CHANGES IN TURBULENT MIXING SHIFT COMPETITION FOR LIGHT BETWEEN PHYTOPLANKTON SPECIES

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Abstract. The intriguing impact of physical mixing processes on species interactions has always fascinated ecologists. Here, we exploit recent advances in plankton models to develop competition theory that predicts how changes in turbulent mixing affect competition for light between buoyant and sinking phytoplankton species. We compared the model predictions with a lake experiment, in which the turbulence structure of the entire lake was manipulated using artificial mixing. Vertical eddy diffusivities were calculated from the measured temperature microstructure in the lake. Changes in turbulent mixing of the lake caused a dramatic shift in phytoplankton species composition, consistent with the predictions of the competition model. The buoyant and potentially toxic cyanobacterium *Microcystis* dominated at low turbulent diffusivity, whereas sinking diatoms and green algae dominated at high turbulent diffusivity. These findings warn that changes in the turbulence structure of natural waters, for instance driven by climate change, may induce major shifts in the species composition of phytoplankton communities.

Key words: competition model; harmful algal blooms; Microcystis; *Péclet number; photosynthesis; regime shift; resource competition; temperature microstructure; turbulence.*

INTRODUCTION

Mixing processes affect species interactions (Huffaker 1958, Levin 1974, Hassell et al. 1994, Kerr et al. 2002, Hulot and Huisman 2004). This is particularly true for planktonic species, whose spatial distributions are to a large extent governed by physical mixing processes (Riley et al. 1949, Hutchinson 1967, Spigel and Imberger 1987, Reynolds 1997, Abraham et al. 2000, Diehl et al. 2002). In marine ecosystems, changes in turbulent mixing are often accompanied by shifts from dominance by dinoflagellates at weak turbulent mixing to dominance by diatoms at intense turbulent mixing (Jones and Gowen 1990, Lauria et al. 1999, Irigoien et al. 2000). In lakes, intensified mixing has led to species replacements from buoyant cyanobacteria toward green algae and diatoms (Reynolds et al. 1983, Bailey-Watts et al. 1987, Harris and Baxter 1996, Visser et al. 1996a). In rivers, similar transitions from dominance by buoyant cyanobacteria to dominance by diatoms occur in relation to changes in mixing regime (Bormans and Condie 1998, Sherman et al. 1998). In all these examples, the interplay between turbulent mixing and access to light appears to be a key factor

determining the changes in phytoplankton community structure.

Despite these well-documented studies, a coherent theory to predict the impact of turbulent mixing on competition for light between phytoplankton species is still in its infancy. Existing theory predicts that the population dynamics of competition for light in well-mixed waters depend on the ''critical light intensities'' of the phytoplankton species. During intense mixing, the species with lowest critical light intensity should competitively exclude all other species (Huisman and Weissing 1994, Weissing and Huisman 1994). Competition experiments in light-limited chemostats confirm this prediction (Huisman 1999, Huisman et al. 1999a). During weak mixing, however, species with low critical light intensities may lose their competitive advantage, if other species are able to gain better vertical positions in the light gradient (Huisman et al. 1999c, Klausmeier and Litchman 2001, Elliott et al. 2002). Under pure light limitation and poor mixing, game theory predicts that the evolutionarily stable strategy for the position of a single species is at the surface (Klausmeier and Litchman 2001). Buoyant phytoplankton species, for instance, may float upwards during weak mixing, forming dense surface blooms (Ibelings 1996, Kononen et al. 1996, Walsby et al. 1997, Villareal et al. 1999). As a result, these buoyant species enhance their own access to light while shading other phytoplankton species. Weak mixing thus gen-

erates asymmetric interactions that may shift the competitive balance in phytoplankton communities.

Here, we develop a competition model to predict how turbulent mixing affects competition for light between buoyant and sinking phytoplankton species. We compare the model predictions with a field study, in which the turbulence structure of a hypertrophic lake was manipulated by means of artificial mixing. Controlled mixing of the lake allowed us to rigorously assess whether the observed changes in turbulent mixing and phytoplankton species composition matched theoretical predictions, thus providing a direct quantitative link between physical mixing processes and phytoplankton community structure.

COMPETITION MODEL

Our competition model is an extension of earlier competition models developed by Huisman and co-workers (Huisman and Weissing 1994, Huisman et al. 1999*a*, *c*). It extends these previous competition models by incorporation of the vertical velocity of buoyant and sinking phytoplankton species.

We consider a vertical water column with several phytoplankton species. We assume that the water is highly eutrophic, such that all nutrients are in ample supply and the growth rates of the phytoplankton species are governed by light availability. Losses of phytoplankton may result from cell lysis, grazing, or virus attacks. Vertical transport of phytoplankton species is driven by sinking or buoyancy of the phytoplankton cells, and by turbulent mixing of the cells through the water column. More precisely, let z denote the depth within the water column, where z runs from 0 at the top to a maximum depth, z_m, at the bottom. Let $I(z, t)$ denote the light intensity at depth z and time t, and let $\omega_i(z, t)$ denote the population density (cells per unit volume) of phytoplankton species i. Accordingly, competition for light between a number of phytoplankton species, n, can be described by a series of n reaction–advection–diffusion equations:

$$\frac{\partial \omega_i}{\partial t} = p_i(I)\omega_i - L_i\omega_i + v_i\frac{\partial \omega_i}{\partial z} + D\frac{\partial^2 \omega_i}{\partial z^2} \quad (1)$$

where $i = 1, \ldots, n$.

Here, $p_i(I)$ is the specific growth rate of species i as a function of light intensity, L_i is the specific loss rate of species i, v_i is the vertical velocity of species i (with $v_i < 0$ for sinking species and $v_i > 0$ for buoyant species), and D is known as the turbulent diffusion coefficient or vertical eddy diffusivity. We assume that the light dependence of phytoplankton growth is described by a Monod function, $p_i(I) = p_{max,i} I/(H_i + I)$, where $p_{max,i}$ is the maximal specific production rate of species i, and H_i is the half-saturation constant of light-limited growth. Other $p_i(I)$ functions of similar shape might also be used (Jassby and Platt 1976), and lead

to similar results (Weissing and Huisman 1994, Behrenfeld and Falkowski 1997).

Light intensity decreases with depth because photons are absorbed by water, dissolved organic matter, phytoplankton species, and many other light-absorbing substances in the water column. More precisely, the light gradient can be described by Lambert-Beer's law applied to nonuniform population density distributions (Huisman et al. 1999*c*):

$$I(z, t) = I_{in}\exp\left\{-\int_0^z \left[\sum_{j=1}^n k_j\omega_j(\sigma, t)\right] d\sigma - K_{bg}z\right\} \quad (2)$$

where I_{in} is the incident light intensity at the top of the water column, k_j is the specific light attenuation coefficient of phytoplankton species j, K_{bg} is the total background turbidity caused by all nonphytoplankton components in the water column, and σ is an integration variable. We note, from Eq. 2, that the light gradient is dynamic. Changes in the population density distributions of the phytoplankton species cause concomitant changes in the light gradient. Thus, the species interact with each other via modification of the light gradient, that is, via shading.

