

Article

Contrasting pelagic plankton in temperate Irish lakes: the relative contribution of heterotrophic, mixotrophic, and autotrophic components, and the effects of extreme rainfall events

K. Sparber,¹ C. Dalton,¹ E. de Eyto,² E. Jennings,³ D. Lenihan,⁴ and F. Cassina¹

¹ *Mary Immaculate College, University of Limerick, Ireland*

² *Marine Institute, Newport, Mayo, Ireland*

³ *Dundalk Institute of Technology, Ireland*

⁴ *Kerry County Council, Tralee, Ireland*

* *Corresponding author: catherine.dalton@mic.ul.ie*

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Abstract

The mobilisation of energy from allochthonous carbon by heterotrophic bacterioplankton can be proportionally more important than autotrophic production in humic lakes. Moreover, increasing levels of dissolved organic carbon (DOC) in many aquatic systems linked to increases in precipitation, which in turn may be related to changing climate, mean that this heterotrophic component of the food web may play an increasing role in the overall transfer and production of energy, particularly within peatland catchments. While such catchments are common in the temperate northwest Atlantic regions of Europe, studies describing the seasonal dynamics of the heterotrophic, mixotrophic, and autotrophic components of their aquatic food webs are rare. In this study, the biomass of these pelagic components was enumerated over 1 year in 2 oligotrophic lakes, both situated in peatland catchments in the west of Ireland but with contrasting DOC concentrations. Bacterial biomass dominated the pelagic food web of the more humic lake, Lough Feeagh, while autotrophic phytoplankton biomass was greatest in the clearwater lake, Lough Guitane. The biomass of potentially mixotrophic flagellates was also slightly larger in the Lough Guitane, while phagotrophic ciliate biomass was comparable between the 2 lakes. An extreme precipitation event led to a significant increase in bacterial biomass while simultaneously depressing autotrophic production for several months in the humic lake. Extreme precipitation in the clearwater lake also depressed autotrophic production but did not give rise to significant increases in bacterial biomass. This quantification of autotrophic, mixotrophic, and heterotrophic components provides a vital first step in understanding how pelagic communities contribute to net ecosystem productivity, and thus how Irish peatland lakes may be affected by projected climate changes.

Key words: autotrophic, clearwater lakes, extreme precipitation, heterotrophic, humic lakes, mixotrophic, pelagic plankton

Introduction

The relative proportions of carbon derived from allochthonous and autochthonous sources vary widely among lakes and can change substantially over the annual cycle at an individual site. These variations have consequences for both the composition of the lake biota and for ecosystem

functioning. In highly productive lakes, primary production from phytoplankton (autochthonous carbon) is generally the dominant carbon source, while in many oligotrophic lakes, particularly in humic catchments with organic peat soils, allochthonous carbon can be more important (Jansson et al. 2000, Kritzberg et al. 2004, Guillemette et al. 2013). When levels of humic compounds

are high, bacterioplankton are likely to be the main pathway by which carbon enters the base of the pelagic food web (Del Giorgio et al. 1997, Attermeyer et al. 2013). These bacteria utilise and mobilise energy from humic substances (Jones 1992, Laybourn-Parry et al. 1994) and then pass it through the food web via phagotrophic flagellates and ciliates to zooplankton, and hence to fish. A significant proportion of fish biomass can be supported by this terrestrial energy source, particularly in forested catchments (Tanentzap et al. 2014) where leaf litter is a significant source of energy (Carpenter et al. 1998). There is also now strong evidence that many waterbodies, even clearwater lakes, may be net heterotrophic aquatic systems, with respiration exceeding gross primary production over the annual cycle (Rubbo et al. 2006, Bass et al. 2010, Ojala et al. 2011, Obrador et al. 2014).

Humic lakes are common in the northern temperate climate zone, where extensive peat soils are common (Dillon and Molot 1997, Kortelainen 1999, Ojala et al. 2011). These lakes play a significant role in regional and global carbon cycles (Cole et al. 2007, Tranvik et al. 2009). While temperate zones are generally net sinks of carbon dioxide (CO₂) from the atmosphere (Apps et al. 1993), the lakes within these zones may be significant sources of CO₂ to the atmosphere (Bass et al. 2010). Even minor changes in the quality and quantity of the humic compounds exported to these lakes can have considerable significance for carbon cycling and have substantial ecological consequences in aquatic systems (Cole et al. 2000, Porcal et al. 2009), including shifts in the structure and function of the microbial components of food webs (Jones 1992, Sucker and Krause 2010, Kostrzevska-Szla-kowska and Jasser 2011).

The biota in humic lakes includes not just autotrophs and heterotrophic bacteria, but also mixotrophs. Mixotrophic phytoflagellates can obtain energy via both autotrophy and heterotrophy and thus function on more than one trophic level by acting as producers and consumers of organic carbon (Jones 1994, 2000, Jansson et al. 2000). Mixotrophy is evident during reduced light conditions (Jones 1997) and enables mobile phytoflagellates to outcompete purely autotrophic species in nutrient limited conditions (Gervais 1997, Bergström et al. 2001). This strategy is particularly advantageous in humic lakes, where access to nutrients can be restricted due to competition with heterotrophic bacteria (Riemann et al. 1995, Jansson et al. 2001). In these lakes, autotrophic production can also be restricted either by poor light availability (Eloranta 1978, Arvola et al. 1999a) or by inorganic nutrient limitation (Meili 1992) or by both these factors (Drakare et al. 2002, 2003). Humic lakes therefore provide conditions favourable for the growth of a diverse pelagic

community of mixotrophic phytoflagellates, heterotrophic nanoflagellates, ciliates, and bacteria (Isaksson et al. 1999, Jansson et al. 2000, Drakare et al. 2002).

Humic ecosystems are especially sensitive to climate change (Tarnocai 2006, Ise et al. 2008), both to gradual warming and any increased incidence of extreme precipitation. The positive feedback between higher atmospheric CO₂ levels, rising temperatures (IPCC 2013), and then further loss of soil carbon through increased decomposition, has major implications for lakes. Higher dissolved organic carbon (DOC) export as a result of climate warming (e.g., Naden et al. 2010) is likely to further enhance the role of heterotrophs in lakes (De Senerpont Domis et al. 2013), leading to even greater carbon emissions to the atmosphere. In addition, while changes in DOC export have received considerable attention (e.g., Jennings et al. 2010, Miller and McKnight 2010), the drivers of particulate organic carbon (POC) export are also influenced at broad spatial scales by climate (Ryder et al. 2014) and therefore also likely to change in the future.

