


# Legacy effects of drought alters the aquatic food web of a northern boreal peatland

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## Abstract

1. Compared to other temporary aquatic ecosystems, we know relatively little about how inundation frequency and duration (i.e. hydrologic regime) influences the structure of aquatic communities in northern peatlands. In this study, we examined patterns in nutrient availability and aquatic community structure during a natural flooding event in an Alaskan fen where water-table position had been manipulated in three large-scale experimental plots during previous years to simulate both drought (lowered water-table treatment) and flooding (raised water-table treatment) conditions relative to a control without manipulation. Although the natural flood disrupted the long-term experimental manipulation, it provided an opportunity to evaluate how variation in past hydrologic regime influences nutrient dynamics and aquatic food web structure during periods of inundation in a northern boreal peatland.
2. Despite similar water depth among experimental plots during the time of sampling (i.e. water was above the peat surface in all plots), water-column nutrient concentrations were significantly greater in the drought treatment (where water table had been lowered during the previous growing season) compared to the raised water-table treatment and the control.
3. Algal production increased with enhanced nutrient availability across all water-table treatments and was most elevated following the rewetting of dry sediments in the drought treatment. Consumer biomass (heterotrophic bacteria and macroinvertebrates) increased with algal production and was significantly greater in the drought treatment compared to the raised water-table treatment and the control. Consumer biomass decreased into the second year of constant inundation as algal production was constrained by reduced nutrient availability.
4. Stable isotope analysis (<sup>13</sup>C and <sup>15</sup>N) showed that elevated levels of periphyton (i.e. the intact biofilm) associated with enhanced nutrient availability promoted energy transfer to higher trophic levels (grazers and predators) rather than living or dead mosses or vascular plant material.
5. Consumption of algal material by grazers altered the size and composition of the algal community. The algal community shifted from coccoid (edible) to filamentous (inedible) growth forms with increased grazer abundance in the drought treatment, possibly owing to selective grazing. Conversely, there was a similar

proportion of edible and inedible taxa in the control and raised treatments where grazers were lower in abundance.

6. Our results show that the legacy effects of drought can regulate aquatic community structure in northern peatlands. Within a predictive context, our findings suggest that conditions of more variable hydrology expected with climate change (i.e. increased frequency of drought) occurring across northern latitudes will promote energy flow to higher trophic levels by releasing nutrient constraints on microalgae during periods of inundation.

#### KEYWORDS

Alaska, algae, climate change, hydrologic regime, macroinvertebrates

## 1 | INTRODUCTION

Photosynthetic carbon fixation by primary producers sustains heterotrophic organisms and the propagation of energy through ecosystems. In northern peatlands, primary production is limited by nutrient availability and plant communities in these ecosystems are comprised of taxa that can tolerate waterlogged soils and a low-nutrient environment (Wieder, 2006). Although peatland plants (e.g. mosses) are essential to the formation and maintenance of peat (Moore & Basiliko, 2006; Turetsky, 2003), they may minimise energy flow to higher trophic levels owing to their poor nutritional value (van Duinen et al., 2013). Consequently, the current paradigm in peatland ecology is that energy flow is constrained by recalcitrant detrital pathways. However, microalgae can also be abundant primary producers on submersed surfaces (i.e. saturated photic zone) in northern peatlands (Rober, Wyatt, Stevenson, & Turetsky, 2014; Wyatt, Bange, Fitzgibbon, Bernot, & Rober, 2015; Wyatt et al., 2012), and may provide an alternative avenue for energy transfer to higher trophic levels.

Unlike mosses, which are resistant to grazing, algal material is rapidly transferred to consumers in aquatic ecosystems (Feminella & Hawkins, 1995; Rober, Wyatt, & Stevenson, 2011). Algal taxonomic groups (e.g. diatoms, chlorophytes, cyanobacteria) vary in their cell storage products (i.e. lipids, starch, protein) and thus, the quality of algae as a food source and the proportion of biomass available for trophic transfer is related to community structure (Guo, Kainz, Sheldon, & Bunn, 2016; Müller-Navarra, Brett, Liston, & Goldman, 2000). Morphological differences also occur among various algal growth forms (e.g. colonial, filamentous) which can affect substratum available for bacteria colonisation as well as consumption by herbivores (Bell, 2002). Consumers can in turn regulate the structure of algal communities through selective grazing of small edible taxa in favour of large cells or more resistant forms, such as filamentous cyanobacteria (Agrawal, 1998). Despite known associations between algal community structure and energy transfer (Torres-Ruiz, Wehr, & Perrone, 2007), we know relatively little about how environmental conditions regulate energy flow from these basal resources to higher trophic levels in northern peatlands.

