Macro- to fine-scale spatial and temporal distributions and dynamics of phytoplankton and their environmental driving forces in a small montane lake in southern California, USA

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Abstract

A wireless network of buoys, two autonomous robotic boats, and an autonomous tethered vertical profiling system were used to characterize phytoplankton dynamics and spatiotemporal changes in chemical and physical forcing factors in a small montane lake (Lake Fulmor, Idyllwild, California). Three deployments each year were conducted in 2005 and 2006 to examine seasonal changes in the structure of the lake and phytoplankton assemblage, as well as fine-scale temporal and spatial variations. The buoys yielded fine-scale temporal patterns of in situ fluorescence and temperature, while the vertical profiling system yielded two-dimensional, cross-sectional profiles of several parameters. The autonomous vehicles provided information on fluorescence and corresponding temperature patterns across the surface of the lake. Average, lake-wide chlorophyll concentrations increased 10-fold seasonally, and strong anoxia developed in the hypolimnion during the summer. The latter process dramatically affected vertical chemical gradients in the 5 m water column of the lake. Small-scale spatial (<1 m) and temporal (minutes) heterogeneity in fluorescence were surprisingly large. These variations were due predominantly to vertical mixing of the phytoplankton assemblage and to phytoplankton vertical migratory behavior. Large peaks in fluorescence at 0.5-m occurred at very short time intervals (minutes) during all deployments, and appeared to be due to upward mixing of deeper dwelling eukaryotic phytoplankton during early–mid-summer, or downward mixing of surface-associated cyanobacteria during late summer.

The development, application, and continued sophistication of environmental sensor platforms in ocean science have become common themes in research programs investigating water quality and large-scale oceanographic processes (Dickey 2003; Glasgow et al. 2004; Dickey and Bidigare 2005). These sensor platforms have provided valuable environmental data for modeling biogeochemical cycles of important chemical constituents, particularly over long temporal or broad geographical scales (Dickey 2004). More recently, emphasis has been directed towards the application of embedded networks of sensors that can obtain and collate information from several locations to provide a detailed characterization of the ecosystem under study (Szewczyk et al. 2002; Pottie and Kaiser 2005; Fries et al. 2007).

Environmental sensors also have been extensively used to support limnological research, but sensor networks have been less frequently employed in fresh water relative to studies of marine ecosystems. This disparity may in part be a consequence of the greater accessibility of many freshwater ecosystems relative to large expanses of the world ocean (obviating the need for autonomous networks in remote areas), and the high cost of manned oceanographic field programs. The latter fact makes sensor platform development and deployment cost efficient for

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oceanographic research. Nevertheless, the investigative power of sophisticated sensor platforms for describing the physical and chemical environment at multiple temporal and spatial scales has not gone unnoticed by the limnological community (Harmon et al. 2007; Sukhatme et al. 2007). The available sources of basic sensors has increased in recent years and costs have declined, resulting in a rapid expansion in the application of sensor networks to river and lake ecosystems (Kratz et al. 2003; Porter et al. 2005).

Sensor networks represent a dramatic improvement in our ability to study natural ecosystems at multiple scales of time and space. Porter et al. (Porter et al. 2005) has noted the paucity of ecological studies that obtained information across multiple temporal and spatial scales. Embedded sensor networks have the potential to yield information on time scales ranging from seconds to months, and on spatial scales ranging from microscopic to many kilometers. Such investigation across scales is still uncommon in aquatic biology, but is increasingly recognized as fundamental to understanding the ecology of species and communities on our planet (Carpenter and Turner 1998). In aquatic ecosystems, we have only a rudimentary understanding of how natural variability in the abundances and distributions of microbial plankton assemblages compare at different time and space scales, and how these dynamics are connected across these scales. This lack of information is in part due to the inability to observe natural communities across very different scales of time and space. Robotic sensor networks provide essential tools for addressing this gap in our observational capabilities and, thus, our knowledge of community ecology.

In this study we describe a large effort to develop and apply a network of environmental sensors that can provide highly resolved spatiotemporal measurements as well as system-level measurements within a freshwater ecosystem. This sensing approach has been employed in a small, montane lake in southern California to characterize phytoplankton distributions and pertinent chemistry and physics. A range of temporal and spatial scales from minutes to season, and centimeters to whole-system (100 s of meters) analyses was examined. These studies bring together expertise in engineering, computer science, robotics, and aquatic biology in order to develop and apply approaches for obtaining chemical, physical, and biological data. Our initial efforts provide unique insights into the small-scale heterogeneity of lake plankton, and have important implications for measurements of the dynamics of phytoplankton biomass dynamics, nutrient acquisition, and photophysiology.

Robotic sensing approaches

The sensor network employed in this study is the outcome of a collaborative effort to design and implement a sensor array that is capable of monitoring water quality within freshwater ecosystems. The field program was carried out during a period of continuous network design and component improvements, and new advances were progressively applied at our study site during 2005 and 2006.

The basic network merges two independent research projects, NAMOS (Networked Aquatic Microbial Observing Systems) and NIMS RD (Networked InfoMechanical Systems—Rapidly Deployable). The systems have been described in detail elsewhere (Jordan et al. 2007; Singh et al. 2007; Sukhatme et al. 2007). Briefly, NAMOS consists of up to 10 stationary monitoring nodes (sensor-equipped buoys) that provide continuous monitoring of basic physical parameters spatially throughout an aquatic ecosystem. Thermistors record water temperature at six fixed depths, and in situ chlorophyll fluorescence is obtained continuously by means of a CYCLOPS-7 submersible fluorometer (Turner Designs) at a single depth of 0.5 m. A prototype mobile surface vehicle (robotic boat; Roboduck I, Fig. 1E) equipped with a thermistor and submersible fluorometer collected information on temperature and chlorophyll fluorescence at a depth of ~10 cm during the 2005–2006 study period. This robotic boat is equipped with Global Positioning System (GPS; Garmin 16A) and a compass (Honeywell HMR 300 Digital Compass Module) for navigation. The boat is capable of autonomous navigation, accepting way-point information wirelessly from the stationary sensor nodes, or directly from shore. The advantages of employing a network consisting of both stationary and mobile components to aid each other has been recently examined (Batalin et al. 2005). Stationary buoys can provide low-resolution spatial sensing but high temporal resolution. The mobile robotic boat can provide relatively low temporal resolution but high-resolution spatial sensing. Collectively, we believe this network provides unprecedented coverage of fine-scale spatiotemporal distributions of sensed parameters, and thus unique insight into microbial plankton distributions and dynamics.

A second-generation robotic boat (Roboduck-II; Fig. 1F) became available in 2006. It is 2.3 m long, 0.5 m wide, and is equipped with dual thrusters and a single rudder (Ocean Science). It is equipped with a winch, which enables the boat to conduct vertical profiling of conductivity, temperature, depth, and chlorophyll using a Sonde sensor package (Hydrolabs). The robotic boat is capable of executing line-of-sight GPS way-point following missions using an onboard GPS (Garmin 16A) and an Inertial Measurement Unit (IMU, Microstrain® 3DM-G) aided by an Extended Kalman filter which fuses information from the two sensors in real time.

The NIMS RD is a tethered, robotic sensing platform, which consists of a sensor package that is supported and transported along a horizontally deployed wire cable. The sensor package is moved horizontally and vertically by means of a series of cables and two motors. The design allows precise horizontal and vertical positioning of the sensor package within the water column to yield high-resolution two-dimensional (2-D) cross-sections of sensed parameters through a body of water. Transit speeds (horizontally and vertically) are controlled to minimize water disturbance. Total transit time is a compromise between high spatial resolution, the degree of water disturbance (which increases with transit speed), and the total time required to perform the entire cross-section. In
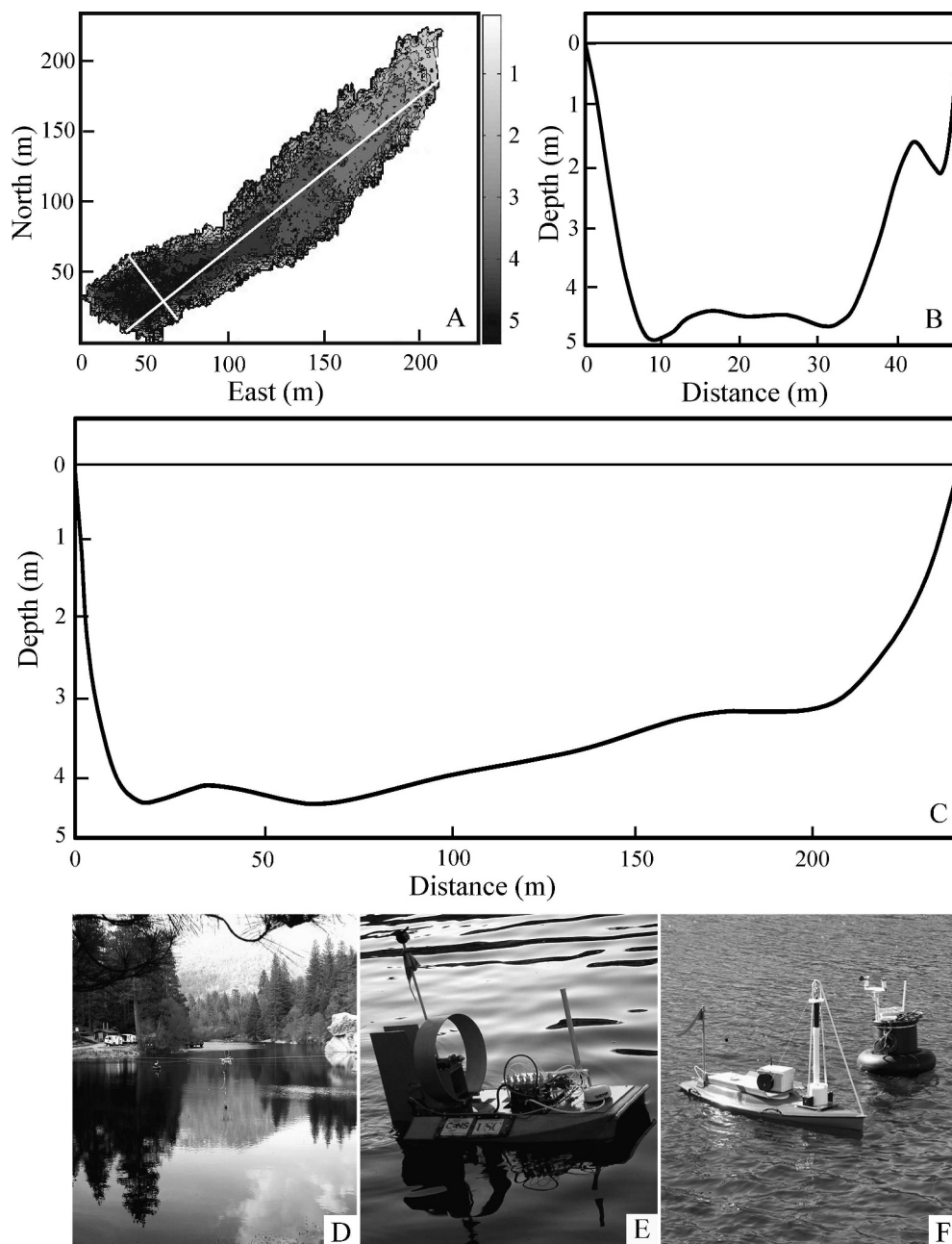
Fig. 1. (A) Bathymetric plot of Lake Fulmor, Idyllwild, California, and (B) cross-sections of lake depth along its long axis and (C) across its short axis. The solid white lines in panel A indicate the approximate location of the NAMOS buoys (along the long axis of the lake), and the location of the NIMS RD deployments (across the short axis of the lake). (D) Picture of the lake along its long axis showing the NAMOS buoys deployed and the NIMS RD mid-lake, (E) the prototype robotic boat (Roboduck I) and (F) Roboduck II near a NAMOS buoy.

