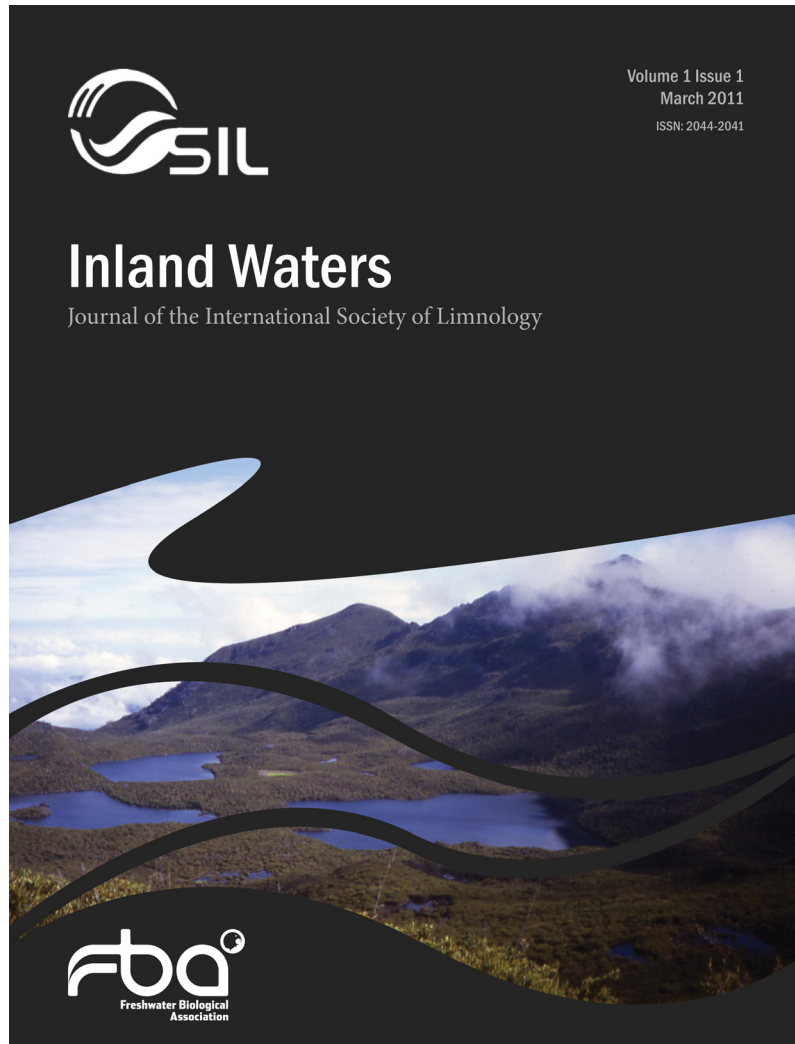


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A Global Lake Ecological Observatory Network (GLEON) for synthesising high-frequency sensor data for validation of deterministic ecological models

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Abstract

A Global Lake Ecological Observatory Network (GLEON; www.gleon.org) has formed to provide a coordinated response to the need for scientific understanding of lake processes, utilising technological advances available from autonomous sensors. The organisation embraces a grassroots approach to engage researchers from varying disciplines, sites spanning geographic and ecological gradients, and novel sensor and cyberinfrastructure to synthesise high-frequency lake data at scales ranging from local to global. The high-frequency data provide a platform to rigorously validate process-based ecological models because model simulation time steps are better aligned with sensor measurements than with lower-frequency, manual samples. Two case studies from Trout Bog, Wisconsin, USA, and Lake Rotoehu, North Island, New Zealand, are presented to demonstrate that in the past, ecological model outputs (e.g., temperature, chlorophyll) have been relatively poorly validated based on a limited number of directly comparable measurements, both in time and space. The case studies demonstrate some of the difficulties of mapping sensor measurements directly to model state variable outputs as well as the opportunities to use deviations between sensor measurements and model simulations to better

inform process understanding. Well-validated ecological models provide a mechanism to extrapolate high-frequency sensor data in space and time, thereby potentially creating a fully 3-dimensional simulation of key variables of interest.

