# Effects of the flow field on small scale phytoplankton patchiness

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**Abstract** We present an example of small scale (10–100 m) horizontal, subsurface patchiness of phytoplankton (*Ceratium)* during an intensive bloom in August 1993 and link it to the flow field. In the small Lake Belau (1.1 $km^2$) in northern Germany large areas of the water surface are sheltered from wind, due to vegetation. Wind sheltering effects decrease with wind speed and below 2 m/s a spatially homogeneous wind field is observed. Under weak wind conditions near-surface *Ceratium* patches with local chlorophyll-concentrations up to 200 $mg/m^3$ were observed in the south bay (0.3 m depth) as well as in parts of the central basin (1 m depth). Detailed flow simulations show very good agreement between location and size of current gyres and phytoplankton patches. Inside the gyres we find low flow velocities with low vertical turbulence. This allows *Ceratium* to form distinct vertical layers with high densities close to the water surface, according to the light gradient. Especially in the south bay flow eddies are determined by the course of the coastline and their location and intensity is, to a large degree, independent of prevailing wind directions.

**Keywords** Algae bloom; *Ceratium*; currents; lake

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## Introduction

It is well known that phytoplankton is strongly influenced by physical determinants leading to spatial variability in its distribution (e.g. Reynolds 1994). With an increasing number of spatially high resolution measurements during the last decades it became obvious that plankton patchiness is not limited to a certain spatial scale. In marine systems a large horizontal variability is observed at mesoscales (1–100 km) even in the absence of marked physical patterns. Under conditions of relative physical uniformity in marine systems, patchiness is rather a consequence of ecological processes than of purely physical forcing (Steele and Henderson 1992).

In lakes with their closed basins we find a different situation. Wind induced surface currents and the connected three-dimensional flow cells are often seen as the main reason for phytoplankton patchiness. Phytoplankton is transported with the wind towards the downwind end of the lake and accumulates there. The degree of accumulation depends on the ability of algae to resist down-welling by floating. In large lakes, like Lake Erie, wind stress shows no increase of chlorophyll concentrations at the downwind end (Stauffer 1982). Similar studies conducted in lakes of smaller size, like Lake Mendota and Lake Delavan, did not show pronounced patchiness of this kind. Camarero and Catalan (1991) conclude that little is known about small scale variability and the effect of basin morphometry on patchiness in small lakes. The kind of phytoplankton patchiness, which is observed in small lakes, is an interaction between physics and the behaviour of the phytoplankton. It depends very much on the floating and swimming abilities of the prevailing phytoplankton species.

The presented results give an example of a strong small scale (10–100 m) horizontal *Ceratium* patchiness in Lake Belau, resulting from a morphometrically influenced flow pattern. In Lake Belau, *Ceratium hirundinella* and *Ceratium furcoides* dominated during summer 1993 (Barkmann personal communication). In eutrophic temperate lakes the armoured K-strategists very often dominate the phytoplankton aspect in late summer and are known for intensive blooms (Heaney and Talling 1979; Hickel 1985; Sommer *et al.* 1986; Sommer 1991, 1993, Landmesser 1993). These large flagellates have good swimming abilities and are able to level themselves, according to light gradients. *Ceratium* is known too, for daily vertical migrations of several metres (Nauwerck 1963; Galvez *et al.* 1988; Jones 1993) and often show strong horizontal heterogeneity in its distribution (Pollingher and Berman 1975; Heaney 1976).



## Materials and methods

Lake Belau in North Germany (54°N, 10°E) has a surface area of 1.1 $km^2$, a maximum length of 2.2 km, an average depth of 9 m (maximum depth of 26 m) and is stratified from May to November (Fig. 1). The lake is divided into two significant different parts: the large deep central area in the north and the shallow south bay. The south bay has a surface area of $0.15 \times 10^6 m^2$, a volume of $0.18 \times 10^6 m^3$, a maximum depth of 1.8 m and an average depth of 1.2 m. The water quality is strongly influenced by the inflow of the small creek Alte Schwentine and the preceding lakes. Along the east and west coast steep slopes rise up from the lake shore to a plateau with an elevation of more than 20 m above the lake level. The slopes as well as some parts of the plateau on the west coast are forested and shelter the lake from easterly and westerly winds. The south bay is surrounded by a reed belt of 5 m to 30 m width and 1.5 m average height above water level (Fig. 1). It obtains additional small scale shelter by alder bogs and single beech trees standing directly at the shore line.

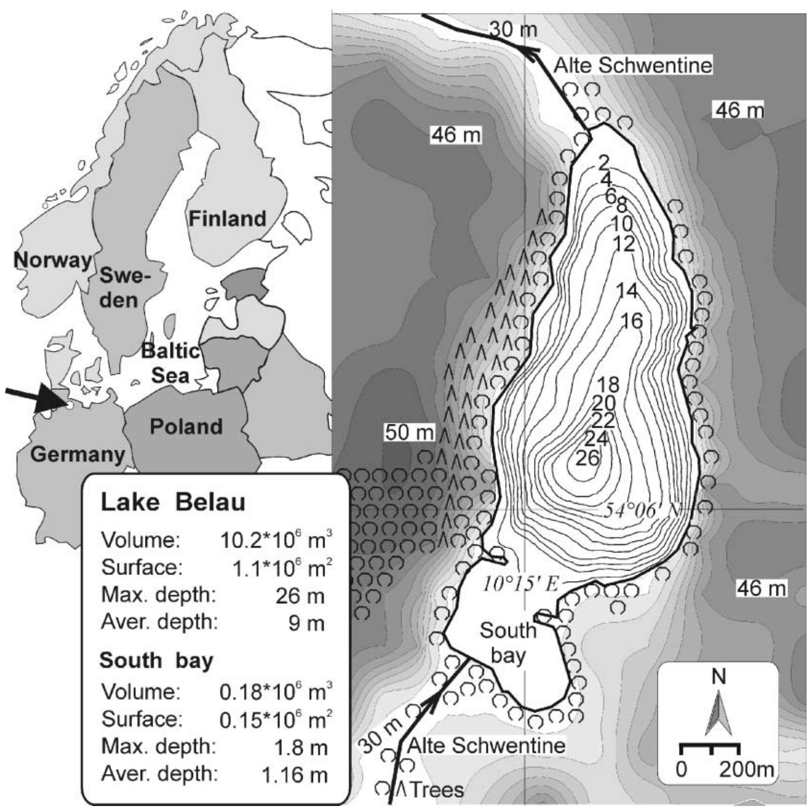


**Figure 1** Location and basic information on Lake Belau in northern Germany

General wind data was provided by a meteorological station (16 m height, 10 min. recording interval). The station is located on agricultural land, about 200 m from the western shoreline of Lake Belau on the highest parts of the plateau. For 1997 and 1998 additional wind data from a floating lake station on Lake Belau (1 m height, 10 min. recording interval) was available. Additional spatial measurements of wind speed and direction at a height of 1 m above lake level were conducted with a mobile anemometer by Thiessen Co. Recorded wind was averaged over one minute intervals.

