

# The relation between the type of antenna pigments of dominant cyanobacteria and the ambient stratification condition in reservoirs

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**ABSTRACT:** We found from field observation data in two reservoirs that the hydraulic state affect the type of antenna pigments of dominant cyanobacteria. To clarify the processes of this phenomenon, we analyzed theoretically the effects of hydraulic states on phytoplankton community based on characteristics of absorption by antenna pigments and underwater light regime. By theoretical analysis we found that phycocyanin-rich cyanobacteria (PC-type) favor shallow stable stratification based on the relationship between the absorption characteristics of antenna pigment and red light penetrative optical condition. Furthermore, this hypothesis can also explain the growth condition of bloom forming cyanobacteria. This stratification condition can be estimated as the critical buoyancy frequency ( $N_{cr}^2$ ). This hypothesis is verified using field data.

**Key Words:** antenna pigment, cyanobacteria, phytoplankton competition, stratification

## Introduction

Algal blooms caused by harmful cyanobacteria is an important subject in water environmental management. Therefore, numerous studies have been already carried out during the past several decades. Particularly, requirement of shallow stable hydraulic states for bloom forming was pointed out by Oliver & Ganf (2000). One of the most important measures for prevention of algal bloom is the artificial circulation (Reynolds 1997), which destroy the stable hydraulic structure. From field observation data of reservoirs in which the equipment were installed, we found that hydraulic states seemed to affect the antenna pigment type of dominant cyanobacteria. Although some studies pointed out the effects of underwater light regime upon antenna pigment type of dominant phytoplankton (Glover *et al.* 1986, Callieri *et al.* 1996, Pick 1991, Vörös *et al.* 1998), the effect of hydraulic states remains unknown. We analyze theoretically the effects of hydraulic condition on phytoplankton community based on characteristics of absorption by antenna pigments and extinction of underwater light, and attempt to explain this phenomenon using our hypothesis.

## Field Observation Data

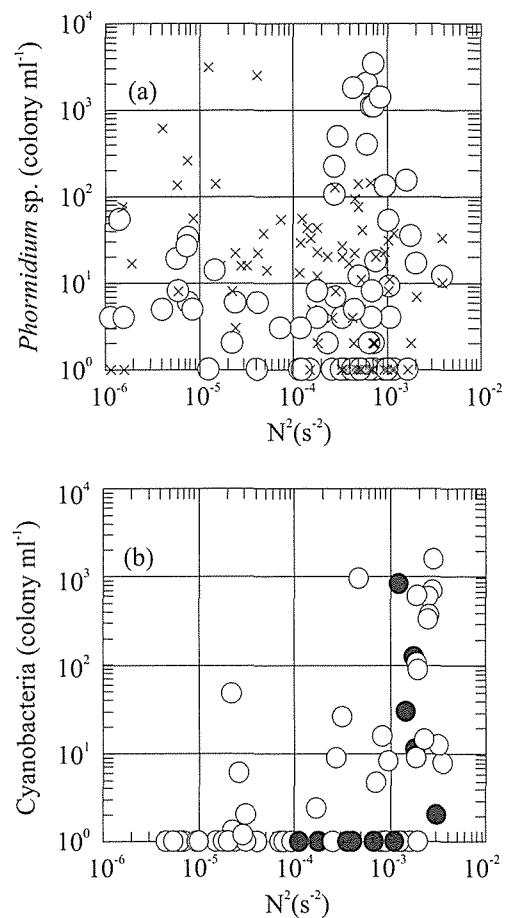
In order to optimize planning and managing artificial destratification, useful, simple, and a reasonable index is necessary. We investigated the relationship between the abundance of cyanobacteria and buoyancy frequency ( $N^2$ ) in two eutrophic reservoirs in Japan (Fig. 1). Different type of artificial destratification equipments were installed in each reservoir for the prevention of water bloom. The dominant cyanobacteria was *Phormidium tennue* in the K dam reservoir and was mainly *Microcystis aeruginosa* in the H dam reservoir.