To complete the model, we assume zero-flux boundary conditions at the top and the bottom of the water column:

$$v_i\omega_i(z, t) + D\frac{\partial \omega_i}{\partial z}(z, t) = 0 \quad (3)$$

at $z=0$ and $z=z_m$.

Numerical simulation of Eqs. 1–3 was based on techniques from computational fluid dynamics tailored to light-limited phytoplankton. Formally, our competition model is an n-dimensional system of integro-partial differential equations (integro-PDEs). The integral in Eq. 2 introduces a nonlocal term in the competition model. Moreover, the various species are coupled through this nonlocal term. As a result, numerical simulation of this system of integro-PDEs is computationally quite demanding. We based our simulations on a finite volume method, with spatial discretization of the differential operators and integral term (Ferziger and Perić 1999). The resulting system of stiff ordinary differential equations was integrated over time using an implicit integration method (Brown et al. 1989). Our simulation techniques are explained in full detail in Huisman and Sommeijer (2002).

EXPERIMENTAL LAKE

The lake

We applied the competition model to Lake Nieuwe Meer, a recreational lake in the city of Amsterdam, The Netherlands (see Plate 1). Lake Nieuwe Meer is a hypertrophic lake, with a surface area of 1.3 km², a mean depth of 18 m, and a maximum depth of 30 m. To the despair of water management authorities, dense surface
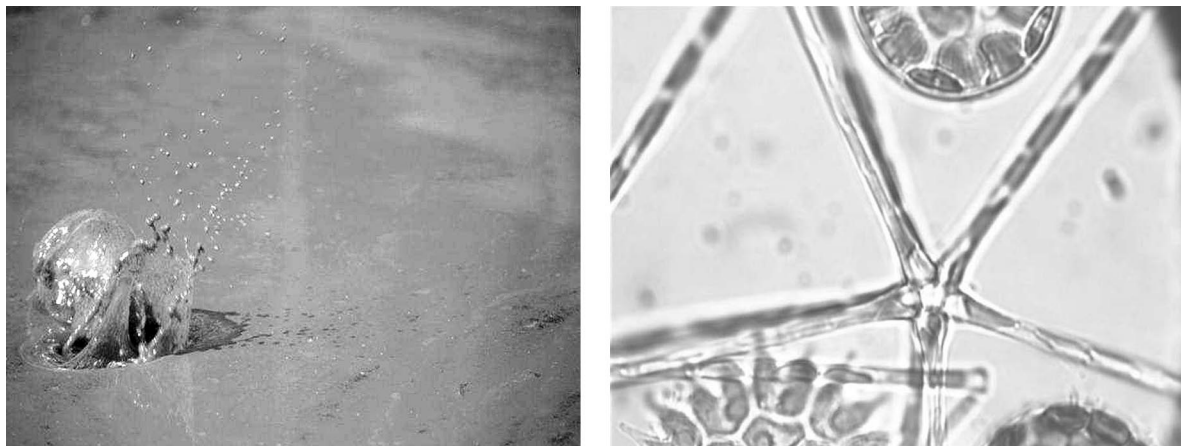
PLATE. 1. (Left) A stone is thrown in a dense surface bloom of the buoyant cyanobacterium *Microcystic* in Lake Nieuwe Meer. (Right) Increased mixing of the lake led to a major change in species composition; sinking phytoplankton species became dominant, like the diatom *Asterionella* (the large ''star'' in the middle) and the green alga *Pediastrum* (the ''rising sun'' at the bottom left). Photo credit: Petra M. Visser and Josje Snoek.

blooms of the cyanobacterium *Microcystis aeruginosa* dominated the lake during the summer months for many years. *Microcystis* is a widespread cyanobacterium that can form nearly monospecific blooms in a variety of eutrophic freshwaters (Zohary and Robarts 1990, Ibelings 1996, Visser et al. 1996*a*). *Microcystis* contains gas vesicles, which give the cells buoyancy (Walsby 1994). Die-off of dense surface blooms of *Microcystis* in summer and autumn spread a disgusting smell and caused anoxia. Moreover, many *Microcystis* strains produce a family of toxins, called microcystins. These microcystins are hepatotoxins that can damage the liver of fish, birds, and mammals, including humans. As a result, *Microcystis* blooms provide a serious threat for water quality, fisheries, and human health (Chorus and Bartram 1999, Codd et al. 1999).

Since Lake Nieuwe Meer has an open connection to the water storage basin of the adjoining polder area and a connection to the canals of Amsterdam, substantial
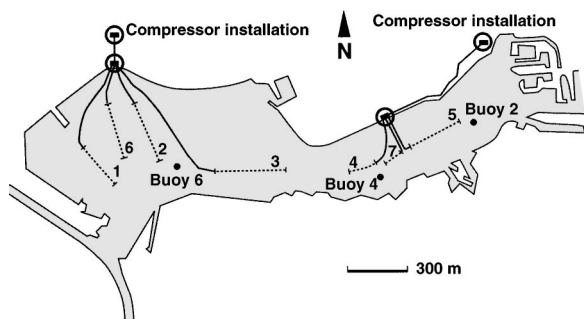

FIG. 1. Map of Lake Nieuwe Meer. The lines numbered from 1 to 7 indicate the seven air tubes used for artificial mixing of the lake; the dashed parts correspond with the perforated parts of the air tubes, providing the aeration. The three sampling stations (buoy 2, buoy 4, buoy 6) are also indicated.

reduction of nutrient loading was not feasible. In 1993, Water Board Rijnland, the water authority responsible for Lake Nieuwe Meer, started artificial mixing of the lake by means of air bubbling, using a system of seven perforated air tubes installed just above the lake sediment (Fig. 1). Artificial mixing led to major changes in phytoplankton species composition (Visser et al. 1996*a*). *Microcystis* was replaced by a mixture of diatoms (mainly *Cyclotella* and *Stephanodiscus*) and large green algae (mainly *Scenedesmus* species).

To test the competition theory, we estimated model parameters for the dominant phytoplankton species of Lake Nieuwe Meer. Furthermore, we exploited recent advances in measurement techniques of turbulent mixing to estimate the vertical turbulent diffusivities in Lake Nieuwe Meer, both with and without artificial mixing. This allowed us to assess whether the outcome of competition predicted by the parameterized competition model matched the observed changes in species composition in the lake.

Phytoplankton parameters

Model parameters for the dominant phytoplankton species of Lake Nieuwe Meer were estimated based on data provided by earlier phytoplankton studies in this lake (Visser 1995, Visser et al. 1996*a, b*). Since the growth kinetics and sinking velocities of the dominant diatoms and green algae were quite similar, they were lumped into a single category ''diatoms and greens'' (Table 1). The maximal specific growth rates of the diatoms and greens are much higher than the maximal specific growth rate of *Microcystis*. However, *Microcystis* is a buoyant species, whereas the diatoms and greens are sinking species.

