Freshwater Biology

Freshwater Biology (2012) **57**, 589–601 doi:10.1111/j.1365-2427.2011.02729.x

Effects of weather-related episodic events in lakes: an analysis based on high-frequency data

ELEANOR JENNINGS*, STUART JONES†, LAURI ARVOLA‡, PETER A. STAEHR§, EVELYN GAISER¶, IAN D. JONES**, KATHLEEN C. WEATHERS††, GESA A. WEYHENMEYER‡‡, CHIH-YU CHIU§§ AND ELVIRA DE EYTO¶¶

**Centre for Freshwater Studies and Department of Applied Sciences, Dundalk Institute of Technology, Dundalk, Ireland*

†University of Notre Dame, Notre Dame, IN, U.S.A.

‡Lammi Biological Station, University of Helsinki, Helsinki, Finland

§Department of Marine Ecology, National Environmental Research Institute, University of Aarhus, Frederiksborgvej, Roskilde, Denmark

¶Department of Biological Sciences, Florida International University, Miami, FL, U.S.A.

***Centre for Ecology and Hydrology, Lancaster Environment Centre, Bailrigg, Lancaster, U.K.*

††Cary Institute of Ecosystem Studies, Millbrook, NY, U.S.A.

‡‡Department of Ecology and Genetics/Limnology, Uppsala University, Uppsala, Sweden

§§Biodiversity Research Center, Academia Sinica, Taipei, Taiwan

¶¶Marine Institute, Furnace, Newport Co. Mayo, Ireland

SUMMARY

1. Weather-related episodic events are typically unpredictable, and their duration is often short. Abiotic and biological responses are often missed in routine monitoring. These responses are, however, now of particular relevance given projected changes in extreme weather conditions.
2. We present data from high-frequency monitoring stations from lakes in Europe, North America and Asia that illustrate two classes of abiotic effects of weather events: (i) generally short-lived effects of storms on lake thermal structure and (ii) the more prolonged effects of high rainfall events on dissolved organic matter levels and water clarity. We further relate these abiotic effects to changes in dissolved oxygen or in chlorophyll *a* levels.
3. Three differing causes for weather-related decreases in surface dissolved oxygen levels were observed: (i) entrainment of anoxic water from depth, (ii) reduction in primary productivity and (iii) increased mineralisation of organic carbon delivered from the catchment.
4. The duration of in-lake effects tended to be longer for events driven by weather conditions with a longer return period, that is, conditions that were relatively more severe and less frequent at a site. While the susceptibility of lakes to change was related in part to the severity of the meteorological drivers, the impacts also depended on site-specific factors in some cases.
5. The availability of high-frequency data at these sites provided insight into the capacity of the lakes to absorb current and future pressures. Several of the changes we observed, including increases in carbon availability, decreases in photosynthetically active radiation and increased disturbance, have the capacity to shift lakes towards an increased degree of heterotrophy. The magnitude and direction of any such change will, however, also depend on the magnitude and direction of climate change for a given location and on lake and catchment characteristics.

Keywords: climate, episodic events, Global Lake Ecological Observatory Network, *in situ* sensors, lakes

Introduction

The effects of episodic events have been a recurring theme in aquatic research in recent decades (Junk, Bayley & Sparks, 1989; Reid & Ogden, 2006; Wantzen, Junk & Rothhaupt, 2008). In lakes, events are characterised by abrupt changes in physical, chemical and/or biological parameters that are distinct from previous background

Correspondence: Eleanor Jennings, Department of Applied Sciences, Dundalk Institute of Technology, Dundalk, Ireland. E-mail: eleanor.jennings@dkit.ie

© 2012 Blackwell Publishing Ltd

levels and are often driven by sudden changes in weather and in particular extremes in precipitation, wind or temperature. High wind speeds, for example, can cause a stratified lake to mix, resulting in a breakdown in stability and a concurrent increase in thermocline depth (Imberger, 1994). Mixing can, however, also be convectively driven: as surface waters cool, they become denser than the underlying water and induce convective stirring (MacIntyre, Eugster & Kling, 2001; MacIntyre, Romero & King, 2002; Eugster *et al.*, 2003). Intense precipitation may also result in physical disturbance of the water column (Yount, 1961; Jones & Elliott, 2007) and can be accompanied by a pulse in the export of dissolved and particulate substances to the lake (Weyhenmeyer, Willén & Sonesten, 2004; Arvola, Järvinen & Hakala, 2006). This potential for flood pulses to have an impact not only on rivers but also on recipient lake ecosystems is an aspect of weather–lake interactions that has often been ignored (Wantzen *et al.*, 2008). Flood events and mixing events may also co-occur during storms, compounding and amplifying the effects.

Biological responses to these episodic changes can be varied and complex and range from short-term, reversible changes to those that are more persistent. They can include changes in bacterial and phytoplankton community structure and productivity and resultant changes in lake metabolism. Cyanobacteria generally dominate in lakes during calm, warm conditions for example, while diatoms and green algae are dominant at higher turbulent diffusivity (Huisman *et al.*, 2004; Jöhnk *et al.*, 2007; Wilhelm & Adrian, 2008). Wash-out of the smallest fraction of plankton can also occur following high turbulence (Arvola *et al.*, 1996) or rainfall (Jones *et al.*, 2011). Relatively high levels of disturbance may sometimes result in only a short-lived biological response (Flöder & Sommer, 1999; Millie *et al.*, 2003; Paidere, Gruberts & Škute, 2007), possibly reflecting the tendency for maximum responses to occur at intermediate levels of disturbance (Connell, 1978). The biological impact of an episodic event may also be long-lived, particularly where concentrations of nutrients or coloured dissolved organic matter (CDOM) have increased. Primary production in Antarctic lakes, for example, was reduced during large flood events but increased in the following year owing to resulting higher availability of nutrients (Foreman, Wolf & Priscu, 2004). Decreased light availability caused by increased CDOM concentrations following floods can also shift lake metabolism from autotrophy to heterotrophy for short or sometimes prolonged periods (Cotner, Johengen & Biddanda, 2000; Drakare *et al.*, 2002; Lohrenz *et al.*, 2004). Other longer-term consequences of episodic events include reductions in water clarity (Bachmann, Hoyer & Canfield, 1999) and shifts to turbid, phytoplankton-dominated states (Hargeby, Blindow & Hansson, 2004; Scheffer & Jeppesen, 2007).

A greater insight into both short-term and long-term responses in lakes to abrupt changes in meteorological drivers is now of particular relevance given recent (Kunkel, Andsager & Easterling, 1999; Klein Tank & Können, 2003) and projected (Beniston *et al.*, 2007) changes in the severity and frequency of meteorological events. By definition, these events are typically of short duration and are therefore easily missed by routine monitoring programmes. Developments in technology and increases in the number and type of lakes with high-frequency monitoring stations, along with the human networks designed to analyse and synthesise high-frequency data (e.g. the Global Lake Ecological Observatory Network – GLEON), now allow exploration of both the meteorological drivers of episodic events and their limnological consequences.

Here, we analyse and synthesise the characteristics of episodic events using a combination of high- and moderate-frequency data from sites in Europe, the U.S.A. and Taiwan. Where data were collected at lower frequencies, high-frequency data can aid in interpretation by providing a record of conditions between sampling occasions. The focal events had either resulted in observed responses in lake biota (Jones *et al.*, 2008; Ojala *et al.*, 2011) or were from sites where a sensitivity to current or future climatic extremes has been noted (Gaiser *et al.*, 2009a and b; Jennings & Allott, 2006; Staehr & Sand-Jensen, 2006; Jones & Elliott, 2007; Naden *et al.*, 2010). Specifically, we aimed to quantify the meteorological conditions that drive episodic events, and the magnitude and duration of effects on abiotic conditions, including thermal structure, CDOM levels and light availability. In addition, we assess the relationship between these changes and in-lake biological responses as indicated by chlorophyll *a*, dissolved oxygen data and gross primary productivity and discuss the potential for longer-term effects on lake biota.