Key words: DYRESM-CAEDYM, ecological modelling, GLEON, grassroots network, lake metabolism, network science, sensors

Introduction

Major anthropogenic stressors are confronting many lake ecosystems across the globe, including altered hydrology, invasions of exotic species, eutrophication, pollution, unsustainable withdrawal, and climate change (Vitousek et al. 1997, Millennium Ecosystem Assessment 2005, Carpenter et al. 2011). Lake ecosystems have already been highly altered as a result of these human-accelerated global changes, and future global change scenarios indicate that some aquatic ecosystems will be even more severely impacted (Mooney 2010, Carpenter et al. 2011). Managing these issues relies on a holistic understanding of the complex processes that govern lake dynamics. Conventional scientific approaches (e.g., reductionism), which have typically confined these issues to studies by disparate disciplinary groups and at single sites, are not well suited to deal with such complex and interdependent processes that are inherent properties of natural ecosystems (e.g., Rigler and Peters 1994).

Advances in sensor technology provide the opportunity to monitor many key ecological variables at temporal scales not possible with conventional sampling techniques. For example, our understanding of lake hydrodynamics (Wüest and Lorke 2003, Klug et al. 2012), metabolism (Van de Bogert et al. 2007, Staehr et al. 2010), effects of episodic events (Jones et al. 2008, Shade et al. 2009, Jennings et al. 2012), and air–water gas transfers (Read et al. 2012) has been strongly driven by the capacity of sensor networks to provide high-frequency data. In contrast, infrequent manual measurements are often unsuitable for detecting rapid changes in variables such as dissolved oxygen and chlorophyll that are a central focus of limnological studies (e.g., Banas et al. 2005).

A global community of ecologists, engineers, computer scientists, and information technologists is studying how anthropogenic stressors affect lake ecosystems through the Global Lake Ecological Observatory Network (GLEON; www.gleon.org; Hanson 2007, Weathers et al. 2013). One important objective of the network is to coordinate local sensor measurements on the global scale and to advance understanding of ecological processes in lakes. The wealth of data arising from this network offers new opportunities to improve ecological modelling methods (Beck et al. 2009, Trolle et al. 2011a, Bennett et al. 2012).

Our objective was 2-fold. First, we demonstrated the

application of GLEON high-frequency data to test the predictive capabilities of a deterministic model (i.e., a dynamic model where state variables are determined by parameters in the model and values from the previous time step). Second, we compared output of different time scales from the model with automated and manual methods of data collection. Our focus was on a deterministic model with widespread application to lake ecosystems irrespective of geographical position, which allows inclusion of process information without “reinventing the wheel” (compare with Mooij et al. 2010). While our focus here is on the utility of GLEON data for modelling applications, readers should refer to Hanson (2007) and Weathers et al. (2013) to learn more on the history and background of GLEON.

Methods

As of May 2014, GLEON consisted of 82 lakes in 34 countries, with 410 members from 40 countries. The larger GLEON network represents 3 interrelated networks of people, data, and lakes (Weathers et al. 2013). Here, we focus on the data. Examples of different lake sensor platforms (Fig. 1) illustrate the grassroots nature of GLEON buoys in which a variety of sensors, deployment settings, and monitoring frequencies are adopted according to the data requirements of the local GLEON site or the availability of funding. Data are often collated across sites by subsampling the high-frequency measurements to adopt a standard time scale for comparative lake analyses or alignment with model output frequency (e.g., Read et al. 2011, Klug et al. 2012, Solomon et al. 2013). While the selected examples of GLEON lake sensor platforms (Fig. 1) range in latitude from 38.1°S (Lake Rotorua, New Zealand) to 59.8°N (Lake Erken, Sweden), GLEON has other platforms in both Antarctica and the Arctic and in all continents except Africa. GLEON platforms thus span a wide range of climate regimes as well as lake sizes and morphologies (Fig. 2).