Turbulence structure

Artificial mixing of Lake Nieuwe Meer was switched off on 19 July 2002, and switched on again on 7 August

TABLE 1. Parameter values for *Microcystis* and the diatoms and green algae of Lake Nieuwe Meer (based on Visser 1995, Visser et al. 1996*a, b*).

| Symbol | Meaning | Parameter values | | Units |
		Diatoms and greens	*Microcystis*	
Species parameters				
v_i	vertical velocity	−5	+50	cm/h
$p_{max,i}$	maximal specific growth rate	0.050	0.008	h^{-1}
H_i	half-saturation constant of light-limited growth	40	40	$\mu mol\ photons \cdot m^{-2} \cdot s^{-1}$
L_i	specific loss rate	0.006	0.004	h^{-1}
k_i	specific light attenuation coefficient	0.700	0.034	$cm^2/10^6\ cells$
Environmental parameters				
I_{in}	incident light intensity	350		$\mu mol\ photons \cdot m^{-2} \cdot s^{-1}$
K_{bg}	background turbidity	0.6		m^{-1}
z_m	water-column depth	18		m

2002, to measure the turbulence structure of the lake under both mixing regimes. We monitored changes in the temperature profile using a permanently moored vertical array of temperature loggers, slightly north of buoy 6 (Fig. 1). The temperature loggers recorded the temperature every 10 minutes.

Vertical turbulent diffusivities can be calculated from detailed profiles of the temperature microstructure (Imberger and Ivey 1991, Kocsis et al. 1999, MacIntyre 1999, Sharples et al. 2001). This requires that the temperature structure is resolved at very small scales, on the order of 1 mm, accomplished by the use of a Self-Contained Autonomous Microstructure Profiler (SCAMP).[7] Using a SCAMP, we measured the vertical microstructure of light, temperature, and chlorophyll fluorescence at three sampling stations (buoy 2, buoy 4, buoy 6; Fig. 1). At each sampling station, we collected 10 consecutive SCAMP profiles within ~40 minutes to capture the intermittent nature of turbulent mixing. Turbulent diffusivities were calculated from the temperature microstructure according to Sharples et al. (2001).

When artificial mixing was switched off, the lake stratified within 10 days, with a thermocline at ~5 m depth (Fig. 2A). The phytoplankton population concentrated in the upper 2.5 m of the water column (Fig. 2B). Turbulent diffusivity ranged from $D = 0.02–0.7$ cm^2/s below the thermocline to $D = 0.1–4$ cm^2/s above the thermocline. Turbulent diffusivities were log-transformed to improve the homoscedasticity of the data. Averaged over all depths and sampling stations, turbulent diffusivity equaled $D = 0.17$ cm^2/s (average(log D) = −0.78, 1 SD(log D) = 0.53, $N = 105$).

After the onset of artificial mixing, the temperature stratification disappeared within a few days (Fig. 2A), and the phytoplankton population was uniformly mixed over depth (Fig. 2C). Turbulent diffusivity ranged from $D = 0.3$ cm^2/s to $D = 100$ cm^2/s. Averaged over all depths and sampling stations, turbulent diffusivity

[7] ⟨http://www.pme.com/scamp.htm⟩

equaled $D = 5.1$ cm^2/s (average(log D) = 0.71, 1 SD(log D) = 0.73, $N = 110$).

The difference in turbulent diffusivity between the two treatments, artificial mixing off vs. artificial mixing on, was highly significant (t test: $t_{213} = 17.2$; $P < 0.0001$).

GROWTH IN MONOCULTURE

We first investigate how turbulent mixing would affect the species separately, in monoculture. We ran numerous simulations with the single-species version of our competition model, for a wide range of water-column depths and turbulent diffusivities. We will say that there is bloom development if a phytoplankton population can increase in abundance when rare.

Fig. 3A shows the model predictions thus obtained for a monoculture of the buoyant cyanobacterium *Microcystis*. If water-column depth exceeds a critical depth (sensu Sverdrup 1953) and turbulent mixing exceeds a critical turbulence (sensu Huisman et al. 1999*b*), the *Microcystis* population would be mixed to great depths and the light conditions thus experienced are so dark that losses exceed production. Hence, *Microcystis* cannot develop blooms if water-column depth exceeds a critical depth and turbulent mixing exceeds a critical turbulence. Comparison with the turbulent diffusivities measured in Lake Nieuwe Meer shows that monocultures of *Microcystis* can develop blooms when artificial mixing is off. Conversely, when artificial mixing is on, monocultures of *Microcystis* would be on the edge of the parameter region that permits bloom development (Fig. 3A).

Fig. 3B assumes that the sinking diatoms and green algae grow alone, in the absence of *Microcystis*. The model predicts that, similar to buoyant phytoplankton, sinking phytoplankton species cannot develop a bloom if water-column depth exceeds a critical depth and turbulent mixing exceeds a maximal turbulence. In addition, if turbulent mixing is too weak, sinking phy-
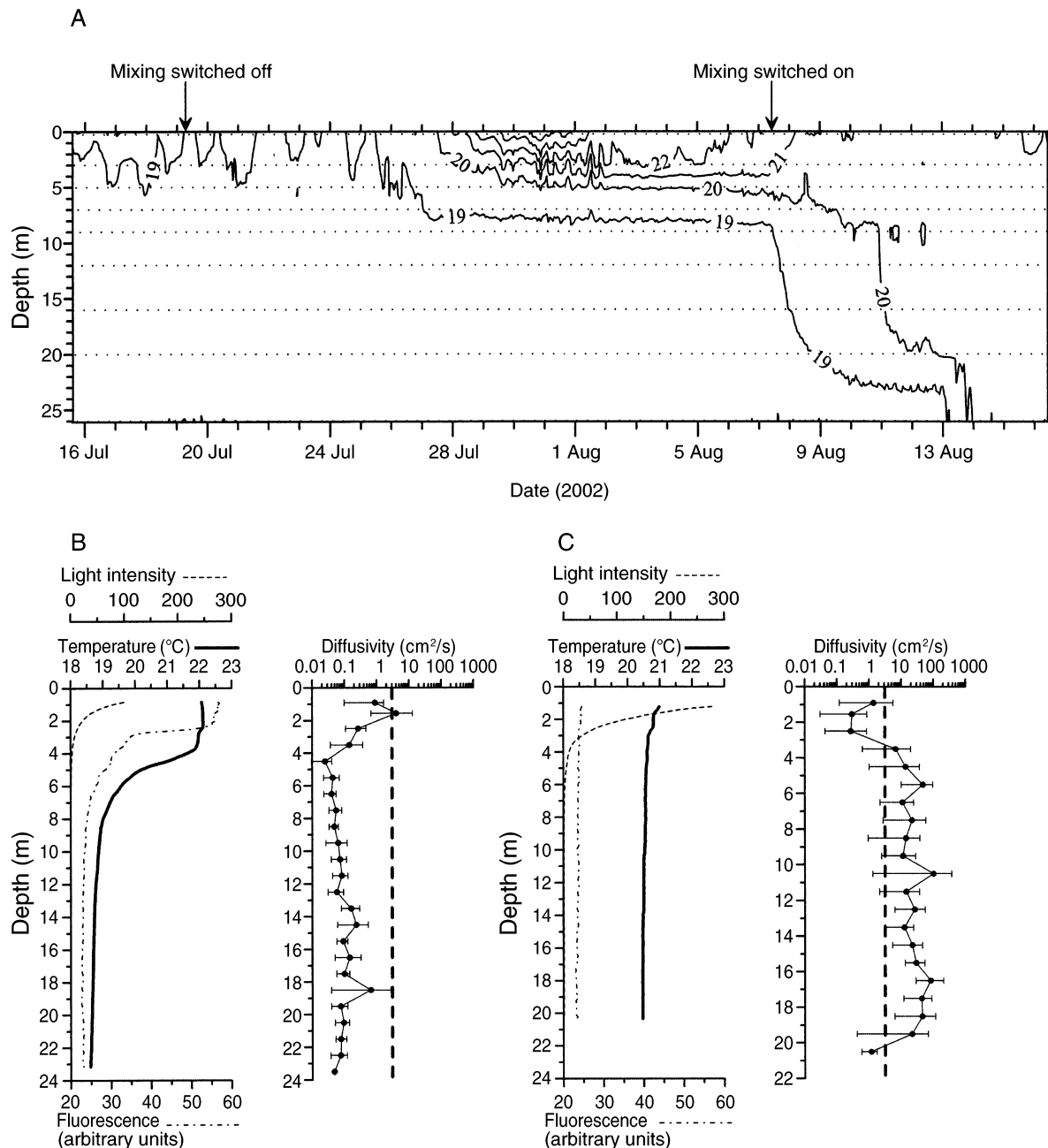
FIG. 2. Changes in the physical structure of Lake Nieuwe Meer during the 2002 experiment. (A) Time series of temperatures (19°–22°C) measured by the moored temperature loggers at buoy 6. (B) Physical structure without artificial mixing, measured at buoy 6 on 5 August 2002. (C) Physical structure with artificial mixing, measured at buoy 6 on 16 August 2002. In (B) and (C), light intensity is measured in μmol photons·m^{-2}·s^{-1} (PAR range of 400–700 nm); chlorophyll fluorescence is used as a relative measure of phytoplankton biomass. Closed circles in the right-hand panels of parts (B) and (C) indicate turbulent diffusivity (with 95% confidence limits; $N = 10$).