Inundation frequency and duration (i.e. hydrologic regime) plays a critical role in regulating community structure in aquatic ecosystems (Datry, Larned, & Tockner, 2014; Kneitel, 2014). In northern peatlands, shallow open water pools are largely intermittent (seasonal or episodic), resulting in both wet and dry phases in the same location at different points in time. Biogeochemical cycling tends to be enhanced at the interface of wet and dry phases (McClain et al., 2003), and is expected to become more common in northern peatlands as a consequence of more variable hydrologic conditions associated with climate change (Schuur et al., 2013). Specifically, warming has increased the frequency of drought associated with evapotranspiration as well as flooding associated with permafrost thaw and melt-water runoff (Osterkamp et al., 2009; Roach, Griffith, Verbyla, & Jones, 2011; Schuur et al., 2013). Recent studies have demonstrated that hydrologically induced biogeochemical hotspots enhance biological activity and subsequently influence food web structure (McClain et al., 2003; Schulz et al., 2015; Soininen, Bartels, Heino, Luoto, & Hillebrand, 2015). However, there is currently a lack of knowledge on the connection between terrestrial and aquatic phases of northern peatlands, including how the timing and duration of desiccation (the dry phase) influences aquatic community structure during the wet phase (i.e. legacy effects; Sala, Gherardi, Reichmann, Jobbagy, & Peters, 2012).

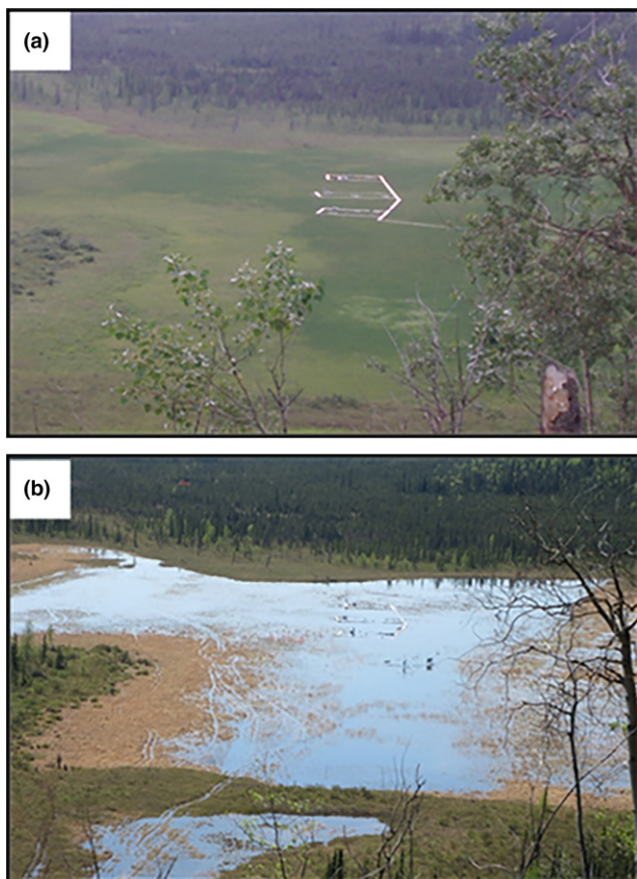
The Alaska Peatland Experiment (APEX) was established in 2005 to evaluate the long-term effects of changing hydrology on ecosystem processes in northern boreal peatlands. The site is made up of three water-table treatment plots with experimentally manipulated water-table position that includes both drought and flooding conditions relative to a control without manipulation. Since its establishment, all three experimental plots have also experienced natural flooding that briefly confounded the water-table manipulation. Previous studies have shown that rewetting of dry sediments during natural flooding events tends to elevate nutrient levels and results in greater overall biofilm production on peat surface layers (Rober, Wyatt, Turetsky, & Stevenson, 2013; Wyatt et al., 2012). To determine if these effects propagate to higher trophic levels, we evaluated patterns of heterotrophic bacteria and macroinvertebrates in relation to algal production and nutrient availability during a natural flooding event across all treatment plots for two growing seasons