The severity and frequency of extreme precipitation events is projected to increase in the coming decades (Beniston et al. 2007), a change that could affect the normal seasonal cycle of pelagic food webs. Some recent studies have shown that responses can be varied, depending on the magnitude and timing of the event (Jones et al. 2007, Jennings et al. 2012). Increases in nutrient concentrations associated with high flows or mixing events can have a positive impact on both primary and heterotrophic production (Bergström and Jansson 2000, Drakare et al. 2002). High flow events in humic catchments can result in a pulse of coloured water and reduced light availability in the lake that can persist for months or years (Jennings et al. 2012). Intense precipitation may also result in physical disturbance of the water column (Jones et al. 2007) and can be accompanied by increased export of dissolved and particulate substances to the lake (Weyhenmeyer et al. 2004, Arvola et al. 2006). There is, however, little information available on the effects of such extreme events on the bacterioplankton in temperate humic lakes.

The Intergovernmental Panel for Climate Change (IPCC) recently recommended that emissions from wetlands (including peatlands and lakes) be incorporated into national estimates of greenhouse gas emissions (IPCC 2013). To ensure successful implementation, a greater understanding of the role of heterotrophic and mixotrophic components in the carbon cycle is required. While the literature describing the plankton of humic lakes is immense, there are regions that have never, or rarely, been studied. For example, Ireland is estimated to have >12 000 lakes (Irvine et al. 2007). Approximately one-fifth (~18%) of the country has peaty soils (Montanarella et al. 2006),

and therefore a significant proportion of these lakes are humic. Despite this, only one summary paper exists on plankton biomass functional groups (de Eyto and Irvine 2005) and no published material on the seasonal dynamics of pelagic food webs in these lakes.

The purpose of this study was to quantify and describe the components of the pelagic autotrophic (phytoplankton), mixotrophic (phytoflagellates), and heterotrophic (bacteria and ciliates) fractions of the pelagic communities over an annual cycle in 2 temperate lakes. Both lakes are located in peatland catchments but differ greatly in their water colour levels, one being classified as a humic lake and one as a clearwater lake. The study also documents the effects of extreme precipitation events on the pelagic community in both lakes.

Methods

The 2 study lakes, Feeagh and Guitane, are of a relatively similar size, and both have catchments dominated by peatland, but they differ in their catchment area to lake area ratio (Fig. 1). Feeagh (53°94'05"N, 9°57'59"W) is located within the Burrishoole catchment (County Mayo) on the northwestern coast of Ireland and is part of the Global Lake Ecological Observatory Network (GLEON, www.gleon.org). It is also an internationally important index site for the monitoring of diadromous fish. The lake has a surface area of 3.95 km², a maximum depth of 46 m, a mean depth of 14.5 m, a retention time of 164 days, and a lake catchment area of 89.5 km², yielding a catchment area:lake area ratio of 22.7. Guitane (52°00'48"N, 9°41'83"W) is located within the Leane catchment (County Kerry) in the southwest of Ireland and is the primary water source for approximately 59 000 people (EIS 2009). It has a lake area of 2.46 km², with slightly deeper maximum (56 m) and mean (18.7 m) depths, and a retention time of 167 days, but it has a lake catchment area of only 18.69 km² and therefore a catchment area:lake area ratio of 7.6. The land cover in the Feeagh catchment includes 58% peatland, 22% coniferous forestry, and 5% waterbodies as well as some natural grassland, transitional woodland, and agricultural land (CORINE 2006). The Guitane catchment includes 69% peatland, 14% waterbodies, and 7% pasture together with limited broadleaved forest and sparsely vegetated areas. There is no coniferous forestry in the Guitane catchment (CORINE 2006). Rainfall and air temperature data were available from meteorological stations within or close to the catchments. The average annual precipitation at the meteorological station in the Burrishoole catchment (1970–2012) was 1586 mm yr⁻¹, while that for the Muckcross meteorological station 15 km from Guitane (1990–2009) was 1833 mm yr⁻¹.

The 2 lakes were monitored from April 2009 to May 2010. An Automatic Water Quality wire sensor, lab facility) and high frequency turbidity using a nephelometer (Chelsea Scientific Minitracka mk II). Daylight hours were quantified using the NOAA ESRL calculator (<http://www.esrl.noaa.gov/gmd/grad/solcalc/sunrise.html>). Vertical water temperature profiles from Guitane were collected on a monthly basis. Thermocline depth was calculated using Lake Analyzer (<http://lakeanalyzer.gleon.org>; Read et al. 2011). Secchi depth was recorded on all sampling occasions at both sites. The Automatic Water Quality Monitoring System (AWQMS) on Feeagh measured vertical temperature profiles using platinum resistance thermometers (PRTs: PT100 1/10DIN 4).

Vertically integrated open-water samples were collected every month from the deepest point of each lake. Poor weather in November necessitated collection of an outflow sample (Finow River) from Guitane. Water samples were collected using a 2.5 cm diameter tube sampler with 2 lengths: 1.5 m for Feeagh and 5 m for Guitane. The different lengths accommodated the annual average Secchi depths of the last 5 years (2003–2008; n = 60), or the mean depth of the euphotic zone (Håkanson and Peters 1995, Arvola et al. 1999b). A 250 mL

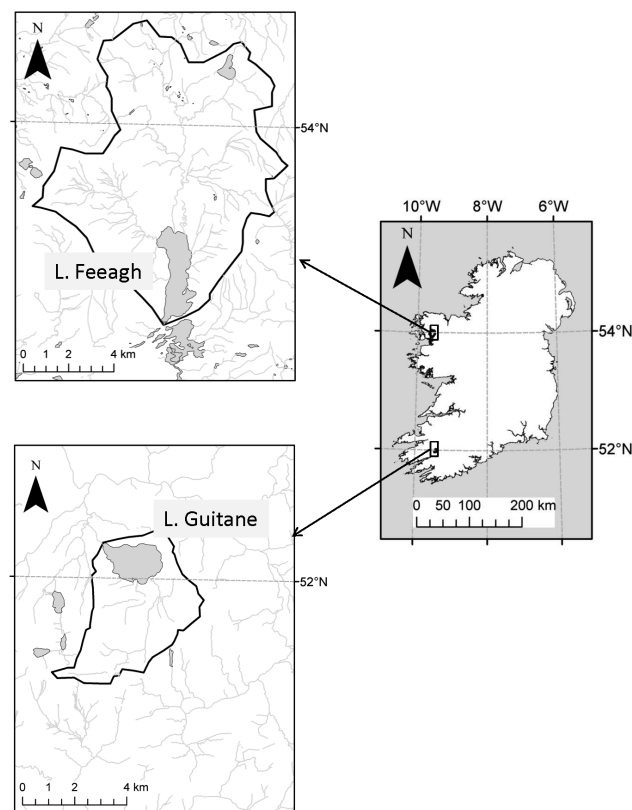


Fig. 1. Location of the 2 study sites, Loughs Feeagh and Guitane and their catchment boundaries.