Spatial current measurements were conducted from a small boat, fixed by two anchors. The boat's position was determined using small buoys, GPS and also estimated by triangulation to fixed objects at the shoreline. We used a small mobile inductive current meter (ISM-2000 MesSen Nord) for flow measurements. The current meter recorded 64 values/s and saved the data averaged over one second intervals. Reliable values down to less than 1 mm/s were obtained after taking three-minute averages. In the pelagic zone, currents were measured in one or two metre vertical intervals, starting from a depth of 0.2 m down to the lake bottom. In the shallow south bay measurements in 0.2 m and 1 m water depth were conducted. The time needed for flow data collection was 1.5 h (3 June 1998), 3 h (21 Oct. 1997) and 4.5 h (16 Sept. 1997).

The intensive phytoplankton patchiness on 4 August 1993 was observed accidentally during data collection for monitoring purposes. Due to this it was not possible to adjust the data collection well to the requirements and neither the instrumentation nor the accompanying data collection was optimal. The campaign started in late afternoon and lasted about 4 hours until sunset. For fast chlorophyll determination we used a one-channel (turbidity, chlorophyll a) BackScat fluorimeter by Haardt Co. (Chl.a: excitation 380–540 nm, emission 863 nm). Fluorescence data was collected at 103 sites at a depth of 0.3 m in the south bay. The remaining time allowed only incomplete data collection at 90 sites in the central basin, where values from a depth of 1 m were stored. The position of the sites has been determined by small buoys together with additional estimations by using fixed objects at the shoreline. Vertical fluorimeter profiles with 10 cm resolution were conducted in three locations in the central bay beside one coarse profile in the south bay. To prepare the contour maps, we calculated variograms and used Kriging as an interpolation method. The validity and methodological independence of the pattern has been tested by using different interpolation methods like Minimum Curvature and Inverse Distance (Schernewski 1992).

To transfer the fluorescence voltage data into chlorophyll values ($mg/m^3$), chlorophyll samples determined by the photometric standard method (Nusch 1980) were used. During August and early September 1993 the measured chlorophyll concentrations in the central basin had their maximum at 2 m to 3 m depth with high values always above 60 $mg/m^3$ (Barkmann personal communication). The calculated transfer factor from voltage to concentration showed stable values between 39 and 43 during the whole *Ceratium* bloom (July–September 1993). For the situation of 4 August 1993 the factor was 39. The applied linear conversion factor of 39 is a conservative assumption. In other years, like 1994, 1996 or 1997 these factors even exceed 60 during summer. The analysis of the intensive and patchy phytoplankton bloom of 4 August 1993 suffers from a lack of photometric measured chlorophyll a data as well as an analysis of the species composition on this specific day.

The main focus of the work was on the very shallow south bay of Lake Belau. Therefore, current simulations were made with a two-dimensional finite element flow model (FemFlow 2D, Podsetchine and Schernewski 1999). It is based on depth averaged hydrodynamic equations. The system of "shallow water" equations is solved with the modified Utnes scheme (1990) which is characterized by a semi-decoupling algorithm. The continuity equation is rearranged to Helmholtz equation form. The upwinding Tabata method (1977) is used to approximate convective terms. For details see Podsetchine and Schernewski (1999).

The linear triangular mesh in Figs. 2 and 3 consist of 516 nodes and 869 elements. The presented wind as well as the flow field show the location of the nodes. The element size varies from 10 m in the south bay to 100 m in the central part of the lake. For detailed simulations in the south bay the grid was locally increased to 900 nodes altogether, shown in Fig. 4. In all computations we used a horizontal diffusion coefficient of $0.01\ m^2/s$, a Coriolis value of $1.176 \times 10^{-4}\ s^{-1}$ and a spatial uniform Manning roughness coefficient of $0.015\ m^{-1/3}\ s$. The zero normal flow condition was applied at the closed boundary instead of the slip boundary condition, which takes a small value of horizontal diffusion into consideration. Otherwise this would have required a considerable refinement of the boundary layer and would have been too time-consuming. An integration period of 2.5 h (with time steps of 15 s) was sufficient to reach a steady state solution in this small lake. The wind field was kept constant during simulations.



## Results

For 50% of the time wind from the west to south-west is dominating in North Germany. This dominance is further increased to 75% when only strong wind events with a speed above