Methods

Study sites

For this study, we collated high-resolution data from seven lakes: Belham Tarn (north-west England), Frederiksborg Slotssø (Denmark), Lough Leane (southwest Ireland), Lough Feeagh (west Ireland), Yuan Yang Lake (north-central Taiwan), Lake Annie (south-central Florida, US) and Lake Pääjärvi (southern Finland) (Table 1). The lakes encompass a range of areas, from 3.6 ha (Yuan

Table 1 Location and characteristics for the seven case study lakes (mono = monomictic, di = dimictic, oligo = oligotrophic, meso = mesotrophic, eu = eutrophic)

Site	Lat	Long	Area (ha)	Max depth (m)	Mean depth (m)	Residence time (days)	Mixing regime	Trophic status	Colour
Yuan Yang Taiwan	24° 35′ N	121° 24′ E	3.6	4.5	1.7	30	Mono	Oligo	Coloured
Blelham U.K.	54° 21′ N	2° 59′ W	10	14.5	6.8	54	Mono	Eu	Clear
Slotssø Denmark	55° 56′ N	12° 17′ E	22	8	3.5	180	Mono	Eu	Clear
Annie U.S.A.	28° 68′ N	81° 54′ W	37	21	10.0	730	Mono	Oligo	Coloured
Feeagh Ireland	53° 56′ N	09° 34′ W	390	45	14.5	164	Mono	Oligo	Coloured
Pääjärvi Finland	61° 07′ N	25° 13′ E	1340	87	14.4	1205	Di	Oligo-meso	Coloured
Leane Ireland	52° 05′ N	9° 36′ W	1990	64	13.1	204	Mono	Meso-eu	Clear

Yang) to 1990 ha (Leane), and mean depths, from 1.7 (Yuan Yang) to 14.5 m (Feeagh). They also range in trophic status from oligotrophic to eutrophic, based on chlorophyll *a* concentrations, and include both clear-water and coloured lakes (Table 1).

Three of the lakes, Blelham, Leane and Slotssø, are clear-water lakes that are mesotrophic or eutrophic. Belham and Slotssø are persistently eutrophic, with a long stratified period from spring to late autumn and a hypolimnion that is highly anoxic during the summer. Slotssø is fed by surface streams that deliver high concentrations of nutrients causing large summer algal blooms of up to 210 mg chlorophyll *a* m^{-3} (Staehr & Sand-Jensen, 2007). Leane also has high nutrient loading (Jennings & Allott, 2006) but is monomictic and is situated in a coastal region with a cool, oceanic climate: assessment of historical data has indicated that algal blooms only occur during times of unusually calm and warm water (H. Twomey, unpubl. data). The other four lakes are coloured by humic substances. Feeagh is also monomictic and has the same oceanic climate as Leane but is coloured (mean annual colour *c.* 90–100 mg L^{-1} PtCo) and oligotrophic. Pääjärvi is a deep, dimictic lake that is also oligotrophic and has high colour levels (*c.* 90 mg L^{-1} PtCo) that drive steep thermal stratification during the short stratified period (June–August). Yuan Yang and Annie are both subtropical and monomictic. Yuan Yang is slightly coloured from input from its forested catchment that reduces light penetration, limiting algal production and increasing thermal stability. Annie is a groundwater-fed lake but is also susceptible to pulses of CDOM from the catchment, causing transparency to vary as much as 8 m within a decade (Gaiser *et al.*, 2009a), depending on long-term rainfall cycles (Gaiser *et al.*, 2009b).

Instrumentation and data

An automatic monitoring buoy stationed at the deep point of Blelham measured *in situ* lake temperatures at eight depths (Platinum Resistance Thermometer; Labfacility Ltd, Bognor Regis, U.K.), wind speed (Vector instruments A100L2-WR, Rhyl, U.K.) and other meteorological variables every 4 min; these data were combined for hourly averages. Monitoring data for an array of additional limnological variables, including dissolved oxygen (DO) concentration (WTW oxi 340i probe; WTW, Weilheim, Germany), were taken every metre at fortnightly intervals. High-frequency meteorological data were measured every 5 min at a similar monitoring buoy situated at the deepest point in Leane, using the same instrumentation as used at Blelham. Water temperature profile data were measured every 2 min at 12 depths at the same point. The lake was also sampled at six sites on a weekly or fortnightly basis for a range of parameters, including dissolved oxygen concentration and chlorophyll *a* (American Public Health Association, 1992). The instrumented platform on Feeagh was also situated at the deepest point. Measured parameters included wind speed and water temperature at 12 depths using the same instruments as used on Blelham, and surface dissolved oxygen concentrations (Hydrolab/OTT hydrometry, Chesterfield, U.K.). CDOM fluorescence (Seapoint, Exeter, U.S.A.), a proxy for dissolved organic carbon (DOC) concentrations, was measured every 2 min on the Glenamong River, one of the two main inflows that drains 18 km^2 of the 38-km^2 catchment. These data were converted to mg DOC L^{-1} based on a relationship with DOC measured on a Shimadzu TOC 5000A analyser (Shimadzu Scientific Instruments, Columbia, MD, U.S.A.) ($r^2 = 0.85$; $P < 0.0001$, $n = 50$). Stream flow data (OTT hydrometry) were also available for the site, while rainfall data were available from a meteorological station located on the shores of the lake. Wind speed, temperature and irradiance in air and oxygen, temperature and photosynthetically active radiation (PAR) were measured continuously at different depths in the water at Slotssø using sensors mounted on a floating raft in the centre of the lake and averaged every 10 min (Staehr & Sand-Jensen, 2007). Weekly values of surface water chlorophyll *a* concentrations were also available.

Temperature profiles, wind speed and dissolved oxygen were measured every 10 min by an instrumented buoy installed at Yuan Yang. The buoy was equipped with a thermistor chain with sensors at seven depths (Apprise Technologies, Duluth, MN, U.S.A.), a Greenspan DO100 dissolved oxygen sensor at the surface (TYCO Integrated Systems, Cambridge, U.K.) and an RM Young wind vane and anemometer to measure wind speed and direction (Campbell Scientific, Logan, VA, U.S.A.). Additional meteorological data were collected at a nearby station (around 500 m from the buoy) including air temperature and rainfall (Campbell Scientific). An automatic monitoring buoy stationed at the deepest point of Annie, installed in February 2008, measured water temperature profiles and surface concentrations of dissolved oxygen at 15-min intervals. A meteorological station located within 2.5 km of the lake includes a tipping bucket rain gauge and 10-m anemometer, recording the total rainfall received and average 10-s wind speed every 15 min. On Pääjärvi, an automatic monitoring buoy stationed at the deep point of the lake measured *in situ* lake temperature profiles and meteorological variables, including net irradiance in air and PAR at 1 m water depth. The instrumentation was similar to that on Leane, Feeagh and Blelham. The measurements were taken every 10–30 min. Additional monitoring data for an array of limnological variables, including DOC concentrations, were collected from different depths of the water column at three to four weekly intervals. Inflowing river discharges were measured on a daily basis and DOC on a weekly basis. Precipitation was measured at the nearby meteorological station belonging to the Finnish Meteorological Institute.

Wind speeds were scaled to a 10-m reference height using the formulation of Amorocho & DeVries (1980). Depth of thermal stratification was analysed with an empirical curve-fitting equation (van Genuchten, modified by Rimmer *et al.*, 2005) for the measured temperature profiles:

$$T(z) = T_h + (T_e - T_h)\left(\frac{1}{1 + (\alpha \cdot z)^n}\right)^{\left(1-\frac{1}{n}\right)} \quad (1)$$

where T (°C) is temperature at depth z (m), T_e and T_h (°C) are temperatures at the surface and the lake bottom, respectively, α (m^{-1}) is a curve-fitting parameter that determines the depth of thermal stratification and n (dimensionless) is a curve-fitting parameter that controls the steepness of the temperature gradient in the metalimnion. T_e and T_h were defined as measured temperatures at the surface and bottom, respectively, and α and n were fitted to each temperature profile.