subsample for phytoplankton and ciliate analysis was fixed with 1.5 mL of Lugol's iodine solution (Merck with a composition of $I_2 = 3.2 \text{ g L}^{-1}$ and $KI = 6.8 \text{ g L}^{-1}$; European Union 2009). Samples for picoplankton and bacterioplankton analysis were fixed with prefiltered (0.2 μm pore size, Whatman GTTPO2500) 20% formaldehyde buffered with sodium cacodylate 0.1 M to final concentrations of 1% and 4%, respectively (Hayat 1981), and stored in sterilized amber glass bottles (Callieri and Stockner 2002); the use of 20% formaldehyde is considered less stressful for cells (Callieri and Stockner 2002). The samples were kept refrigerated in the dark and were processed as soon as possible after sampling to avoid loss of cell numbers (Turley and Hughes 1992) and to decrease problems with bleaching of autofluorescent pigments (Olrík et al. 1998, Callieri and Stockner 2002). Alkalinity, conductivity, pH, total phosphorus (TP), dissolved molybdate reactive phosphorus (DMRP), total nitrogen (TN), nitrate (as nitrogen $\text{NO}_3\text{-N}$), and chlorophyll *a* (Chl-*a*) were analysed using standard methods (Eisenreich et al. 1975, Korolef 1983, Standing Committee of Analysts 1983, Davison 1990, Clesceri et al. 1999). Filtered samples (Whatman glass microfiber filter GF/F 0.45 μm pore size) were measured for colour using a Hach DR 5000 UV Vis Spectrophotometer in platinum cobalt units ($\text{mg L}^{-1} \text{ PtCo}$), while DOC (in mg L^{-1}) was measured using a TOC Elementar (model Vario TOC cube) analyzer (Clesceri et al. 1999).

Phytoplankton and ciliate cell enumeration was determined using the Utermöhl (1958) sedimentation technique. The characterization of autotrophic and mixotrophic species of phytoplankton was carried out according to Jansson et al. (1996) with modifications according to Isaksson et al. (1999). Bacterioplankton and picoplankton samples were processed when possible within 1 week in the laboratory following the method described by Sherr et al. (1993) and MacIsaac and Stockner (1993). A wetted white polycarbonate filter (Millipore, Ireland, type HAWPO2500) was placed on the filtering device to support the membrane filter to facilitate even distribution of the sample. Subsamples of 1 and 5 mL were filtered onto 0.2 μm pore-sized black isopore membrane filters (Millipore, Ireland, type GTBP 2500) and, in semi-darkness, 0.1 and 0.5 mL, respectively, of $0.1 \mu\text{g mL}^{-1}$ 4',6'-diamidino-2-phenylindole (DAPI) were added. The whole sample was drawn through the filter with a vacuum pump under low pressure (5–10 kPa; Kuppoo-Leinikki and Kuosa 1989, MacIsaac and Stockner 1993). For the picoplankton, two 5 mL subsamples underwent the same procedure without the addition of DAPI. The filters were dried after removal from the holder and directly mounted on glass slides on a small drop of 50% glycerol–water solution (Callieri and Stockner

2002a) with a cover slip. The slides were stored at $-20 \text{ }^\circ\text{C}$ to minimize bleaching of the autofluorescent pigments (MacIsaac and Stockner 1993).

Bacteria and picoplankton were counted under an epifluorescence microscope (ZEISS Axioplan). Bacteria were counted using a UV filter (G365, FT395, LP420), while picoplankton were examined using filters for blue (BP450-490, FT510, LP520) and green light excitation (LP510-KP560, FT580, LP590). The fluorescent cells observed on the filters were enumerated in random fields at the highest magnification ($\times 1250$). At least 400 cells were counted with an upper limit set at 30 fields to obtain a precision of 10% (Lund et al. 1958). The heterotrophic bacteria appeared bright blue in colour against a dark background. Conversion factors and other methodological specifications followed Straškrabová et al. (1999). Note that the picoplankton samples were not always processed immediately after field sampling, and therefore picoplankton counts are probably underestimated. Heterotrophic nanoflagellates were not enumerated for this study.

Phytoplankton and ciliate biomass were calculated by multiplying the number of cells of a given species counted in a sample by its average cell volume (calculated using digital photographs and the direct measurement of the linear dimensions; Potapova and Snoeijs 1997, Hillebrand et al. 1999). The biovolume of the dominant species was calculated according to 20 different geometric shapes and respective equations taken from the literature (e.g., Hillebrand et al. 1999, Sun and Liu 2003, Vadrucci et al. 2007). Digital images (Image Pro Plus v4.5.1) of picoplankton and bacterioplankton were used to measure volume of at least 100 cells according to the algorithms given in Massana et al. (1997). Multivariate analysis of the biological data was carried out using the package VEGAN (Oksanen et al. 2013) in R (v3.0.2; R Core Team 2013). Ordination of samples was carried out using multidimensional scaling (NMDS) whereby the placement of samples reflects the similarity of their biological communities. Biological data were square root transformed to down-weight the effect of abundant groups. Formal tests for differences between assemblages were carried out using ANOSIM (analysis of similarity), which tests the null hypothesis that there are no assemblage differences between groups of samples.

Results

Annual rainfall totals of 1657 mm yr^{-1} in Burrishoole (Feeagh) and 2023 mm yr^{-1} in Leane (Guitane) were recorded between May 2009 and April 2010. The wettest months in Burrishoole were July ($243.8 \text{ mm month}^{-1}$), August ($254.7 \text{ mm month}^{-1}$), and November ($322.9 \text{ mm month}^{-1}$), and the coldest temperature of $-1 \text{ }^\circ\text{C}$ was

registered at the end of December 2009. An extreme rainfall event occurred on 2 July 2009 on the east side of the Burrishoole catchment when 52 mm of rain was recorded over a period of 2 hours. This type of extreme rainfall event has an estimated expected return period in excess of 250 years in Ireland (Fitzgerald 2007). At Guitane, the wettest months were July (218.3 mm month⁻¹), October (223.3 mm month⁻¹), and November (485.1 mm month⁻¹) 2009, while the coldest temperature of -6.6 °C was recorded at the beginning of January 2010. A deep Atlantic depression brought wet and windy conditions to the southwest of Ireland in November and persistent and heavy rain, the highest on record (Walsh 2010), which led to unprecedented levels of flooding in many parts of the catchment in that month. The variation in daylight hours in Feeagh ranged from a maximum of 17.2 hours in July 2009 to a minimum of 7.5 hours in January 2010. Daylight hours in Guitane ranged between 16.7 in July 2009 and 7.9 hours in January 2010.