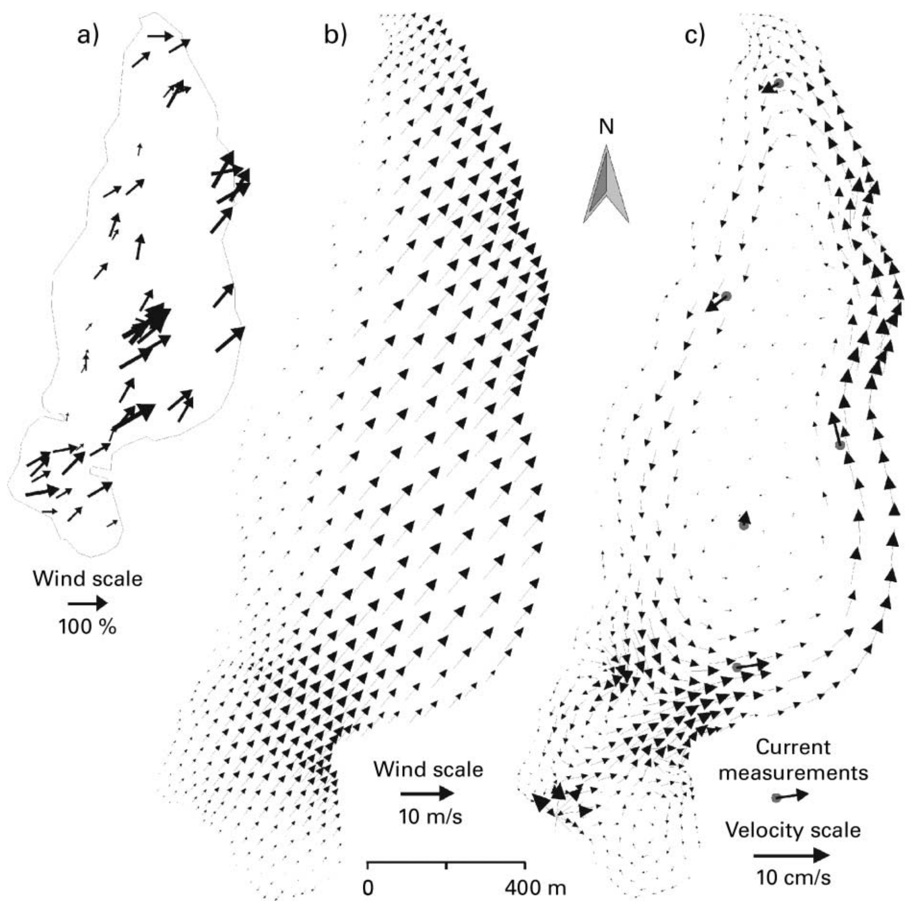


**Figure 2** (a) Measured wind data on Lake Belau (1 m above water surface). Compilation of 5 data collections with prevailing wind from SW with wind speeds above 4 m/s (7 April, 27 July and 16 September 1997, 23 July, 8 August 1998). To allow the comparison of different dates and to visualize sheltering effects, relative wind speeds are given. (b) Calculated spatial heterogeneous wind field used in simulation (max. 6 m/s). (c) Depth integrated flow field during SW-wind situation of 16 September 1997 as well as depth integrated flow measurements on 5 sites of this day (from Podsetchine and Schernewski 1999)

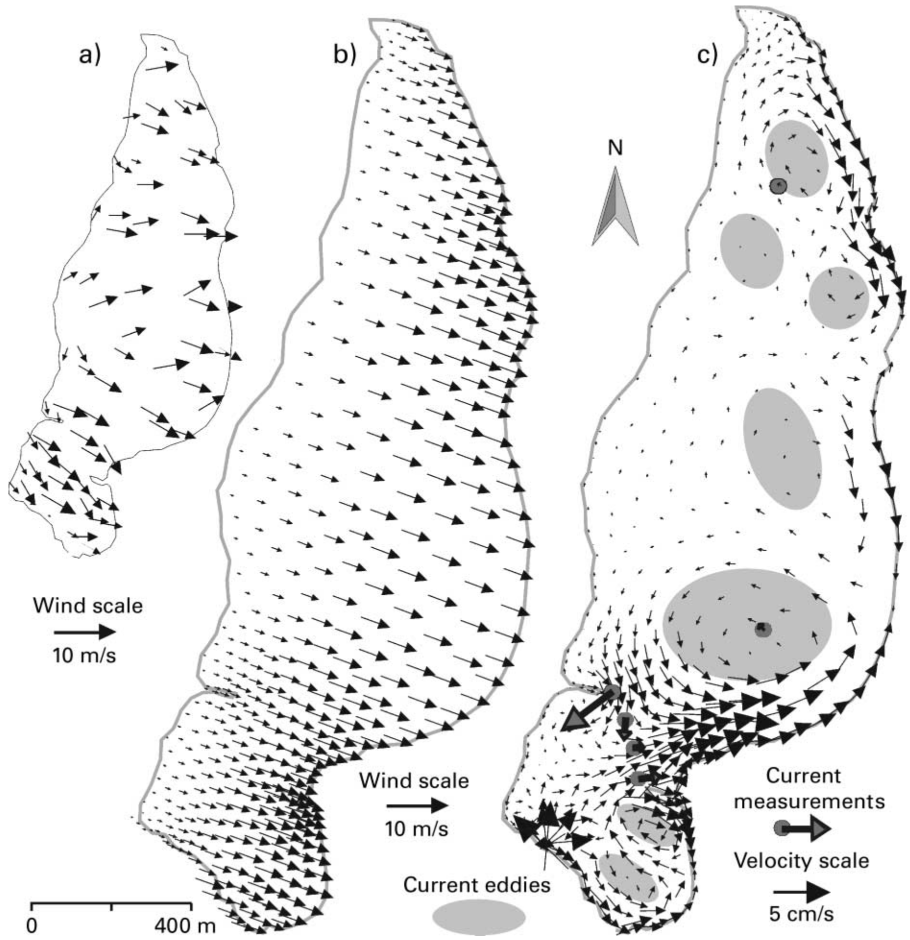


**Figure 3** (a) Wind measurements of 24 February 1998 on Lake Belau. (b) Calculated spatial heterogeneous wind field used in simulation (280° direction, max. speed 5 m/s). (c) Depth integrated flow field during situation of 6 June 1998 as well as depth integrated flow measurements on 6 sites of this day. Current eddies are indicated as shaded areas

4 m/s are considered. Most coastal parts of Lake Belau are, to a limited extent, sheltered from the wind by topography and vegetation. The narrow north–south oriented valley with relatively high ridges along the east and west coasts provides additional strong shelter from easterly and north-westerly winds. On the other hand, wind coming from south to west is channelled, slightly turned when passing the valley and meets the main axis of Lake Belau. Winds between south and west have the highest share, are more often connected with strong wind events than other directions and coincide with the main axis of the valley and the lake. West to south-west wind and the resulting flow field have a dominating impact on Lake Belau. Therefore, flow simulations are mainly restricted to these situations.