Although the scatter of data is high in Fig.1, the colony number of both PC-type of *Phormidium* (Fig.1(a)) and cyanobacteria (*Microcystis*) (Fig.1(b)) increase in higher  $N^2$  condition. In a qualitative point of view, this relationship agrees with many previous studies (Oliver & Ganf 2000). However, in the quantitative view point, what  $N^2$  means in phytoplankton dynamics is not yet resolved. In addition to above, the increase of phycoerythrin-rich type (PE-type) *Phormidium* in lower  $N^2$  condition (Fig. 1(a)) cannot be explained from previous studies (Glover *et al.* 1986, Callieri *et al.* 1996, Pick 1991, Vörös *et al.* 1998). To explain this tendency, we attempt to analyze theoretically as shown in the following sections.

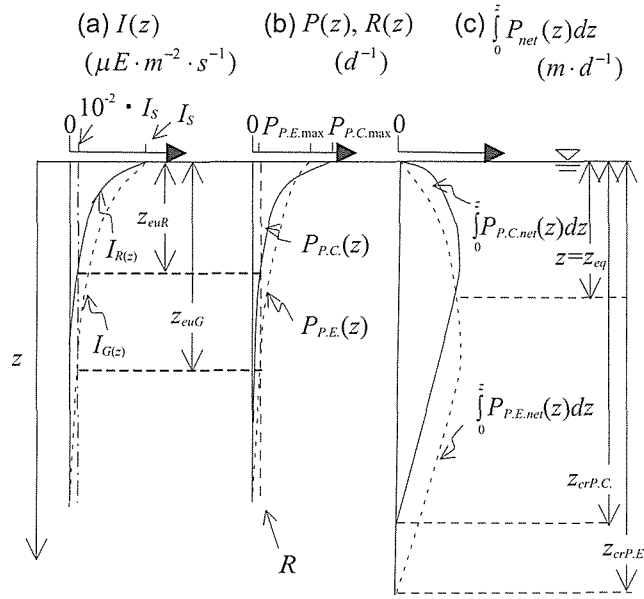
## Theory — Antenna Pigments and Buoyancy Frequency Hypothesis —

We propose a hypothesis of antenna pigments-buoyancy frequency. This theory explains how optical and hydraulic characteristics of water bodies affect *in situ* phytoplankton population competition.

As described above, there have been already some studies, which focused on the relationship between antenna pigment and underwater light spectrum. For example in cyanobacteria, roughly, there are two types of antenna pigment; PC-type, which mainly absorb red color long-wave light; PE-type, which mainly absorb green color shorter-wave length than red (Vörös *et al.* 1998). Which type becomes dominant depend on most penetrative wave length underwater light in many lakes and reservoirs. However, based on that photosynthetic ability of phytoplankton subject to depend on hydraulic states, such as mixed depth (Reynolds 1997) or critical depth (Sverdrup 1953) and critical turbulence (Huisman *et al.* 1999), we tried to propose a new theory. That is, phytoplankton population competition can be affected by not only



**Fig. 1.** The relationship between  $N^2$  and cyanobacteria abundance. (a) *Phormidium* sp in the K dam reservoir. ○, PC type; ×, PE type.  $N^2$  was calculated at total (15~20m) depth. (b) large colony cyanobacteria (mainly *Microcystis*) in the H dam reservoir. ○, before artificial circulation; ●, after artificial circulation.  $N^2$  was calculated at 5m depth.



