photosynthesis of total phytoplankton and nannoplankton collected from the upper layer was measured by the 14C technique (Dotty and Oguri, 1959) in the laboratory at 1,100-1,130 under photoflood lamps (500 W, Iwasaki Electric Co.) and in situ water temperature. The light intensity for measurement of photosynthesis was in the range of 0-0.7×10^17 quanta sec^-1 cm^-2. Incubation time was 10-15 min. The rate thus obtained was regarded as nearly gross photosynthesis (Arima, 1968). Chlorophyll a amount of phytoplankton on the Whatman GF/C glass fiber filter was determined by the method of Lorenzen (1967). Solar radiation was measured using an Eppley 180°-pyranometer (Ishikawa, S-110) on the roof of the Otsu Hydrobiological Station, Kyoto University, located on the south basin. Filtrates through Whatman GF/C glass fiber filter were put to determinations of DIN (NO_3^-N, NO_2^-N and NH_4^-N) and DIP (see Nakanishi et al., 1986). The daily primary production rate was estimated using a mathematical model proposed by Ikusima (1967, 1970).

3. Results

3.1. Variations of some variables related to assimilation number and primary productivity

Vertical profiles of water temperature and concentrations of Chl.a, DIN and DIP were nearly uniform at any stations during the investigated period. Figure 2 shows seasonal changes in water temperature at the depth of 0.5 m below the surface and concentrations of DIN and DIP on averages of the upper and lower layers at the study sites. In addition, daily solar radiation (SR) is also shown in Fig. 2 as an average value at intervals of ten days in each month. Water temperature was not significantly different among the investigated

Fig. 1. Map of the south basin of Lake Biwa showing the investigated stations.

Fig. 2. Seasonal changes in water temperature (W.T.), daily solar radiation (SR), DIN and DIP.
Assimilation Number and Primary Productivity

stations and change seasonally within the range of
5°C in January - 29°C in July and August. The
seasonal changes in DIN concentration showed a
similar pattern at each station in relation to the
other stations, evidencing mostly a depletion
condition (minimum : 0.7 μg at. N • 1⁻¹) from July
to November. This pattern agrees with the
observations by TEZUKA (1982, 1984). Except for
the depletion period, however, the fluctuation of
DIN concentration was great at the littoral sites,
especially at Sta. 2 on the east side of the basin,
compared with that at pelagic Sta. 3.

DIP concentration changed greatly and rapidly at
Sta. 2 with the range of 0.20-1.50 μg at. P • 1⁻¹
(average : 0.40 μg at. P • 1⁻¹), but was relatively
constant at Sta. 3 with the range of 0.10-0.25 μg at.
P • 1⁻¹ (average : 0.16 μg at. P • 1⁻¹) throughout the
investigated period. Such great fluctuations of
DIN and DIP concentrations at littoral sites may
have been related to variation of loadings from
land. As a whole, DIN and DIP concentrations
tended to be highest at Sta. 2, and slightly higher at
Sta. 1 than at Sta. 3. Solar radiation was in the
range of 6 MJ • m⁻² • d⁻¹ (average) in December -
15 MJ • m⁻² • d⁻¹ in July. A special feature of the
seasonal changing pattern appears to be the
marked decrease in radiation observed in late June
in the middle of the rainy season.

Figure 3 shows seasonal changes in Chl.a concen-
trations (average of the upper and lower layers)
of total phytoplankton and nannoplankton at Stas.
1, 2 and 3. The seasonal changing pattern of the
total phytoplankton was similar at all stations with
the exception of April 1978 at Sta. 2, though Chl.a
concentration at the peaks was always higher at
littoral Stas. 1 and 2 than at pelagic Sta. 3. The
seasonal variation of nannoplankton was not so
noticeable as that of the total phytoplankton.
Nannoplankton tended to contribute greatly to
total phytoplankton during April - July 1978 and
January - April 1979, while share of nannoplankton
in total phytoplankton was noticeably lowered by
propagation of netplankters like Anabaena macros-
pora, Pediastrum binuc, Lyngbia limnetica and
Staurastrum dorsidentiferum during August -
December 1978 (NAKANISHI et al., 1986).

3-2. Seasonal variation of assimilation
number

The assimilation numbers of total phytoplankton
and nannoplankton changed seasonally with a
pattern which was quite similar at all stations (Fig.