practice, 1–2-m horizontal and 0.15-m vertical resolution was attained in this study. Environmental parameters were measured during descent into the lake to minimize the effect of disturbance on sensor values. Dwell times at each depth were determined in accordance with sensor equilibration rates. The NIMS RD was equipped with either a Hydrolab Datasonde models 4A and DS5 equipped for measurements of depth, temperature, power of hydrogen (pH), dissolved oxygen, turbidity (uncalibrated), specific conductivity, and oxidation reduction potential (Hydrolab), and chlorophyll fluorescence using a CYCLOPS-7 submersible fluorometer (Turner Designs) for deployments in Lake Fulmor.

Study site and field program methods

Lake Fulmor is a small (12,000 m²), narrow, artificial impoundment lake located at ~1600-m elevation in the San

Jacinto Mountains, Idyllwild, California created by the damming of the Indian Creek ravine (Fig. 1). The lake has a maximal depth of ~5 m near its southwestern end (Fig. 1A,C) and a total volume of <40,000 m^3 at its maximal seasonal depth. The creek leads into the northeastern end of the lake and it is dammed at its southwestern end, but flow into and out of the lake for most of the period from late spring through autumn is negligible. Precipitation is low and averages 12 cm $month^{-1}$ throughout the May–August period. The lake is heavily used seasonally for recreational fishing and swimming, and freezes over completely during most winters.

Fine-scale spatial and temporal measurements of temperature at six depths and in situ chlorophyll fluorescence at 0.5 m in Lake Fulmor were obtained during field studies conducted 17–20 May, 27–30 July, and 27–30 October 2005 using NAMOS buoys. The work during 2005 was conducted primarily to test hardware and software components of NAMOS but yielded useful preliminary information on the distribution of the phytoplankton (i.e., chlorophyll fluorescence) and depth-resolved temperature in the lake. A minimum of five buoys was deployed along the long axis (north–south) of the lake for each of the deployments (Fig. 1). Fluorometers on all buoys were fixed at a single depth (0.5 m), while thermistors were fixed at depths of 0.1, 0.65, 1.15, 1.65, 2.15, and 2.65 m (water-depth permitting). Measurements of fluorescence and temperature were recorded every 5 s from each sensor for periods ranging from ~48 h to 60 h. Data were stored onboard each buoy, and also relayed wirelessly to an onshore monitoring station in real time.

The robotic boat (Roboduck I) was deployed on 28 November 2005 to characterize surface area of the lake and to examine the fine-scale spatial patterns of near-surface (~0.1 m) temperature and chlorophyll fluorescence throughout the lake. Sensor information was collected every 5 s, and relayed wirelessly to an onshore station. Two-dimensional patterns of temperature and chlorophyll fluorescence were constructed using a 2-D Gaussian filter. The boat was employed in a similar manner on 09–10 May 2006 to obtain system-level spatial patterns of temperature and chlorophyll fluorescence across the surface of the lake.

The second robotic boat (Roboduck II) was employed to obtain detailed information on the depth and topography of the lake bottom. The boat was equipped with an Imagenex 881 L digital multifrequency profiling sonar for this work. The sonar was mounted at the front end of the boat to the left side of the hull, and the center of the sonar was 10 cm below the surface of the water. Data from the GPS and onboard Inertial Measurement Unit (Microstrain®, 3DM-G) were gathered continuously by the boat and logged with time stamps. Sonar data across the lake was gathered by performing 180° sweeps at 0.3° resolution. This procedure yielded 600 bathymetric data points per completed scan. The sweep corresponded to moving from left to right and back (anticlockwise, pointed downward towards the bottom of the lake). The sonar data included time stamp, head orientation, and also amplitude of the back scatter information for the returned ping. These data, along with GPS and IMU data, were fused to generate a

bathymetric map of the lake. The sonar had an accuracy of (<10 cm) for our data sets.

The resulting 2-D pattern of the lake bottom is shown in Fig. 1A. In addition, the depth information was interrogated to provide cross-sectional depth contours of the lake along the long axis of the lake at the approximate location of the NAMOS buoys, and also along the short axis of the lake at the approximate location of the deployment of the NIMS RD robotic sensing platform (Fig. 1B,C).

Field studies in Lake Fulmor using both the NAMOS and NIMS RD were conducted 09–10 May, 20–22 June, and 29 August–01 September 2006. A limited number of field deployments were possible, and these dates were chosen to obtain representative information for spring, mid-summer and late-summer periods. A minimum of seven buoys were deployed along the long axis of the lake for each of the NAMOS deployments. Sensors and deployment depths were as employed during 2005. Sensor measurements of fluorometry and temperature were recorded every 10 s from each sensor for periods ranging from ~60 h to 84 h, and data handled as described above. The lengths of the deployments were limited to short deployments because of the cost to keep the 12–15-person team in the field. The NIMS RD system was erected above the lake forming a transect line that bisected the short axis of the lake at approximately the deepest region (Fig. 1A, B,D). The sensor package was deployed three to eight times per field period at different times of day along this transect line during the three study periods in order to obtain information representative of all times of day. Sensor measurements were recorded every 0.15-m depth for each vertical profile along the horizontal transect. Horizontal spacing of the vertical profiles ranged from 1 m to 2 m. This density of measurements was a compromise between the desire to sense at high spatial resolution, the time involved with each set of sensor measurements, and the physical disturbance to the water (which was affected by the rate of movement of the sensor package). The sensor package was lowered to each depth, time was allowed for sensor equilibration, and then sensor measurements were recorded. Data were binned according to specific horizontal and vertical position in the water column to yield an average measurement for each parameter at each position.

Meteorological information was collected at the lake's edge north of Lake Fulmor during 2005 and 2006 by the University of California James San Jacinto Mountains Reserve. Meteorological measurements included precipitation, air temperature, wind direction, and wind speed. Additionally, wind direction and wind speed were measured on board a NAMOS buoy located centrally in the lake during the late-August deployment in 2006.

Samples of plankton were collected during the 2006 field studies to examine seasonal changes in phytoplankton biomass and species composition. Samples were preserved in acid Lugol's solution (Stoecker et al. 1994), concentrated in settling chambers (Utermöhl 1958), and examined using a compound inverted microscope. Samples for carbon, hydrogen, and nitrogen (CHN) analysis of particulate material and for measurements of extracted chlorophyll were collected from five to six depths in the upper 3.5 m of

the water column, filtered onto GF/F filters and stored frozen until analyzed. Frozen samples used for chlorophyll measurements were extracted with 100% acetone at $-20°C$ and analyzed fluorometerically using standard methods (Parsons et al. 1984). Samples for CHN measurements were dried and sent to the Marine Science Institute Analytical Lab for analysis (University of California, Santa Barbara).

The in situ Cyclops 7 fluorometers were calibrated prior to deployment against a mixture of laboratory cultures (a prasinophyte, a dinoflagellate, and a pelagophyte) serially diluted to chlorophyll concentrations ranging from 4.8 μg L^{-1} to 291 μg L^{-1}. Each fluorometer was calibrated to each dilution at all three gain settings when algal densities were sufficiently high to warrant it, and regression analysis between fluorometer voltage and extracted chlorophyll was used to determine the calibration. Calibrations were conducted prior to deployments and checked following deployments to examine stability of the calibration. Individual deployments were sufficiently short that biofouling was not a significant problem. Although calibrated to extracted chlorophyll, in situ fluorometric measurements do not provide an exact measure of chlorophyll concentration, and these data must be considered a measure of relative estimates.

The penetration of photosynthetically active radiation (PAR) into the lake was measured during each field study using a quantum radiometer and photometer (model LI-185B; LI-COR Biosciences) equipped with a submersible sensor.