To a varying degree, all wind fields show spatial inhomogeneity over the lake (Figs 2 and 3) and it is important to consider this in flow simulations. With spatially homogeneous wind from the south-west the model predicted a two-cell circulation system that covered most parts of the lake (Podsetchine and Schernewski 1999). The flow field changed drastically, when spatial variation in wind speed was taken into account (Fig. 2(a) and (b)). The two-gyre system was replaced by one large cell with a strong reverse jet along the western shore (Fig. 2(c)). The depth averaged flow field fitted well to the current measurements from 16

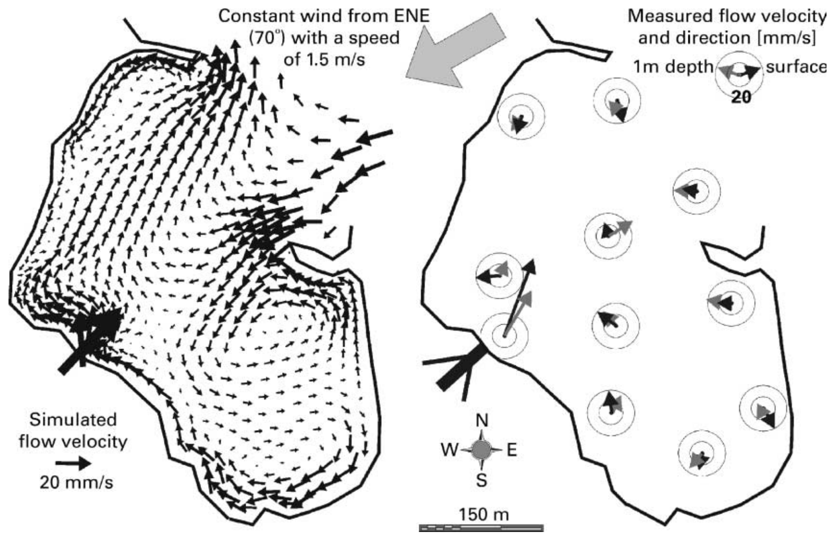


**Figure 4** Simulated depth integrated flow field in the south bay of Lake Belau. Measurements in 11 locations of 25 September 1997 between 1 pm and 4 pm at a depth of 0.2 m and 1 m. Prevailing wind from ENE (70°) with a speed of 1.5 m/s. A spatial homogeneous wind field was applied in the simulation

Sept. 1997 conducted on five locations in the lake. In the simulation we assumed a wind speed of 6 m/s from the south-west. Wind data from 69 different locations from 24 February 1998 show that the coastal wind shelter effect is still intensified under west wind conditions (Fig. 3(a) and (b)). Taking into account spatial wind inhomogeneity detailed flow simulations under west wind situations were possible, which fitted well to the measured depth integrated currents in six locations from 3 June1998 (Fig. 3(c)). Under westerly winds the circular flow field is dissolved into less defined flow structures with several horizontal flow gyres in the central basin as well as in the shallow south bay. The highest flow velocities again occur at the east coast.

The flow field under a south-west wind as well as under a west wind showed a complex spatial structure in the south bay of Lake Belau. The horizontal solution of the grid used in Figs 2 and 3 is sufficient for the central basin, but insufficient to resolve details of the flow pattern in the south bay. Therefore, a similar grid in the central basin with increased density in the south bay was applied for simulations in Figs 4 and 6. For comparisons between simulation and measurements we had to switch to an ENE-wind situation. On 25 September 1997 flow data was collected at 11 points (0.2 m and 1 m depth) in the south bay with one additional measurement in the Alte Schwentine. The data collection took about three hours and the weak wind (2 m/s) died down slowly. This fact caused some uncertainties, but the simulated flow field again fitted well to the depth integrated measured data (Fig. 4). In this simulation a spatial homogeneous wind field was applied. We displayed the measurements at 0.2 m as well as at 1 m depth to indicate that, apart from the river mouth, no significant vertical flow shear was observed in this shallow bay and that a two-dimensional model is well suited. One has to keep in mind that the bay has an average depth of about 1 m and differences between data at 0.2 m and 1 m might be caused by disturbances resulting from the boat.

Between July and September the phytoplankton biomass in Lake Belau is usually dominated by a varying proportion of two groups: Cyanophyceae and Dinophyceae. In some years like in 1990 (Landmesser 1993) and in 1993 the dinoflagellates *Ceratium hirundinella* and *Ceratium furcoides* can contribute up to 95% of the biomass. In 1993, the absolute *Ceratium* dominance lasted the whole summer, from early June until the end of September.

During late August 1993 *Ceratium* caused an extreme biomass peak of nearly 35 g/m$^3$ at 0.5 m depth in the central basin. Brown clouds of *Ceratium* were visible in the water at that time. The average annual chlorophyll concentration at 0.5 m depth at the centre of the lake was 18 mg/m$^3$ with a maximum of 71 mg/m$^3$ in August, during the peak of this strong algae bloom. The vertical chlorophyll distribution, measured in late morning, indicated that these flagellates are concentrated between the water surface and a depth of about 6 m. Below 6 m depth a strong decline in chlorophyll concentrations was found (Barkmann personal communication). The thermocline was located at 8 m at that time.

On 4 August 1993, the *Ceratium* development approached its maximum. During this day, the weak south-westerly wind never exceeded 1 m/s in the afternoon and early evening (Fig. 7). The calm conditions allowed fast chlorophyll measurements at 103 points at a depth of 0.3 (Fig. 6) m in the south bay and at over 90 points in the central bay of Lake Belau at a depth of 1 m (Fig. 5) as well as a reliable determination of the boat position. The measurement points were irregularly distributed, depending on the observed lateral gradients of the chlorophyll concentration.

In the central basin a strong horizontal variability of chlorophyll distribution was evident (Fig. 5). In all areas along the eastern and western shoreline of the lake, where sufficient measurement points were available, a narrow coastal belt with low chlorophyll concentrations became obvious. The lowest values were found directly near the shore, in front of the narrow reed zones, and increased with increasing distance from the coast. The highest chlorophyll concentrations (above 140 mg/m$^3$) were observed in distinct patches in the eastern part of the lake.