The water temperatures in Guitane were generally slightly higher than those in Feeagh, although the 2 study lakes had a relatively similar pattern in their temperature profiles over the study period (Fig. 2), with both lakes exhibiting thermal stratification in summer months. In Feeagh, the maximum temperature differential between the epilimnion and hypolimnion was recorded in July at 5.1 °C, while that of Guitane was 8.9 °C in the same month. This difference between the sites reflected, in part, colder deepwater temperatures in Guitane during summer. The water column of both lakes mixed in November 2009, remaining isothermal over the winter and early spring. The 2 lakes had similar pH and alkalinity levels (mean pH 6.9 for both lakes and mean alkalinity of 5 and 5.5 mg L⁻¹ CaCO₃ for Feeagh and Guitane, respectively), while Feeagh had generally higher conductivity, DOC, colour, and nutrient levels, and Guitane had higher concentrations of Chl-*a* (Table 1). Water colour was on average 4 times higher in Feeagh than in Guitane (84 and 21 mg L⁻¹ PtCo, respectively) and reached a maximum in August 2009 in Feeagh and in November 2009 in Guitane (Fig. 3). DOC concentration ranged from 6.2 to 11.4 mg L⁻¹ in Feeagh and from 1.5 to 6.4 mg L⁻¹ in Guitane. Secchi depth in Feeagh was 1.2–2.1 m while that of Guitane was 4.4–5.7 m, reflecting the difference in water colour at the 2 sites. Chl-*a* values were low (average 1.1 and 2.1 mg L⁻¹ in Feeagh and Guitane, respectively) but indicated similar seasonal patterns of phytoplankton dynamics in the 2 lakes, with highest values in midsummer, dropping to winter lows in January and February (Fig. 3). TP was generally low in both lakes, with annual averages falling into the oligotrophic class (<10 µg L⁻¹) as defined by the Organisation of Economic Co-operation and Development (OECD 1982). The exception to this was the sample taken

in November from Guitane, which spiked to 16 µg L⁻¹. This sample was taken from the lake outflow rather than mid-lake due to poor weather conditions, although note that none of the other physical or chemical variables seem to be affected. A proxy measurement for turbidity (nephelometer readings in millivolts; Fig. 4) increased after the July flood event in Feeagh. These readings did not return to pre-flood values for 3 months. No turbidity measurements were available for Guitane.

The total biomass of pelagic organisms quantified in this study differed significantly between the 2 lakes (t-test, $t = -2.4901$, $df = 22$, p -value = 0.021; Fig. 5). The average pelagic biomass of Feeagh was 366 mm³ m⁻³ over the annual cycle, while that of Guitane was 581 mm³ m⁻³. In general, the largest portion of the pelagic biomass in Feeagh was made up of bacteria (average of 153 mm³ m⁻³), followed by autotrophic phytoplankton (average 134 mm³ m⁻³). In Guitane, autotrophic phytoplankton biomass was higher (average of 355 mm³ m⁻³; Fig. 5) than that of bacteria (103.4 mm³ m⁻³). The ratio of phytoplankton (P, including mixotrophic species) to bacteria (B) biomass for each sampling occasion summarises this difference in the sites, with the annual P:B ratio in Feeagh averaging 1.17 (i.e., roughly similar biomass of phytoplankton and bacteria when mixotrophic species are included). In contrast, the P:B ratio of Guitane averaged 4.27 (i.e., 4 times more phytoplankton than bacteria over the annual cycle; Fig. 5). When potentially mixotrophic species (*Rhodomonas* sp., *Cryptomonas* sp., *Chrysochromulina parva* (Lackey), *Dinobryon* sp., *Ochromonas tuberculata* (D.J.Hibberd), *Gymnodinium uberrimum* (G.J.Allman) Kofoid & Swezy, and *Gymnodinium triceratium* (Skuja) are considered independently of the rest of the phytoplankton, Feeagh clearly supports a lower biomass of potential mixotrophs than Guitane (annual average of 30.9 and 82.7 mm³ m⁻³ respectively); however, the relative contribution of mixotrophic species in the overall phytoplankton biomass was similar in both lakes (annual average of 21% in Feeagh and 25% in Guitane). The biomass of phagotrophic ciliates was roughly similar in the 2 lakes, averaging 48 mm³ m⁻³ in Feeagh over 12 months and 37 mm³ m⁻³ in Guitane. The average annual biomass of autotrophic phytoplankton, bacteria, potentially mixotrophic phytoplankton, and ciliates represented 36, 43, 6, and 15%, respectively, of the pelagic biomass in Feeagh. In Guitane, the equivalent respective percentages were 57, 20, 15, and 8%.

The biomass of the constituent parts of the pelagic biomass also varied significantly between lakes (ANOSIM statistic $R = 0.46$, $p < 0.001$), resulting in clear separation of Feeagh samples from Guitane samples when plotted using NMDS (Fig. 6). The high relative biomass of autotrophic Chrysophyta (*Mallomonas akrokomos* and

Table 1. Physical and chemical characteristics of the 2 study sites, Lough Feeagh and Lough Guitane. Summary water chemistry characteristics are presented for monthly samples collected between May 2009 and April 2010.

	Feeagh			Guitane		
	Mean	Min.	Max.	Mean	Min.	Max.
Catchment area (km ²)	89.5			12.04		
Surface area (km ²)	3.95			2.46		
Max. (average) depth (m)	46 (14.5)			56 (18.7)		
pH	6.9	6.7	7.1	6.9	6.7	7.1
Alkalinity (mg L ⁻¹ CaCO ₃)	5.5	4.0	6.0	5.0	4.0	7.0
Conductivity (μS cm ⁻¹)	82	76	92	49	46	53
Colour (mg L ⁻¹ PtCo)	84	64	110	21	16	26
DOC (mg L ⁻¹)	7.7	6.2	11.4	3.3	1.5	6.4
TP (μg L ⁻¹)	8.1	5.0	12	5.3	2.0	15
DMRP (μg L ⁻¹)	1.6	0.9	3.0	1.1	0.9	3.0
TN (μg L ⁻¹)	462	200	870	340	210	530
NO ₃ -N (μg L ⁻¹)	70	38	83	113	75	180
Chl- <i>a</i> (μg L ⁻¹)	1.1	0.2	3.0	2.2	0.8	4.3