The thermocline depth (Z_{mix}) was defined as the depth with the maximal temperature gradient (Hutchinson, 1975) and was calculated from eqn 1 as the plane where $d^2T/dz^2 = 0$:

$$Z_{mix} = \alpha^{-1}\left(1 - \frac{1}{n}\right)^{-1/n} \quad (2)$$

The empirical curve-fitting equation only applies to temperature profiles with thermal stratification. If surface water temperature was colder than 4 °C ($T_e < 4$ °C) or colder than the bottom temperature ($T_e < T_h$), the empirical eqn (1) does not hold, and mixing depth was automatically set to maximal lake depth.

The stability of thermal stratification at the calculated thermocline depth was evaluated with the Brunt–Väisälä (BV) buoyancy frequency (N, s^{-1}):

$$N = \left(-\frac{g}{\rho_o}\frac{\delta\rho}{\delta z}\right)^{1/2} \quad (3)$$

where g is gravitational acceleration (9.82 m s^{-2}), ρ_o is mean density of the water column (g cm^{-3}), $\delta\rho$ is change in water density (g cm^{-3}) over depth and δz is defined as the 0.5 m extension above as well as below the mixing depth (Gill, 1982). Water density (ρ, g cm^{-3}) was calculated from temperature (T, °C) according to Kalff (2002):

$$\rho = 1 - 6.63 \cdot 10^{-6}(T - 4)^2 \quad (4)$$

In Slotssø, weekly sampling of chlorophyll *a* (Chl *a*) in the epilimnion and vertical light profiles provided a highly significant linear model of Chl *a* concentration (Chl *a*, μg L^{-1}) as a function of light attenuation (K_D, (m^{-1})): Chl *a* = 0.297 K_D + 0.556 ($r^2 = 0.98$, $P < 0.001$). Applying this model to daily estimates of light attenuation (see Staehr & Sand-Jensen, 2007) yielded daily estimates of Chl *a*. Oxygen concentrations recorded every 10 min in Slotssø were used to calculate daily rates of gross primary production (GPP) according to Staehr *et al.* (2010).

Relative changes in BV buoyancy frequency, thermocline depth and DO levels were calculated as the number of standard deviations from the mean change. The return period (RP) for precipitation and wind speed was calculated as

$$\mathrm{RP} = n - 1/m \tag{5}$$

where n is the rank of the event and m is number of years in the record (Wilson, 1990). Where the rank of an event was <1, a within-season return time was calculated and expressed as a fraction of the number of days in that season. In that case, n is the rank in days for the season in which event occurred and m is days in that season: for example, for June, July, and August, m = 92.

Results

A total of 13 weather-related episodic events occurred in the seven lakes during the time periods examined (Table 2). These included single events in Blelham (U.K.), Annie (U.S.A.) and Feeagh (Ireland), two events each in Slotssø (Denmark), Pääjärvi (Finland) and Leane (Ireland), and four events in Yuan Yang (Taiwan). All occurred between June and October. The drivers of the episodic events were either increases in wind speed, increases in precipitation, or a combination of both (Table 2). With the exception of one of the four events at Yuan Yang, all meteorological conditions were greater than two standard deviations from the seasonal mean (Table 2). The impacts of these extremes in weather conditions manifested themselves as changes in lake thermal structure and stability, changes in DOC loading and underwater PAR levels or changes in DO concentration and primary productivity.

Effects on lake thermal structure and stability

Mixing resulted in changes in lake water temperature profiles (Fig. 1a–d) and water column stability (Fig. 2e–h) following all events, with the exception of Pääjärvi (not shown), the deepest lake, where the two high rainfall events in the summer 2004 had no impact on stratification. A mixing event in Blelham in early September 2006 was driven by winds of about 4 m s^{-1} (Fig. 1a,c; Table 2). In contrast, a series of four mixing events in Yuan Yang in the summer of 2005 were principally related to high precipitation (daily precipitation of 103–443 mm day^{-1}) during tropical storms (Fig. 1b,d;

Table 2 Characteristics of the events including maximum mean daily wind speed (m s^{-1}), maximum daily precipitation (PPT) (mm day^{-1}), number of standard deviations from the seasonal mean for the main meteorological driver, meteorological driver return period (years), pre-event and decrease in Brunt–Väisälä (BV) buoyancy frequency (s^{-1}), recovery time (days) for BV buoyancy frequency and underwater photosynthetically active radiation (PAR) (na = not applicable; event occurred at end of period of stratification)

Site	Date	Event wind speed (m s^{-1})	Event PPT (mm day^{-1})	Main event driver	Driver (no. standard deviation from mean)	Driver return period (years)	Pre-event BV (s^{-1})	Decrease BV (s^{-1})	BV recovery time (days)	PAR recovery time (days)
Yuan Y.	18/7/05	4.0	442.5	PPT	5	1.0	0.088	0.065	8	
	5/8/05	3.7	354.5	PPT	4	0.5	0.087	0.069	5	
	12/8/05	3.5	102.5	PPT	1	0.3	0.061	0.031	5	
	31/8/05	2.6	296.5	PPT	3	0.3	0.072	0.047	7	
Blelham	4/9/06	4.0	0.1	Wind	3	0.1	0.100	0.012	12	
Slotssø	3/9/06	5.7	0.0	Wind	2	0.2	0.103	0.018	14	
	7/10/06	5.7	8.5	Wind	2	0.2	0.075	0.070	na	
Annie	18/8/08	8.0	77.7	PPT/wind	4	1.0	0.168	0.025	9	56
Feeagh	23/6/04	8.9	39.9	PPT	7	6.0	0.074	0.009	45	
Pääjärvi	30/6/04		45.2	PPT	5	8.0 } 32				360
	28/7/04		50.3	PPT	5	9.0				
Leane	26/6/97	9.3	0.5	Wind	2	0.3	0.067	0.025	17	
	28/8/97	10.9	9.8	Wind	3	8.0	0.089	0.012	na	