Fig. 2 shows the flow field of 16 Sept. 1997. The comparison of this flow field with the one in Fig. 5 showed an obvious and important difference. In both situations south-westerly wind

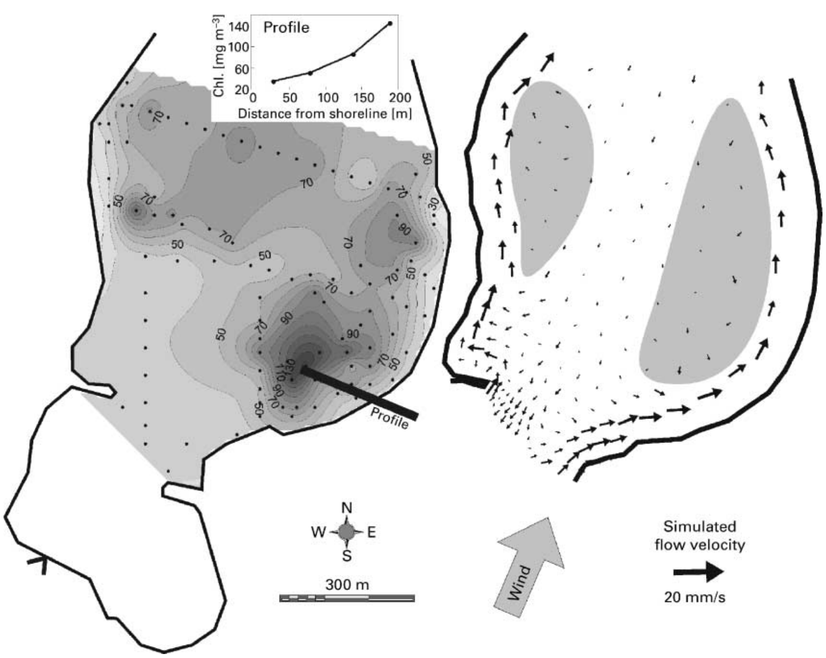


**Figure 5** Phytoplankton patchiness on 4 August 1993 during a *Ceratium* bloom in central parts of Lake Belau and the simulated flow field for this situation. Shown are chlorophyll a concentrations (mg/m$^3$) derived from fluorimeter data. Calculations are on the basis of 90 measurements at a water depth of 1 m between 6 pm and 7 pm. Before and during the measurements very weak south-westerly to westerly winds with a speed below 1 m/s prevailed

prevailed, but the wind speed was very different. In Fig. 2 we observed a wind speed up to 6 m/s with a pronounced heterogeneity of the wind field, which was taken into account in the flow simulations. Under SW-wind conditions below 2 m/s (4 August 1993), the sheltering effect of the surroundings on the wind field became less important and was negligible. Wind shear is the driving force of water movement. At 2 m/s wind speed it is only 1/9 of the surface shear at 6 m/s. Therefore, flow simulations are sensitive to changes in wind speed. When a spatial homogeneous wind field (Fig. 5) is applied, the flow field in the central basin switched to a two-cell system, as reported in Podsetchine and Schernewski (1999). On 4 August 1993 the simulation yielded strong north directed currents along the shore and a south directed backflow in the centre of the lake, which is less obvious due to the greater depth. As a result we received two large cells with low circular currents in their centres.

Comparing the location of the phytoplankton patches and the coastal belt of low chlorophyll concentrations with the flow pattern during that day showed good accordance. The patches are linked to the centre of these large gyre systems (indicated as shaded areas in Fig. 5) where very low flow velocities prevail. On the other hand, the coastal belts with low chlorophyll concentrations are located in areas where the highest current velocities occur. Despite this coincidence one has to state that the measurements in the central basin are too coarse to generate a complete picture of phytoplankton patchiness and its relation to the flow field in the central basin.

On 4 August 1993, the highest chlorophyll concentrations were found in the eastern part of the south bay (Fig. 6). In this area a few distinct and clearly defined patches with chlorophyll concentrations up to 200 mg/m$^3$ were found. In some cases the diameter of these patches was less than 30 m. Besides that, a local maximum with 100 mg/m$^3$ was found in the western part of the bay, 150 m north of the Alte Schwentine inflow. The minimum values, less than 20 mg/m$^3$, were found in a belt 20 m wide directly in front of the reed zone at the western shore line. In all parts of the bay a decline of values near the front of the reed belts was indicated. Other local minimum values of 29 mg/m$^3$ were found at the inflow of the Alte Schwentine.

The flow field in the south bay during 4 August 1993 is shown in Fig. 7 at three times. During noon wind from SSW with a speed of 2 m/s prevailed. Later the wind died down slowly and turned towards the west as indicated in Fig. 7. The simulation at 3 pm showed the situation under SW wind with a speed of 1 m/s and at 6 pm 0.4 m/s wind speed from the west was applied. In all figures the direct influence of the Alte Schwentine inflow on the currents in the south bay was weak and limited to the vicinity of its mouth. The currents in the bay were mainly wind driven. All situations in Fig. 7 showed the highest flow velocities along the west coast and near the peninsula at the east coast. Slightly increased values were observed at the south eastern coast of the south bay, too. The lowest currents occurred inside the different gyre systems. At noon three gyres systems, indicated as shaded areas (Fig. 7), were found. Two flow eddies covered nearly the whole eastern part of the south bay and one extended gyre was found 150 north of the Alte Schwentine discharge. With changing wind direction during the afternoon of 4 August 1993 the gyres were slightly modified but remained more or less stable.

The observed phytoplankton patchiness during 4 August 1993 (Fig. 6) corresponded well with the simulated flow field. Phytoplankton patches with high chlorophyll concentrations were always linked to gyres and the maximum chlorophyll a concentrations were located in their centres. The patches in the eastern part of the south bay showed an intensive small scale structure which, in general, fitted well to the gyre systems. But the structures could not be explained in detail by one flow situation. The reason may be the slight modifications in size, location and intensity of the gyres with changing wind conditions during the afternoon as well as the long time of altogether 2 hours needed to collect all the fluorimeter data in the