Results

Large-scale temporal and spatial patterns—Seasonal changes in total phytoplankton biomass were substantial in Lake Fulmor during 2005 and 2006 (Table 1). Seasonal changes in the average phytoplankton standing stock, as indicated by extracted chlorophyll concentrations, in either year were much greater than differences between similar seasons in different years. Similar trends were observed for measurements of in situ fluorometry. For example, fluorometric values observed at 0.5-m depth using the NAMOS buoys during May 2005 were similar to values observed during May 2006, and values observed during late July 2005 overlapped with those observed in June and August 2006. In situ fluorescence values averaged over a 24-h period during May were 6.2 μg L^{-1} during 2005 and 5.0 μg L^{-1} during 2006. Similarly, concentrations averaged over a 24-h period during late July during 2005 were 13.6 μg L^{-1}, while daily averages were 20.9 μg L^{-1} and 21.8 μg L^{-1} during late August and early September, respectively, during 2006. Coefficients of variation for in situ fluorescence values during individual campaigns were high (25–110%) due to large daily excursions in fluorescence and differences related to different sampling depths and locations within the lake. Given the slight differences in dates of deployment during 2005 and 2006, the patterns and general magnitudes were quite similar for the two years. In contrast, average daily extracted chlorophyll concentrations and in situ fluorometry within either year, measured in early and late summer, differed by 2–13-fold (Table 1).

Table 1. Summary of seasonal ranges (and averages) for meteorological, chemical, physical, and biological parameters from field studies in Lake Fulmor during 2005 and 2006. Air temperatures represent averages of the daily minimum and maximum for the week encompassing each deployment.

Parameter	Daily range (2005)			Daily range (2006)		
	May	Jul	Oct	May	Jun	Aug
Air temp. (°C)	2.8–28.9	13.3–30	0.6–20.6	5–25	6–26	10–29
Precipitation (mm)	0	0.02	0	0	0	0
Surface water (0.1 m) Temp. (°C)						
Range (Average)	12.5–19 (15.3)	3.7–25.3 (22.2)	5.2–22.8 (10.1)	11.2–19 (16.0)	18.2–23.4 (20.4)	18.1–22.8 (20.0)
Max. daily photosynthetically active radiation (PAR) (W m^{-2})	1210	1060		942	1038	1166
Extracted chlorophyll, 0–3 m, discrete* (μg L^{-1})						
Range (Average)	1.3–7.5 (2.6)	12.8–20.1 (16.8)	65–74.5 (69.2)	2.7–21.5 (5.0)	34.0–68.8 (47.0)	21.8–121 (50.9)
Sensed fluorometry, 0.5 m, NAMOS†						
Range (Average)	5.0–7.5 (6.2)	8.3–39.2 (13.6)	18.2–184 (82.0)	4.1–8.6 (5.0)	10.0–28.9 (20.9)	9.8–79.7 (21.8)
C:N ratio (0–3 m)				6.7–11.6	8.1–11.2	7.3–9.9

* Extracted chlorophyll determined fluorometrically from discrete samples collected within the epilimnion of the lake (5–6 depths at 2–3 locations).
† Fluorometric measurements recorded by a Networked Aquatic Microbial Observing Systems (NAMOS) fluorometer suspended at 0.5 m centrally in the lake.
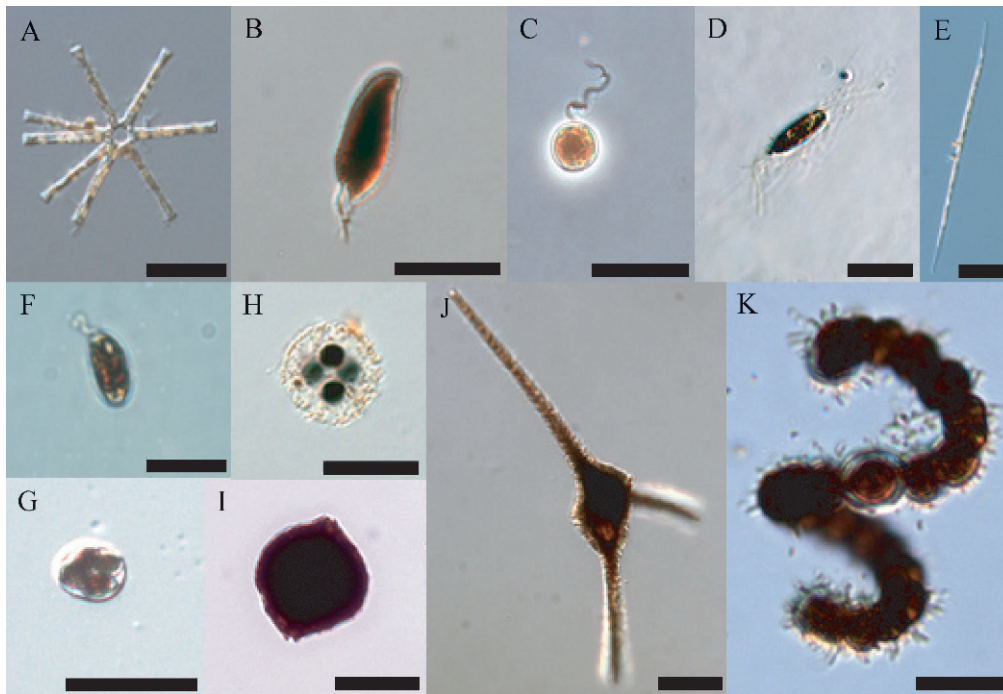
Fig. 2. Phytoplankton communities present in surface waters of Lake Fulmor on 09–10 May, 20–22 June and 29 August–1 September 2006. (A) The assemblage in May was highly dominated by the diatom *Asterionella formosa*. (B) Cryptophytes, (C) a large unidentified flagellate, and (D) small euglenid flagellates were also abundant at the surface and at depth. The plankton community in late June showed strong dominance by (E) diatoms, dinoflagellates, and (G, H) colonial *Gloeocapsa*-like cyanobacteria. (K) A persistent surface scum in late August was composed of the cyanobacterium *Anabaena spiroides* that formed in the late mornings. Dominant phytoplankton in the water column at that time included (I, J) large *Peridinium* and *Ceratium* dinoflagellates, diatoms, and a (F) large aggregation of small flagellates at the 3-m depth. Markers bars in panels D, F, K are 15 μm. Markers bars in all other panels are 35 μm.

Species composition of the phytoplankton assemblage also changed dramatically from May to August during 2006 (Fig. 2). The phytoplankton assemblage was strongly dominated by the diatom *Asterionella formosa* during May (Fig. 2A) with a number of other small flagellates present at subdominant abundances (Fig. 2B–D). Dinoflagellates, diatoms and colonial *Gloeocapsa*-like cyanobacteria shared dominance during June (Fig. 2E,G,H,J). A persistent surface accumulation composed of the cyanobacterium *Anabaena spiroides* was present during August (Fig. 2K), and large *Peridinium* and *Ceratium* dinoflagellates, diatoms, and small flagellates were present at subdominant abundances throughout the water column (Fig. 2F,I,J). The vertical distributions of extracted chlorophyll concentration determined from discrete water samples during the day were also markedly different during the three study periods in 2006 (Fig. 3). Phytoplankton biomass in the upper 3 m during May was fairly low and uniformly distributed throughout the water column with a subsurface peak of chlorophyll below 2 m. The June assemblage during midday was significantly more abundant at depth, with maximal chlorophyll concentration observed at or below 3 m. In contrast, exceptionally high concentrations of chlorophyll were measured during the day at the surface during August as a consequence of the presence of buoyant cyanobacterial colonies (largely *A. spiroides*). Despite these

differences in the standing stocks and vertical distributions of the phytoplankton assemblages between May and August, penetration of photosynthetically active radiation (PAR) did not vary dramatically throughout the summer, presumably due to high suspended particle loads in the water column (Fig. 3). Surface irradiances were high due to the elevation of the lake (1600 m) and cloudless sky. Nevertheless, extinction coefficients were consistently high during all three field studies (1.5–1.7) resulting in dramatic attenuation of light at 3-m depth for the three study periods.

Spatial heterogeneity in water temperature and in situ fluorescence at a depth of 0.1 m in Lake Fulmor was investigated using the robotic boat on 28 November 2005 and 09 May 2006 (Fig. 4). Temperature showed little spatial heterogeneity during either deployment (Fig. 4A,B). The overall range of fluorometric values was low during the November 2005 deployment relative to the seasonal ranges of in situ fluorescence at 0.5 m, and extracted chlorophyll concentrations at different depths (Fig. 4B and Table 1). This result was not surprising given the timing of the first deployment of the boat (late autumn). Nevertheless, spatial heterogeneity in near-surface (0.1 m) fluorescence was significant across the lake (range of 2–10 μg chlorophyll L^{-1} based on calibration with cultures as noted above). No obvious spatial
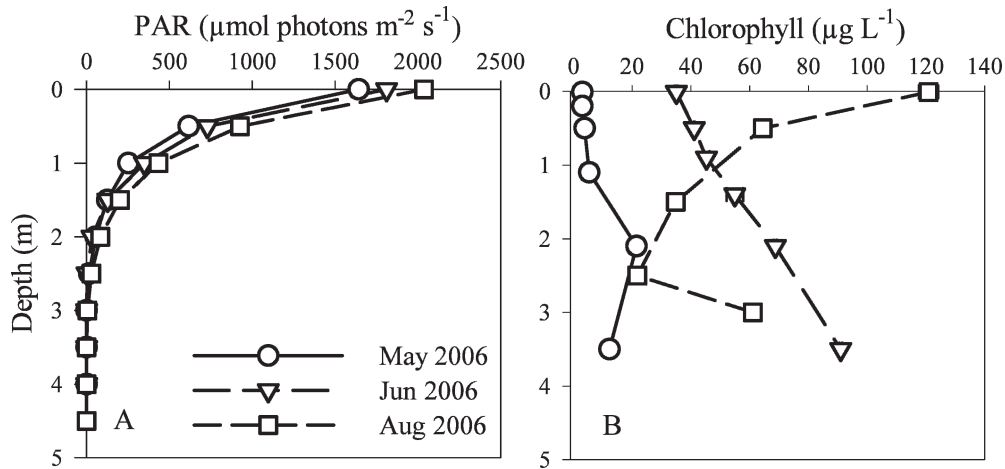
Fig. 3. (A) Penetration of photosynthetically active radiation (PAR) and (B) concentrations of chlorophyll in samples collected at specific depths in Lake Fulmor on 09 May, 21 June, and 30 August 2006. Chlorophyll was determined fluorometrically after extraction.

correlation between fluorescence and temperature was apparent at that time. In contrast, fluorescence values were substantially higher during the May 2006 deployment (Fig. 4C,D), although spatial heterogeneity in near-surface fluorescence was less pronounced (~10% of the absolute concentrations) than observed in November of the previous year. The overall range of all measurements obtained by the robotic boat was 56.0–63.5 μg chlorophyll L^{-1} when converted from fluorescence based on the calibration with cultured algae. Highest near-surface fluorescence values during May 2006 (Fig. 4D) were clearly inversely related to water temperatures at a depth of 0.1 m (Fig. 4C).