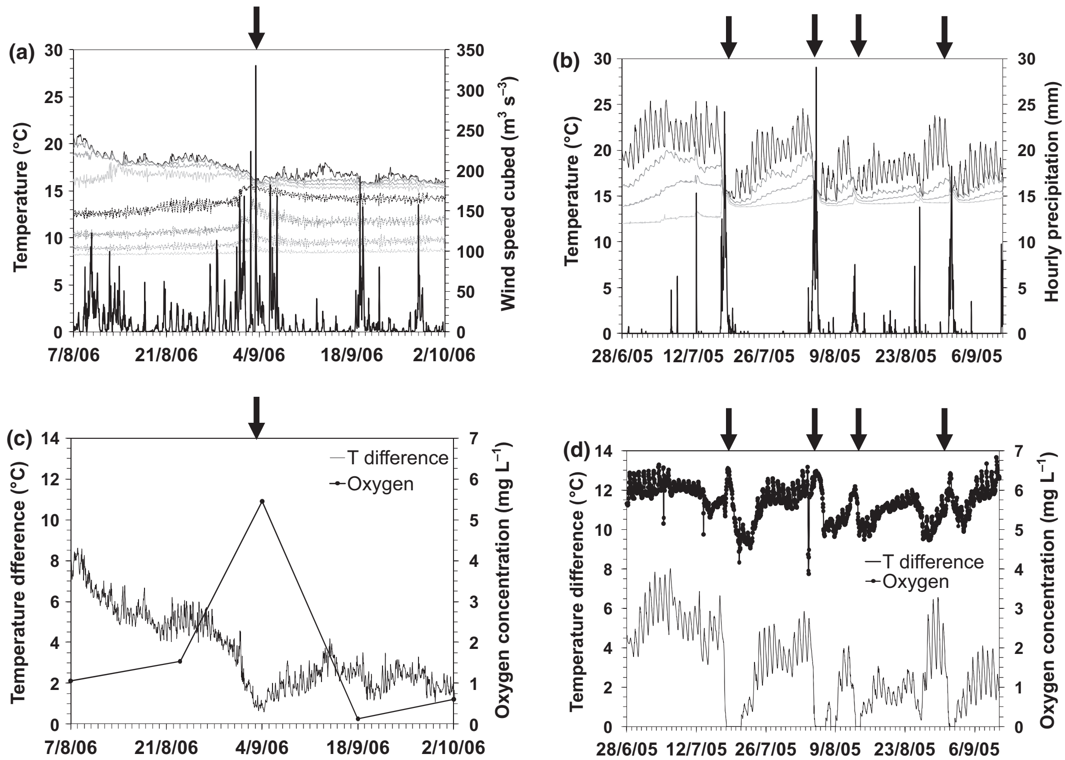

Fig. 1 (a) water temperatures in Blelham at depths of 1–8 m (thin black line–thin grey line and dashed thin black line–dashed thin grey line) and cube of the wind speed (thick black line); (b) temperatures at Yuan Yang at depths of 0–3 m (thin black line–thin grey line) and hourly precipitation (thick black line); (c) temperature difference in Blelham between 1 and 5 m (thin line) and oxygen concentration at 5 m (thick line and circles); (d) temperature difference in Yuan Yang between epilimnion and hypolimnion (thin line) and oxygen concentration at 0.5 m (thick line and circles). Black arrows indicate timing of change in meteorological driver.

Table 2). In Blelham, the sharp increase in turbulent wind energy flux, together with a reduction in surface heating owing to overcast conditions, coincided with a decrease in the temperature difference between the surface and deep water from 4.6 to 1.6 °C in a little over half a day (Fig. 1c). There was also an increase in the dissolved oxygen concentration at a depth of 5 m, suggesting the entrainment of oxygenated water from the mixed layer. The recovery in stratification to over a 4 °C temperature difference took about 2 weeks (Fig. 1c). In Yuan Yang, the temperature difference between the surface and deep waters was between 4 and 6 °C during periods of stratification but was reduced to zero following each of the four precipitation events (Fig. 1d). The dissolved oxygen concentration of the surface water also decreased during mixing. However, as with Blelham, the lake restratified relatively rapidly (5–8 days) after each event (Fig. 1c,d; Table 2).

Wind-driven mixing events also occurred in Slotssø (Fig. 2a,e) and Leane (Fig. 2b,f). In Slotssø, both mixing events occurred in the autumn. Elevated wind speeds of 4.4–5.7 m s^{-1} occurred between 28 August 2006 and 4 September 2006; a second period of high wind speeds was centred on 6 October (Fig. 2a). These episodes, which occurred when air temperatures were declining, caused an immediate decrease in water column stability, and a concurrent deepening of the thermocline (Fig. 2e). The Brunt–Väisälä (BV) buoyancy frequency, a measure of water column stability, did not return to pre-event levels after this but remained at approximately 0.085 s^{-1} until the second mixing event in October, after which it declined to 0.004 s^{-1}.

The first mixing event in Leane occurred during a period of high wind speeds of 5–9 m s^{-1} in late June 1997 (Fig. 2b). Water column stability (BV) decreased from 0.067 to 0.025 s^{-1}, while the thermocline deepened from 15 to 21 m (Fig. 2f). As with the events in Blelham and Yuan Yang, the lake restratified relatively rapidly, with both stability and thermocline depth returning to pre-event levels within 17 days. A second mixing event in Leane in late August was driven by higher wind speeds of 10.9 m s^{-1}. Thermocline depth did not recover following this event and continued to decline over the following weeks (Fig. 2f).

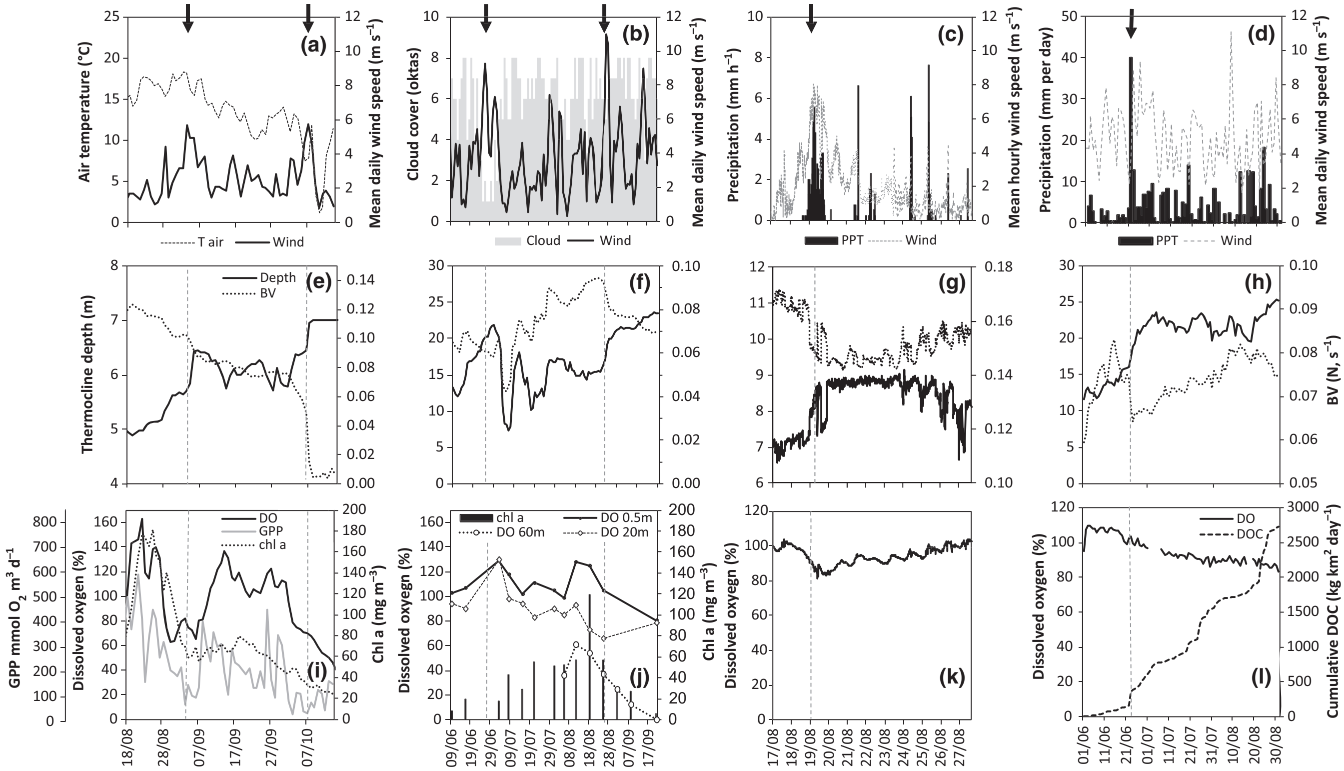

Fig. 2 Episodic events at Slotssø (a, e, i), Leane (b, f, j), Annie (c, g, k) and Feeagh (d, h, l): meteorological drivers (a–d), Brunt–Väisälä (BV) buoyancy frequency and thermocline depth (e–h), dissolved oxygen levels, chlorophyll *a* (Slotssø and Leane only) and gross primary productivity (Slotssø only), and inflow DOC load (Feeagh only) (i–l). Black arrows and grey dashed lines indicate timing of change in meteorological driver.