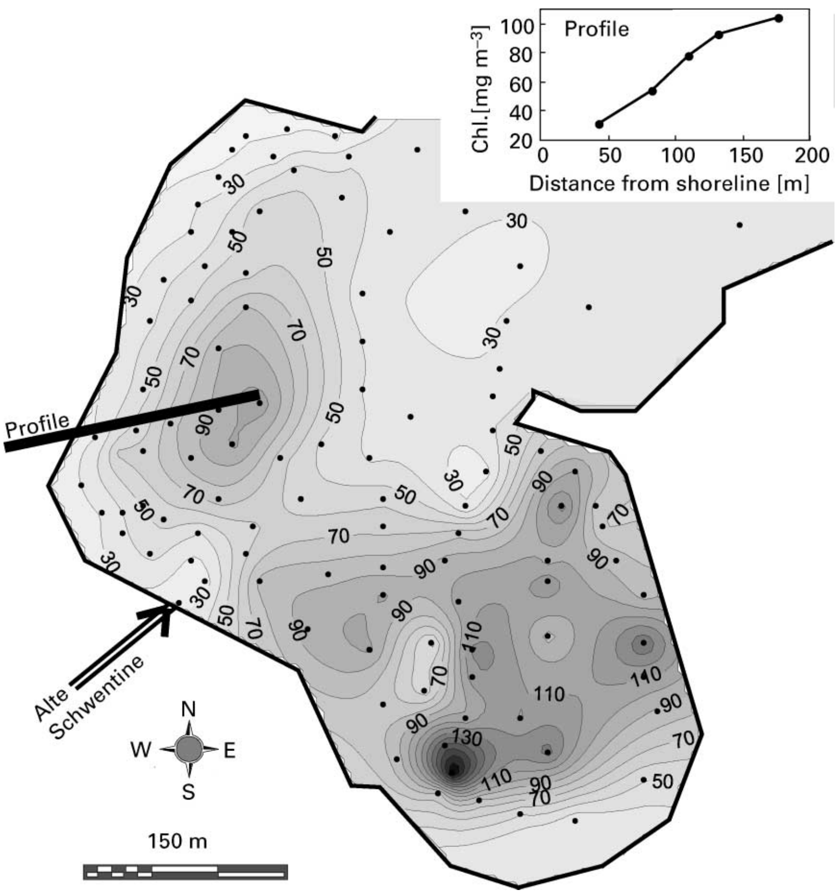


**Figure 6** Phytoplankton *p*atchiness on 4 August 1993 during a *Ceratium* bloom in the shallow south bay of Lake Belau. Shown are chlorophyll a concentrations (mg/m$^3$) derived from fluorimeter data. Calculations are on the basis of 103 measurements at a water depth of 0.3 m between 3 pm and 6 pm

south bay. It is likely that some smaller patches are not a result of recent flow conditions. They were possibly formed during late morning and noon, when stronger wind prevailed and may be regarded as relicts. The current velocity distribution indicates that all areas showing low chlorophyll values are connected to relatively high current speeds.

All fluorimeter measurements of 4 August 1993 were restricted to a depth of 1 m in the central basin and 0.3 m in the south bay. The surprising occurrence of this intensive patchiness and the intensive horizontal measurements left only time for very few vertical chlorophyll profiles (Fig. 8). In the lake centre, the chlorophyll maximum was observed at 1 m (50 mg/m$^3$) depth and decreased continuously with greater depth. Two measurements in the south-westerly part of the central bay, in an area where the patches with the highest chlorophyll concentrations of the central basin were found, showed maximums above 100 mg/m$^3$ close to the water surface. In the south bay only one coarse vertical profile, consisting of three measurements, indicate a maximum around the general measurement depth at 0.3 m.

## Discussion and conclusion

The comparison of measured and depth averaged simulated currents showed a good agreement in the central basin as well as in the south bay. The model is able to take spatial variable Manning roughness coefficients into account to simulate detailed effects of reed

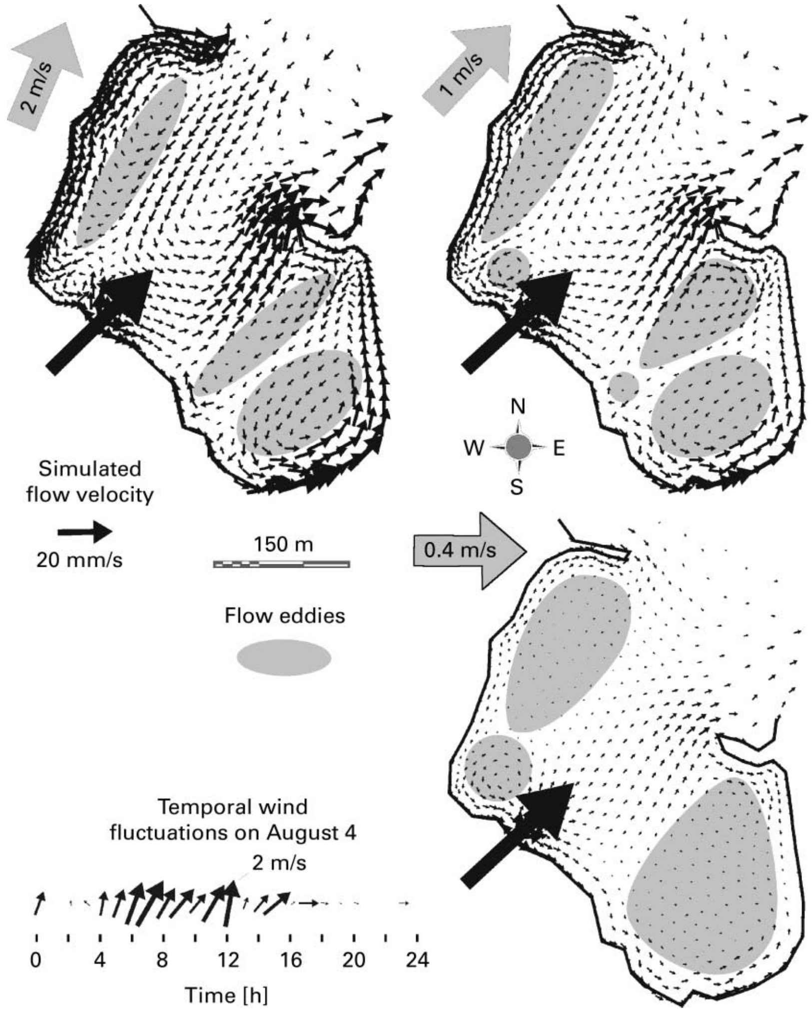


**Figure 7** Simulation of flow pattern in the south bay of Lake Belau on 4 August 1993. The simulations show the flow field at 12 am (wind speed 2 m/s from SSW), 3 pm (1 m/s SW) and 6 pm (0.4 m/s W). The temporal wind fluctuations during the day are indicated too. The shaded areas illustrate horizontal circulations

belts on the flow field (Schernewski *et al.* 2000). The effects of spatial differences in bottom roughness were tested for the simulations presented here, too, but were negligible. Much more important were the consideration of wind shelter effects and the application of spatial variable wind fields during flow simulations, where wind speeds of 5–6 m/s prevailed. In situations with wind speeds below 2 m/s a spatial uniform wind field has to be applied and wind sheltering effects are negligible. One important result is that the general flow field under a south-westerly wind shows a completely different characteristic depending on the prevailing wind speed. Wind speeds of 5 m/s and above induce one large anti-clockwise circulation cell. Wind speeds below 2 m/s cause a switch to a two-cell system. The strong currents near the western shore have a southerly direction under strong winds and a northerly direction under weak winds.