(Figure 1). This period of flooding, although unexpected, allowed us to examine the effects of past hydrologic regime (experimental drought and flooding maintained during previous years through manipulation) on the relationship between algal production and consumer biomass in a northern boreal peatland. Furthermore, the duration of the natural flooding event allowed us to evaluate the extent to which past drought can influence nutrient cycling and community dynamics after rewetting (i.e. legacy effects). We hypothesised that low nutrient levels in conditions of stable hydrology constrain energy transfer to higher trophic levels. We expected that elevated nutrient levels in conditions of more variable hydrology (i.e. rewetting of dry sediments) would promote algal production on the peat surface, with increased energy transfer to all trophic levels.

## 2 | METHODS

### 2.1 | Study site

The APEX study site is a moderately rich fen located near the Bonanza Creek Experimental Forest, approximately 35 km southeast of Fairbanks, Alaska (64.82°N, 147.87°W). APEX is made up of three 30 m × 40 m experimental plots positioned 25 m apart and outlined



**FIGURE 1** Image of the APEX water-table plots during (a) experimental manipulation in 2012 and (b) the flooding event during our study period in 2013 [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

by a raised boardwalk to prevent disturbance of the peat surface during regular sampling. Water table is manipulated within experimental plots by pumping ground water during a time period from approximately the spring snowmelt until the ground freezes (Chivers, Turetsky, Waddington, Harden, & McGuire, 2009). Drought conditions (lowered water-table treatment) are maintained by a series of drainage canals that divert water away from the treatment plot to reduce water-table position 10 cm below the control plot (ambient). Flooding conditions (raised water-table treatment) are maintained by solar-powered bilge pumps that increase water-table position 5 cm above the control (Turetsky et al., 2008). Despite experimental manipulation, natural variation in hydrology that is characteristic of flood plain landscapes within interior Alaska (i.e. flooding following the spring snowmelt) continues to occur and can overwhelm the ability for pumps to maintain experimental differences in water-table position. Consequently, periodic episodes of natural flooding that result in standing water above the peat surface in all three plots have briefly confounded the experiment (Churchill, Turetsky, McGuire, & Hollingsworth, 2015; Kane, Turetsky, Harden, McGuire, & Waddington, 2010; Wyatt et al., 2012). This study was conducted during such an event in 2013, when heavy precipitation resulted in standing water above the peat surface in all plots throughout the growing season (May–August; Figure 1b), and flooding conditions in 2013 were sustained into 2014. This study was conducted from 30 May to 18 July 2013 and from 28 May to 4 June 2014 (when the water table fell below the peat surface in all plots).

### 2.2 | Environmental parameters

Environmental parameters were monitored at six locations within each of the three water-table plots each week. Water-table height above the peat surface was measured inside polyvinyl chloride wells located in each treatment plot. Surface water temperature, pH and dissolved oxygen (DO) were measured with a Hach model 40d multi-probe (Hach Company, Loveland, CO, U.S.A.). Water samples for dissolved nutrient analysis were collected from 5 cm above the peat surface and filtered through a 0.45- $\mu\text{m}$  filter (Millipore Corporation, Bedford, MA, U.S.A.) into 20-ml acid-washed polyethylene bottles. Dissolved nutrient samples were stored on ice in the field and frozen until analysis for nitrate ( $\text{NO}_3^-$ ) and phosphate ( $\text{PO}_4^{3-}$ ) concentration with a Dionex ion chromatograph (Dionex Corporation, Sunnyvale, CA, U.S.A.) (APHA, 1998). Environmental parameters were measured at the same six locations within each water-table plot and at the same time of day (between 10 a.m. and 2 p.m.) as the collections of algae, bacteria and macroinvertebrates described below.

### 2.3 | Algal parameters

Algae were sampled at six locations within each of the three water-table plots using non-destructive methods as a conservation measure to limit disturbance of plant material at this long-term study site. Each composite sample ( $n = 6$ ) included four subsamples collected from the peat surface and the submersed portions of four *Carex*

*utriculata* (Cyperaceae) stems (the dominant emergent macrophyte) within a 25 cm<sup>2</sup> area. A plastic syringe was used to gently remove algae from each quadrat until there were no loosely attached algae or biofilms present on the peat surface and tightly attached algae were removed from the submersed portions of plant stems by scraping and brushing (Rober et al., 2013). The length and width of each stem was measured and the surface area of each stem was adjusted in subsequent calculations. Care was taken to eliminate plant material from composite samples during sample collection and when present, small pieces of flocculent plant material were removed from each composite sample with forceps.