toplankton cannot be entrained in the upper part of the water column and will vanish into the deep (Riley et al. 1949, Shigesada and Okubo 1981). Thus, theory predicts that sinking phytoplankton species can develop blooms in deep waters only if turbulent mixing takes an intermediate value, between a minimal and a max-imal turbulence (Huisman et al. 2002). Comparison with the turbulent diffusivities measured in Lake Nieuwe Meer shows that, in the absence of *Microcystis*, conditions are suitable for bloom development of the diatoms and green algae both when artificial mixing is on and when artificial mixing is off (Fig. 3B).
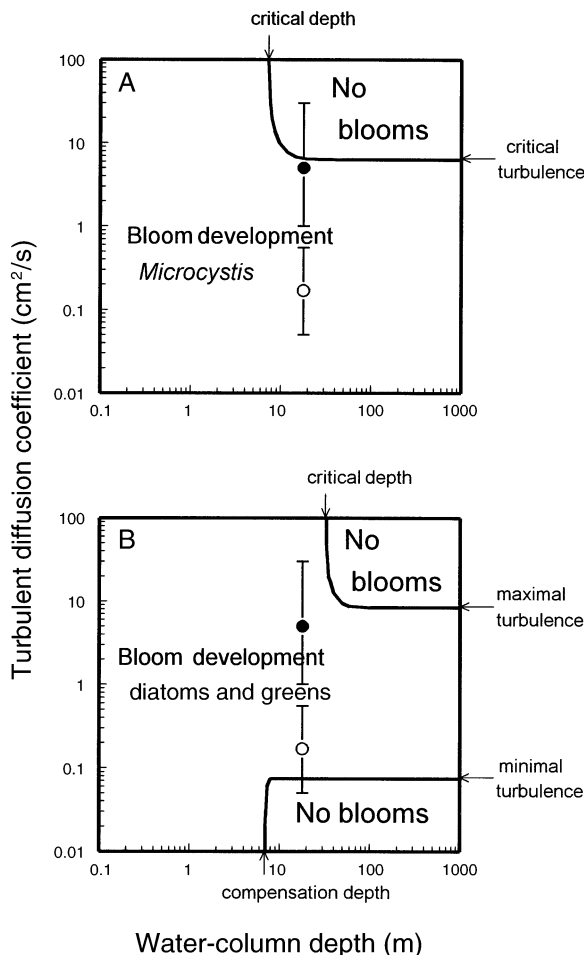
FIG. 3. Model prediction of the conditions that allow bloom development for (A) a monoculture of the buoyant cyanobacterium *Microcystis* and (B) a monoculture of the sinking diatoms and green algae, plotted as a function of water-column depth and turbulent diffusion coefficient. The position of Lake Nieuwe Meer is indicated in the graphs, both without artificial mixing (open circles) and with artificial mixing (solid circles). Error bars indicate ±1 SD. The graphs are each based on a grid of 41 × 41 = 1681 simulations. For model parameters, see Table 1.

COMPETITION

Two simulation examples

Species that would develop blooms in monoculture may be prevented from doing so in the presence of competing species. This section presents two simulation examples of the species in competition. At the onset of the simulations, the species are uniformly distributed over depth, with a low initial population density.

Fig. 4A assumes that artificial mixing is switched off, and hence vertical turbulent diffusivity is low. *Microcystis* cells float upwards, and develop a surface bloom from the first days onwards. In contrast, the diatoms and green algae remain distributed over the

entire water column. Initially, both *Microcystis* and the diatoms and green algae increase. The surface bloom of *Microcystis* expands to population densities that exceed 5×10^6 cells/mL (note the changing scales of the different panels in Fig. 4A). As a result of this dense surface bloom, nearly all light is absorbed in the upper meter of the water column. The diatoms and green algae are shaded by the surface bloom, and they start to decline. *Microcystis* wins (Fig. 4A).

Fig. 4B assumes that artificial mixing is switched on. The vertical turbulent diffusivity is sufficiently high to prevent a surface bloom of *Microcystis*. Instead, *Microcystis* is mixed over the upper 10 m of the water column, and thus exposed to the dark conditions in the deeper parts of the water column. Initially, both *Microcystis* and the diatoms and green algae increase. As a result, more light is absorbed, and the light gradient steepens. *Microcystis* is a less efficient species at low light than the diatoms and green algae, however, and hence *Microcystis* starts to decline after ~10 days. The diatoms and green algae win (Fig. 4B).