**Fig. 2.** Diagrammatic representation of vertical profiles of optical and photosynthetic factors. (a) photon flux of red and green light (b) photosynthesis and respiration at depth  $z$  of PC type and PE type (c) depth integral net photosynthesis (DINP) of each antenna pigments type. ( $z_{eu}$  is euphotic depth for each type,  $z_{eq}$  is equilibrium depth for each types competition,  $z_{cr}$  is critical depth (Sverdrup 1953))

$$\int_0^{z_m} P_{P.C.net} = \frac{P_{P.C.max}}{\epsilon R} \cdot \log \left( \frac{I_{kp.C.} + I_{R_s}}{I_{kp.C.} + I_{R_s} \exp^{-\epsilon R \cdot z_m}} \right) - R_{P.C.} \cdot z_m \quad (1)$$

Where, PP.C. is the gross photosynthetic rate ( $d^{-1}$ ),  $P_{P.C.max}$  is the light saturated gross photosynthetic rate ( $d^{-1}$ ),  $I_{R_s}$  is the underwater photon flux density of red light at surface ( $\mu E m^{-2} s^{-1}$ ),  $\epsilon R$  is the extinction coefficient of red light ( $m^{-1}$ ),  $I_{kp.C.}$  is the half saturation photon flux density corresponding to red light of PC-type ( $\mu E m^{-2} s^{-1}$ ). The equations for PE-type can be expressed by converting PC given in the subscript into PE and R into G.

Following assumptions are used: First, PC-type depends on only red light and PE-type depends on only green light in their photosynthesis (Callieri *et al.* 1996). Second, each wave length of light attenuated has an inherent extinction coefficient. Third, each type of phytoplankton is distributed uniformly in the mixed layer.

underwater light regime but also hydraulic state through the absorption characteristics of antenna pigments.

For example, if we assume competition between two types of antenna pigment cyanobacteria, that is PC-type and PE-type, the explanation given below seems possible. Shallow mixed depth would make the conditions favorable for the PC-type because red light exist only in the shallow layer. Converse condition favor the PE-type. Under some assumptions, this competition state can be estimated by whether mixed depth reach the equilibrium depth ( $z_{eq}$ ).  $N^2$  is a useful index of hydraulic stability (Imberger & Patterson 1990) and based on this, we propose that  $N^2$  between surface and arbitrary depth would be useful index for the estimation of phytoplankton population competition.

## Theoretical Analysis

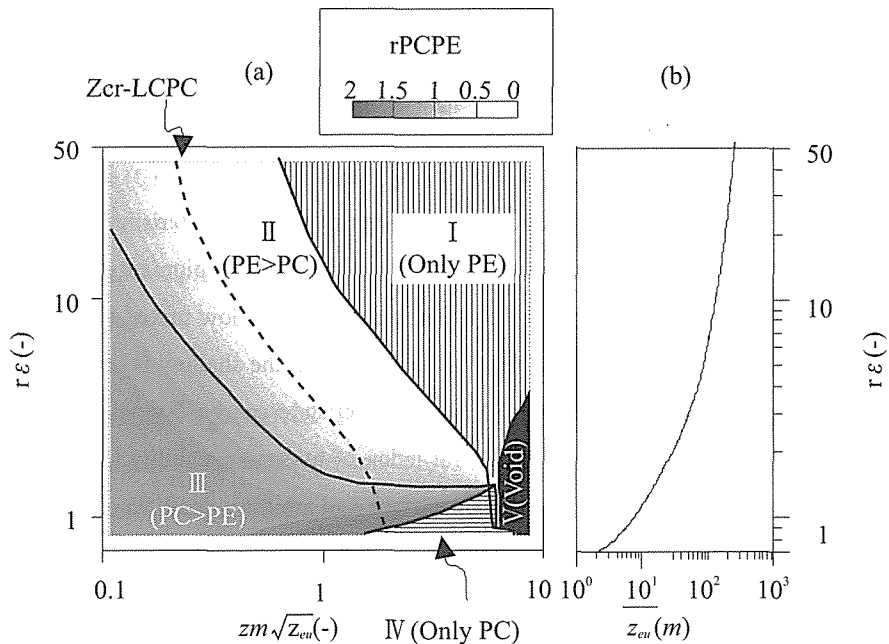
### The effect of mixed depth on competition between PC-type and PE-type