Each composite sample was diluted to a known volume with filtered fen water and inverted several times before separating into subsamples for algal chlorophyll *a* (chl-*a*), cell density and taxonomic composition. A subsample was transported to the lab on ice where it was filtered onto a glass fibre filter (0.7 µm GF/F Whatman, Springfield Mill, U.K.), placed into a 20-ml centrifuge tube with 90% ethanol and steeped in the dark overnight in a refrigerator. Chl-*a* was measured from the extract with a Shimadzu UVmini-1240 spectrophotometer (Shimadzu Corporation, Kyoto, Japan) at 665 and 750 nm before and after acidification to correct for phaeopigments (American Public Health Association (APHA), 1998). Subsamples for algal composition analysis were preserved in 2% formalin solution. Algal abundance and taxonomic composition were characterised by counting and identifying ≥300 natural units per composite sample using a Palmer-Maloney nanoplankton counting chamber (Charles, Knowles, & Davis, 2002). Algae were identified to genus at 400× magnification with a Leica DM 4000 microscope (Leica Microsystems, Wetzlar, Germany) and categorised by division and functional group.

## 2.4 | Bacterial biomass

We examined bacterial biomass on plant stems collected at each of six sampling locations within each of the three water-table plots using epifluorescence microscopy. The submersed portions of two *C. utriculata* stems were collected at each location in a sterile glass vial and preserved in the field with formalin. Bacterial cells were detached from stems by a combination of probe ultrasonication and brushing and aliquots of each sample were stained with 4', 6-diamino-2-phenylindole (DAPI) (Porter & Feig, 1980). The stained aliquots were filtered onto a 0.2-µm pore-size black filter (OSMONIC INC., Livermore, CA, U.S.A.) and a minimum of 300 cells or 25 fields were counted per filter at 1000× magnification using a light microscope with fluorescence (Leica Microsystems model DM 4000, Wetzlar, Germany). Cell volume (µm<sup>3</sup>) was calculated from measurements of length (*l*) and width (*w*) using the formula:  $V = w^2/4 \times (l - w) \times \pi + w^3/6 \times \pi$  and bacterial biomass was calculated according to Loferer-Kröbächer, Klima, and Psenner (1998).

## 2.5 | Measures of macroinvertebrate abundance and taxonomic composition

Macroinvertebrates were collected for abundance and community composition three times during the 2013 growing season (early,

middle, late) and only once in 2014 (owing to the rapid reduction in water level). Macroinvertebrates were collected from six locations within each treatment plot using a dipnet and each sample was a composite of three sweeps that were 1 m in length (Genet & Bourdagh, 2006; Hannigan & Kelly-Quinn, 2012). Macroinvertebrates were separated from detritus and plant material in 15 × 21 cm white pans and preserved in 70% ethanol in the field. Macroinvertebrates were counted and identified to family level following Merritt, Cummins, and Berg (2008). Following identification, biomass of macroinvertebrates was determined by drying 10 individuals of each taxon in pre-weighed aluminium pans for 24 hr at 60°C and then multiplying the dry mass (mg) by the number of individuals of each taxon.