In Annie and Feeagh, mixing was related to the combined pressures of high precipitation rates and high wind speed. Tropical Storm Fay began to pass over Annie on 18 August 2008 with maximum rainfall occurring on 19 August (Fig. 2c and Table 2). By 22 August, the lake had received approximately 152 mm of rainfall over 4 days and experienced 5-min average wind speeds up to 8 m s^{-1}. Water column stability declined immediately after the storm from 0.168 to 0.143 s^{-1} and remained lower than pre-storm values throughout the following week (Fig. 2g). This resulted in a deepening of thermocline from 7 to 9 m until 28 August. In Feeagh, high rainfall (40 mm day^{-1}) on 23 June 2004 was also the initial driver of mixing (Fig. 2d). This high rainfall was followed by an increase in wind speeds from 4.3 to 8.6 m s^{-1} on 24 June 2004. The water column stability (BV) decreased from 0.074 to 0.065 s^{-1} before increasing slowly over the next 5 weeks (Fig. 2h). The thermocline depth declined from 15 to 22 m and, in contrast to all other mixing events, remained at approximately this lower depth for the rest of the summer until the lake fully mixed in late September.

Effects on DOC loading and underwater PAR variations

High rainfall also resulted in a rapid influx of coloured dissolved organic matter at some sites. In addition to the effects on lake stability and thermocline depth described above, Tropical Storm Fay caused a rapid reduction in light transmission as measured by underwater PAR in groundwater-fed Annie (Fig. 3a). The reduction in light transmission occurred rapidly, had a curvilinear relationship to cumulative precipitation and continued to decline after peak rainfall on 19 August 2008 ($r^2 = 0.84$; $P < 0.001$). The percentage transmission decreased from 63 to 45% within 5 days of the storm. The effect of the storm on underwater PAR levels persisted for 56 days. At Pääjärvi, discharge in the period June to August 2004 was nearly double the long-term average (from 1972 to present). The increase was primarily related to two high rainfall events, one on 30 June 2004 (45 mm day^{-1}) and one on 20 July 2004 (50 mm day^{-1}). The DOC load to the lake (Fig. 3b) peaked as a result of both increasing discharge and higher DOC concentrations of the inflowing water (not shown). Two large pulses in the export of DOC led to a decrease in

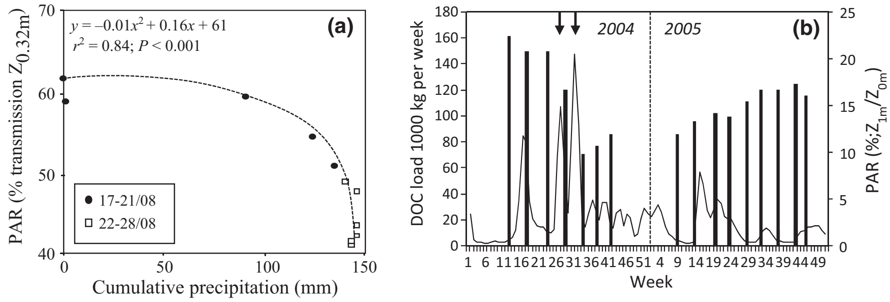

Fig. 3 Short-term and longer-term changes in underwater photosynthetically active radiation (PAR) levels: (a) PAR (% transmission at 0.32 m) plotted against cumulative precipitation (mm) in Annie following Tropical Storm Fay (black circles = 17–21 August; open circles = 22–28 August); (b) DOC load (1000 kg DOC week^{-1}, black line) and ratio of surface to underwater PAR (at 1 m, black bars) in Pääjärvi, 2004 and 2005. Black arrows indicate timing of rainfall events.

the ratio of underwater to surface PAR by a factor of 1.9 (Fig. 3b). Underwater PAR levels did not return to pre-event levels until August of 2005. In-lake DOC concentrations or PAR levels were not available for Feeagh; however, the DOC load associated with the event in June 2004 was 189 kg DOC km^{-2} day^{-1} (Fig. 2l). In contrast, similar and higher DOC loads were associated with relatively low rainfall later in the summer: for example, 2 days with rainfall of 9 and 18 mm day^{-1} in late August had loads of 165 and 268 kg DOC km^{-2} day^{-1}, respectively.

Effects on dissolved oxygen levels, chlorophyll a levels and primary production

Three differing patterns of change in dissolved oxygen levels were observed following the changes in meteorological conditions. In Annie (Fig. 2k), surface water DO concentrations dropped rapidly by 1 mg L^{-1} (from about 100 to 85% saturation) during mixing but then returned to their pre-event levels within 10 days. This decrease was coincident with the increase in wind speed and precipitation, and the decline in water column stability and in thermocline depth (Fig. 4a), indicating entrainment of deoxygenated water from depth. A similar reduction in surface water DO levels and subsequent rapid reoxygenation occurred following all four events in Yuan Yang (Fig. 1d). In Feeagh, surface water DO levels declined only slightly, from about 105% prior to the event to 97% immediately after, but then continued to decline steadily over the next 2 months. This slower decline coincided with continued DOC loading in the inflowing stream (Fig. 3l). In this case, BV buoyancy frequency declined on the day of the high rainfall (23 June), while thermocline depth decreased over the subsequent days: however, there was no decline in DO levels concurrent with mixing (Fig. 4b).

In contrast, the initial decrease in the DO content of the upper mixed layer in Slotssø was coincident with the decline in gross primary production (Fig. 2i). The first mixing event in Slotssø began during an algal bloom that was characterised by hypertrophic chlorophyll *a* levels (150–175 mg Chl *a* m^{-3}). DO levels decreased from more than 125% DO to about 70% DO. This decline occurred on

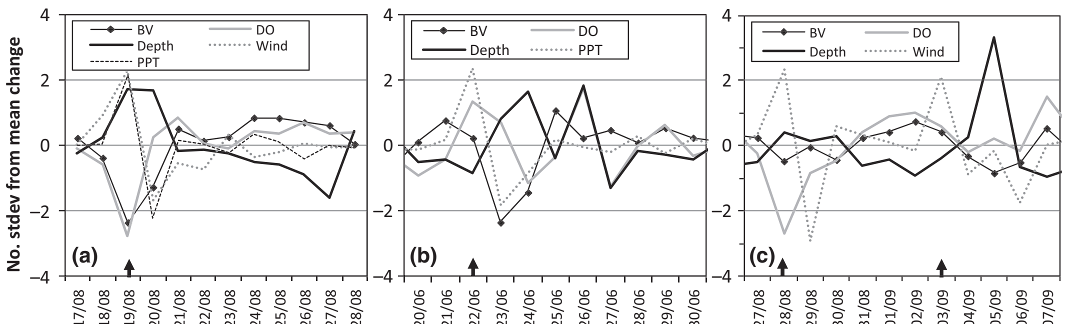

Fig. 4 Three differing patterns in the sequence of relative change (number of standard deviations from mean change) in Brunt–Väisälä (BV) buoyancy frequency, thermocline depth and surface dissolved oxygen (DO) levels following changes in weather: (a) Annie, (b) Feeagh and (c) Slotssø. Black arrows indicate timing of change in meteorological driver.

the first day on which wind speeds increased (28 August 2006), while the increase in thermocline depth occurred following a second increase in wind speed on 5 September (Figs 2a,e & 4c). However, chlorophyll *a* levels remained relatively high (60–70 mg Chl *a* m^{-3}) after the period of higher wind speed and epilimnetic dissolved oxygen levels returned to supersaturated levels (100–125%) within 3 days of wind speeds declining. The lake became fully mixed during the second event in October: surface water DO levels again declined to 50% saturation but then remained low.

The hypolimnion was not deoxygenated in Leane prior to the mixing event in June 1997, and therefore, no reduction in epilimnetic DO levels occurred (Fig. 2j). This period coincided with unusually clear skies (Fig. 2b), and while Chl *a* remained low, surface DO levels rose from 103 to 129% (Fig. 2j). In mid-August, following another unusually bright and calm day (cloud cover 1 okta, wind speed 1.2 m s^{-1}), high Chl *a* concentrations (118 mg m^{-3}), identified as a bloom of the cyanobacterium *Anabaena flos-aquae,* were recorded. These coincided with a peak in surface water temperatures (maximum 20 °C) and high water column stability (Fig. 2f). Chlorophyll concentrations declined following the second mixing event in late August. Following deposition of this bloom, anoxic conditions were recorded in the bottom waters of the lake (Fig. 2j). They remained anoxic until November of that year.