Small-scale temporal-spatial patterns—Changes in the distribution of the phytoplankton over small-scales temporally and vertically (≤ 1 m) in the water column of Lake Fulmor were examined using data collected using the NAMOS buoys in 2005 and the NAMOS buoys and NIMS RD robotic sensing platform in 2006. Patterns observed employing the buoys in 2005 were very similar to patterns observed in the following year, albeit for differences presumably owing to the differences in timing of the field studies conducted in each year. Therefore, the information presented in the following sections is limited to 2006.

The lake-wide pattern of near-surface in situ fluorescence obtained using the robotic boat in May 2006
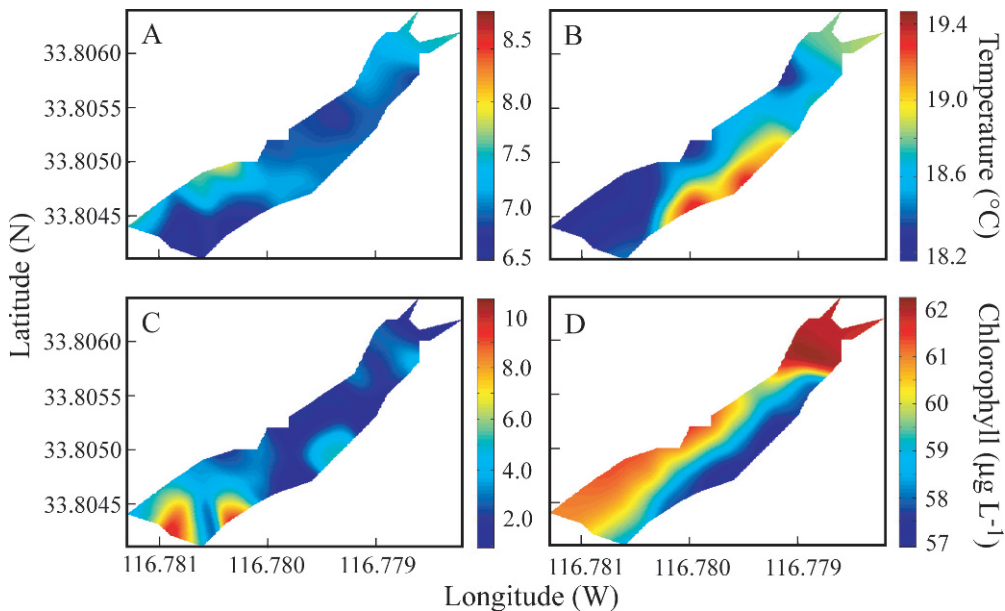

Fig. 4. (A, B) Spatially resolved temperature and (C, D) in situ chlorophyll fluorescence at 0.1 m in Lake Fulmor on (A, C) 28 November 2005, and (B, D) 09 May 2006. Data collected using the NAMOS robotic boat and contours generated using a 2-D Gaussian filter. Chlorophyll values were based on sensor calibration with cultured algae (*see* study site and field program methods).
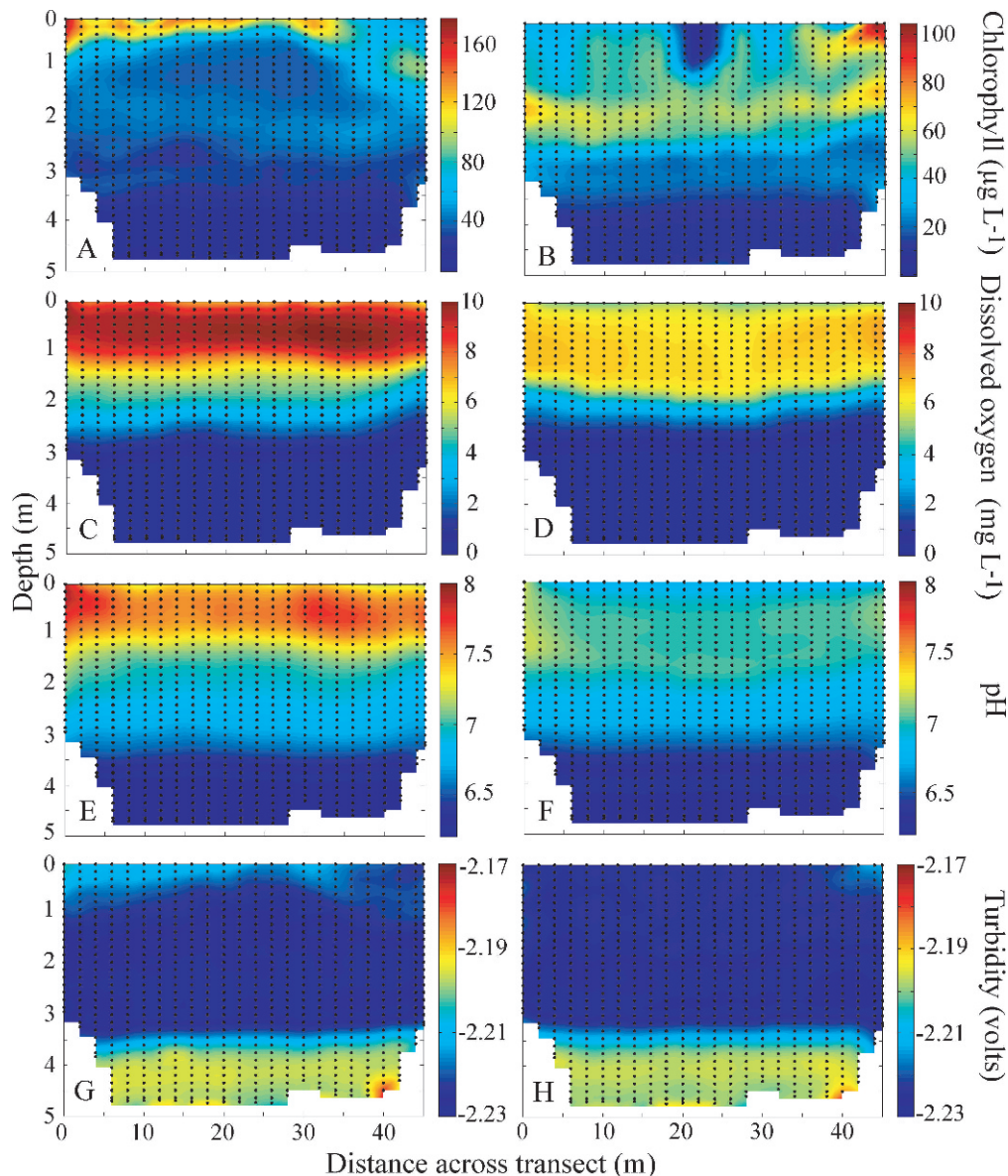
Fig. 5. (A, B) Cross-sectional contour plots of chlorophyll fluorescence, (C, D) dissolved oxygen, (E, F) pH and (G, H) turbidity across the deepest region of Lake Fulmor obtained using NIMS RD. Transects were performed 29–30 August 2006 and are representative of daytime (panels A, C, E, G: 29 August 16:50 h to 19:44 h) and nighttime (panels B, D, F, H: 30 August 06:47 h to 09:44 h) distributions of these parameters. Vertical and horizontal locations in the water column from which sensor measurements were recorded are depicted by closed circles. All times are local. Chlorophyll values were based on sensor calibration with cultured algae (*see* study site and field program methods).

indicated that the system-level (large-scale) variability in phytoplankton abundance was relatively minor at a given time of day. However, investigation of the short-term temporal and spatial patterns of fluorescence indicated substantial variability in the small-scale patterns. These patterns, and the probable forces resulting in these patterns, became apparent through examination of temporal changes in fluorescence at 0.5 m in the water column over time scales of minutes to hours using the NAMOS sensor platform, and temporal changes of hours to days

throughout a cross-sectional area of the lake studied using the NIMS RD.