## 2.6 | Isotopic analysis

During peak algal biomass (13 June 2013), we used isotopic analysis to evaluate trophic structure and energy transfer through the peatland food web. Samples of macroinvertebrates (grazers and predators) and potential basal resources (periphyton, plants, detritus) collected from each of the experimental plots were aggregated and analysed for natural abundances of carbon (<sup>13</sup>C) and nitrogen (<sup>15</sup>N). Algal biofilms were collected as described above. Because we were unable to separate autotrophic and heterotrophic components of the biofilm for isotopic analysis, we hereafter refer to this basal resource as periphyton. Macroinvertebrate samples were collected using methods described above and snails were removed from their shell prior to analysis. We collected living vascular plants (*Equisetum fluviatile* [Equisetaceae], *C. utriculata*; the dominant macrophytes in the system), detritus (i.e. dead plant material), moss (composite of *Sphagnum* [Sphagnaceae] and brown moss species [Amblystegiaceae and Brachytheciaceae]), and peat during the same timeframe. We removed sediment, non-plant material and attached periphyton from plant material in the lab with distilled water. All samples were dried at 60°C for 48 hr, ground into a fine powder, and isotopic composition was determined with a continuous flow isotopic ratio mass spectrometer (PDZ Europa, Sercon Ltd., Cheshire, U.K.) at the University of California Davis Stable Isotope Facility. All stable isotope values have been reported in the δ notation as parts per thousand (‰) deviation from established standards (Pee Dee belemnite for δ<sup>13</sup>C and atmospheric N for δ<sup>15</sup>N) where δ<sup>13</sup>C or δ<sup>15</sup>N =  $([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000$ , where *R* is <sup>13</sup>C:<sup>12</sup>C or <sup>15</sup>N:<sup>14</sup>N. Analytical precision was 0.2‰ for δ<sup>13</sup>C and 0.3‰ for δ<sup>15</sup>N. The δ<sup>15</sup>N signatures were used to estimate trophic position as the δ<sup>15</sup>N of a consumer is typically enriched by 3‰–4‰ relative to the prey (Peterson & Fry, 1987). The δ<sup>13</sup>C signatures were used to determine the source(s) of C propagated through the food web (e.g. periphyton versus plant versus detritus) and were based on the assumption that δ<sup>13</sup>C changes <1‰ per trophic level (Post, 2002).

## 2.7 | Statistical analysis

We used repeated measures general linear models (RM-GLM) and Tukey's Honestly Significant Difference (HSD) tests for post hoc



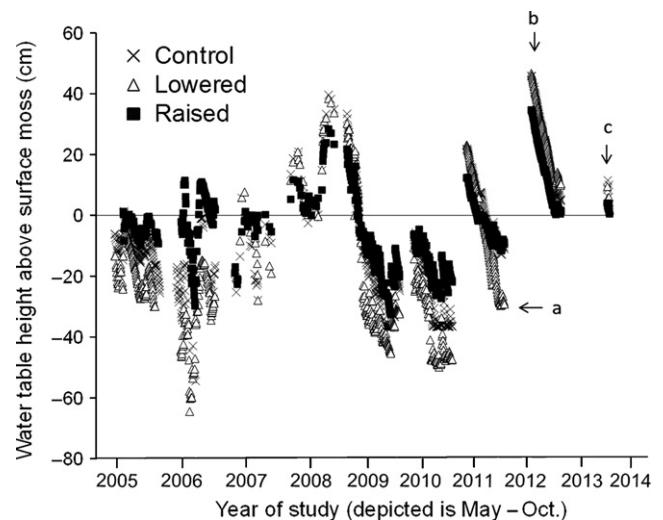
comparison of means to determine if algal and heterotrophic parameters were different among water-table treatments over time. We included  $\text{NO}_3^-$  and  $\text{PO}_4^{3-}$  in the model as predictors of algal biomass, heterotrophic bacteria and macroinvertebrates because univariate RM-GLM indicated significant differences among treatments. Environmental parameters that were not significantly different among water-table treatments were not included in the model and have been reported as the mean  $\pm 1$  SE for each growing season. Linear regression analyses were used to evaluate relationships between measures of nutrients, algae, heterotrophic bacteria and macroinvertebrate abundance in the water-table manipulation. Repeated measures multivariate analysis of variance (RM-MANOVA) and Tukey's test for post hoc comparisons of means was used to evaluate differences in algal taxonomic composition among water-table treatments for taxa present at  $\geq 10\%$  relative abundance. Differences in macroinvertebrate taxonomic richness among water-table treatments were evaluated using RM-ANOVA and Tukey's post hoc comparison of means. It is important to note that our water-table treatment was not replicated (i.e. one plot per treatment) and therefore, the effects of water-table treatment were tested with a small number of  $df$  and some caution is warranted given the lack of true replicates. Statistical analyses were performed with SPSS 20 (IBM Statistics, Chicago, IL, U.S.A.).