DYRESM-CAEDYM is a 1-dimensional (vertically resolved) water quality model developed by and available from the Centre for Water Research at The University of Western Australia. It is a coupled hydrodynamic (DYRESM) and ecological model (CAEDYM) that links vertical transport and distributions of temperature, salinity, and density with fluxes of nutrients, dissolved oxygen, and

ecological state variables (e.g., phytoplankton biomass) at hourly time scales (Hamilton and Schladow 1997, Bruce et al. 2006, Hipsey et al. 2007). Input data are either fixed (in the case of hypsography) biogeochemical rate constants and an initial water column profile of the state variables to commence a simulation, or dynamic (in the case of meteorological variables such as radiative, conductive and convective heat transfers, rainfall, and wind speed) inflows (discharge and composition of state variables) and outflows (discharge).

In this study, DYRESM-CAEDYM was applied to 2 lakes: dimictic Trout Bog, Wisconsin, USA (latitude 46.0°N, area 0.056 km², maximum depth 7.9 m, oligotrophic) and monomictic Lake Rotoehu, North Island, New Zealand (latitude 38.0°S, area 7.9 km², maximum depth 13.5 m, eutrophic). We chose these 2 lakes on opposing ends of gradients of mixing, latitude, trophic state, and surface area to highlight the wide range of lakes for which the DYRESM-CAEDYM model is applicable. Model input data for Trout Bog and measurements at a central lake station for comparison with simulation output, including details of monitoring instruments and methods, were available from the North Temperate Lakes Long Term Ecological Research program (www.lternet.edu/sites/ntl/data) and a sensor data repository (www.lter.limnology.wisc.edu). Model input data for Lake Rotoehu have previously been described by Trolle et al. (2011b) and include solar radiation data obtained from Rotorua Airport Meteorological Station, 20 km west of Lake Rotoehu. High-frequency chlorophyll *a* and phycocyanin data were collected at Lake Rotoehu with a Trios microFlu (Germany) sensor deployed at 0.2 m depth from a platform at the central monitoring station used by Trolle et al. (2011b).



Fig. 1. Representative lake buoy deployments in (A) Lake Rotorua, New Zealand; (B) Lake Erken, Sweden; (C) Trout Bog, Wisconsin, USA; and (D) Yuan-Yang Lake, Taiwan.