The overall picture

We ran numerous simulations with the competition model, for a wide range of water-column depths and turbulent diffusivities. For each simulation, we documented the final outcome of competition. The results thus obtained are plotted in Fig. 5. If the species are mixed over great depths, none of the species survives (upper right corner of Fig. 5; compare with Fig. 3). The model predicts that diatoms and green algae will win the competition when Lake Nieuwe Meer is intensely mixed. Conversely, *Microcystis* will float upwards and outcompete the other species during weak mixing. The boundary between *Microcystis* dominance and dominance by diatoms and greens in Lake Nieuwe Meer, with an average water-column depth of 18 m, is predicted at a turbulent diffusivity of $D \approx 3.4$ cm²/s. When artificial mixing is off, turbulent diffusivity is clearly in the range where *Microcystis* dominates. When artificial mixing is on, turbulent diffusivity is just sufficient to shift the system toward dominance by diatoms and green algae (Fig. 5).

Two features of Fig. 5 attract immediate attention. First, coexistence is confined to a narrow band only. This is a robust result that we also found in the model simulations when using other parameter values reflecting different species combinations. Apparently, competition for light does not create many opportunities for species coexistence. Second, the pattern in Fig. 5 is surprisingly simple. For shallow waters, <30 m deep, the boundary between the two regions of competitive dominance is described by a diagonal line with a slope of 1 when plotted on a log-log scale. Again, this is a robust result that we also found when using other species combinations.
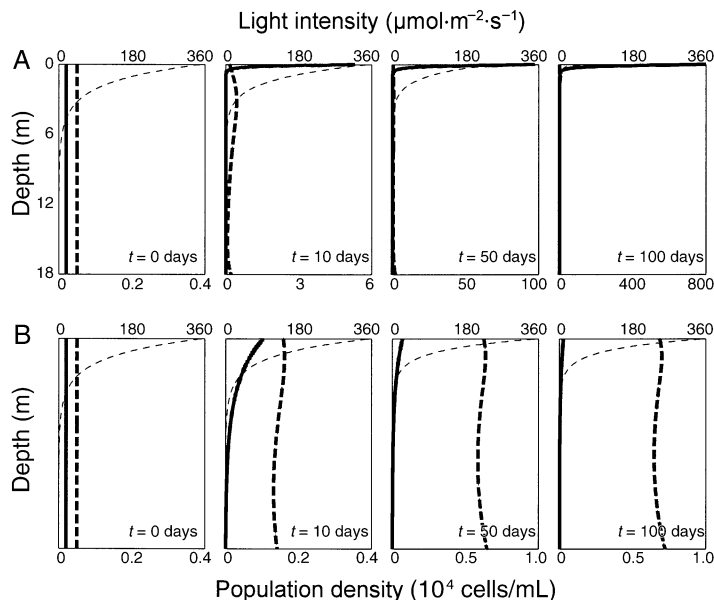
FIG. 4. Model simulation of competition for light between the buoyant cyanobacterium *Microcystis* and the sinking diatoms and green algae, assuming (A) weak mixing ($D = 0.17$ cm²/s), and (B) intense mixing ($D = 5.1$ cm²/s). Bold solid lines indicate the population density distributions of *Microcystis*; bold dashed lines indicate the population density distributions of the diatoms and green algae; thin dashed lines indicate the light gradient. For parameter values, see Table 1.

Dimensional analysis

The diagonal boundary line in Fig. 5, for waters <30 m deep, can be explained by the time scale of turbulent mixing vs. the time scale of the vertical velocity of the species. The time scale of turbulent mixing
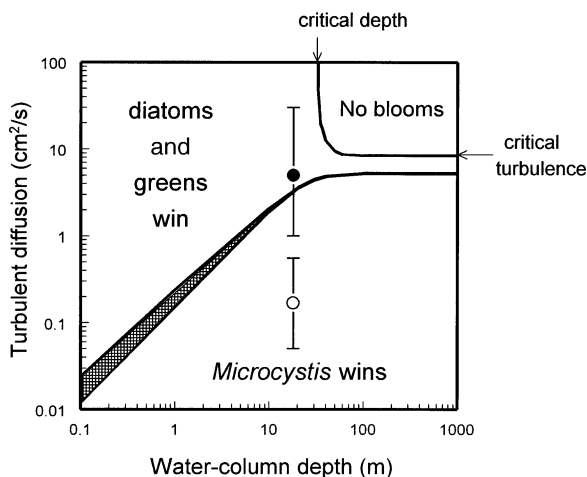

FIG. 5. Model prediction of the outcome of competition for light between *Microcystis* and the diatoms and green algae, plotted as a function of water-column depth and turbulent diffusion coefficient. In the narrow hatched area, *Microcystis* and the diatoms and greens coexist. The position of Lake Nieuwe Meer is indicated in the graphs, both without artificial mixing (open circle) and with artificial mixing (solid circle). Error bars indicate standard deviation. The graph is based on a grid of 41 × 41 = 1681 simulations. For model parameters, see Table 1.

indicates the time required for a phytoplankter to travel through the water column by means of turbulent mixing, and is given by $\tau_{mix} = z_m^2/D$. The time scale of the vertical velocity of a species indicates the time required for a phytoplankter to travel through the water column by means of its sinking rate or buoyancy, and is given by $\tau_{vv} = z_m/v$. The dimensionless Péclet number, Pe, gives the ratio of these two time scales (e.g., Condie 1999):

$$\text{Pe} = \frac{\tau_{mix}}{\tau_{vv}} = \frac{z_m v}{D}. \quad (4)$$

We note that the Péclet number is species specific, because the vertical velocity is different for different species. We focus here on the Péclet number from the perspective of *Microcystis*, as our simulations indicate that the buoyant *Microcystis* wins the competition when it is able to overtop the sinking species. The diagonal boundary line between dominance of *Microcystis* and dominance of the diatoms and greens, in Fig. 5, is described by the simple equation Pe = 7. That is, the boundary line depends on the ratio of the time scales of turbulent mixing and vertical flotation. If the rate of vertical flotation dominates over the rate of turbulent mixing (i.e., Pe > 10), *Microcystis* will form a surface bloom, and hence outcompetes the diatoms and greens. Conversely, if turbulent mixing dominates over vertical flotation (i.e., Pe < 1), *Microcystis* cannot form a surface bloom, and the diatoms and green algae win.

In waters deeper than 30 m, the boundary line that separates the two domains of dominance bends off and takes a constant value, irrespective of water-column

depth. In these deep waters, there is sufficient time for a phytoplankter to produce daughter cells before the phytoplankter is transported throughout the entire depth of the water column by mixing or flotation. As a result, a third time scale, the time scale of phytoplankton growth, plays a role as well. From simple model considerations, analogous to the classic KISS model of Skellam (1951) and Kierstead and Slobodkin (1953), it can be shown that the asymptotic expansion rate of a growing population of a neutrally buoyant species (i.e., $v_i = 0$) with a net specific growth rate μ is given by the square root of $4\mu D$. If the vertical flotation velocity of a buoyant species exceeds this vertical expansion rate, the entire population becomes concentrated in the upper part of the water column, and hence the outcome of competition will be independent of water-column depth. (That is, imagine an ocean several kilometers deep; competition for light in the upper 100 m is independent of the depth of the ocean.) We therefore define a second dimensionless number that compares the vertical expansion rate of a growing population with the vertical flotation velocity. We have called this dimensionless number the Riley number, Ry, in honor of the early work of Gordon Riley on plankton dynamics and turbulent mixing (Riley 1942, Riley et al. 1949):

$$Ry = \frac{v^2}{4[p(I_{in}) - L]D}. \qquad (5)$$

The horizontal boundary line in Fig. 5, between dominance of *Microcystis* and dominance of the diatoms and greens in waters deeper than 30 m, is described by the simple equation Ry = 9. That is, if, in deep waters, the vertical flotation rate of *Microcystis* dominates over the vertical expansion rate of the *Microcystis* population (Ry > 10), *Microcystis* will form a surface bloom irrespective of water-column depth, and will outcompete the diatoms and greens. Conversely, if, in deep waters, the vertical expansion rate dominates over the vertical flotation rate (Ry < 1), *Microcystis* cannot form a surface bloom, and the diatoms and green algae will win.