Relative magnitude and duration of episodic events

The reduction in BV frequency coefficient was linearly related to precipitation for the four mixing events in Yuan Yang and the events in Feeagh and Annie (Fig. 5a). The high rainfall levels that drove the events in Yuan Yang (all >103 mm day^{-1}), although extreme in general terms, are relatively common at this site with return times of <1 year (Table 2). There was no relationship between wind speed and reduction in BV frequency coefficient for the four events at Yuan Yang (not shown). The relationship between the reduction in BV frequency coefficient and mean daily wind speed at the other sites was less clear than that with rainfall but showed a generally positive relationship (Fig. 5b).

The duration of changes in water column stability ranged from 5 to 45 days across the sites (Fig. 5c). Lake thermal structure returned to pre-event conditions within 17 days of all mixing events, with the exception of the event in Feeagh, where the reduction in stability and increase in thermocline depth was apparent until the lake

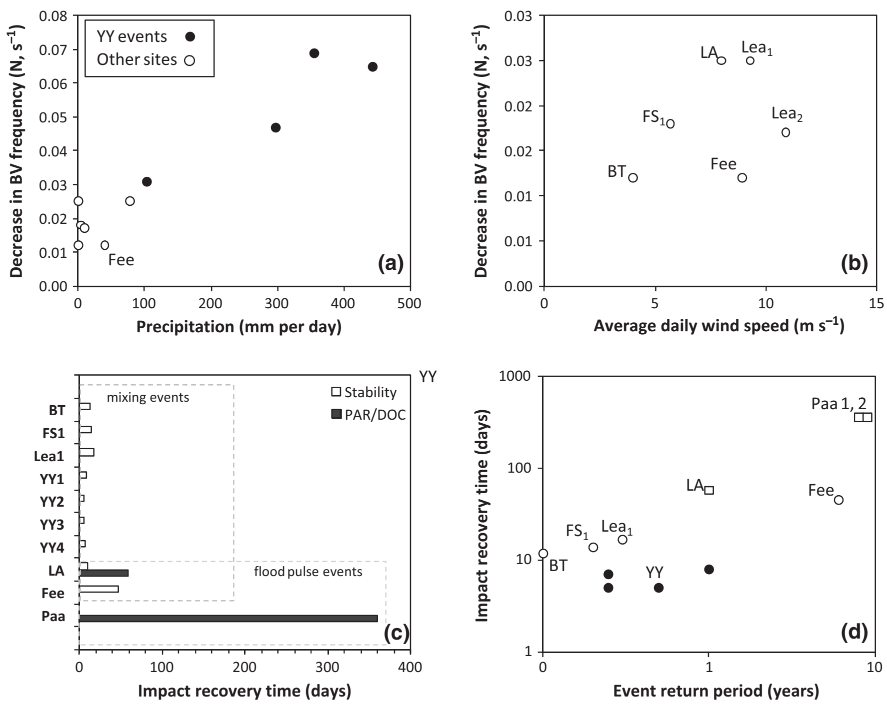

Fig. 5 Relationship between the reduction in BV frequency coefficient (s^{-1}) and daily precipitation (mm day^{-1}) (a) and wind speed (m s^{-1}) (b) (Yuan Yang events = black circles, all other sites = open circles); (c) time taken for recovery of in-lake parameter following event (impact recovery time, days); (d) impact recovery time (days: log scale) plotted against event return period (years: log scale), circles = thermal profile impacts; squares = PAR impacts (BT = Blelham, FS = Slotssø, Fee = Feeagh, LA = Annie, Lea = Leane, Paa = Pääjärvi, YY = Yuan Yang).

fully mixed in September (45 days). The changes in underwater PAR levels at Annie and Pääjärvi were more prolonged, lasting for 56 and 360 days, respectively (Table 2). The duration of impacts tended to be longer for events with longer return periods, that is, those that are less frequent and more severe at a site (Fig. 5d; Table 2). The two flood pulse events in Pääjärvi, where peak rainfall was 45 and 50 mm day^{-1}, respectively, had individual return periods of 8 and 9 years. However, analysis of the precipitation data for the site showed that no two events of this magnitude co-occurred in any other summer in the 32-year record (Table 2).

Discussion

Abrupt changes in weather have long been recognised as drivers of episodic events in lakes, including sudden changes in stability and stratification (Imberger, 1994; Wilhelm & Adrian, 2008), increases in the availability of dissolved nutrients (Drakare *et al.*, 2002; Foreman *et al.*, 2004) and both short-term and longer-term biological responses (Flöder & Sommer, 1999; Hargeby *et al.*, 2004; Paidere *et al.*, 2007). These studies, however, generally report effects for a specific site or event. The case studies that we presented were from lakes that differed in size, trophic status and climatic region. The range in the magnitude of the meteorological drivers, and the number of events occurring in a season provides insight into the consequences of increases in the severity and the frequency of these drivers across a wide range of sites.

Consequences of weather-related episodic events for abiotic conditions: the importance of high-frequency data

The changes in wind speed and rainfall in our case studies were all of short duration, necessitating the use of automated high-resolution monitoring to resolve them. Nevertheless, they had rapid and substantial impacts on abiotic conditions within the lakes that persisted for periods varying from several days to an entire year. Two types of effects were identified: (i) generally short-lived effects of even very intense storms on lake thermal structure and (ii) more prolonged changes in coloured dissolved organic matter export and underwater light levels following high rainfall. Two of the case studies used in this paper, Blelham and Slotssø, clearly demonstrated the rapid but short-lived consequences of relatively low-severity wind speeds for thermal structure. Leane, one of our largest lakes, also restratified rapidly after mixing. More surprisingly, some lakes experiencing what might be considered severe conditions (for example, the storms at Yuan Yang and Annie) also restratified within days. Our results also illustrated the compound effects of flood events compared to those events where only an increase in wind speed occurred. A decrease in stability, a deepening of the thermocline, a reduction in underwater PAR levels and a reduction in surface water DO levels all occurred in Annie following Tropical Storm Fay. In addition, where successive flood pulse events occur, as illustrated by the two sequential events in Pääjärvi, the changes in CDOM levels and on underwater PAR levels can be cumulative.

Biological responses to weather-related episodic events

These changes in abiotic conditions also resulted in some cases in rapid biological responses. Decreases in algal biomass occurred in both Slotssø and Leane when wind speeds increased. A decline in surface water DO levels and in estimated GPP was coincident with the decrease in Chl *a* at Slotssø. Other reductions in surface water DO levels may have been due, in part, to increased bacterial mineralisation of DOC, for example in Feeagh. In Pääjärvi, where an influx of DOC was recorded but where mixing did not occur, a peak in CO_2 and CH_4 fluxes from the water column was recorded following the 2004 events owing to increased mineralisation (Ojala *et al.*, 2011). The bacterial community composition in Yuan Yang was also perturbed immediately following each of the events described in 2005 but recovered to pre-event conditions within 3–4 weeks (Jones *et al.*, 2008). The reductions in light availability in Annie and Pääjärvi would also potentially influence phytoplankton species composition. In Annie, *Chrysophyte* communities dominate in the metalimnion in storm-free, transparent years, while these communities are absent from the lake in years where CDOM concentrations have increased following storms (Battoe, 1985). Such increases in carbon availability, decreases in PAR and increased disturbance all have the potential to shift lake ecosystems away from net autotrophy towards net heterotrophy.