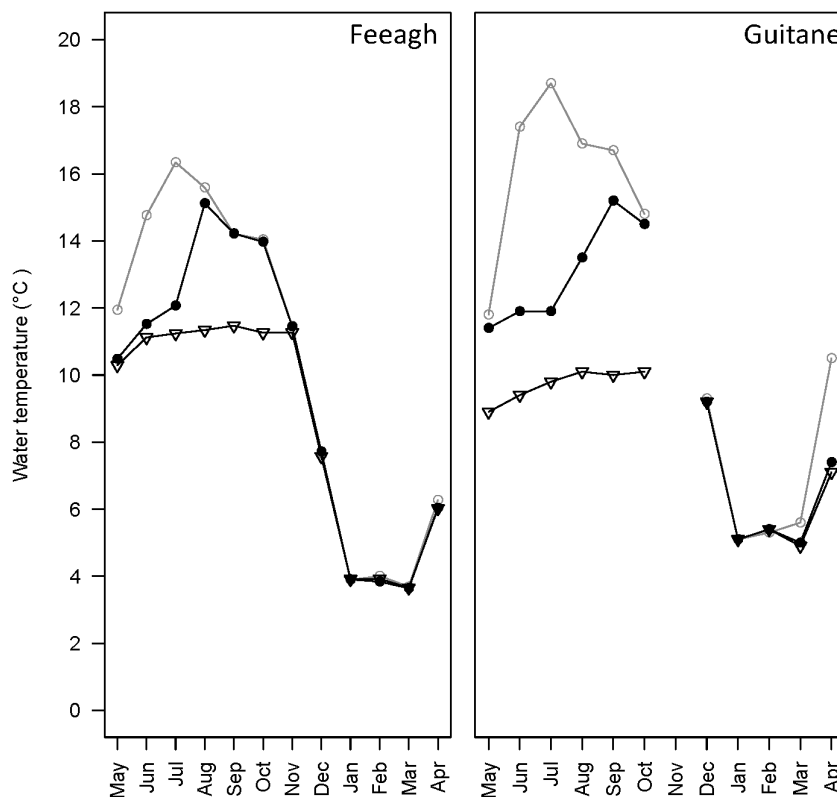


Fig. 2. Water column temperatures (°C) between May 2009 and April 2010 in Feeagh (left) and Guitane (right) at subsurface (2–2.5 m: open grey circles), mid-water (20 m: black filled circles), and at the lake bottom (40–42 m: triangles).

Mallomonas caudate), bacteria, and picoplankton distinguished the pelagic community of Feeagh. In contrast, the pelagic plankton of Guitane had relatively high biomass of the potentially mixotrophic Dinophyte *Ceratium hirundinella*, along with substantial biomass of cyanophytes and chlorophytes. Significant environmental vectors overlayed on the NMDS plot ($p < 0.05$; Fig. 6) indicate that the split between the pelagic food webs of the 2 lakes (i.e., top left to bottom right) can be best explained by the humic characteristics of the water (as indicated by colour and Secchi depth). The perpendicular vectors of pH, light,

and temperature indicate the difference between summer samples (plotted toward the bottom left of Fig. 6) and winter samples (plotted toward the top right of Fig. 6) in both lakes. The presence of the autotrophic dinophyte *Ceratium hirundinella* (O.F. Müller) characterised the samples taken in July 2009 from both lakes.

In Feeagh, the biomass of autotrophic phytoplankton (including picoplankton) was highest in the first 2 months of sampling during spring 2009 (Fig. 5). This biomass decreased substantially after the flood event on 2 July (the July sample was taken 3 weeks after the flood event),

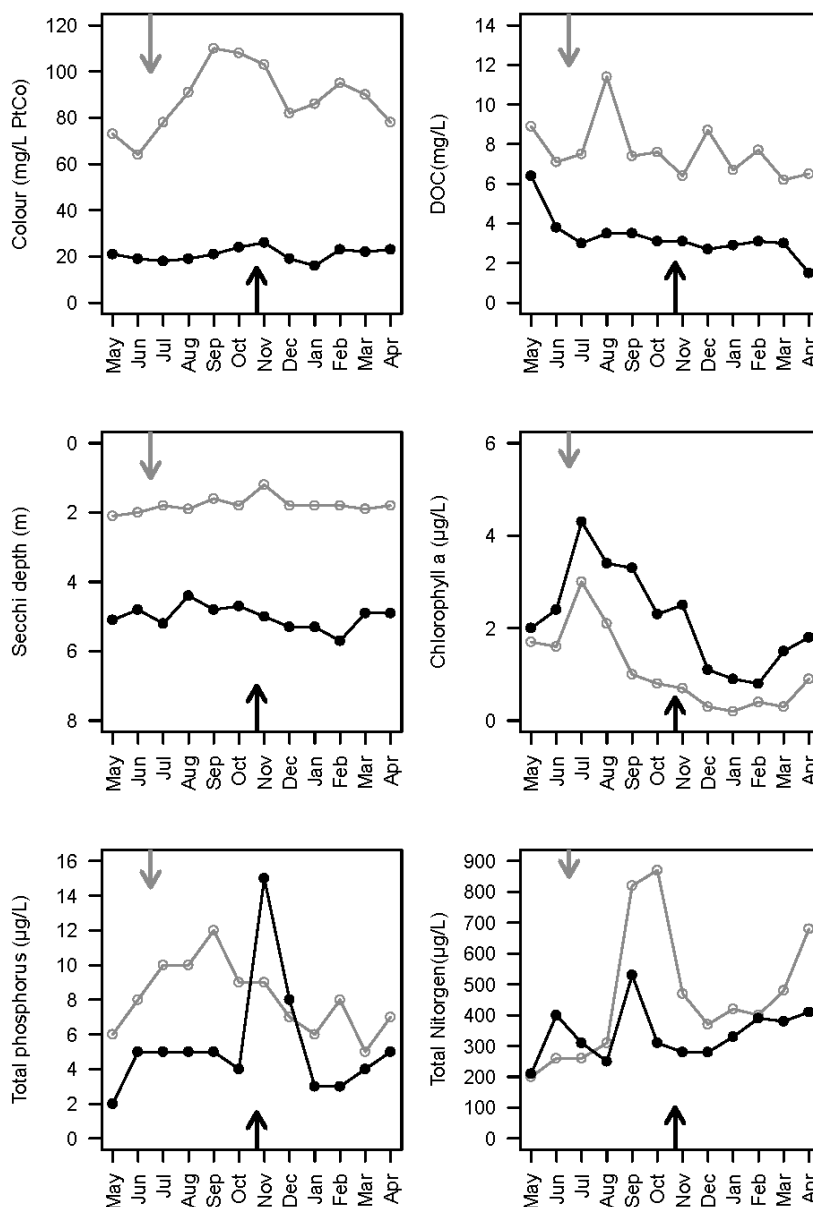


Fig. 3. Seasonal variation in colour, DOC, Secchi depth, chlorophyll *a*, total phosphorus, and total nitrogen in Loughs Feeagh (grey open circles) and Guitane (black filled circles) between May 2009 and April 2010. Arrows indicate the timing of heavy rainfall events in the Feeagh (grey) and Guitane (black) catchments.