Altogether the flow results shown as well as results reported earlier (Podsetchine and Schernewski 1999; Schernewski *et al.* 2000) allow the conclusion that the model is able to simulate the flow field in a reliable and detailed way. This permits a model application in situations where no direct flow data is available.

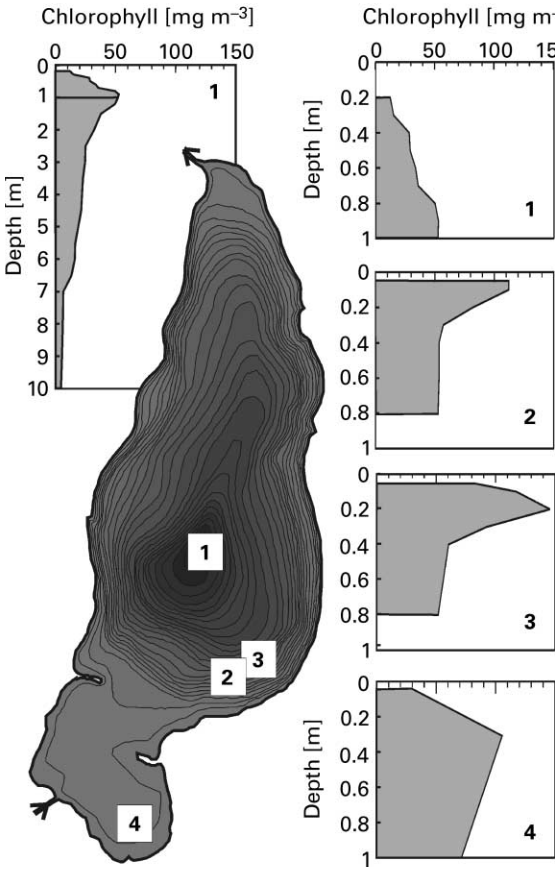


**Figure 8** Vertical distribution of chlorophyll a concentration at 4 sites during the strong *Ceratium* bloom of 4 August 1993. The location of the measurement points is indicated in the bathymetrical map (1 m isobath distance)

Concerning 4 August 1993 fluorimeter data yields local maxima in chlorophyll a concentrations of 140 mg/m$^3$ in the central basin and 200 mg/m$^3$ on one site in the south bay. There is no doubt that these values are unusually high. Data provided by Barkmann (unpublished) show that the highest measured chlorophyll a concentration of 71 mg/m$^3$ was at a depth of 4 m on 24 August 1993. The data show further that during summer 1993 the chlorophyll a concentrations in the centre of the lake (7 sampling dates) are evenly distributed between a depth of 1 m and 5–7 m.

On every sampling date the daily average wind speeds were higher (between 1.6 m/s and 4.2 m/s) than on 4 August (1.4 m/s). This means that wind induced mixing was responsible for the evenly vertical distribution of chlorophyll a concentration on all regular sampling dates. Due to the decreasing wind in the afternoon of 4 August, an accumulation of phytoplankton close to the water surface was possible. The observed high chlorophyll concentrations per m$^3$ in patches have not necessarily caused an increased concentration per surface area. Besides, extremely high chlorophyll a concentrations have been observed during the *Ceratium* bloom in 1990 too. On 28 August 1990 the chlorophyll a maximum reached 194 mg/m$^3$ at a depth of 1 m in the centre of Lake Belau (Landmesser 1993). This again was a day with a weak wind of 1.9 m/s (daily average). A comparison of the biomass and species composition between two locations (centre of the lake and centre of the south bay) in 1989 and 1990 has been carried out by Landmesser (1993). The general species composition between these two sampling sites differed neither in 1989 nor 1990. We think that the calculated chlorophyll a concentrations are realistic and that the phytoplankton patchiness in August 1993 can be attributed to *Ceratium* (*Ceratium hirundinella*, *Ceratium furcoides*).

*Ceratium hirundinella* and *Ceratium furcoides* are some of the largest and most common flagellates in temperate lakes. In sheltered, eutrophic lakes the armoured K-strategists often dominate the phytoplankton aspect in late summer and are known for intensive blooms (Heaney and Talling 1979; Hickel 1985; Sommer *et al.* 1986; Sommer 1991, 1993). Due to their considerable swimming ability they are able to level themselves, according to light gradients, and to perform daily migrations of several metres (Nauwerck 1963; Galvez *et al.* 1988; Jones 1993). Even for these species, the turbulence induced by wind speeds of 3 m/s is sufficient to prohibit a pronounced maximum of flagellates in the depth of their light optimum (Lampert and Sommer 1993). This explains why no strong vertical separation of *Ceratium* was found during other sampling dates in summer 1993.

It is well known that *Ceratium* shows strong horizontal heterogeneity in their distribution (Pollingher and Berman 1975; Heaney 1976). One most important type of spatial heterogeneity is an accumulation at the downwind side of the lake (Webster and Hutchinson 1994; Verhagen 1994). In several cases a downwind accumulation of phytoplankton, indicated by increased oxygen saturation near the surface, was observed in Lake Belau, too (Schernewski 1992) and a pronounced phytoplankton patchiness was never found when wind speeds exceeded 3 m/s. The *Ceratium* patchiness in the south bay in August 1993 is different. The south bay of Lake Belau is shallow and does not allow a large scale vertical circulation. The vertical structure of the flow field in this bay is uniform and the observed horizontal gyres are a result of basin morphometry, the course of the shore line and prevailing wind directions. In the central basin a three-dimensional vertical circulation was suggested several times (Schernewski 1992), but in the case of 4 August 1993 this circulation was less important compared to large horizontal eddies. In all gyre systems low current speeds were found close to the centre. This is connected to weak vertical turbulence, which allows a vertical movement and a separation of algae at a depth where preferred light conditions prevail. Direct wind driven transport with the weak wind towards the north were of minor importance. Different than *Micocystis*, *Ceratium* is not accumulating at the water surface but is able to create maxima in dependence of the light gradient. The strong light directly at the surface is not optimal. This means that only low *Ceratium* concentrations are to be found in the uppermost surface layer and their direct transport with the wind as well as their accumulation on the downwind side of the lake is negligible. The floating and swimming abilities of different species as well as their light optima therefore determine the phytoplankton patchiness to a large degree.