The magnitude of the effects on our case study lakes was related to the intensity of the event but also in some cases to site-specific characteristics that may reflect lower inherent resilience to such disturbance. While rainfall initiated the deepening of the thermocline in Feeagh, for example, this site experiences a cool oceanic climate and the persistence of the lower thermocline was likely to have been a function of subsequent wind speed, precipitation and air temperature. The size of the pulse of coloured DOC exported from the Feeagh, Pääjärvi and Annie catchments would depend on the amount of rainfall but also on the availability of DOC in flow pathways in catchment soils (Vogt & Muniz, 1997; Worrall *et al.*, 2002). The magnitude of subsequent changes in lake DOC concentrations and in underwater PAR levels would be related to both DOC loading and to lake residence time. Repeated years with frequent storms in Lake Annie have been shown to result in persistent elevation of CDOM levels. Recovery to pre-event levels requires a recovery period without storms, equal to the water residence time of 2 years (Gaiser *et al.*, 2009b).

Future changes in the severity and frequency of extreme weather conditions

Changes in both the frequency and/or severity of storms are predicted as a result of global climate change. While there is a greater degree of uncertainty associated with future projections for precipitation and wind speed than those for warming (Beniston *et al.*, 2007; Samuelsson, 2010), upward trends in the occurrence of extreme precipitation have already been reported for both Europe (Klein Tank & Können, 2003) and the United States (Kunkel *et al.*, 1999). Overall, the consequences of these changes will depend on the direction of climate change at a given location and on lake and catchment characteristics. Our humic case study lakes lie in four different climatic regions. For three of these regions, those where Annie, Yuan Yang and Pääjärvi are located, increases in the severity and/or frequency of summer storms are projected (Knutson & Tuleya, 2004; Walsh, 2004; Diffenbaugh *et al.*, 2005; Beniston *et al.*, 2007; Samuelsson, 2010). In contrast, warmer, drier, and calmer conditions are projected for the Feeagh catchment in summer, with higher rainfall in winter and early spring (Samuelsson, 2010). The bacterial community in lakes that experience frequent storms, such as Yuan Yang, appears to be well adapted to these conditions (Jones *et al.*, 2008, 2009), and changes in intensity may have little effect. However, the occurrence of more intense and frequent storms could lead to longer periods with decreased transparency in lakes such as Annie, which fluctuate between clear-water and more coloured phases (Gaiser *et al.*, 2009a,b). Similarly, an increase in extreme precipitation could increase DOC loading and decrease light levels in northern lakes such as Pääjärvi. Although drier and calmer summers are expected at Feeagh, modelling of future DOC export to the lake suggests increased rates of aerobic decomposition in soils and a subsequent increase in annual mean DOC inflow to the lake (Naden *et al.*, 2010).

The three clear-water, eutrophic lakes all lie in western and north-western Europe, a region where drier, calmer conditions are expected in mid- to late summer, with higher rainfall in spring and early summer (Christensen *et al.*, 2007; Samuelsson, 2010). Here, mixing events will be rarer, and higher stability could lead to more frequent algal blooms, similar to that experienced in Leane, and less frequent reoxygenation of deeper water. Increased nutrient loading in spring and early summer has also been projected for Leane and would contribute to the potential for blooms (Jennings *et al.*, 2009). However, experimental work at Slotssø has suggested that, even in this clear-water site, predicted changes in climate will drive the lake towards net heterotrophy in summer and autumn (Staehr & Sand-Jensen, 2006, 2007).

These case studies highlight the importance of high-frequency data in exploring and quantifying the consequences of such intermittent changes in lakes. The analysis and synthesis of ongoing high-frequency measurements, both at GLEON lakes and at other sites, will provide further insight into the capacity for lakes to absorb such impacts. The availability of data from a network of sites will also facilitate comparative investigations and allow assessment on both regional and global scales. These insights will be increasingly important given the global nature of many current influences, episodic or chronic, on lake ecosystems, especially those related to climate change.

Acknowledgments

The authors wish to thank all involved in data collection at their respective sites. Additional meteorological data were provided by Met Éireann (Ireland) and the Finnish Meteorological Institute. They also wish to thank the two reviewers who provided very useful guidance on the paper. This work benefited from participation in or use of the Global Lake Ecological Observatory Network (GLEON).

References

American Public Health Association (1992) *Standard Methods for the Examination of Water and Wastewater*, 18th edn. American Public Health Association, Washington, U.S.A..

Amorocho J. & DeVries J.J. (1980) A new evaluation of the wind stress coefficient over water surfaces. *Journal of Geophysical Research*, **85**, 433–442.

Arvola L., Kankaala P., Tulonen T. & Ojala A. (1996) Effects of phosphorus and allochthonous humic matter enrichment on the metabolic processes and community structure of plankton in a boreal lake. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 1646–1662.

Arvola L., Järvinen M. & Hakala I. (2006) Nutrient export from small boreal catchments: the influence of annual and seasonal hydrology. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **29**, 2031–2034.

Bachmann R.W., Hoyer M. & Canfield D. (1999) The restoration of Lake Apopka in relation to alternative stable states. *Hydrobiologia*, **394**, 219–232.

Battoe L.E. (1985) Changes in vertical phytoplankton distribution in response to natural disturbances in a temperate and a subtropical lake. *Journal of Freshwater Ecology*, **3**, 167–174.

Beniston M., Stephenson D.B., Christensen O.B., Ferro C.A.T., Frei C., Goyette S. *et al.* (2007) Future extreme events in European climate: an exploration of regional climate model projections. *Climatic Change*, **81**, 71–95.

Christensen J.H., Hewitson B., Busuioc A., Chen A., Gao X., Held I. *et al.* (2007) Regional climate projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (Eds S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt *et al.*), pp. 848–940. Cambridge University Press, Cambridge, United Kingdom and New York, U.S.A.

Connell J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, **24**, 1302–1310.

Cotner J.B., Johengen T.H. & Biddanda B.A. (2000) Intense winter heterotrophic production stimulated by benthic resuspension. *Limnology and Oceanography*, **45**, 1672–1676.

Diffenbaugh N.S., Pal J.S., Trapp R.J. & Giorgi F. (2005) Fine-scale processes regulate the response of extreme events to global climate change. *Proceedings of the National Academy of Science of the United States of America*, **102**, 15774–15778.

Drakare S., Blomqvist P., Bergström A.-K. & Jansson M. (2002) Primary production and phytoplankton composition in relation to DOC input and bacterioplankton production in humic Lake Örträsket. *Freshwater Biology*, **47**, 41–52.

Eugster W., Kling G., Jonas T., McFadden J.P., Wüest A., MacIntyre S. *et al.* (2003) CO_2 exchange between air and water in an Arctic Alaskan and midlatitude Swiss lake: importance of convective mixing. *Journal of Geophysical Research*, **108**, 4362. doi: 10.1029/2002JD002653.

Flöder S. & Sommer U. (1999) Diversity in plankton communities: an experimental test of the intermediate disturbance hypothesis. *Limnology and Oceanography*, **44**, 1114–1119.

Foreman C.M., Wolf C.F. & Priscu J.C. (2004) Impact of episodic warming events on the physical chemical and biological relationships of lakes in the McMurdo Dry Valleys, Antarctica. *Aquatic Geochemistry*, **10**, 239–268.

Gaiser E.E., Deyrup N., Bachmann R., Battoe L. & Swain H. (2009a) Effects of climate variability on transparency and thermal structure in subtropical monomictic Lake Annie, Florida. *Fundamental and Applied Limnology*, **175**/3, 217–230.

Gaiser E., Deyrup N., Bachmann R., Battoe L. & Swain H. (2009b) Multidecadal climate oscillations detected in a transparency record from a subtropical Florida lake. *Limnology and Oceanography*, **54**, 2228–2232.

Gill A.E. (1982) *Atmosphere-Ocean Dynamics*. Academic Press, London.

Hargeby A., Blindow I. & Hansson L.-A. (2004) Shifts between clear and turbid states in a shallow lake: multi-causal stress from climate, nutrients and biotic interactions. *Archiv für Hydrobiologie*, **161**, 433–454.