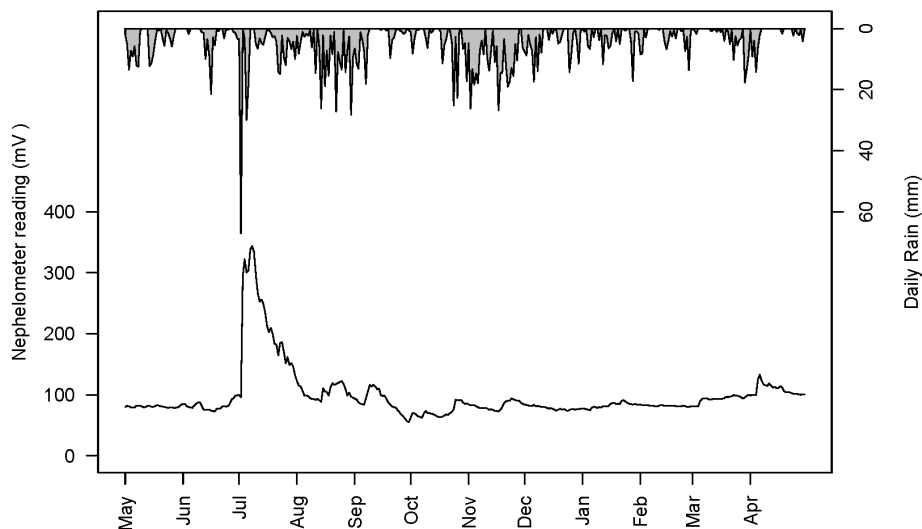


Fig. 4. Daily rainfall and average daily turbidity measurements from Lough Feeagh between May 2009 and April 2010. Turbidity was measured using an *in situ* nephelometer.

recovered slightly over the summer, and then dropped to a winter low between November and February 2009/2010. The potentially mixotrophic phytoplankton biomass followed a relatively similar pattern, being highest in May and then decreasing in the weeks after the flood. A small increase in biomass was noted in August before declining for the rest of the year. In contrast, both phagotrophic ciliate biomass and heterotrophic bacterial biomass increased in the month after the flood. Ciliate biomass also exhibited a peak in January 2010. Diatoms (predominantly *Asterionella formosa* Hassall and *Aulacoseira alpigena* [Grunow] Krammer) were common in all months. Samples from June to September were characterised by the presence and relatively high abundance of the autotrophic dinophyte *Ceratium hirundinella*. A bloom of the cyanophyte *Woronichinia naegelianana* (Unger) Elenkin was noted in August. The Cryptophyta *Rhodomonas* sp. and *Cryptomonas* sp. were also relatively frequent over the summer months.

Despite the seemingly obvious effect of the flood event on the biomass of various groups (Fig. 5), neither rainfall nor turbidity was significantly correlated with the ordination (Fig. 6). Instead, the pelagic communities seem to be most affected by seasonal changes in temperature, light, and pH, which enabled diverse summer populations of cyanophytes, mixotrophic cryptophytes, dinophytes, and chrysophytes to develop. In contrast, when the lake was fully mixed in winter, the winter samples were dominated by bacteria, ciliates, and picoplankton.

The autotrophic phytoplankton bloom in Guitane lasted longer than that of Feeagh, with high biomass being recorded until September 2009 (Fig. 5). Chlorophyte

biomass was highest between June and September and contained a diverse mix of species including *Cosmarium tinctum* Ralfs, *Crucigenia tetrapedia* (Kirchner) Kuntze, *Monoraphidium minutum* (Nägeli) Komárková-Legnerová, *Sphaerocystis Schroeteri* Chodat, and *Spondylosium planum* (Wolle) West & G.S. West. Late spring and early summer samples were characterised by relatively high biomass of autotrophic Chrysophyta and Dinophyta. While cell densities of colonial picocyanobacteria (*Aphanocapsa* sp., *Aphanothece* sp., and *Merismopedia* sp.) were high in the summer months, their relative biomass was low. The extensive precipitation of November had no noticeable effect on the species composition of the pelagic community; however, a notable bloom of *Tabellaria flocculosa* var. *asterionelloides* (Grunow) Knudson ($198 \text{ mm}^3 \text{ m}^{-3}$) was recorded in December. In general, diatom biomass remained consistently important throughout the annual cycle, as indicated by its placement in the centre of the ordination plot.

In both lakes, extreme precipitation events led to a decrease in phytoplankton biomass as indicated by Chl-*a* values (Fig. 7). When viewed in comparison to long-term monthly average Chl-*a* values (2007–2014 for Feeagh, 1999–2008 for Guitane), the Chl-*a* values after the precipitation events in both lakes were considerably lower than normal for the relevant time of year (Aug–Jan in Feeagh and Dec–Mar in Guitane), indicating depressed autotrophic production. While bacterial biomass increased in Feeagh after the flood from 218 to $324 \text{ mm}^3 \text{ m}^{-3}$, a similar pattern was not observed in Guitane, with bacterial biomass remaining low ($\sim 95 \text{ mm}^3 \text{ m}^{-3}$) in the months following heavy rainfall in November 2009 (Fig. 5).