4). The assimilation number of total phytoplank-
ton, showing considerable oscillation at short
intervals, attained the maximum (5.0 - 5.8 mg C • mg
Chl.a⁻¹ • hr⁻¹) during summer - mid - autumn and the
minimum (0.2 - 0.3) during winter - early spring.
The assimilation number of nannoplankton was
mostly the same as that of the total phytoplankton except September and October. Taking into consideration the fact that the greater part of total phytoplankton was nannoplankton during April - July 1978 and January - April 1979 (Fig. 3), it may be considered that the assimilation number of total phytoplankton during these periods depended mainly on nannoplankton. However, during the rest period (August - December), when the ratio of the netplankton Chl.a concentration to the total phytoplankton became relatively high, the assimilation number of the total phytoplankton must have been strongly influenced not only by nannoplankton but also by netplankton. In comparison of the assimilation number of the total phytoplankton with that of nannoplankton during the latter period, it is considered that the nannoplankton assimilation number was not always higher than the netplankton one or rather low in September and October.

In order to examine what variables would be related to variation in the assimilation numbers, a step-wise multiple regression analysis was done using water temperature, solar radiation (average daily radiation for ten days before sampling), Chl. a, DIN and DIP as independent variables (Table 1). The assimilation number of total phytoplankton was related significantly to water temperature, solar radiation and/or Chl.a: 65.5% water temperature and solar radiation at Sta. 1, 72.6% water temperature at Sta. 2, and 79.2% water temperature, solar radiation and Chl.a at Sta. 3. That of nannoplankton was related to water temperature and Chl.a with 78.2% at Sta. 1, water temperature with 73.0% at Sta. 2, and water temperature and solar radiation with 70.5% at Sta. 3. In the variables being significant in the regression, the contribution of water temperature was very high in both the total and nannoplankton at all stations, ranging from 59.0 to 73.0%. Though solar radiation and/or Chl.a also were significant in the regression at Stas. 1 and 3, their contribution was very low as compared with water temperature (solar radiation, 6.4-16.2% ; Chl.a, 3.1-9.3%). Nutrients (DIN and DIP) were not significant varying assimilation number in any case.

3-3. Seasonal variation of primary productivity

The daily gross primary production rate of total phytoplankton was not so different in its seasonal

### Table 1. Step-wise multiple regression analysis of assimilation number (dependent variable) and related independent variates.

#### Total phytoplankton

<table>
<thead>
<tr>
<th>Station</th>
<th>Step</th>
<th>Variate</th>
<th>Multiple $R$</th>
<th>$R^2$</th>
<th>$\Delta R^2$</th>
<th>Overall $F$</th>
<th>Regression coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>W.T.</td>
<td>0.768</td>
<td>0.590</td>
<td>0.590</td>
<td>47.57</td>
<td>0.199</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>SR</td>
<td>0.809</td>
<td>0.655</td>
<td>0.064</td>
<td>30.34</td>
<td>-0.154</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
<td>W.T.</td>
<td>0.852</td>
<td>0.726</td>
<td>0.726</td>
<td>87.31</td>
<td>0.171</td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td>W.T.</td>
<td>0.774</td>
<td>0.599</td>
<td>0.599</td>
<td>49.26</td>
<td>0.235</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>SR</td>
<td>0.872</td>
<td>0.761</td>
<td>0.162</td>
<td>50.90</td>
<td>-0.238</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>Chl.a</td>
<td>0.890</td>
<td>0.792</td>
<td>0.031</td>
<td>39.37</td>
<td>-0.047</td>
</tr>
</tbody>
</table>

Constants are 0.077, -0.423 and 0.694 at Stations 1, 2 and 3, respectively.

#### Nannoplankton

<table>
<thead>
<tr>
<th>Station</th>
<th>Step</th>
<th>Variate</th>
<th>Multiple $R$</th>
<th>$R^2$</th>
<th>$\Delta R^2$</th>
<th>Overall $F$</th>
<th>Regression coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>W.T.</td>
<td>0.830</td>
<td>0.689</td>
<td>0.689</td>
<td>73.01</td>
<td>0.110</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Chl.a</td>
<td>0.884</td>
<td>0.782</td>
<td>0.093</td>
<td>57.44</td>
<td>-0.074</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
<td>W.T.</td>
<td>0.854</td>
<td>0.730</td>
<td>0.730</td>
<td>89.15</td>
<td>0.164</td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td>W.T.</td>
<td>0.783</td>
<td>0.614</td>
<td>0.614</td>
<td>50.82</td>
<td>0.214</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>SR</td>
<td>0.840</td>
<td>0.705</td>
<td>0.092</td>
<td>37.11</td>
<td>-0.183</td>
</tr>
</tbody>
</table>