We used the Bayesian mixing model Stable Isotope Analysis in R (SIAR; Parnell et al., 2013) approach to investigate the relative contributions of periphyton, plants and detritus to peatland aquatic macroinvertebrate diets using R (R Core Team, 2015). We ran the model for primary consumers and predators using the mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for periphyton, *C. utriculata*, *E. fluviatile*, plant detritus, moss and peat as possible basal resources. We used trophic fractionation factors of  $0.47 \pm 1.23\text{‰}$  for  $\delta^{13}\text{C}$  and  $3.46 \pm 0.23\text{‰}$  for  $\delta^{15}\text{N}$  according to Vander Zanden and Rasmussen (2001).

### 3 | RESULTS

#### 3.1 | Environmental parameters

In contrast to previous years when water-table position was regulated by experimental manipulation, the natural flood over experimental plots resulted in an elevated water table that remained above the peat surface in all treatments during the growing season in 2013 (Figure 1b). Mean ( $\pm$  SE) water depth was  $40.3 \pm 1.2$  cm (control),  $40.3 \pm 1.7$  cm (lowered) and  $36 \pm 1.6$  cm (raised) above the peat surface following the spring thaw (in May 2013) and decreased over time to  $5.44 \pm 0.3$  (control),  $10.6 \pm 0.3$  (lowered) and  $1.13 \pm 0.2$  (raised) above the peat surface in July 2013 (Figure 2). Saturated soil conditions at the end of the growing season 2013 were sustained into the 2014 growing season (Figure 2). Mean water depth was similar among control ( $6.63 \pm 1.29$  cm), lowered ( $4.78 \pm 0.89$  cm) and raised ( $2.59 \pm 0.48$  cm) experimental treatments in 2014 until the water table dropped below the peat surface 2 weeks following the spring thaw (4 June). Water depth was not significantly different between control and lowered water-table treatments throughout the



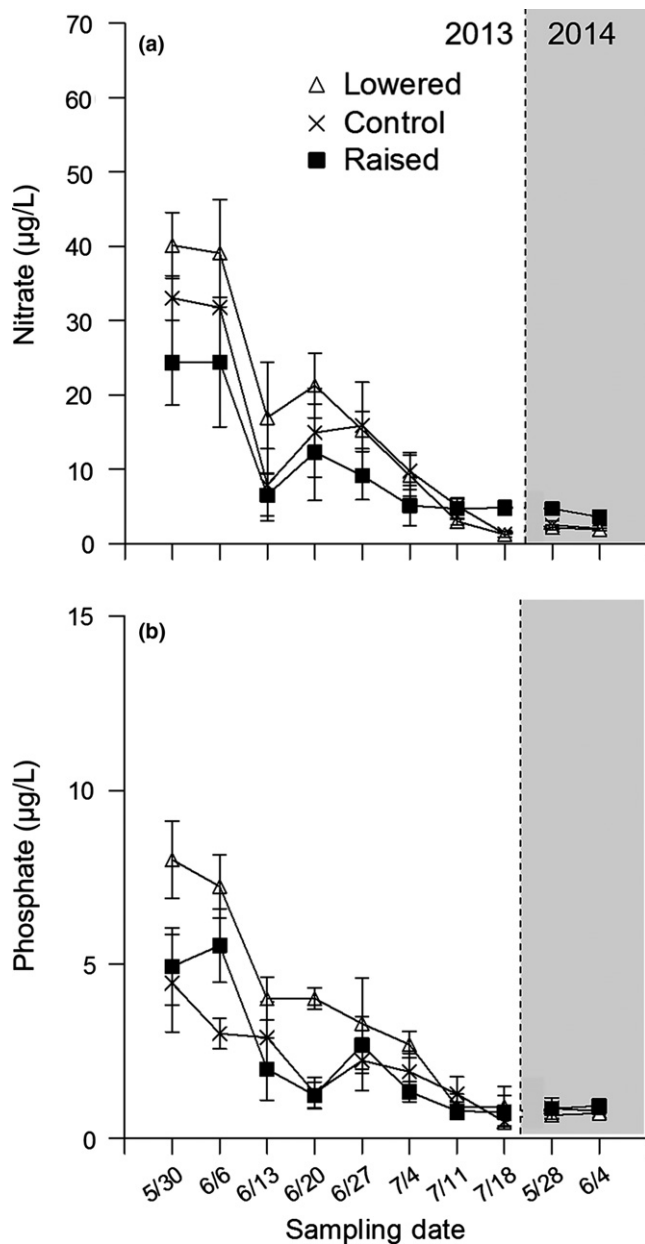
**FIGURE 2** Long-term seasonal trends in water-table position across the control, lowered and raised water-table treatments (negative values indicate water-table position below the surface of the peat). Letters depict the period of manipulation in 2012 (a) and during the flooding event when water was above the peat surface in 2013 (b) and 2014 (c)