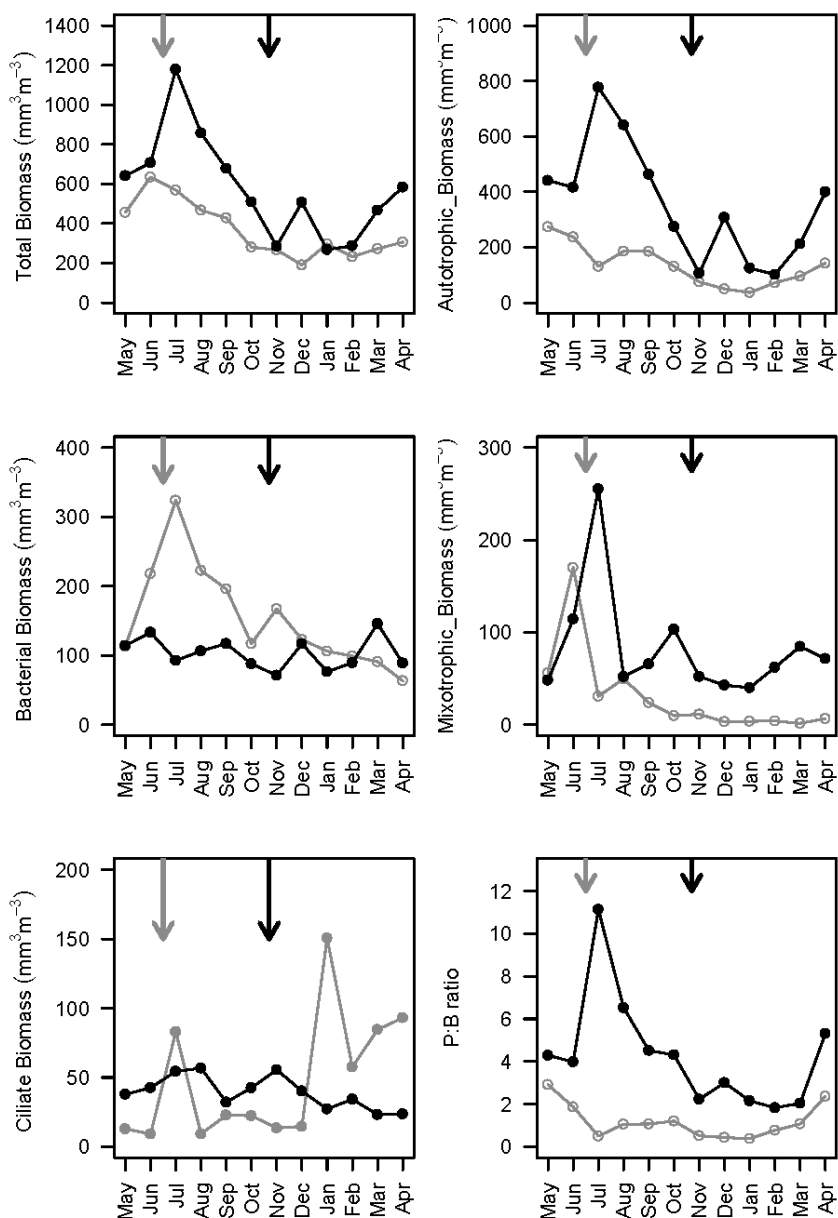


Fig. 5. Biomasses ($\text{mm}^3 \text{m}^{-3}$) of total open-water plankton, autotrophic phytoplankton, bacteria, potential mixotrophic phytoplankton, ciliates, and the phytoplankton:bacteria (P:B) ratio in Feeagh (grey open circles) and Guitane (black filled circles) between May 2009 and April 2010. Arrows indicate the timing of heavy rainfall events in the Feeagh (grey) and Guitane (black) catchments.

Discussion

Comparisons of water colour and nutrient concentrations from both lakes confirm the contrasting characteristics of Feeagh and Guitane, despite their similar peatland-dominated catchments and their similar Irish EPA preliminary Water Framework Directive (WFD) typology classification (Lake Type 4: deep [average >4 m and maximum depth >12 m], surface area >50 ha, and low alkalinity [$<20 \text{ mg L}^{-1}$

CaCO_3]; Free et al. 2006). Catchment percentage of peat cover is sometimes cited as a reliable predictor for DOC concentrations in catchment streams (e.g., Hope et al. 1994, Aitkenhead et al. 1999); however, if the most recently formulated classification scheme for the WFD (Poikane 2009) is applied, Feeagh and Guitane actually fall into separate lake types within the Northern Geographical Inter-calibration Group: humic (water colour 30–90 mg PtCo L^{-1}) and clearwater (water colour <30 mg PtCo L^{-1}), respectively.

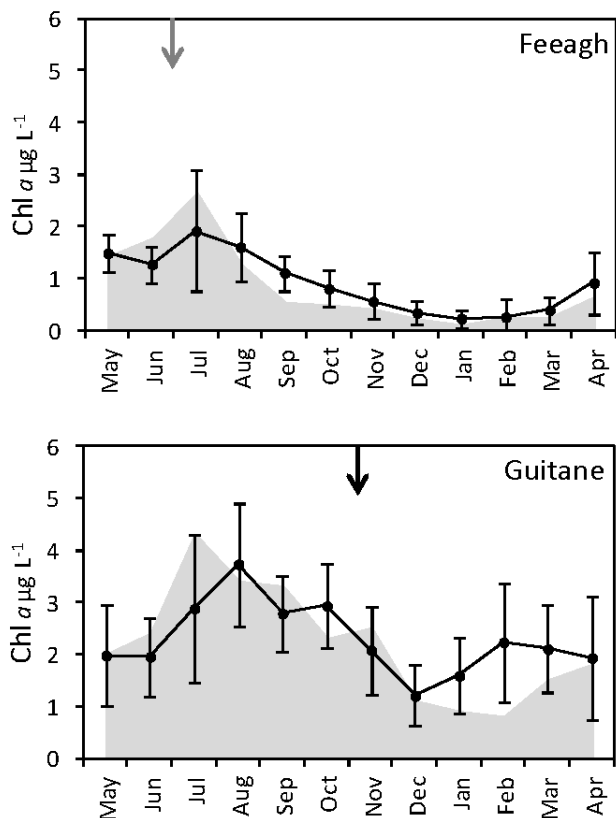


Fig. 7. Ethanol extracted Chl-*a* ($\mu\text{g L}^{-1}$) measured in open-water samples in Lough Feeagh (top) and Lough Guitane (bottom). The grey shaded areas indicated samples taken between May 2009 and April 2010. The black lines represent long-term monthly averages during 2007–2014 for Feeagh and 1999–2008 for Guitane, excluding the period of interest 2009–2010. Error bars indicated the standard deviation in long-term averages. Arrows indicate the timing of heavy rainfall events.

The P:B biomass ratio is generally low in humic lakes (Tranvik 1989, Bergström et al. 2003), and the bacterial production may be several times higher than the planktonic primary production (Tranvik 1989). This was evident in the study lakes with an annual mean ratio of 1.7 in Feeagh and 4.27 in Guitane. Moreover, the purely autotrophic biomass (phytoplankton not including mixotrophs) was generally lower over the annual cycle in Feeagh (except spring when diatoms increased) compared to the bacterial biomass. In contrast, phytoplankton dominated the pelagic biomass in Guitane. These results conform to several studies in humic lakes documenting that biomass and productivity of the heterotrophic bacteria can equal or be much greater than that of autotrophic communities in the euphotic zone (Jansson et al. 1996, 2001, Nürnberg and Shaw 1999, Staehr et al. 2012), a finding with implications for the role that individual lakes play in carbon cycling within a catchment. Because of the predominance of bacterial biomass in the pelagic zone,

Feeagh is likely a net heterotrophic lake over the annual cycle and thus acts as a carbon source to the atmosphere. Recent metabolism studies (Solomon et al. 2013) of Feeagh have indicated that this may be the case, with respiration exceeding gross primary production in the epilimnion in 2006, resulting in negative net ecosystem productivity (NEP) over the whole year. Guitane is also situated in a predominantly peat catchment, and we expected that heterotrophic bacteria would likewise play an important role in processing allochthonous carbon. The data presented here indicate that gross primary production in the epilimnion is likely to be higher than respiration, given the relatively higher biomass of autotrophs. If the whole lake is examined, however, significant heterotrophic productivity may be evident because considerable respiration may occur below the euphotic zone (Obrador et al. 2014).