Constants are 0.592, -0.306 and -0.082 at Stations 1, 2 and 3, respectively.
changing pattern among the investigated stations (Fig. 5). It was maximum (1.93, 2.74 and 2.17 g C \cdot m^{-2} \cdot d^{-1} at Stas. 1, 2 and 3, respectively) in late August or early September, and minimum (0.07 g C \cdot m^{-2} \cdot d^{-1} at all stations) in January. It was common at all stations for the nannoplankton contribution to the daily production rate of total phytoplankton to be very high, averaging 77% during April - July 1978 and January - April 1979, against the relatively low 39% during August - December 1978 (cf. Fig. 6).

The nannoplankton daily production ($P_{nanno}$) : total daily production ($P_{total}$) ratio changed dependently on the nannoplankton Chl.a ($Chl_{nanno}$) : total Chl.a ($Chl_{total}$) ratio as a whole, while the $P_{nanno}$ : $P_{total}$ ratio did not show any tendency to exceed consistently the $Chl_{nanno}$ : $Chl_{total}$ ratio at any station (Fig. 6). This tendency suggests that the productivity per unit Chl.a of nannoplankton is not always higher than that of netplankton.

The annual gross primary production rate of total phytoplankton estimated was 191, 302 and 225 g C \cdot m^{-2} \cdot yr^{-1} at Stas. 1, 2 and 3, respectively. The percentage contribution of nannoplankton to the total annual gross production was similar among the stations and 49-54%.

4. Discussion

4-1. Variation in assimilation numbers

The assimilation numbers of total phytoplankton and nannoplankton did not vary much in their seasonal changing pattern and in the ranges between littoral and pelagic sites. These results suggest that there is little local difference in photosynthetic activity of phytoplankton in the south basin of Lake Biwa except for a hypereutrophic area (NAKANISHI et al., unpublished).

From multiple regression analysis, water temperature was the most significant contributor with 59.0-73.0% of the variation in the assimilation numbers of both the total and nannoplankton at any station. In addition, daily solar radiation and/or Chl.a contributed from 3.1 to 16.2% at Stas. 1 and 3. This statistical result, in which water temperature was a major contributor, is consistent with that reported by MANDELLI et al. (1970), EPPLEY (1972), PLATT and JASSBY (1976), LASTEIN and GARGAS (1978) and HARRISON and PLATT (1980). However, despite the change in assimilation numbers mainly in terms of water temperature as a whole, considerable fluctuation in the assimilation
numbers was observed at short intervals under a given water temperature (Fig. 7). Variables other than water temperature are required to explain the fluctuation. In some cases, a part of the fluctuation may be explained by contribution of daily solar radiation and/or biomass (Chl.a).

The assimilation numbers are influenced in complex fashion not only by water temperature, daily solar radiation and biomass but also by nutrients, algal composition and biochemical properties. The assimilation numbers are often lowered by nutrient depletion in temperate waters except for very shallow waters with rapid nutrient regeneration (Epplle, 1972). Glosschenko et al. (1974) and Gachter et al. (1974) suggested also that the assimilation numbers in Lake Erie and Lake Ontario were related to nutrient status. Takahashi et al. (1973) found that the assimilation number of phytoplankton in the surface layer of Fraser River estuary was lowered drastically under a condition of nitrate concentration below 1 μg at. N · l⁻¹ during summer stagnation period with water temperature above 16°C.

As for the present study, despite frequent observation of DIN concentration below 1 μg at. N · l⁻¹ during July - August 1978 with water temperature above 20°C, the assimilation numbers did not show any distinct decrease, even though they fluctuated irregularly. Further, as a result of the multiple regression analysis, neither the DIN nor DIP contributed significantly to the variation in the assimilation number. As pointed out by Epplle (1972), nutrients may be passably supplied by rapid regeneration in very shallow waters like the south basin of Lake Biwa. Thus, the DIN concentration below 1 μg at. N · l⁻¹ may have been an apparent depletion of phytoplankton in the south basin.