This dimensional analysis illustrates how the time scales of turbulent mixing, vertical flotation or sinking, and population growth determine the impact of turbulent mixing on competition between buoyant and sinking phytoplankton species. We emphasize, though, that a dimensional analysis provides, at best, only a rough approximation of the full competition model.

DISCUSSION

Although many theoretical studies predict that changes in mixing processes affect species interactions (e.g., Levin 1974, Powell and Richerson 1985, Hassell et al. 1994, Durrett and Levin 1997, Huisman et al. 1999*c*, Bracco et al. 2000, Hulot and Huisman 2004), only a limited number of empirical studies have tested these model predictions (Huffakker 1958, Eppley et al.
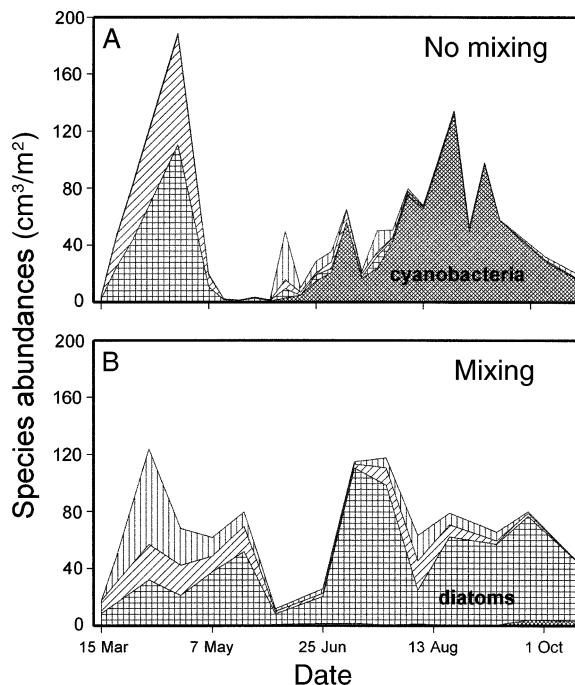

FIG. 6. Seasonal patterns in phytoplankton species composition in Lake Nieuwe Meer. (A) Example of a year without artificial mixing (1990). (B) Example of a year with artificial mixing (1993). Species abundances are expressed in biovolumes per unit surface area of the lake. Dark hatched area (finely spaced cross-hatching) = cyanobacteria (mostly *Microcystis*); boxes (wider cross-hatching) = diatoms; diagonal lines = green algae; vertical lines = small flagellates.

1978, Chao and Levin 1981, Reynolds et al. 1983, Kerr et al. 2002). The theory and field experiment reported in this paper show that changes in turbulent mixing may shift competition for light between phytoplankton species. When artificial mixing of Lake Nieuwe Meer was switched off, field measurements showed that the vertical turbulent diffusivity was low (Fig. 2B). In this case, the parameterized competition model predicts that the buoyant cyanobacterium *Microcystis* will become dominant because its vertical flotation velocity exceeds the rate of turbulent mixing (Fig. 5). When artificial mixing was switched on, the field measurements showed that turbulent diffusivity was much higher (Fig. 2C). Consequently, the parameterized competition model predicts that diatoms and green algae should become dominant, because turbulent mixing exceeds the vertical flotation velocity of *Microcystis*. These model predictions are consistent with the observations on phytoplankton species composition in Lake Nieuwe Meer. Dense surface blooms of *Microcystis* dominated the lake almost every summer during the 1980s and early 1990s, when the lake was not artificially mixed (Fig. 6A shows an example). From 1993 onwards, the lake was artificially mixed, and ever since then diatoms and green algae have dominated the lake throughout the summer period (Fig. 6B).

The theory developed in this paper is consistent not only with the observations in Lake Nieuwe Meer, but also with numerous other field observations on shifts in the competitive balance between buoyant and sinking phytoplankton species in freshwater ecosystems (Reynolds et al. 1983, Harris and Baxter 1996, Sherman et al. 1998) and marine ecosystems (Walsby et al. 1997, Lauria et al. 1999). Moreover, the patterns are also consistent with the physiological adaptations of the species involved. Generally speaking, diatoms and green algae seem better adapted to fluctuating light conditions experienced in well-mixed waters than buoyant cyanobacteria (Ibelings et al. 1994, Flameling and Kromkamp 1997, Litchman 2000). Although these qualitative patterns have been known for a long time, a major advance of the competition theory advocated in this paper is that quantitative prediction of the impact of turbulent mixing on phytoplankton species composition comes into reach.

Interestingly, the model predicts that the phytoplankton species would all have grown well in Lake Nieuwe Meer, irrespective of the mixing regime, if they had grown in monoculture isolation (Fig. 3). It is because of competitive interactions, mediated by shading, that the diatoms and greens are predicted to competitively displace *Microcystis* in well-mixed waters, whereas buoyant *Microcystis* competitively displaces the others during weak mixing. Hence, the theory and lake experiment reveal that changes in species composition observed in response to changes in turbulent mixing are not so much related to the physiological limits of these species, but are largely driven by shifts in the competitive balance between the plankton species.

In contrast with most theoretical studies on mixing processes, which generally predict high species diversity at low mixing intensity (e.g., Levin 1974, Powell and Richerson 1985, Hassell et al. 1994, Kerr et al. 2002), our competition model predicts little opportunity for species coexistence (Huisman et al. 1999*c*). This matches the observations in Lake Nieuwe Meer, where a nearly monospecific bloom of *Microcystis* dominates the phytoplankton during summers without artificial mixing (Fig. 6A). The lack of species coexistence during weak mixing can be attributed to the asymmetric nature of competition for light. That is, once a buoyant species forms a dense surface bloom, there is little opportunity for sinking or neutrally buoyant species to escape from shading. As a result, weak vertical mixing will have a tendency to reduce phytoplankton species diversity in eutrophic waters.