Information obtained using the NIMS RD robotic sensing platform indicated substantial spatial (vertical) variations in water column physics, chemistry, and biology, and substantive changes in some of these distributions within 24 h during the June and August 2006 study periods (Figs. 5, 6, 7). Examples of the vertical distributions of sensed parameters obtained from the NIMS RD are given in Fig. 5 for two sampling times (mid–late afternoon and
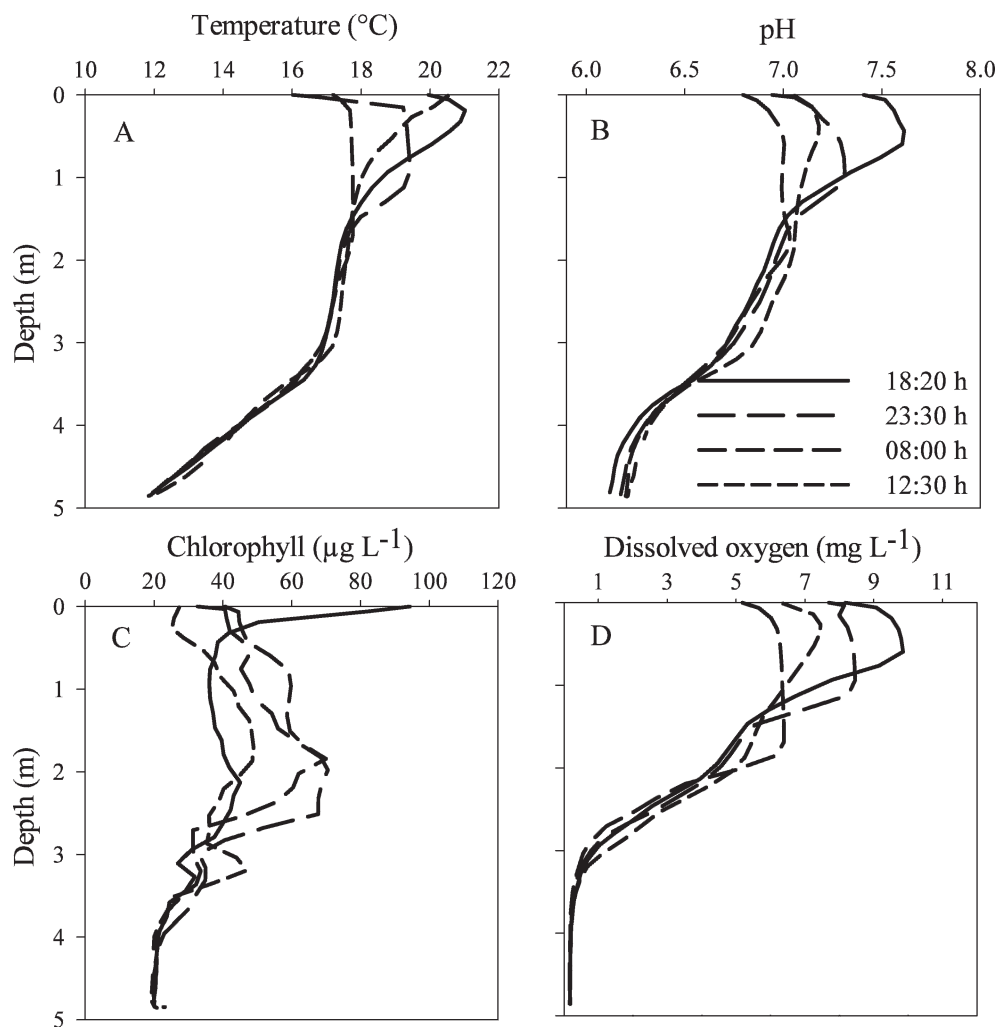
Fig. 6.   (A) Depth-resolved profiles of temperature, (B) pH, (C) in situ fluorescence, and (D) dissolved oxygen in Lake Fulmor on 29–31 August 2006 using NIMS RD. Cross-sections of the lake were conducted at four times of day as depicted in Fig. 5. Each profile presented here was constructed by averaging three vertical sensing profiles from the NIMS RD obtained centrally in the lake along the transect line. All times are local.

early morning) during August 2006 when diel differences in vertical structure in the lake were most pronounced. A well-developed epilimnion and hypolimnion were apparent in the lake at that time. Horizontal gradients in the measured parameters were not large, but vertical gradients were extreme, and the magnitude and vertical zonation changed significantly over a 24-h period (compare Fig. 5A,C,E,G to Fig. 5B,D,F,H). In situ fluorescence during mid–late afternoon was strongly associated with the surface of the lake during August (Fig. 5A). Fluorometry values near the surface corresponded to chlorophyll concentrations in excess of 150 μg L^{-1} at that time. Chlorophyll fluorescence showed a markedly different vertical pattern at the beginning of the daylight period with a clear subsurface maximum of abundance at 1.5–2 m (Fig. 5B). However, it is important to note that changes in fluorescence characteristics of the phytoplankton due to photoadaptation must be considered when interpreting data derived from fluorescence sensors.

The 2-D spatial distributions obtained using the NIMS RD (Fig. 5) were processed to obtain mid-lake distributions of sensed parameters at four times of day during the August deployment (Fig. 6). These vertical profiles were obtained by averaging three profiles conducted centrally in the lake. Profiles obtained in this manner demonstrated that the subsurface maximum of in situ fluorescence persisted through the night and into midday (Fig. 6C). Only the mid–late-afternoon profile revealed a large maximum in fluorescence near the surface. This maximum coincided with the highest temperatures of surface waters and the time of day exhibiting the strongest thermal stratification (Fig. 6A). However, diel changes in the vertical distribution of fluorescence in the lake were not the same as diel changes in the vertical distribution of temperature, implying that biological processes as well as physical processes were affecting phytoplankton vertical distribution.

Dissolved oxygen concentrations during late afternoon in August 2006 varied from ~10 mg L^{-1} (~280 μmol L^{-1})
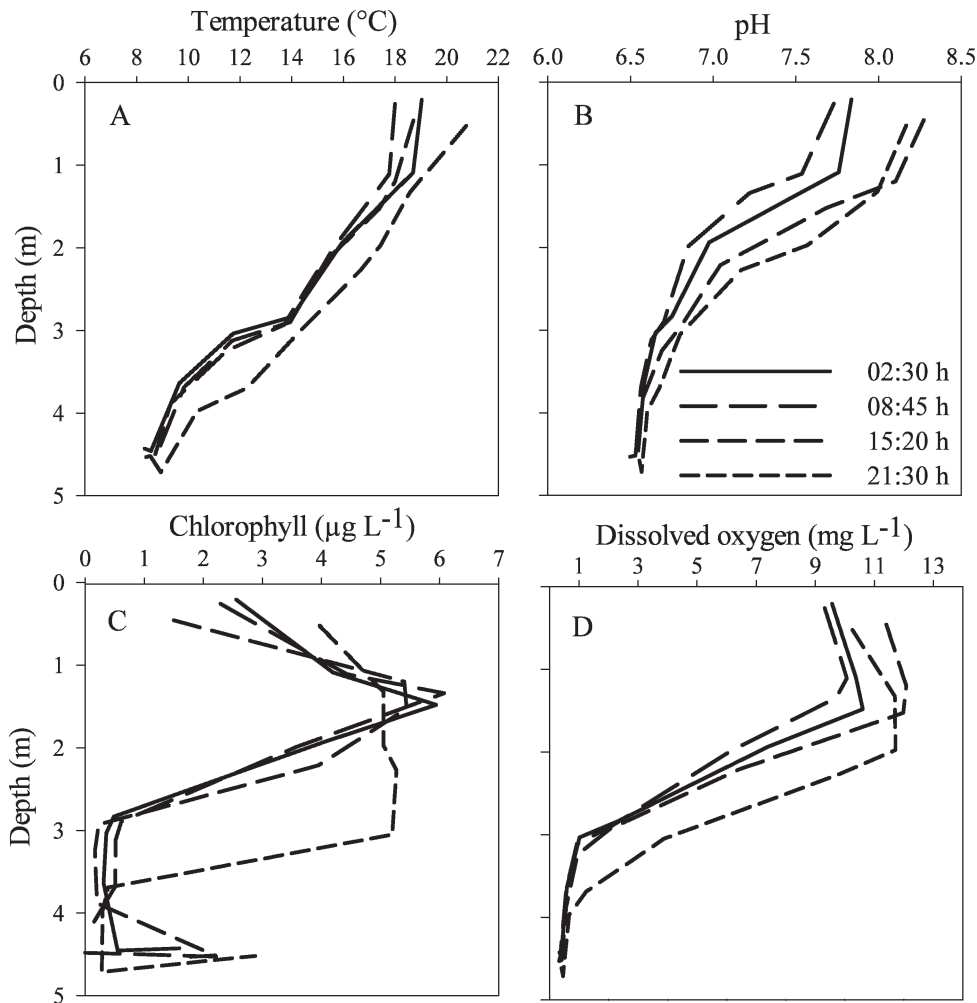
Fig. 7. (A) Depth-resolved profiles of temperature, (B) pH, (C) chlorophyll fluorescence, and (D) dissolved oxygen in Lake Fulmor on 20–22 June 2006 using NIMS RD. Cross-sections of the lake were conducted at four times of day as depicted in Fig. 5. All times are local. Each profile presented here was constructed by averaging three vertical sensing profiles from the NIMS RD obtained centrally in the lake along the transect line.

at 0.5 m to 0 mg L^{-1} below 3 m (Fig. 5C). Maximal values in surface waters during the night were ~6 mg L^{-1} (170 μmol L^{-1}; Fig. 5D) indicating a substantial diel signal in this parameter resulting from community primary production and respiration. Gross primary productivity was estimated for the August 2006 campaign based on depth-integrated differences in oxygen concentrations at different times of day. Assuming a constant rate of community respiration, minimal loss or gain of oxygen to or from the atmosphere, a respiratory quotient of 0.9, and a 2-m euphotic zone at that time, primary production was estimated to be 4.8 gC m^{-2} d^{-1}. This value indicates a highly productive ecosystem.

The vertical structure of dissolved oxygen (specifically, the subsurface maximum at 0.5 m) became less pronounced during the night and the vertical distribution was relatively uniform throughout the epilimnion by morning (Fig. 6D). It is noteworthy that the dissolved oxygen concentration at 2-m depth was greatest in early morning. This early morning distribution is in contrast to the distribution at

the end of the daylight period which showed a distinct maximum at 0.5 m. Unlike fluorescence, the diel vertical pattern for dissolved oxygen strongly mimicked the diel vertical patterns observed for temperature (compare Fig. 6A,D). Maximal temperature at 2-m depth in the water column was observed in early morning.