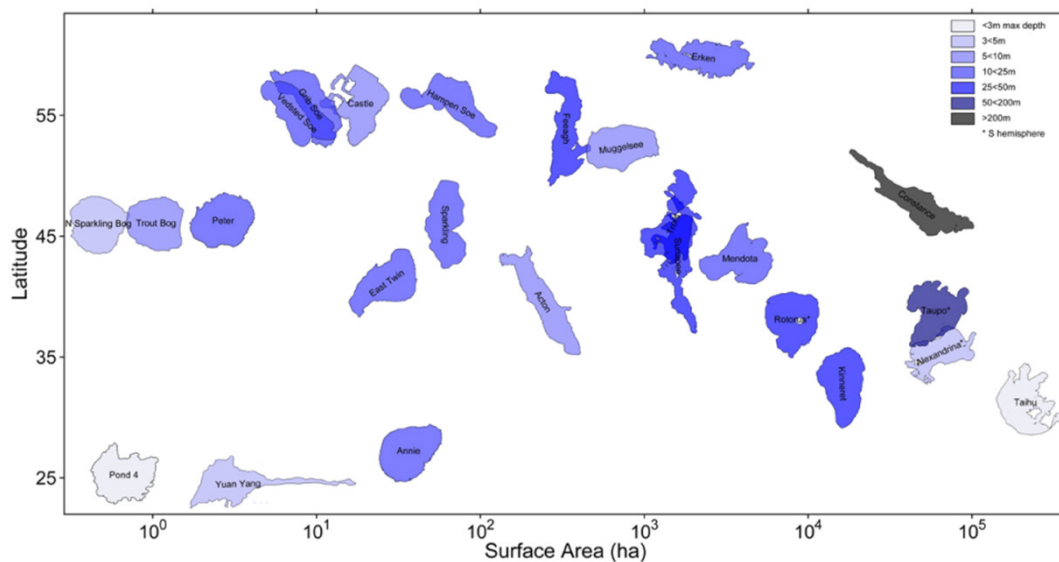


Fig. 2. Surface area, shape, depth, and absolute latitude for 25 of the instrumented lakes in the GLEON network. Size and location of each lake correspond to the centre of area of each lake shape. Southern hemisphere lakes are marked with an asterisk.

Results

A late-summer (northern hemisphere) cooling phase (23 Aug to 1 Nov 2006) leading to complete water column mixing was chosen to compare model simulation outputs of water temperature in Trout Bog with measurements at fixed depths taken both manually on a fortnightly resolution and from sensors subsampled to 1 h intervals. The pronounced vertical gradients of water temperature in Trout Bog make this lake particularly suitable for comparisons of measured data against temperature output from simulations using DYRESM-CAEDYM. The frequency of manual observations is sparse compared with sensor data and model output and provides limited opportunity for a process-based interpretation of the physical drivers of temperature changes.

Small hour-to-hour variations in observed sensor temperature, driven by minute internal waves, were not captured with the deterministic 1-dimensional model, although model forcing data were derived from hourly meteorological sensor measurements on the lake buoy (Fig. 3). The major point of difference between model simulations and observations was the apparent step-like entrainment process as the surface mixed layer (SML) cooled and deepened to entrain deeper water layers in the model, which contrasted with sensor observations of a more progressive warming of deeper waters as they were entrained into the SML. For the case of model output temperature at a depth of 3 m, this entrainment into the SML occurred ~23 days earlier than was indicated by the temperature sensor at this depth. Nevertheless, the large diurnal changes in water temperature in the SML during

the period when the thermocline deepened from an initial depth of 2 m until turnover on 22 October were mostly well captured in the model simulations.

Sensor output is shown at hourly intervals for chlorophyll fluorescence and phycocyanin at a depth of 0.2 m in Lake Rotoehu during late autumn (14 May) to mid-winter (18 Jul) of 2011 (Fig. 4). These data are presented as relative chlorophyll (RFU) and phycocyanin units (RPU) and have not been corrected to equivalent concentrations of chlorophyll *a* or biomass of phytoplankton or cyanobacteria communities, respectively. Both phycocyanin and chlorophyll fluorescence are highly variable on diurnal time scales. These sensor data were compared with DYRESM-CAEDYM chlorophyll output representing the 2 groups of phytoplankton: cyanobacteria and the remaining phytoplankton biomass (Fig. 4). Temporary increases in phycocyanin corresponding to short-term stratification events (data not shown) were generally captured well with the model simulations of cyanobacteria chlorophyll using phycocyanin units normalised to the initial (14 May) simulated cyanobacteria chlorophyll. The observed pattern of decrease in phycocyanin during the study period was also reproduced in the simulations, including the consistently low values later in winter.

The observed chlorophyll fluorescence at 0.2 m depth showed a strong diurnal fluctuation as well as 2 small peaks over the study period, one near the start and the other at the end of the 3-month period. The model simulations of phytoplankton chlorophyll (excluding the contribution by cyanobacteria) did not show the regular diurnal fluctuations in the observed chlorophyll fluores-