sampling period ( $p = .64$ ), and was consistently lower in the raised water-table treatment ( $p < .001$ ; Figure 2). Mean ( $\pm$  SE) water temperature ( $19 \pm 0.25$  and  $17 \pm 0.52^\circ\text{C}$ ) and pH ( $6.52 \pm 0.09$  and  $6.34 \pm 0.04$ ) were similar among treatments throughout the growing season in 2013 and 2014 respectively ( $p > .05$ ). Dissolved oxygen concentration (mg/L) peaked with algal biomass and was similar among the lowered ( $6.37 \pm 0.97$ ), raised ( $5.90 \pm 1.32$ ) and control water-table treatments ( $6.13 \pm 0.90$ ) in both 2013 and 2014 growing seasons ( $p = .26$ ).

Surface water nutrient concentrations (mean  $\pm$  SE) peaked in all water-table treatments following the spring thaw in 2013 and were the most elevated in the lowered (i.e. drought) treatment ( $\text{NO}_3^-$ :  $40.1 \pm 3.97$   $\mu\text{g/L}$ ;  $\text{PO}_4^{3-}$ :  $8.00 \pm 0.99$   $\mu\text{g/L}$ ), where concentrations of  $\text{NO}_3^-$  (RM-GLM,  $F_{2,150} = 4.56$ ,  $p = .012$ ) and  $\text{PO}_4^{3-}$  (RM-GLM,  $F_{2,150} = 13.6$ ,  $p < .0001$ ) were significantly greater compared to the raised ( $\text{NO}_3^-$ :  $24.3 \pm 5.15$   $\mu\text{g/L}$ ;  $\text{PO}_4^{3-}$ :  $4.93 \pm 1.00$   $\mu\text{g/L}$ ) and control ( $\text{NO}_3^-$ :  $33.0 \pm 2.69$   $\mu\text{g/L}$ ;  $\text{PO}_4^{3-}$ :  $4.45 \pm 1.26$   $\mu\text{g/L}$ ) treatments (Figure 3a,b). Nutrient concentrations declined in all water-table treatments over the remainder of the 2013 growing season (Figure 3). Low nutrient concentrations ( $\text{NO}_3^-$ :  $2.82 \pm 0.21$   $\mu\text{g/L}$ ;  $\text{PO}_4^{3-}$ :  $0.79 \pm 0.05$   $\mu\text{g/L}$ ) were sustained into the 2014 growing season following continuously saturated soil conditions from the previous year, and were similar among water-table treatments ( $p = .75$ , Figure 3a,b).

#### 3.2 | Algal biomass

Measures of algal biomass increased with greater nutrient availability. Chl-*a* peaked shortly following the maxima in nutrient concentrations and was significantly greater in the lowered (i.e. drought) treatment compared to the control and raised treatments (RM-GLM,



**FIGURE 3** Mean ( $\pm 1$  SE;  $n = 6$ ) surface water (a) nitrate and (b) phosphate concentrations in the control, lowered and raised water-table treatments on each sampling date during the 2013 and 2014 (shaded portion) growing seasons in the APEX fen

$F_{2,150} = 31.2$ ,  $p < .0001$ ), which were not significantly different from each other ( $p = .55$ ; Figure 4a). Elevated algal chl-*a* was related to increases in both N and P concentrations ( $\text{NO}_3^-$ :  $r^2 = .52$ ,  $p < .0001$ ;  $\text{PO}_4^{3-}$ :  $r^2 = .43$ ,  $P < .0001$ , Figure 5a). Algal chl-*a* remained consistently higher in the lowered water-table treatment throughout the remainder of the 2013 growing season but declined with nutrient concentrations. In contrast to conditions in 2013, mean ( $\pm$  SE) chl-*a* was low following the spring thaw in 2014 ( $2.67 \pm 0.37$  mg/m<sup>2</sup>), when saturated soil conditions had been sustained from the previous growing season, and was similar among water-table treatments ( $p = .56$ , Figure 4a).