The pH of the lake observed using the NIMS RD ranged from ~8 near the surface to <6 below 3 m (Fig. 5E). The pH of the water column above 3 m increased by nearly one unit during the day, and returned to a starting value of ~7 by 08:00 h (Fig. 5F). Changes in the vertical distribution of this parameter over a diel cycle were similar to diel changes in temperature in that maximal surface pH occurred in late afternoon while maximal values in the deep epilimnion (>2 m) occurred during the night (Fig. 6B).

High turbidity was restricted to the hypolimnion throughout the August 2006 study period and was relatively unchanging (Fig. 5G,H). However, a minor increase in turbidity was associated with the surface accumulation of phytoplankton (largely colonial cyano-
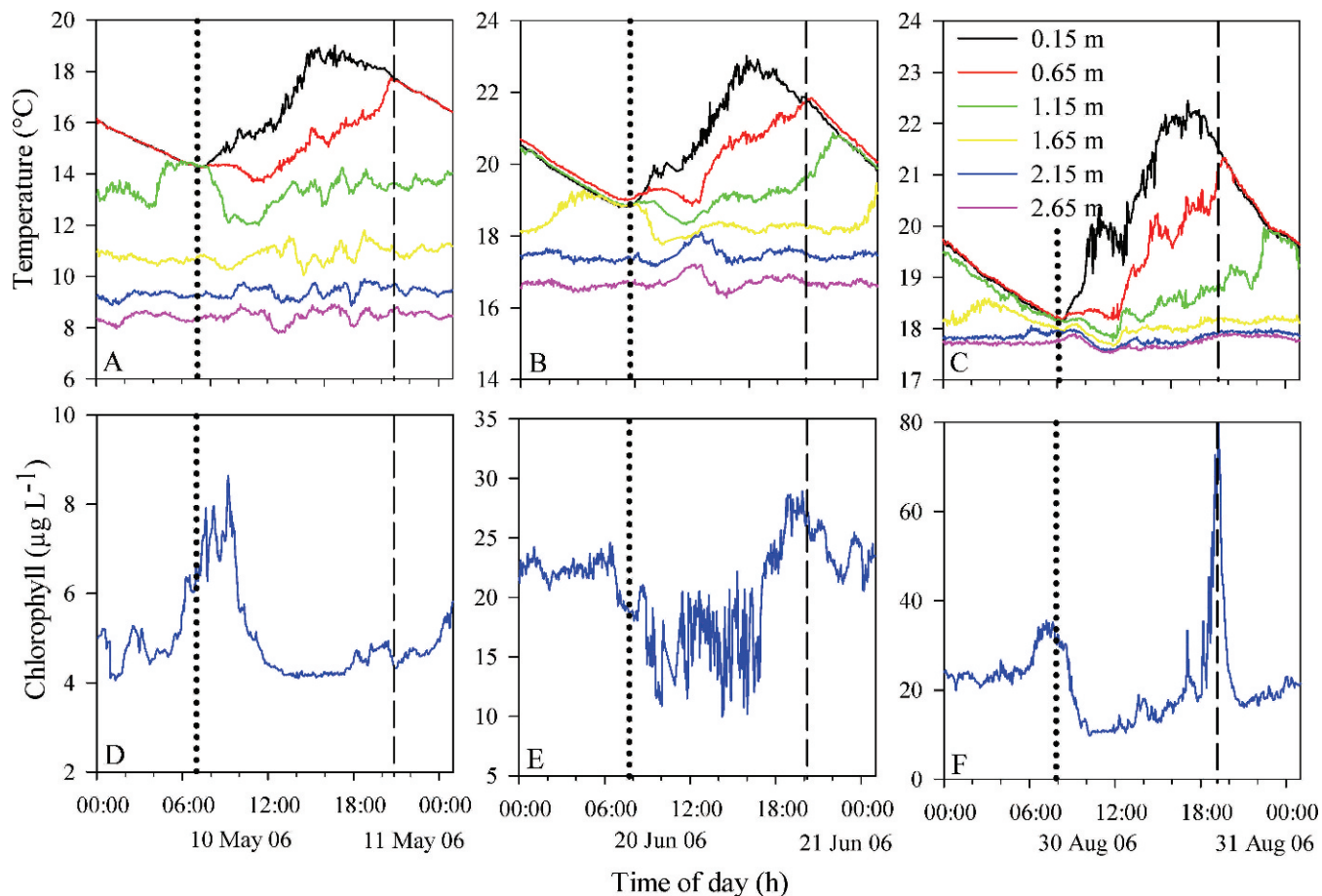
Fig. 8. (A, B, C) Diel changes in depth-resolved temperature and (D, E, F) chlorophyll fluorescence in Lake Fulmor on (A, D) 10 May, (B, E) 22 June, and (C, F) 28 August 28 2006. A representative 24-h period is depicted for NAMOS buoys located centrally in the lake. Dotted vertical lines in each panel indicate the times when thermal stratification began each day. Dashed vertical lines indicate the approximate times when surface waters were isothermal with water at the depth of the fluorometer. All times are local. Chlorophyll values were based on sensor calibration with cultured algae (*see* study site and field program methods).

bacteria) at the surface of the lake during mid–late afternoon (Fig. 5G).

Information on the small-scale spatial variability of these parameters was also obtained for June 2006 (Fig. 7). Diel patterns and changes in the vertical profiles of temperature were similar to profiles obtained during August albeit less pronounced (Fig. 7A). Radiative warming was apparent down to a depth of 1.5–2 m, but temperature did not vary over a diel cycle below that depth during the June study period. Vertical profiles of in situ fluorescence indicated that the phytoplankton assemblage maintained a subsurface maximum in the epilimnion throughout the day during this time and did not exhibit the strong near-surface maximum observed during August (Fig. 7C). This pattern for June was consistent with the results of chlorophyll analyses performed on extracted chlorophyll from samples collected from discrete depths throughout the top 3.5 m of the water column. The latter analyses also indicated a subsurface distribution of the phytoplankton (Fig. 3B). The vertical profiles of dissolved oxygen, and to a lesser extent pH, reflected the subsurface maximum in phytoplankton biomass at that time (Fig. 7B,D). In addition, the

magnitude of the diel changes in these parameters were less pronounced during June relative to August.

Diel changes in water-column structure affected the distribution of phytoplankton within Lake Fulmor during all field efforts in 2005 and 2006. Representative data for depth-resolved temperature (0.15–2.65 m) and in situ fluorescence at 0.5 m collected using the NAMOS buoys during the three study periods in 2006 are shown in Fig. 8. Patterns of fluorescence sensed at 0.5 m are presented on the same time scale immediately below the temperature patterns. Intense solar radiation (Fig. 3) resulted in rapid heating of the surface waters of the lake during morning and into mid-afternoon during all three study periods (Fig. 8A–C). Solar heating during May resulted in a diel cycle of warming to a depth of ~1.15 m. The exact depth could not be accurately determined because of the discrete vertical positions of the thermistors. The temperature of the water column at 0.15 m began to diverge from deeper water at ~08:00 h (Fig. 8A). Water temperature near the surface continued to increase until ~16:00 h, at which time surface water began to cool. Note, however, that the water at 0.65 m (Fig. 8A) continued to warm as the surface water

cooled, until the water at 0–0.65 m was isothermal at ~21:00 h. Vertical mixing of the water column was indicated by the fact that the water at 0.65 m continued to increase in temperature while the water at 0.15 m decreased in temperature. Vertical mixing was presumably a consequence of convective and wind-induced mixing because there was no flow into or out of the lake during the study, and there was no indication of advective processes in the pattern of lake-wide surface temperature during the study (Fig. 4). Water at or above 0.65 m continued to cool throughout the night until ~06:00 h at which time the water column from the surface to ~1.15 m was isothermal. As the water from 0 m to 1.15-m became isothermal, the water at 1.15 m depth reached its daily maximal temperature (06:00 h).

Maximal in situ fluorescence at 0.5 m (the depth of the sensor) during May 2006 was observed at the time when the water at 1.15 m became isothermal with the water above that depth (Fig. 8D). Fluorescence at 0.5 m remained elevated until the water column began to warm and stratify again the following day (~ a 4-h period; Fig. 8D). This result appeared to indicate that mixing of deeper water (and its associated phytoplankton) during the evening increased fluorescence at the depth of the sensor. The increase in fluorescence at the depth of the sensor occurred rapidly (<2 h), and fluorescence decreased rapidly as the water column again became stratified during the morning and afternoon. The rapidity of the increase in fluorescence indicated that it is highly unlikely that these changes were due to phytoplankton growth and mortality. Presumably, phytoplankton mixed from deeper waters up to the depth of the fluorometer resulted in the rapid increase in chlorophyll fluorescence, and reestablishment of stratified water resulted in the decrease in fluorescence through sinking, migration, or other removal processes (e.g., grazing by herbivores).

Similar diel patterns of thermal stratification and destratification of the water column occurred during June and August 2006 but the magnitude of the temperature fluctuations and the depth of mixing were greater for the latter deployments. Also, the patterns of temporal changes in fluorescence at 0.5 m were different for subsequent deployments. Water temperature changed over the diel cycle to a depth of ≥1.65 m during June (Fig. 8B), although the daily timing was similar to May. Water temperature at 0.15 m in June began to cool at ~17:00 h, and became isothermal with water at 0.65, 1.15, and 1.65 m at 20:00, 22:00, and 04:00 h, respectively (Fig 8B). The transfer of heat deeper into the water resulted in the warmest water temperature at 1.65 m in June (>19°C) occurring at 04:00 h (Fig. 8B). Similar to the pattern observed during May, in situ fluorescence at 0.5 m during June showed generally higher values during the period of isothermal surface water, and lower values during the period of thermal stratification, although the extent of these effects differed during the two deployments (Fig. 8E).