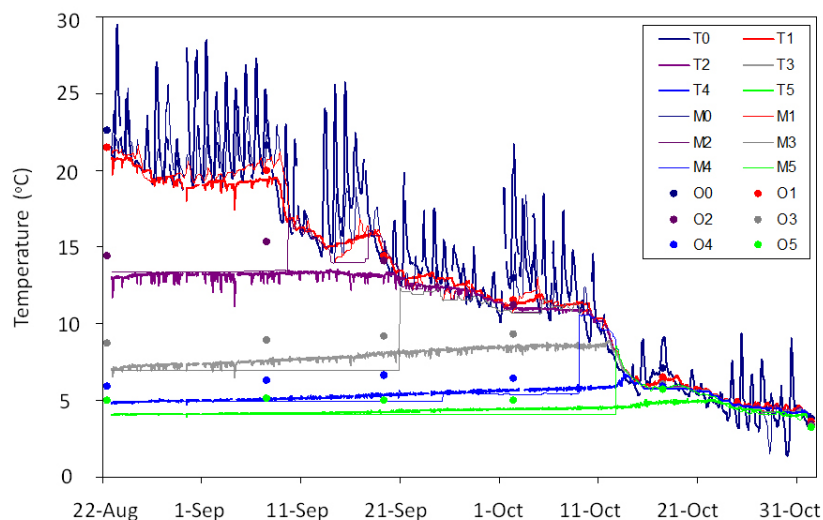


Fig. 3. Temperature sensor readings for Trout Bog at hourly intervals at nominal 1 m depths from the water surface (T0) to 5 m (T5), DYRESM-CAEDYM model output at identical depths and times (M0 to M5), and manual biweekly measurements for Trout Bog from the water surface (O0) to 5 m (O5), 22 August to 1 November 2006. Offset of measured temperatures (T vs. O) is due to thermistor position and model output slightly deeper than the manual measurements.

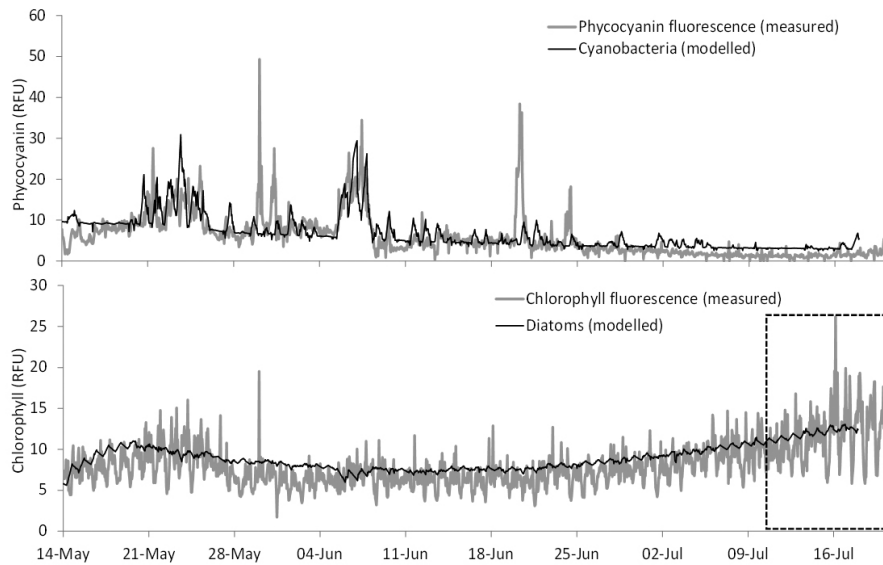


Fig. 4. Phycocyanin (upper panel) and chlorophyll fluorescence (lower panel) measurements (relative units; RPU and RFU, respectively) from 0.2 m depth at 1 h time intervals from 14 May to 20 July 2011 and model simulations of cyanobacteria and remaining phytoplankton biomass for Lake Rotoehu. Sensor data have been normalized to modelled data at 14 May. The box with a dashed line (lower panel, right) has an exploded view in Fig. 5.