All over the lake chlorophyll values are reduced along the shoreline, in front of the reed. This is most obvious at the northwest shore of the bay where the chlorophyll concentration remains below 20 $mg/m^3$. This can be a result of grazing, of its own swimming abilities or of hydrodynamic effects. Due to its size *Ceratium* is not grazed by zooplankton. Bream (*Abramis brama*) and roach (*Rutilus rutilus*) account for nearly 2/3 of the fish biomass in Lake Belau. Fish larvae and young bream are to be found mainly in the littoral and avoid the open parts of Lake Belau. Lampert and Sommer (1993) describe young bream as efficient grazers of zooplankton. But stomach analyses of juvenile fish in Lake Belau (Bertram, personal communication) prove that *Ceratium* is avoided by fish. Biological interactions therefore cannot explain the low chlorophyll a concentrations in front of the reed.

Padisak (1985) investigated the spatial distribution of *Ceratium hirundinella* in Lake Balaton. She concluded that the lowest abundance was consistently found in areas with the highest currents and assumed an active coastal avoidance by *Ceratium hirundinella*. The relatively high current speeds along the shore and the connected high vertical turbulence leads to a stronger mixing than in other parts of the bay. This could prevent a vertical separation of algae near the surface, cause vertical uniformity and lead to reduced chlorophyll a concentrations.

The eddies in the south bay are, to a large degree, independent of wind speed. Due to the morphometry of the coastline all wind directions cause eddies in this bay. They vary in size, intensity and slightly in location, but two areas are predestined for the development of eddies under various wind directions: the eastern part of the south bay and a region 150 m north of the Alte Schwentine. In these areas gyres are a comparatively stable phenomenon and allow algae to adapt to the situation.



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## References

Camarero, L. and Catalan, J. (1991). Horizontal heterogeneity of phytoplankton in a small high mountain lake. *Verh. Int. - Verein. Limnol.*, **24**, 1005–1010.

Galvez, J.A., Niell, F.X. and Lucena, J. (1988). Description and mechanism of formation of a deep chlorophyll maximum due to *Ceratium hirundinella*. *Arch. Hydrobiol.*, **112**, 143–155.

Heaney, S.I. (1976). Temporal and spatial distribution of the dinoflagellate *Ceratium hirundinella* O.F. Müller within a small productive lake. *Freshwater Biol.*, **6**, 531–542.

Heaney, S.I. and Talling, J.F. (1979). *Ceratium hirundinella* – ecology of a complex, mobile, and successful plant. *Freshwater Biol. Assoc. Ann. Rep.*, **48**, 27–40.

Hickel, B. (1985). The population structure of Ceratium in a small eutrophic lake. *Verh. Int. Verein. Limnol.*, **22**, 2845–2849.

Jones, R.I. (1993). Phytoplankton migrations: pattern, processes and profits. *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, **39**, 67–77.

Landmesser, B. (1993). Untersuchungen zur Struktur und zur Primärproduktion des Phytoplanktons im Belauer See. Dissertation am Fachbereich Biologie der Universität Hamburg.

Lampert, W. and Sommer, U. (1993). *Limnoökologie*. Georg Thieme Verlag, Stuttgart.

Nauwerck, A. (1963). Die Beziehungen zwischen Zooplankton und Phytoplankton im See Erken. *Symb. Bot. Upsal.*, **17**, 163.

Nusch, E.A. (1980). Comparison of different methods for chlorophyll and phaeopigment determination. *Ergebn. Limnol.*, **14**, 14–36.

Padisak, J. (1985). Population dynamics of the freshwater dinoflagellate *Ceratium hirundinella* in the largest shallow lake of Central Europe, Lake Balaton, Hungary. *Freshwater Biol.*, **15**, 43–52.

Podsetchine, V. and Schernewski, G. (1999). The influence of spatial wind inhomogeneity on flow patterns in a small lake. *Wat. Res.*, **33**(15), 3348–3356.

Pollingher, U. and Berman, T. (1975). Temporal and spatial distribution of dinoflagellate blooms in Lake Kinneret, Israel (1969–1974). *Verh. Int. Verein. Limnol.*, **19**, 1370–1382.

Reynolds, C.S. (1994). The role of fluid motion in the dynamics of phytoplankton in lakes and rivers. In *Aquatic Ecology*, P.S. Giller, A.G Hildrew and D.G. Raffaelli (Eds.), Blackwell Science, Oxford, pp 141–188.

Schernewski, G. (1992). Raumzeitliche Prozesse und Strukturen im Wasserkörper des Belauer Sees. *EcoSys*, Suppl. 1, 160.

Schernewski, G., Podsetchine, V., Asshoff, M., Garbe-Schönberg, D. and Huttula, T. (2000). Spatial ecological structures in littoral zones and small lakes: Examples and future prospects of flow models as research tools. *Arch. Hydrobiol., Adv. Limnol.*, **55**, 227–241.

Sommer, U., Gliwicz, Z.M., Lampert, W. and Duncan, A. (1986). The PEG-model of seasonal succession of planktonic events in freshwaters. *Arch. Hydrobiol.*, **106**(4), 433–471.

Sommer, U. (1991). The application of the droop-model of nutrient limitation to natural phytoplankton. *Verh. Int. Verein. Limnol.*, **24**, 791–794.

Sommer, U. (1993). Phytoplankton competition in Plusssee: a field test of the resource-ratio hypothesis. *Limnol. Oceanogr.*, **38**(4), 834–845.

Stauffer, R.E. (1982). Wind stress effects on chlorophyll distribution in stratified eutrophic lakes. *Limnol. Oceanogr.*, **27**(1), 66–74.

Steele, J.H. and Henderson, E.W. (1992). A simple model for plankton patchiness. *J. Plankton Res.*, **14**(10), 1397–1403.

Tabata, M. (1977). A finite element approximation corresponding to the upwinding finite differencing. *Mem. Numer. Math.*, **4**, 46–63.

Utnes, T. (1990). A finite element solution of the shallow-water wave equations. *Appl. Math. Modelling*, **14**(1), 20–29.

Verhagen, J.H.G. (1994). Modeling phytoplankton patchiness under the influence of wind-driven currents in lakes. *Limnol. Oceanogr.*, **39**(7), 1551–1565.

Webster, I.T. and Hutchinson, P.A. (1994). Effect of wind on the distribution of phytoplankton cells in lakes revisited. *Limnol. Oceanogr.*, **39**(2), 365–373.