Huisman J., Sharples J., Stroom J.M., Visser P.M., Kardinaal W.E.A., Verspagen J.M.H. *et al.* (2004) Changes in turbulent mixing shift competition for light between phytoplankton species. *Ecology*, **85**, 2960–2970.

Hutchinson G.E. (1975) *A Treatise on Limnology – Geography and Physics of Lakes*. John Wiley & Sons, London, U.K.

Imberger J. (1994) Transport processes in lakes: a review article. In: *Limnology Now a Paradigm of Planetary Problems* (Ed. R. Margalef), pp. 99–193. Elsevier, Amsterdam.

Jennings E. & Allott N. (2006) Influence of the Gulf Stream on lake nitrate concentrations in SW Ireland. *Aquatic Sciences*, **68**, 482–489.

Jennings E., Allott N., Pierson D., Schneiderman E., Lenihan D., Samuelsson P. *et al.* (2009) Impacts of climate change on phosphorus loading from a grassland catchment – implications for future management. *Water Research*, **43**, 4316–4326.

Jöhnk K.D., Huisman J., Sharples J., Sommeijer B., Viser P.M. & Stroom M. (2007) Summer heatwaves promote blooms of harmful cyanobacteria. *Global Change Biology*, **14**, 495–512.

Jones I.D. & Elliott J.A. (2007) Modelling the effects of changing retention time on abundance and composition of phytoplankton species in a small lake. *Freshwater Biology*, **52**, 988–997.

Jones S.E., Chiu C.Y., Kratz T.K., Wu J.T., Shade A. & McMahon K.D. (2008) Typhoons initiate predictable change in aquatic bacterial communities. *Limnology and Oceanography*, **53**, 1319–1326.

Jones S.E., Kratz T.K., Chiu C.Y. & McMahon K.D. (2009) The influence of typhoons on annual CO_2 flux from a subtropical humic lake. *Global Change Biology*, **15**, 243–254.

Jones I.D., Page T., Eliott J.A., Thackery S.J. & Heathwaite A.L. (2011) Increases in lake phytoplankton biomass caused by future climate-driven changes to seasonal river flow. *Global Change Biology*, **17**, 1809–1820.

Junk W.J., Bayley P.B. & Sparks R.E. (1989) The flood pulse concept in river-foodplain systems. *Canadian Special Publications of Fisheries and Aquatic Sciences*, **106**, 110–127.

Kalff J. (2002) *Limnology – Inland Water Ecosystems*, 1st edn. Prentice Hall, New Jersey.

Klein Tank A.M.G. & Können G.P. (2003) Trends in indices of daily temperature and precipitation extremes in Europe, 1946–99. *Journal of Climate*, **16**, 3665–3680.

Knutson T.R. & Tuleya R.E. (2004) Impact of CO_2-induced warming on simulated hurricane intensity and precipitation: sensitivity to the choice of climate model and convective parameterization. *Journal of Climate*, **17**, 3477–3495.

Kunkel K.E., Andsager K. & Easterling D.R. (1999) Long-term trends in extreme precipitation events over the conterminous United States and Canada. *Journal of Climate*, **12**, 2515–2527.

Lohrenz S.E., Fahnenstiel G.L., Millie D.F., Schofield O.M.E., Johengen T. & Bergmann T. (2004) Spring phytoplankton photosynthesis growth and primary production and relationships to a recurrent coastal sediment plume and river inputs in southeastern Lake Michigan. *Journal of Geophysical Research*, **109**, C10S14; doi: 10 1029/2004JC002383.

MacIntyre S., Eugster W. & Kling G.W. (2001) The critical importance of buoyancy flux for gas flux across the air-water interface. In: *Gas Transfer at Water Surfaces* (Eds M.A. Donelan, W.M. Drennan, E.S. Saltzman & R. Wanninkhof), pp. 135–139. AGU, Washington.

MacIntyre S., Romero J.R. & King G.W. (2002) Spatial-temporal variability in surface layer deepening and lateral advection in an embayment of Lake Victoria, East Africa. *Limnology and Oceanography*, **47**, 656–671.

Millie D.F., Fahnenstiel G.L., Lohrenz S.E., Carrick H.J., Johengen T. & Schofield O.M.E. (2003) Physical-biological coupling in southeastern Lake Michigan: influence of episodic sediment resuspension on phytoplankton. *Aquatic Ecology*, **37**, 393–408.

Naden P., Allott N., Arvola L., Jarvinen M., Jennings E., Moore K. *et al.* (2010) Modelling the effects of climate change on dissolved organic carbon. In: *The Impact of Climate Change on European Lakes* (Ed. D.G. George), pp. 221–252. Aquatic Ecology Series Vol. 4. Springer, Amsterdam.

Ojala A., Lo'pez Bellido J., Tulonen T., Kankaala P. & Huotarib J. (2011) Carbon gas fluxes from a brown-water and a clear-water lake in the boreal zone during a summer with extreme rain events. *Limnology and Oceanography*, **56**, 61–76.

Paidere J., Gruberts D. & Škute A. (2007) Impact of two different flood pulses on planktonic communities of the largest floodplain lakes of the Daugava River (Latvia). *Hydrobiologia*, **592**, 303–314.

Reid M.A. & Ogden R.W. (2006) Trend variability or extreme event? The importance of long-term perspectives in river ecology *River Research and Applications*, **22**, 167–177.

Rimmer A., Aota Y., Kumagai M. & Eckert W. (2005) Chemical stratification in thermally stratified lakes, a chloride mass balance model. *Limnology and Oceanography*, **50**, 147–157.

Samuelsson P. (2010) Using regional climate models to quantify the impact of climate change on lakes. In: *The Impact of Climate Change on European Lakes* (Ed. D.G. George), pp. 15–32. Aquatic Ecology Series Vol. 4. Springer, Amsterdam.

Scheffer M. & Jeppesen E. (2007) Regime shifts in shallow lakes. *Ecosystems*, **10**, 1–3.

Staehr P.A. & Sand-Jensen K. (2006) Seasonal changes in temperature and nutrient control of photosynthesis, respiration and growth of natural phytoplankton communities. *Freshwater Biology*, **51**, 249–262.

Staehr P.A. & Sand-Jensen K. (2007) Temporal dynamics and regulation of lake metabolism. *Limnology and Oceanography*, **52**, 108–120.

Staehr P.A., Bade D., van de Bogert M., Koch G., Williamson C., Hanson P. *et al.* (2010) Lake metabolism and the diel oxygen technique: state of the science. *Limnology and Oceanography Methods*, **8**, 628–644.

Vogt R.D. & Muniz I.P. (1997) Soil and stream water chemistry in a pristine and boggy site in mid-Norway. *Hydrobiologia*, **348**, 19–38.

Walsh K. (2004) Tropical cyclones and climate change: unresolved issues. *Climate Research*, **27**, 77–83.

Wantzen K.M., Junk W.J. & Rothhaupt K.-O. (2008) An extension of the floodpulse concept (FPC) for lakes. *Developments in Hydrobiology*, **204**, 151–170.

Weyhenmeyer G.A., Willén E. & Sonesten L. (2004) Effects of an extreme precipitation event on lake water chemistry and phytoplankton in the Swedish Lake Mälaren. *Boreal Environment Research*, **9**, 409–420.

Wilhelm S. & Adrian R. (2008) Impact of summer warming on the thermal characteristics of a polymictic lake and consequences for oxygen nutrients and phytoplankton. *Freshwater Biology*, **53**, 226–237.

Wilson E.M. (1990) *Engineering Hydrology*, 4th edn. Macmillan Publishers, London.

Worrall F., Burt T.P., Jaeben R.Y., Warburton J. & Shedden R. (2002) The release of dissolved organic carbon from upland peat. *Hydrological Processes*, **16**, 3487–3504.

Yount J.I. (1961) A note on stability in central Florida lakes with discussion of the effect of hurricanes. *Limnology and Oceanography*, **6**, 322–325.

(Manuscript accepted 4 December 2011)