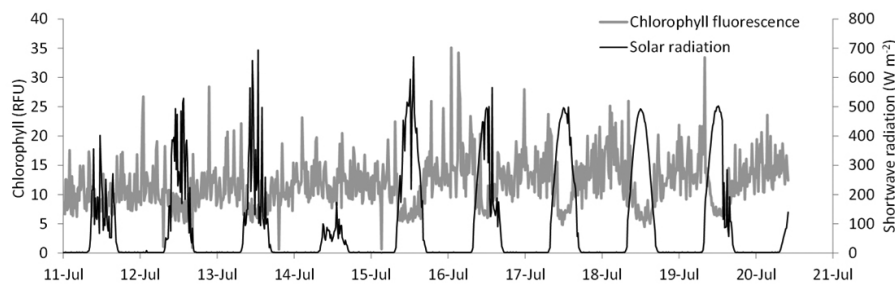


Fig. 5. Chlorophyll fluorescence (relative fluorescence units; RFU) from 0.2 m depth at 1 h time intervals (exploded view from Fig. 4) and shortwave radiation for Lake Rotoehu from 11 to 20 July 2011.

cence but reproduced the trend of 2 peaks during the study period. An expanded view of chlorophyll fluorescence for the period 11 July to 20 July 2011 (Fig. 4 and 5) includes solar radiation to demonstrate the regularity of the reduced chlorophyll fluorescence on days with clear sky indicated by a sinusoidal distribution of radiation over the day.

Discussion

Rarely do the temporal scales of observations and models intersect, but when they do, there are rich opportunities to drive forward hypothesis testing and process representation of models, enhancing dialogue among modelers, engineers, and aquatic scientists. Arguably, not since Volleweider (1968), when limnological dynamics were typically captured by snapshot sampling on a monthly scale, has there been such an opportunity to align observations and model predictions. Today's autonomous sensors

provide a new domain of high-frequency data that will challenge our capacity to adequately simulate some aspects of ecosystem behavior. The resulting improvements in model process representation and performance provide opportunities to move beyond observation and synthesis of data and into a domain of prediction, a fundamental goal for ecologists in a rapidly changing environment (Rigler and Peters 1995). Our chosen case studies highlight some of the challenges relating to both the alignment between sensor readings and model state variable outputs (e.g., chlorophyll fluorescence measurements vs. phytoplankton chlorophyll simulations in Lake Rotoehu) and process representation (e.g., the mixing dynamics of the deep waters in Trout Bog).

The issue of alignment of measured variables with model state variable outputs has been highlighted by Flynn (2005) but is expected to become more acute for many optical sensors that provide only indirect measure-

ments of modelled variables of interest (i.e., model state variables). Kara et al. (2012), for example, used wavelet analysis to show that time-scale-specific variations of chlorophyll fluorescence were not reproduced in simulations of chlorophyll associated with different functional groups of phytoplankton in Lake Mendota (WI, USA). While they highlighted apparent shortcomings in the process representation in DYRESM-CAEDYM, they also pointed to the difficulties inherent in the use of high-frequency indirect measures of phytoplankton biomass (i.e., *in vivo* chlorophyll fluorescence) for which only low-frequency validation data (i.e., biovolume measurements) were available. A further potential difficulty in the use of *in vivo* fluorescence to interpret phytoplankton biomass arises when there is nonphotochemical solar quenching from exposure of phytoplankton to excess light energy, resulting in a decrease in fluorescence quantum yield (Hamilton et al. 2010). Evidence of this effect can be seen clearly in the strong diurnal oscillations in fluorescence in Lake Rotoehu (Fig. 5) where the fluorescence signal is strongly depressed by the solar radiation on clear days. By contrast, the small but regular daily oscillations in simulated phytoplankton chlorophyll (Fig. 4B) point to a diurnal growth cycle regulated by light availability.

Another issue is the alignment of time scales of measurement of interdependent variables such as nutrients or zooplankton, which play a key role in determination of phytoplankton biomass at slightly longer time scales. Nutrient concentrations and zooplankton biomass are generally derived from analyses of grab samples taken manually at low frequency and often with limited spatial resolution. While optical and acoustic sensors show much promise in transposing conventional low-frequency grab samples toward high-frequency autonomous measurements (e.g., McDonagh et al. 2008), there remain concerns about their accuracy because low-level concentration measurements and their uptake have not been widespread compared with sensors that measure physical variables such as temperature (Rundel et al. 2009).