In order to analyze our hypothesis, we used some assumptions (See Fig.2 caption). Following these assumptions, depth integrated net photosynthesis (DINP) of each type can be estimated by the following equation (also see Fig.2). Fig. 2 shows these vertical profiles with a comparison of PC-type and PE-type. This competitive relation can be estimated as the ratio of DINP of each pigments types ( $r_{PCPE}$ ).

$$rPCPE = \int_0^{z_m} P_{P.C.net} / \int_0^{z_m} P_{P.E.net} \quad (2)$$

We analyzed the behavior of  $rPCPE$  as a relationship between the ratio of  $\varepsilon G$  and  $\varepsilon R$  ( $r\varepsilon$ ) and mixed depth. **Fig. 3** shows the analytical results based on biological parameters of picocyanobacteria (*Synechococcus* sp.) (Callieri *et al.* 1996). There are five areas of  $rPCPE$  according to  $z_m/z_{eu}$  and  $r\varepsilon$ . Except for area V, it is possible in four areas that DINP of both or each type is positive. Only in area V, mixed depth is too deep for positive DINP of both types. It gives rise to these five areas that smaller  $r\varepsilon$  and smaller  $z_m/z_{eu}$  make PC-type efficient than PE-type as well as that different critical depths for each pigment type. The dependence characteristics of  $rPCPE$  on  $r\varepsilon$  agrees with previous studies (Glover *et al.* 1986, Callieri *et al.* 1996, Pick 1991, Vörös *et al.* 1998). Particularly, in moderate  $r\varepsilon$ , mixed depth can determine dominant antenna pigment type.

Addition to this analytical results, we try to analyze large colony PC-type cyanobacteria (LCPC) based on the parameters of *Microcystis aeruginosa* (colony form) (Reynolds *et al.* 1981, Reynolds 1989). Although it is similar to the PC-type picocyanobacteria that the critical depth is greater in low  $r\varepsilon$ , critical depth of LCPC is shallower than picocyanobacteria and deepest critical depth is only three times as that of euphotic depth. The reason for this is lower maximum photosynthetic rate of LCPC (Reynolds 1997). Particularly, in the higher  $r\varepsilon$  area, which correspond to a high transparency water body, extremely small  $z_m/z_{eu}$  allows net photosynthesis to become positive. Therefore this is one of the reasons why the growth



**Fig. 3**  $rPCPE$  as a function of  $z_m/z_{eu}$  and  $r\varepsilon$ , and euphotic depth. (a) Solid thick lines indicate boundary of each area and dashed thick line indicates critical depth of LCPC (ex. *Microcystis aeruginosa*). Particularly, the solid thick line bounded between area II and III is  $z_{eq}$  as shown in Fig.1(c). ; (b) wave length-smoothed euphotic depth ( $\overline{z_{eu}}$ ) in accordance with  $r\varepsilon$  based on Jerlov's water types (Jerlov 1976). Since euphotic depth is strictly defined as the depth in which gross photosynthesis is equal to respiration rate, even in same water body it depends on phytoplankton species. Considering conventional water quality index, however, we calculated the euphotic depth using transparency. Thus, this euphotic depth does not consider any specific phytoplankton species.

of LCPC is restricted to eutrophic lakes and reservoirs (Reynolds 1997) that tend to be lower in transparency and has a lower  $re$ . However, even in these eutrophic lakes and reservoirs, the condition that mixed depth exceeds the depth as much as several times of euphotic depth is considered not to be suitable for LCPC.