The quantification of autotrophs and heterotrophs, as presented in this study of 2 contrasting lakes within peatland catchments, is a first step in understanding the role that these lakes play in processing terrestrial carbon stores. Future avenues for exploration include the calculation of whole lake metabolism for a range of temperate peatland catchments in this geographic area to quantify the contribution of pelagic organisms to NEP. Given the reported (Worrall and Burt 2007, Bates et al. 2008) and projected rises in DOC (Naden et al. 2010), this work would be particularly timely.

With the exception of the month after the flood for Feeagh, bacterial biomass in the 2 lakes was of a similar order of magnitude (Fig. 5). It was therefore unexpected that the biomass of potentially mixotrophic species was almost twice as high in Guitane than in Feeagh. Although primary production by autotrophs is probably the main route of energy to higher trophic levels in Guitane, there may be comparable quantities of heterotrophy in the 2 lakes (given the similar quantities of bacterial biomass). Thus, the cumulative amount of energy available to zooplankton and fish from these 2 sources was higher in Guitane than in Feeagh. Bacterial mineralization of terrestrial carbon is known to be significant in clearwater lakes (Karlsson et al. 2002) but is probably sometimes overlooked when there is obvious primary production by phytoplankton. Also noteworthy is that, although assimilation of allochthonous carbon into the pelagic food web via heterotrophs can be substantial, the nutritional quality of this resource is low (Kelly et al. 2014). In addition, the degree of heterotrophy in the potentially mixotrophic species may have varied between lakes and over time. Light attenuation in Feeagh increases the likelihood that the mixotrophic species outcompete other phytoplankton species (Morgan and Kalff 1979) by utilising the bacterial biomass as an energy source. In

Guitane, with a euphotic zone of several metres depth, the mixotrophic species also have the option of boosting their metabolism via autotrophy, leading to larger biomass accumulations despite the similar-sized bacterial resource.

Extreme precipitation events are known to have strong impacts on aquatic ecosystems (Parmesan et al. 2000). Flash floods increase the inflow of allochthonous inorganic suspended solids from the catchment. Jennings et al. (2010) described the effects of pulses in dissolved organic matter (DOM) from rivers into downstream lakes, which included prolonged decreases in lake water clarity. Data collected immediately after large flood events at the Swedish Lake Östräsket showed that such increases in the supply of labile organic substrates from the catchment stimulated bacterial production in the lake (Bergström and Jansson 2000, Drakare et al. 2002). Berggren et al. (2010) have shown that such responses can be the result of assimilation of low-molecular-weight DOM from terrestrial sources in the bacterial food web. The bacterial biomass in Feeagh followed a similar pattern, reaching a peak in the month after the flood event in July 2009 and then decreasing steadily over the following 9 months. The physicochemical data indicated that the main input to Feeagh with the floodwaters was particulate matter because the turbidity sensor showed an immediate spike while DOC and water colour showed no significant rise between June and July. A recent study by Guillemette et al. (2013) indicated that bacterioplankton can utilise both allochthonous and autochthonous sources of carbon, albeit over different time scales, so the increased input of carbon after the flood (especially in particulate form) was likely able to stimulate the growth of bacterial populations. The same stimulating effect of humic substances on growth and abundance of bacteria has been documented in many Scandinavian lakes (e.g., Tranvik 1988, Weyhenmeyer et al. 2004).

Although the rainfall in the Guitane catchment in November 2009 was the highest on record, the biomass of bacteria, ciliates, and mixotrophic phytoplankton remained constant over the subsequent winter months (Fig. 3). A small increase in phytoplankton biomass was evident between November and December, mainly due to *Tabellaria flocculosa* var. *asterionelloides*. Winter blooms of large diatoms are well documented (Kerfoot et al. 2008, Twiss et al. 2012), but without a long-term record, it is impossible to know whether this increase was related to higher precipitation levels. Chl-*a* was low relative to long-term records in the months post-flood at both sites, even though the events occurred at different times in the growing season. Although data were lacking for the physical and chemical effects of the floods in

Guitane, the data from Feeagh suggested that the decrease in Chl-*a* may have been due to increased turbidity; however, it is also noteworthy that Jennings et al. (2000) reported lower winter Chl-*a* in Leane, downstream of Guitane, in winters with a higher North Atlantic Oscillation index, characterised by increased rainfall. Washout of smaller phytoplankton species has also been reported following high rainfall from other lakes (Arvola et al. 1996). Our results suggest that in both lakes, the extreme precipitation events of 2009 can be considered significant disturbances. The Intermediate Disturbance Hypothesis (Connell 1978) predicts a decrease in biomass following a significant disturbance, whereas the normal response of phytoplankton to predictable seasonal rainfall is more likely to be an increase in biomass (Paidere et al. 2007, Mihaljević et al. 2009). The results presented here indicate that one of the likely outcomes of increases in extreme precipitation events in temperate lakes will be an overall decrease in gross primary productivity, as suggested by some future climate simulations (e.g., Jones et al. 2011). The results from Feeagh also indicate that some of this productivity loss may be compensated for by increased bacterial heterotrophy; however, the low nutritional quality of this heterotrophic mobilisation of terrestrial carbon means that overall energy transfer to zooplankton and fish is likely to be lower (Kelly et al. 2014).

Conclusions

The pelagic planktonic communities of Guitane and Feeagh conform to expectations derived from previous studies of clearwater and humic lakes. Despite their common situation in peatland-dominated catchments, the results indicate that a more significant proportion of the pelagic plankton in Feeagh, the more humic lake, was heterotrophic. Light restrictions caused by humic compounds probably limited the role of autotrophs, while the supply of DOC and POC supported significant biomass of heterotrophic bacteria. Bacterial biomass in the humic lake was especially high in the month following a flash flood in the catchment, which brought with it large amounts of particulate matter. In both lakes, Chl-*a* levels were depressed in the months following extreme precipitation events. The results presented here provide valuable empirical information, quantifying the temporal variability in the pelagic communities controlling lake metabolism, and in particular their response to extreme precipitation events. Given the high proportion of humic lakes in western and northern Europe, and the projected increasing levels of aquatic DOC with climate change, carbon emissions from these lakes are likely to increase in the future.

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