The assimilation numbers are influenced by algal composition (Ichimura and Aruga, 1964; Mandelli et al., 1970; Glosschenko et al., 1974) and by cell size (Malone, 1971, 1977, 1980).

In the present study, however, the variation in the assimilation numbers at a given water temperature did not seem to correspond at least with that in dominant species changing successively from August to December, though there are no full data on seasonal succession of algal composition. The assimilation number of nanoplankton was not always higher than that of the total (cf. Fig. 4), nor than that of netplankton. This tendency seems to be different from that of marine phytoplankton in which, for example, the nanoplankton assimilation number is generally higher than that of netplankton (Malone, 1977). This discrepancy may be due to a difference in species specific to freshwater and marine phytoplankters (Glosschenko et al., 1974).

Epplle (1972) found that C : Chl.a ratio as a biochemical property of marine phytoplankton was an important variable in the variation of the assimilation number. Unfortunately, the effect of C : Chl.a ratio on the assimilation numbers could not be examined here because of the lack of data on carbon content of phytoplankton. Thus, it is considered that water temperature is the most significant variable of the variation in the assimilation numbers in the south basin of Lake Biwa, and other related variables are minor.

The maximum assimilation number of total phytoplankton was 5.0-5.8 mg C · mg Chl.a⁻¹ · hr⁻¹ at the investigated stations (Fig. 4). In comparison with the assimilation numbers summarized by Ichimura and Aruga (1964) and Parsons et al. (1984), the maximum assimilation number corresponds to the maximum value of freshwater eutrophic lakes. Recently, Ichiki (1986) obtained a higher assimilation number (ca. 8 mg C · mg Chl. a⁻¹ · hr⁻¹) than that of the present study in June -
September of 1983-1984 at a pelagic site in the south basin of Lake Biwa. This suggests the occurrence of phytoplankton with higher photosynthetic activity as a result of ongoing eutrophication.

4-2. Primary productivity of phytoplankton

It is of interesting that the high nanoplankton contribution to daily production was mostly observed during the period of relatively high DIN concentration, whereas the high netplankton contribution was observed during the period when DIN stock was below 1 mg at. N · l⁻¹ (Figs. 2 and 6). This phenomenon suggests that a certain level of DIN stock may be necessary for a high nanoplankton growth rate in eutrophic waters (HARRIS, 1986). On this assumption, it is considered that regeneration of DIN was insufficient for the growth of nanoplankton during the period of the low DIN stock. Under such a condition (low DIN stock), Anabaena macroura possibly having N-fixing appeared firstly as a dominant netplankter and formed a big peak of the productivity or Chl.a in late August - early September. And then Pediastrum biwae, Lyngbya limnetica and Staurastrum dorsidentiferum occurred successively as netplankters till December (NAKANISHI et al., 1986).

Thus, in the south basin of Lake Biwa, regeneration of N under low DIN stock may have been more favorable for the growth of these netplankters characterized by slow growth, long generation time and/or N-fixing as well as low loss rates than for that of nanoplankters. However, taking into consideration the fact that the assimilation number of nanoplankton was not always lower than that of netplankton during the period of high contribution of netplankton excepting September - October (Fig. 4), the consideration mentioned above seems to be insufficient for explanation of the phenomenon. OKAMOTO et al. (unpublished) found that the grazing rate of Daphnia longispina corresponded to the daily net production rate of nanoplankton at certain times in the north basin of Lake Biwa. In the present study, high loss in the rate of daily nanoplankton production due to zooplankton grazing may be a conceivable cause of low contribution to the total daily production rate in August - December.

The next step requires analysis of the primary production processes in connection with the nitrogen metabolism of nanoplankton and netplankton, and with the effect of zooplankton grazing in the south basin of Lake Biwa.

Acknowledgements

The authors appreciate the valuable comments on the manuscript by members of the Otsu Hydrobiological Station, Kyoto University. They also thank Dr. T. OKINO, Suwa Hydrobiological Station, Shinshu University, for the total inorganic carbon analysis, and Captain A. KAWARATA and Mr. T. UDAGA for their help in the field survey.

References


SUZUKI, Faculty of Education, Shiga University, Hiratsu, Otsu 520; Osamu MITAMURA, Osaka Kyoiku University, Minami-kawahoricho, Ten-noji, Osaka 543)

Received: 14 March 1988
Accepted: 8 June 1988