Whereas the present theory has focused on competition for light as the sole mechanism of species interaction, changes in turbulent mixing may also shift the competitive balance between phytoplankton species by other mechanisms. In particular, reduced turbulent mixing may suppress upward transport of nutrients towards the euphotic zone, which can have a major impact on phytoplankton productivity and species composition in nutrient-limited waters (Mann and Lazier 1996, Longhurst 1998, Wetzel 2001). In Lake Nieuwe Meer and other highly eutrophic lakes, nutrient limitation is not likely to play a major role because these hypertrophic systems are saturated with nutrients. However, clear examples are found in coastal upwelling regions, like those along the Pacific coasts of North and South America, where turbulent mixing of nutrients over the thermocline is greatly reduced during El Niño years, with major effects that cascade from the phytoplankton level throughout the entire food web (Chavez et al. 1999, Stenseth et al. 2002). It would be of considerable interest, as a next step, to extend the light-based competition theory developed here by incorporating effects of turbulent mixing on competition for nutrients as well.

In conclusion, the theory and lake experiment demonstrate that changes in turbulent mixing may shift the competitive balance between buoyant and sinking phytoplankton species in a predictable manner. These findings may find useful application in water management, improving prediction of the mixing intensity required to prevent surface blooms of harmful cyanobacteria. Moreover, our results may also contribute to a better understanding of phytoplankton communities in freshwater and marine ecosystems exposed to natural mixing regimes. Turbulent mixing of natural waters is largely determined by climatic factors like heat exchange and wind action. Accordingly, sinking phytoplankton species, which play an important role in several biogeochemical cycles, tend to become dominant during stormy periods with increased mixing. Conversely, buoyant phytoplankton species, including harmful cyanobacteria like *Microcystis*, tend to be favored during periods with warm weather and weak wind mixing. Climate change will affect the frequency of storms as well as the heat budget of aquatic ecosystems. Our competition model and lake experiment thus warn that changes in turbulent mixing, driven by climate change, are likely to shift the species composition of the phytoplankton, with possible implications for biogeochemical cycles and the incidence of harmful algal blooms.

Literature Cited

Abraham, E. R., C. S. Law, P. W. Boyd, S. J. Lavender, M. T. Maldonado, and A. R. Bowie. 2000. Importance of stirring in the development of an iron-fertilized phytoplankton bloom. Nature **407**:727–730.

Bailey-Watts, A. E., E. J. Wise, and A. Kirika. 1987. An experiment in phytoplankton ecology and applied fishery management: effects of artificial aeration on troublesome

algal blooms in a small eutrophic loch. Aquaculture and Fisheries Management **18**:259–276.

Behrenfeld, M. J., and P. G. Falkowski. 1997. A consumer's guide to phytoplankton primary productivity models. Limnology and Oceanography **42**:1479–1491.

Bormans, M., and S. A. Condie. 1998. Modelling the distribution of *Anabaena* and *Melosira* in a stratified river weir pool. Hydrobiologia **364**:3–13.

Bracco, A., A. Provenzale, and I. Scheuring. 2000. Mesoscale vortices and the paradox of the plankton. Proceedings of the Royal Society of London B **267**:1795–1800.

Brown, P. N., G. D. Byrne, and A. C. Hindmarsh. 1989. VODE: a variable-coefficient ODE solver. SIAM Journal on Scientific and Statistical Computing **10**:1038–1051.

Chao, L., and B. R. Levin. 1981. Structured habitats and the evolution of anticompetitor toxins in bacteria. Proceedings of the National Academy of Sciences (USA) **78**:6324–6328.

Chavez, F. P., P. G. Strutton, C. E. Friederich, R. A. Feely, G. C. Feldman, D. C. Foley, and M. J. McPhaden. 1999. Biological and chemical response of the equatorial Pacific Ocean to the 1997–98 El Niño. Science **286**:2126–2131.

Chorus, I., and J. Bartram, editors. 1999. Toxic cyanobacteria in water: a guide to their public health consequences, monitoring and management. Spon Press, London, UK.

Codd, G. A., S. G. Bell, K. Kaya, C. J. Ward, K. A. Beattie, and J. S. Metcalf. 1999. Cyanobacterial toxins, exposure routes and human health. European Journal of Phycology **34**:405–415.

Condie, S. A. 1999. Settling regimes for non-motile particles in stratified waters. Deep-Sea Research I **46**:681–699.

Diehl, S., S. Berger, R. Ptacnik, and A. Wild. 2002. Phytoplankton, light, and nutrients in a gradient of mixing depths: field experiments. Ecology **83**:399–411.

Durrett, R., and S. A. Levin. 1997. Allelopathy in spatially distributed populations. Journal of Theoretical Biology **185**:165–171.

Elliott, J. A., A. E. Irish, and C. S. Reynolds. 2002. Predicting the spatial dominance of phytoplankton in a light limited and incompletely mixed eutrophic water column using the PROTECH model. Freshwater Biology **47**:433–440.

Eppley, R. W., P. Koeller, and G. T. Wallace, Jr. 1978. Stirring influences the phytoplankton species composition within enclosed columns of coastal sea water. Journal of Experimental Marine Biology and Ecology **32**:219–240.

Ferziger, J. H., and M. Perić. 1999. Computational methods for fluid dynamics. Second edition. Springer, Berlin, Germany.

Flameling, I. A., and J. Kromkamp. 1997. Photoacclimation of *Scenedesmus protuberans* (Chlorophyceae) to fluctuating irradiances simulating vertical mixing. Journal of Plankton Research **19**:1011–1024.

Harris, G. P., and G. Baxter. 1996. Interannual variability in phytoplankton biomass and species composition in a subtropical reservoir. Freshwater Biology **35**:545–560.

Hassell, M. P., H. N. Commins, and R. M. May. 1994. Species coexistence and self-organizing spatial dynamics. Nature **370**:290–292.

Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator–prey oscillations. Hilgardia **27**:343–383.

Huisman, J. 1999. Population dynamics of light-limited phytoplankton: microcosm experiments. Ecology **80**:202–210.

Huisman, J., M. Arrayás, U. Ebert, and B. Sommeijer. 2002. How do sinking phytoplankton species manage to persist? American Naturalist **159**:245–254.

Huisman, J., R. R. Jonker, C. Zonneveld, and F. J. Weissing. 1999*a*. Competition for light between phytoplankton species: experimental tests of mechanistic theory. Ecology **80**: 211–222.

Huisman, J., and B. Sommeijer. 2002. Population dynamics of sinking phytoplankton in light-limited environments: simulation techniques and critical parameters. Journal of Sea Research **48**:83–96.

Huisman, J., P. Van Oostveen, and F. J. Weissing. 1999*b*. Critical depth and critical turbulence: two different mechanisms for the development of phytoplankton blooms. Limnology and Oceanography **44**:1781–1788.

Huisman, J., P. Van Oostveen, and F. J. Weissing. 1999*c*. Species dynamics in phytoplankton blooms: incomplete mixing and competition for light. American Naturalist **154**: 46–68.

Huisman, J., and F. J. Weissing. 1994. Light-limited growth and competition for light in well-mixed aquatic environments: an elementary model. Ecology **75**:507–520.

Hulot, F. D., and J. Huisman. 2004. Allelopathic interactions between phytoplankton species: the roles of heterotrophic bacteria and mixing intensity. Limnology and Oceanography **49**:1424–1434.