### Critical stability and wind speed

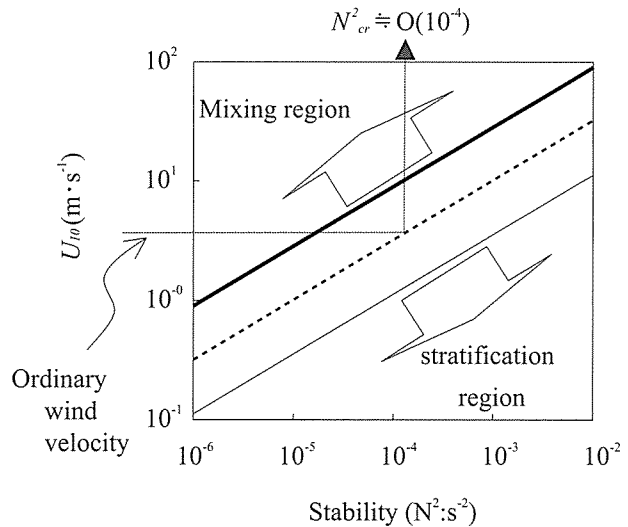
As described below, we analyzed the index of estimation for *in situ* mixing condition for phytoplankton population competition. Generally, the stability of stratification can be estimated by  $N^2$  (Imberger & Patterson 1990). However, this can only represent stability, but not actual mixing states. Considering the time scale of phytoplankton dynamics, the major external forcing factor can be assumed to be the wind. Mixing condition based on wind stirring and stratification can be estimated from Wedderburn number (Imberger & Patterson 1990). Therefore, we combined simply these two parameters and obtained the following equation for critical  $N^2$  ( $N_{cr}^2$ ).

$$N_{cr}^2 = \rho_a / \rho \cdot C_D \cdot L \cdot U_{10} \cdot H^{-3} \quad (3)$$

where  $\rho_a$  is the density of air,  $H$  is the depth,  $C_D$  is the drag coefficient,  $U_{10}$  is the wind speed at height 10 m above water surface,  $L$  is the basin scale. As shown in the Fig. 4, if we assume ordinary wind velocity at  $U_{10}$  as several m/s and depth at  $zm=10m$ ,  $N^2$  under  $O(10^{-4})$ , which corresponding to  $N_{cr}^2$  to represent mixing condition.

### Discussion

As shown in Fig. 2, in the range of medium to low  $re$  condition corresponding to many inland water bodies (Kirk, 1983), stratification condition can affect the competition dynamics of different antenna pigment type. Because maximum photosynthetic rate of large colony algae tends to be smaller (Reynolds 1997), critical depth of LCPC tends to be shallower. Furthermore, from theoretical analysis, actual mixing state can be estimated by  $N^2$ . In both reservoirs shown in Fig. 1,  $N^2$  and the corresponding calculated depth exceeds  $N_{cr}^2$  and  $z_{eq}$ , respectively seems suitable for PE-type dominance. Furthermore,  $N_{cr}^2$  of both reservoirs agree with Reynolds's empirical critical value of S-strategy type phytoplankton (Reynolds



**Fig. 4** The relationship between stability (Buoyancy frequency  $N^2$ ) and wind velocity corresponding to  $W=1$  solid thin line,  $zm=5m$ ; dashed thick line,  $zm=10m$ ; solid thick line,  $zm=20m$ . Each line represents critical values of mixing or sustaining stratification corresponding to each different mixed depth. In this figure, the range of  $N_{cr}^2$  at  $z=10m$  in accordance with ordinary wind speed is indicated

1993) (such as *M.aeruginosa*, *Volvox*, *Peridinium*, characterized by bigger size, and slower growth rate).

However, in this research, there are several limitations such as the effect of other populations, the assumption of steady state, and the generality of  $r\epsilon$  (Prieur & Sathyendranath 1981). Furthermore, for investigation in relation to pigments of cyanobacteria, consideration about chromatic adaptation (Tandeau 1977) is necessary. However, in addition to the agreement with some of previous studies about optical viewpoints (Pick 1991, Vörös *et al.* 1998), and requirement of shallow stable stratification for cyanobacterial bloom (Huisman 1999, Wallane & Hamilton 2000),  $N_{cr}^2$  which we proposed is practical and useful for planning and management of artificial destratification.

In the future, it is necessary to verify this hypothesis using more field data, and also to investigate the relation to other factors such as buoyancy regulation of cyanobacteria (Oliver & Ganf 2000). Moreover, for optimization of artificial destratification, it is necessary to clarify arbitrary equipment specification based on previous hydraulic studies (Asaeda & Imberger 1993).

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