The diel pattern of water temperature during August was similar to June except that water down to 2.65 m was significantly warmer during August (>17°C; Fig. 8C). Water below 3 m (hypolimnion) decreased gradually with

depth to 12°C during this period (*see* NIMS RD profiles, Fig. 6A). Near-surface water in August diverged in temperature from deeper water at ~08:00 h and continued to warm until 16:00 h. Cooling of surface waters ensued after 16:00 h with sequentially deeper layers of water continuing to warm, and then cool again until isothermal conditions down to at least 2.65 m were reestablished each day at ~06:00 h.

The diel pattern of in situ fluorescence at 0.5 m was markedly different during August than the pattern observed in May and June (Fig. 8F). A large, transient increase in fluorescence was recorded at 0.5 m in August, following the daylight period of strong thermal stratification, at the time that the water at 0.15 m became isothermal with the water at 0.65 m (~19:00 h; Fig. 8C,F). This peak appeared very rapidly (<2 h) and decreased rapidly. A smaller peak in chlorophyll fluorescence was observed at the time that the water column became isothermal down to a depth of ≥1.65 m (the depth of the deepest thermistor; 06:00 h).

These diel patterns of depth-resolved temperature and chlorophyll fluorescence at 0.5 m were well-defined by the opposing forces of thermal stratification of the water column during the day due to solar radiation, and vertical mixing at night due to water cooling and convective, advective, and wind mixing (Fig. 9). Wind speed during the August 2006 study period was low and variable over the 3-d deployment period but did not indicate large differences in day/night average speed (Fig. 9A). However, wind direction was consistent and regular for all three days in that wind direction was oriented up the ravine (south to north) from ~09:00 h until ~18:00 h each day, and then changed 180° to directly down the ravine (north to south) from 18:00 h until 09:00 h (Fig. 9B). Heating of air above the Indian Creek ravine caused a regular pattern of warm, rising air during the day followed by cold air drainage that reversed the wind direction in the late afternoon and through the night (Bergen 1969). Moreover, nighttime air temperatures at the study site were much lower than daytime temperatures, with differences between average daily minima and maxima on the order of 20°C (Table 1). Comparison of the pattern of cooling and mixing of Lake Fulmor with this pattern of wind direction and air temperature indicated that cooling of the surface waters of the lake and vertical mixing of water into deeper layers were strongly correlated with the period of cold air drainage (compare diel pattern of temperature in Figs. 6A and 9C with the pattern of wind direction in Fig. 9B). Large increases in fluorescence at 0.5 m during August as recorded by the NAMOS buoys occurred only at the initial period of cooling and mixing of surface waters (Fig. 9).

Discussion

Large seasonal changes in the standing stocks of phytoplankton within eutrophic lakes are well-documented and well-understood phenomena (Kratz et al. 2005). Patterns are often coherent within and between lakes over considerable geographical distances or time (Kratz et al. 2003; Livingstone and Pakisák 2007). Seasonal changes in
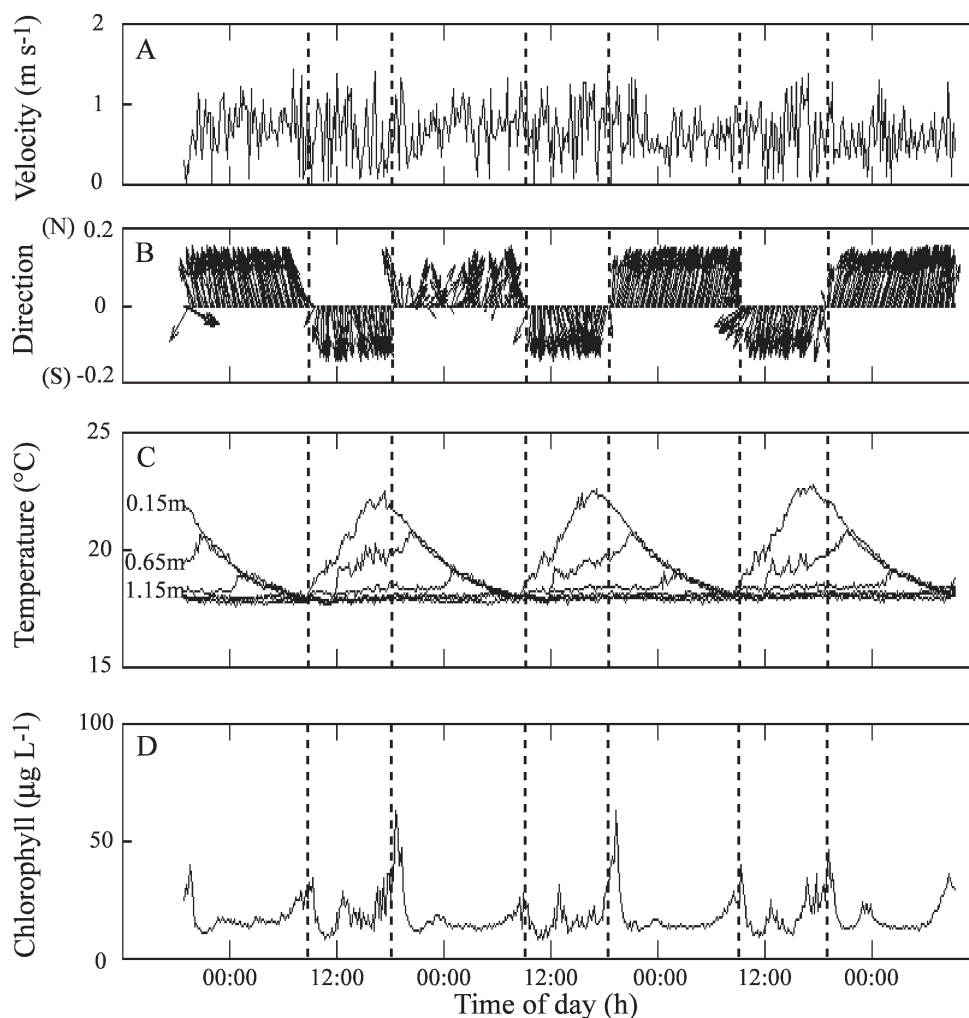
Fig. 9. (A) Relationship between wind speed, (B) wind direction, (C) depth-resolved temperature, and (D) in situ fluorescence at 0.5 m observed using a NAMOS buoy located centrally in Lake Fulmor from 27 August to 01 September 2006. Dotted lines indicate the time of change in wind direction each day. All times are local. Chlorophyll values were based on sensor calibration with cultured algae (*see* study site and field program methods).

phytoplankton standing stock and assemblage composition are controlled by the interaction of chemical, physical, and biological driving forces (Sommer et al. 1986). Dramatic changes in the availability of light and nutrients and the stability of the water column give rise to changes in species composition and the total amount of plankton biomass present in these environments.

Similarly, the magnitudes and forcing factors that bring about short-term (i.e., minutes to days) fluctuations in the abundances of these assemblages, and how these forces might contribute to larger scale plankton dynamics, have been extensively examined in marine and freshwater ecosystems (Harris and Trimbee 1986; Dekshenieks et al. 2001; Rines et al. 2002; Cowles 2003; Mcmanus et al. 2003, 2005; Serra et al. 2007). These processes have been shown to have important implications not only for phytoplankton distributions, but for zooplankton aggregation and feeding, nutrient distributions, and the accumulation of particulate organic material within the water column (Alldredge et al.

2002; Bochdansky and Bollens 2004; Lunven et al. 2005; Menden-Deuer and Grünbaum 2006). Conducting observations across these differing scales is greatly enabled by autonomous instrumentation, and can provide unique insights into ecosystem structure and function.

The use of two robotic approaches in this study allowed observations of both small-scale phenomena within the lake and at the level of the whole ecosystem. Data obtained using the NAMOS buoys and robotic boats and the NIMS RD robotic sensing platform documented the lake-wide horizontal variability in sensed parameters within Lake Fulmor (Figs. 4, 5). The horizontal spatial variability of temperature and chlorophyll were not great relative to changes observed in short-term, temporal variability at a single location and depth (compare magnitude of changes in Fig. 4 relative to changes in Fig. 8). The data obtained from the individual NAMOS buoys deployed along the long axis of the lake exhibited similar patterns at all buoys, indicating only modest horizontal differences in tempera-

ture and chlorophyll throughout much of the lake, and were largely a consequence of differences in lake depth along its length (data not shown). In addition, horizontal variability in chemical parameters observed in the cross-sectional transects of the lake along its short axis using the NIMS RD was minimal relative to vertical changes in these parameters and relative to short-term temporal (diel) changes (Figs. 5, 6, 7). This level of uniformity in the horizontal distributions of the sensed parameters seemed unsurprising given the relatively small size of Lake Fulmor.

Year-round measurements of water-column structure in Lake Fulmor have not been conducted and, therefore, mixis has not been characterized. Given the very shallow nature of the northern end of the lake, vertical mixing may take place regularly in that part of the lake. However, the southern portion of the lake may be quite different, and may even be meromictic based on seasonal measurements of environmental parameters conducted in this study. The narrowness of the lake, its steep-sided bottom contours (Fig. 1B,C) and the generally low wind speed that characterizes this area for much of the spring–autumn may constrain vertical-mixing processes in the deepest (~5-m) region. Vertical gradients in water temperature were already considerable in early spring in the lake (Fig. 8), and sharp vertical gradients in temperature and dissolved oxygen persisted throughout late autumn.

An observation of the present study that was made possible by the sensor network was the appearance of large, short-term (diel) fluctuations in chlorophyll fluorescence at 0.5 m in the data obtained using the NAMOS buoys. Such rapid changes in plankton communities as a consequence of diel changes in physical forcing factors have been reported previously (Talling 2004; Pannard et al. 2007; Staehr and Sand-Jensen 2007). Changes in fluorescence at the stationary sensors at 0.5 m occasionally exceeded an order of magnitude when sensed by the NAMOS buoys, and often lasted only on the order of minutes to a few hours. These transient fluctuations correlated strongly with changes in thermal stratification as surmised from changes in the depth-resolved temperature data (Figs. 8, 9). Reversal of wind direction in early evening, and the dramatically lower air temperature associated with this pattern of cold air drainage, presumably led to cooling of surface waters in the lake and subsequent convective (and possibly advective) and wind-driven mixing. The connectivity between these physical forcing factors in reshaping the phytoplankton distribution of lakes is well-known (Serra et al. 2007).