The ability of the DYRESM-CAEDYM model to reproduce variations in phycocyanin sensor measurements in Lake Rotoehu suggests that the model has captured the dominant processes influencing cyanobacterial concentrations over time scales of hours to several days. Vertical distributions of cyanobacteria are strongly influenced by both physical mixing events and buoyancy of cells, filaments, or colonies. We interpret that temporary stratification events allow buoyant cyanobacteria to migrate vertically toward the water surface, typically over durations >2–3 h (compare with Wallace et al. 2000). Because of the accuracy with which DYRESM-CAEDYM simulates water temperature ($r^2 > 0.97$; Trolle et al. 2011b) and, by implication, stratification and mixing

events, there is a close fit of simulated cyanobacterial biomass to the observed phycocyanin.

High-frequency temperature measurements in Trout Bog provided an opportunity to evaluate discrepancies in model fit at a process level, helping to identify some of the mechanisms that may be incompletely represented in the model formulation. Some of the high-frequency variations of deep-water sensors are likely contributed by propagation of internal waves and other disturbances occurring at frequencies higher than the model time step and output data resolution. Three-dimensional modelling could improve fine-scale representation of these high-frequency disturbances. The deep-water temperature variations were small, however, particularly at the location of the deepest (5 m) sensor. More attention could be paid to the discrepancy between the timing of entrainment of bottom waters into the deepening SML, however, which points to a more systematic issue, either with the model input data or with representation of the SML deepening process prior to water column turnover. Capturing these dynamics may be particularly important in resolving the duration for which, for example, bottom waters are anoxic, and accurate simulation is therefore critical to model applications where a climate change or nutrient loading scenario is generated by altering the data input files for the model.

Obtaining data at high temporal resolution has the potential to address a long-term problem for numerical modellers: inadequate resolution of boundary forcing or in-lake variables to support robust calibration and validation of “data-hungry” deterministic models. There are currently large disparities between measurement frequencies of variables used for model input and in-lake comparisons, however. Many “boundary” variables, such as air temperature and wind speed, and *in situ* variables, such as water temperature and dissolved oxygen, can be resolved autonomously at high frequency in comparison with commonly used manual sampling for chemistry or biological variables. Automated methods such as real-time polymerase chain reaction (PCR) to monitor changes in microbial populations or optical methods for chemical variables are advancing rapidly (e.g., Rasmussen et al. 2008, Shade et al. 2009), however, and could ultimately align biological and chemical variable monitoring frequencies with physical variables to better address key issues of changes in aquatic biodiversity or biogeochemical cycles. For 3-dimensional deterministic models, the requirements for spatial validation may still fall short of what is desired, and other monitoring techniques such as autonomous underwater vehicles or remote sensing may be valuable for ensuring robust spatial validation of these models (Wynne et al. 2011).

Ecologists are increasingly being challenged to model, predict, and forecast future ecosystem state and dynamics

at a variety of spatial and temporal scales (e.g., Biggs et al. 2009). Cause and effect relationships between environmental pressures and ecological responses are unlikely to be linear or intuitive and may exhibit indirect or lagged effects. They are often denoted by complex and interacting factors pertaining to multiple environmental stressors as well as system resilience, hysteresis, and existence of alternate ecological states (Carpenter 2003). Process-based models will be used increasingly to test our understanding of ecological processes and generate scenarios for how lake ecosystems will respond to a changing climate, land use, or an altered hydrological regime. There is also likely to be an increased level of scrutiny and interrogation of the process representation and accuracy of these models, similar to models used to predict future climate change, as they are increasingly integrated into mainstream management and economic considerations for freshwater and watershed protection. Thus, the use of high frequency is critical to advancing ecological modelling as well as to better resolve and understand fine-scale temporal dynamics in lake ecosystems.

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