Hutchinson, G. E. 1967. A treatise on limnology. II. Introduction to lake biology and the limnoplankton. J. Wiley and Sons, New York, New York, USA.

Ibelings, B. W. 1996. Changes in photosynthesis in response to combined irradiance and temperature stress in cyanobacterial surface waterblooms. Journal of Phycology **32**: 549–557.

Ibelings, B. W., B. M. A. Kroon, and L. R. Mur. 1994. Acclimation of photosystem II in a cyanobacterium and a eukaryotic green alga to high and fluctuating photosynthetic photon flux densities, simulating light regimes induced by mixing in lakes. New Phytologist **128**:407–424.

Imberger, J., and G. N. Ivey. 1991. On the nature of turbulence in a stratified fluid. II. Application to lakes. Journal of Physical Oceanography **21**:659–680.

Irigoien, X., R. P. Harris, R. N. Head, and D. Harbour. 2000. North Atlantic Oscillation and spring bloom phytoplankton composition in the English Channel. Journal of Plankton Research **22**:2367–2371.

Jassby, A. D., and T. Platt. 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnology and Oceanography **21**:540–547.

Jones, K. J., and R. J. Gowen. 1990. Influence of stratification and irradiance regime on summer phytoplankton composition in coastal and shelf seas of the British Isles (UK). Estuarine and Coastal Shelf Science **30**:557–568.

Kerr, B., M. A. Riley, M. W. Feldman, and B. J. M. Bohannan. 2002. Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. Nature **418**:171–174.

Kierstead, H., and L. B. Slobodkin. 1953. The size of water masses containing plankton blooms. Journal of Marine Research **12**:141–147.

Klausmeier, C. A., and E. Litchman. 2001. Algal games: the vertical distribution of phytoplankton in poorly mixed water columns. Limnology and Oceanography **46**:1998–2007.

Kocsis, O., H. Prandke, A. Stips, A. Simon, and A. Wüest. 1999. Comparison of dissipation of turbulent kinetic energy determined from shear and temperature microstructure. Journal of Marine Systems **21**:67–84.

Kononen, K., J. Kuparinen, K. Makela, J. Laanemets, J. Pavelson, and S. Nommann. 1996. Initiation of cyanobacterial blooms in a frontal region at the entrance to the Gulf of Finland, Baltic Sea. Limnology and Oceanography **41**:98–112.

Lauria, M. L., D. A. Purdie, and J. Sharples. 1999. Contrasting phytoplankton distributions controlled by tidal turbulence in an estuary. Journal of Marine Systems **21**:189–197.

Levin, S. A. 1974. Dispersion and population interactions. American Naturalist **108**:207–228.

Litchman, E. 2000. Growth rates of phytoplankton under fluctuating light. Freshwater Biology **44**:223–235.

Longhurst, A. R. 1998. Ecological geography of the sea. Academic Press, London, UK.

MacIntyre, S., K. M. Flynn, R. Jellison, and J. R. Romero. 1999. Boundary mixing and nutrient fluxes in Mono Lake, California. Limnology and Oceanography **44**:512–529.

Mann, K. H., and J. R. N. Lazier. 1996. Dynamics of marine ecosystems: biological-physical interactions in the oceans. Second edition. Blackwell Science, London, UK.

Powell, T., and P. J. Richerson. 1985. Temporal variation, spatial heterogeneity, and competition for resources in plankton systems: a theoretical model. American Naturalist **125**:431–464.

Reynolds, C. S. 1997. Vegetation processes in the pelagic: a model for ecosystem theory. Ecology Institute, Oldendorf Luhe, Germany.

Reynolds, C. S., S. W. Wiseman, B. M. Godfrey, and C. Butterwick. 1983. Some effects of artificial mixing on the dynamics of phytoplankton populations in large limnetic enclosures. Journal of Plankton Research **5**:203–234.

Riley, G. A. 1942. The relationship of vertical turbulence and spring diatom flowerings. Journal of Marine Research **5**:67–87.

Riley, G. A., H. Stommel, and D. F. Bumpus. 1949. Quantitative ecology of the plankton of the western North Atlantic. Bulletin of the Bingham Oceanographic Collection **12**:1–169.

Sharples, J., C. M. Moore, and E. R. Abraham. 2001. Internal tide dissipation, mixing, and vertical nitrate flux at the shelf edge of NE New Zealand. Journal of Geophysical Research **106**:14069–14081.

Sherman, B. S., I. T. Webster, G. J. Jones, and R. L. Oliver. 1998. Transitions between *Aulacoseira* and *Anabaena* dominance in a turbid river weir pool. Limnology and Oceanography **43**:1902–1915.

Shigesada, N., and A. Okubo. 1981. Analysis of the self-shading effect on algal vertical distribution in natural waters. Journal of Mathematical Biology **12**:311–326.

Skellam, J. G. 1951. Random dispersal in theoretical populations. Biometrika **38**:196–218.

Spigel, R. H., and J. Imberger. 1987. Mixing processes relevant to phytoplankton dynamics in lakes. New Zealand Journal of Marine and Freshwater Research **21**:361–377.

Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K. S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. Science **297**:1292–1296.

Sverdrup, H. U. 1953. On conditions for the vernal blooming of phytoplankton. Journal du Conseil, Conseil Permanent International pour l'Exploration de la Mer **18**:287–295.

Villareal, T. A., C. Pilskaln, M. Brzezinski, F. Lipschultz, M. Dennett, and G. B. Gardner. 1999. Upward transport of oceanic nitrate by migrating diatom mats. Nature **397**:423–425.

Visser, P. M. 1995. Growth and vertical movement of the cyanobacterium *Microcystis* in stable and artificially mixed water columns. Dissertation. University of Amsterdam, Amsterdam, The Netherlands.

Visser, P. M., B. W. Ibelings, B. Van der Veer, J. Koedood, and L. R. Mur. 1996*a*. Artificial mixing prevents nuisance blooms of the cyanobacterium *Microcystis* in Lake Nieuwe Meer, The Netherlands. Freshwater Biology **36**:435–450.

Visser, P. M., L. Massaut, J. Huisman, and L. R. Mur. 1996*b*. Sedimentation losses of *Scenedesmus* in relation to mixing depth. Archiv für Hydrobiologie **136**:289–308.

Walsby, A. E. 1994. Gas vesicles. Microbiological Reviews **58**:94–144.

Walsby, A. E., P. K. Hayes, R. Boje, and L. J. Stal. 1997. The selective advantage of buoyancy provided by gas vesicles for planktonic cyanobacteria in the Baltic Sea. New Phytologist **136**:407–417.

Weissing, F. J., and J. Huisman. 1994. Growth and competition in a light gradient. Journal of Theoretical Biology **168**:323–336.

Wetzel, R. G. 2001. Limnology. Third edition. Academic Press, London, UK.

Zohary, T., and R. D. Robarts. 1990. Hyperscums and the population dynamics of *Microcystis aeruginosa*. Journal of Plankton Research **12**:423–432.