The timing, magnitude and direction of these rapid changes in chlorophyll fluorescence at 0.5 m were not similar for all deployment periods (Fig. 8), and differences in timing appeared to be a consequence of differences in the dominant phytoplankton species present in the plankton and the corresponding ecologies of these phytoplankton taxa (Fig. 2). In situ fluorescence at 0.5 m increased substantially in May only during the period when water from 1.15 m was mixed up to the depth of the fluorometer (Fig. 8A,D). Consistent with this pattern, chlorophyll extracted from discrete samples showed maximal daytime values at subsurface depths in the lake during May 2006 (Fig. 3B). This subsurface maximum in chlorophyll appar-

ently resulted in a peak in fluorescence at 0.5 m at the time of day when mixing of the lake water was deepest (~08:00 h) and persisted only for the period when the water was isothermal down to 1.15 m (~4 h). Chlorophyll fluorescence decreased rapidly with the onset of water stratification in May, and was relatively low throughout the period of the day with strong thermal stratification in surface waters (Fig. 8A,D).

Diel increases in fluorescence were also recorded by the sensors at 0.5 m in June, but persisted throughout the entire 12-h period of surface-water cooling and mixing (Fig. 8B,E). Chlorophyll fluorescence was relatively low (and variable) throughout the period of thermal stratification (Fig. 8B,E). This pattern was also consistent with a scenario in which cooling and mixing of the water during the night resulted in the upward mixing of a subsurface phytoplankton population.

In contrast, the timing of the large peaks in fluorescence observed by the sensors at 0.5 m during the August deployment (Figs. 8C,F; 9) implicated the downward mixing of phytoplankton that was aggregated near the surface of the lake in late afternoon (Fig. 5A). The most dramatic increase in chlorophyll fluorescence during this period occurred when the water column became isothermal to 0.65 m (~2 h after the period of cold air drainage began; Fig. 8C,F). This pattern was consistently observed on successive days at a single NAMOS buoy, and across multiple buoy platforms (Figs. 8C,F; 9C,D). These striking increases in fluorescence at 0.5 m during August were most likely a consequence of the cyanobacterial-dominated assemblage that accumulated near the surface of the lake during the afternoon being mixed down into the water column (Fig. 9B,C). Values for extracted chlorophyll obtained from surface samples at that time exceeded 120 μg L^{-1} (Fig. 3B). Further mixing of the water column after 20:00 h decreased the fluorescence signal at 0.5 m, presumably due to continued dilution of the cyanobacterial assemblage deeper into the water column. Minor peaks in chlorophyll were also apparent at 0.5 m at the time when the water column became isothermal down to a depth of 2.65 m (Figs. 8C,F; 9C,D). These minor peaks are consistent with a subsurface population of phytoplankton being mixed into the upper water column during those times. A subsurface peak in chlorophyll was observed in the extracted chlorophyll samples from 3 m on that date (Fig. 3B).

The accumulation of colonial cyanobacteria at the surface of the lake during the afternoon in August was clearly evident in the vertical profiles of chlorophyll fluorescence observed using the NIMS RD sensor platform (Fig. 5A). Such accumulations are well-documented in cyanobacterial-dominated lakes, and represent the interplay between cyanobacterial behavior (i.e., positive buoyancy) and physical forcing factors (Hutchinson and Webster 1994; Webster and Hutchinson 1994). The pattern of accumulation in Lake Fulmor was consistent with that theory, although wind speed was quite low relative to wind speeds required to induce physical mixing of these near-surface accumulations. It is probable that cold air drainage taking place at night at the study site resulted in significant

cooling of surface waters, reduced density stratification in surface waters, and promoted convective (and perhaps advective) mixing of the water column. Additionally, diel changes in cyanobacterial physiology may have caused changes in buoyancy, which contributed to the rapid vertical dispersal of the cyanobacterial accumulations. Physiological changes that alter the buoyancy of cyanobacteria have been documented for marine and freshwater colonial forms (Reynolds et al. 1987; Villareal and Carpenter 2003).

It is probable that active vertical migration of the subdominant, non-cyanobacterial, motile species of phytoplankton may have contributed secondarily to the diel pattern of chlorophyll observed at the 0.5-m fluorometer during the three study periods. Diel differences in phytoplankton vertical distributions were observed in the NIMS RD transect data from this study during the August deployment (Fig. 5A,B). However, the results described above are consistent with water stratification/destratification as the primary factor affecting the observed diel cycle of in situ fluorescence at 0.5 m. Moreover, the rapid increases and decreases in fluorescence at 0.5 m were consistent with changes in the vertical position of the phytoplankton either as a result of mixing or diel vertical migration, rather than increases or decreases in overall phytoplankton abundance as a consequence of growth and/or grazing losses. The latter would be expected to occur much more slowly.

The development of a seasonal, relatively stable anoxic layer in this small, shallow lake was observed over the course of this study using sensing at relatively coarse temporal and spatial scale. This layer was a relatively constant feature below 3 m, and may have been a strong selective pressure in determining the composition of the phytoplankton assemblage. Salonen and Rosenberg (2000) noted the dominance of the raphidophyte *Gonyostomum semen* in a small, shallow (6 m) lake in southern Finland. The authors speculated that the strong diel vertical migration pattern demonstrated by the raphidophyte constituted a competitive advantage over other phytoplankton taxa because the population migrated into the anoxic zone during the night where nutrient concentrations were higher and presumably grazing by zooplankton was lower. These larger scale features and characteristics of the water column constitute important aspect of the lake's ecology, and are readily observed using scarce, low-frequency sampling approaches.

Nevertheless, these large spatial and long temporal scales often miss important dynamics that ultimately control the success or failure of microbial assemblages. For example, measurements of in situ fluorescence at a single depth can be misleading with respect to phytoplankton population dynamics. As observed in the present study, phytoplankton biomass (as indicated by situ fluorometry) can change dramatically and rapidly as a consequence of diel mixing events, which can transport phytoplankton populations from above or below the sensor to the depth at which the sensor is deployed (Figs. 8, 9). Thus, short-term fluctuations in chlorophyll fluorescence, which might otherwise be attributed to rapid changes in population abundance due to growth or removal (e.g., grazing, sinking), may in actuality represent a redistribution of a relatively stable population of phytoplankton.

The ordered, temporal redistribution of phytoplankton in the lake as a consequence of diel vertical mixing has implications for the photophysiology of the phytoplankton cells and potentially the availability of growth-limiting nutrients. The rapid changes observed in chlorophyll fluorescence at 0.5 m in the present study imply that mixing occurred more rapidly than the majority of the phytoplankton could reacquire a specific depth stratum. It is unknown whether herbivorous protists or crustacean zooplankton were also mixed by this process or if those assemblages maintained a specific depth distribution. The answer could have important implications for phytoplankton trophodynamics. An awareness and characterization of these small-scale spatial and temporal distributions provide baseline data for generating hypotheses regarding these interactions, and rich contextual information for experimentally testing them.

Most direct experimental measurements of rate processes in aquatic ecosystems (e.g., rates of primary production or community respiration) rely on the containment of small volumes of water for making such measurements. Given the small-scale variability in plankton abundances observed in this study, the validity of the results yielded by these approaches may be called into question. The findings of the present investigation imply that studies employing 'containment-free' measurements of diel fluctuations in the products or reactants of these processes may provide an important independent confirmation of the rates obtained from the incubation of small volumes of water (Cole et al. 2000; Gelda and Effler 2002; Hanson et al. 2003). For example, the use of short-term changes in dissolved oxygen concentrations in the present study (*see* Results) provided an estimate of vertically integrated primary production in the water column of Lake Fulmor.

The small-scale chemical and biological features observed in Lake Fulmor during this study are not unique. Extensive research on thin layers of plankton in marine and estuarine ecosystems provides insight into the potential implications of these features (and their disruption) in planktonic ecosystems (Donaghay et al. 1992; Alldredge et al. 2002; Rines et al. 2002; Cowles 2003; Mcmanus et al. 2003, 2005). These studies have revealed extensive and persistent thin layers of phytoplankton, the physical proximity of these assemblages to important chemical gradients (e.g., the nutricline), the importance of these layers for zooplankton feeding, and the accumulation of particulate organic material at these features. The findings of these studies document the widespread existence and ecological significance of small-scale spatial structure of planktonic ecosystems, and the importance of characterizing and understanding their occurrence and dynamics.

The NAMOS and NIMS RD developed and applied in this study provided unique insights into the small-scale environmental forcing factors for phytoplankton dynamics in Lake Fulmor. New designs and iterative improvements in these platforms continue to expand the capabilities of these sensor platforms for supporting studies of plankton

distributions and dynamics. The second-generation robotic boat described herein is equipped with a small on-board winch to enable vertical profiling of a suite of pertinent environmental parameters. This improvement will enable more detailed information on water column structure. Improvements in boat navigation algorithms allow autonomous navigation to be linked to and controlled by environmental parameters sensed by the stationary nodes. Iterative improvements of the robotic boat and the NIMS RD allow the collection of near-surface water (using the robotic boat) or water at specified depths (using the NIMS RD). Further improvements in the prevention of biofouling and assessment of calibration will be required for deployments longer than a few days. These capabilities, especially when combined with new and future environmental sensors for the detection, identification, and quantification of specific microbial species and relevant chemical constituents (Malkiel et al. 1999; Franks and Jaffe 2001; Egli et al. 2004; ACT 2005; also *see* http://www.act-us.info/workshops_reports.php), will provide powerful investigative tools for examining the distributions and activities of planktonic organisms.

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