### 3.3 | Bacterial and macroinvertebrate biomass

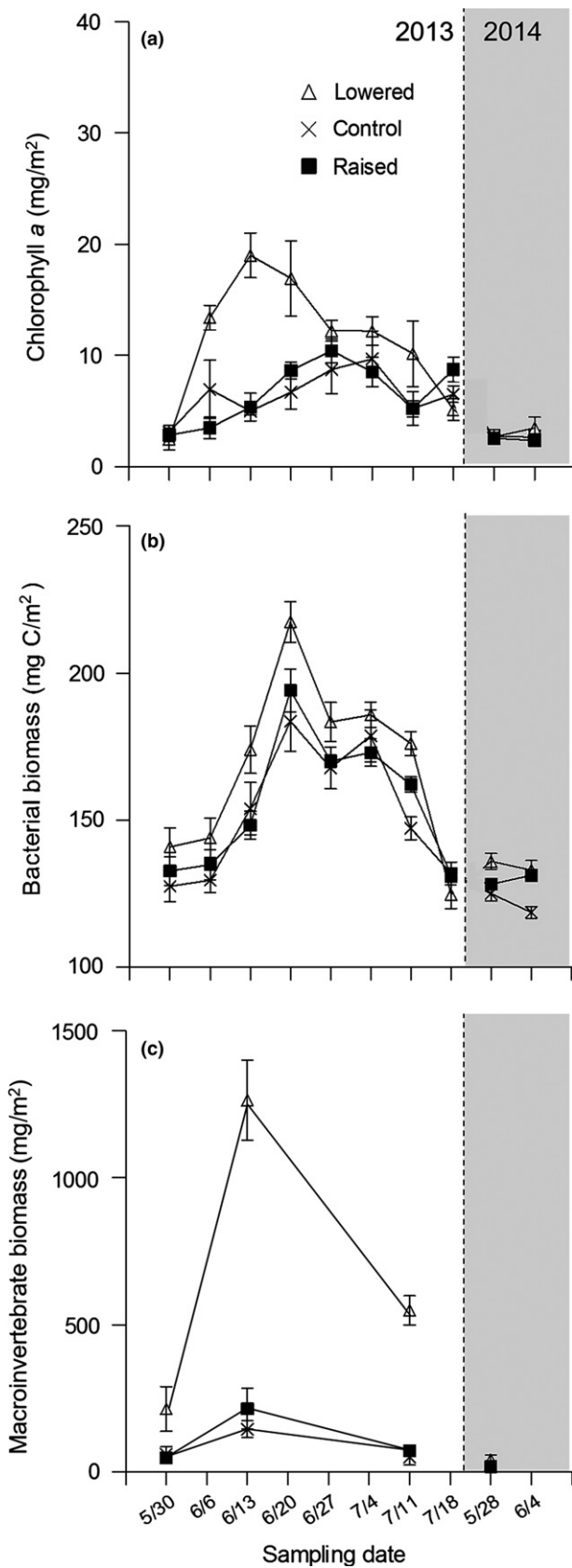
Bacterial biomass was significantly greater in the lowered water-table (i.e. drought) treatment compared to the raised and control treatments in 2013 (RM-GLM,  $F_{2,150} = 25.3$ ,  $p < .0001$ , Figure 4b), and increased bacterial biomass was related to enhanced algal production ( $r^2 = .43$ ,  $p < .0001$ , Figure 5b). Mean ( $\pm$  SE) bacterial biomass was low following the spring thaw in 2014 ( $129 \pm 1.3$  mg C/m<sup>2</sup>) and not significantly different among treatments (RM-GLM,  $F_{2,150} = 2.79$ ,  $p = .07$ , Figure 4b). Macroinvertebrate biomass (mg/m<sup>2</sup>) was greatest in all three water-table treatments during peak algal biomass and was significantly greater in the lowered water-table (i.e. drought) treatment compared to the raised and control treatments (RM-GLM,  $F_{2,35} = 18.9$ ,  $p \leq .003$ , Figure 4c). Macroinvertebrate biomass was similar among treatments when algal biomass accumulation was apparently constrained by low nutrient availability in 2014 ( $p > .92$ , Figure 4c).

### 3.4 | Isotopic analysis

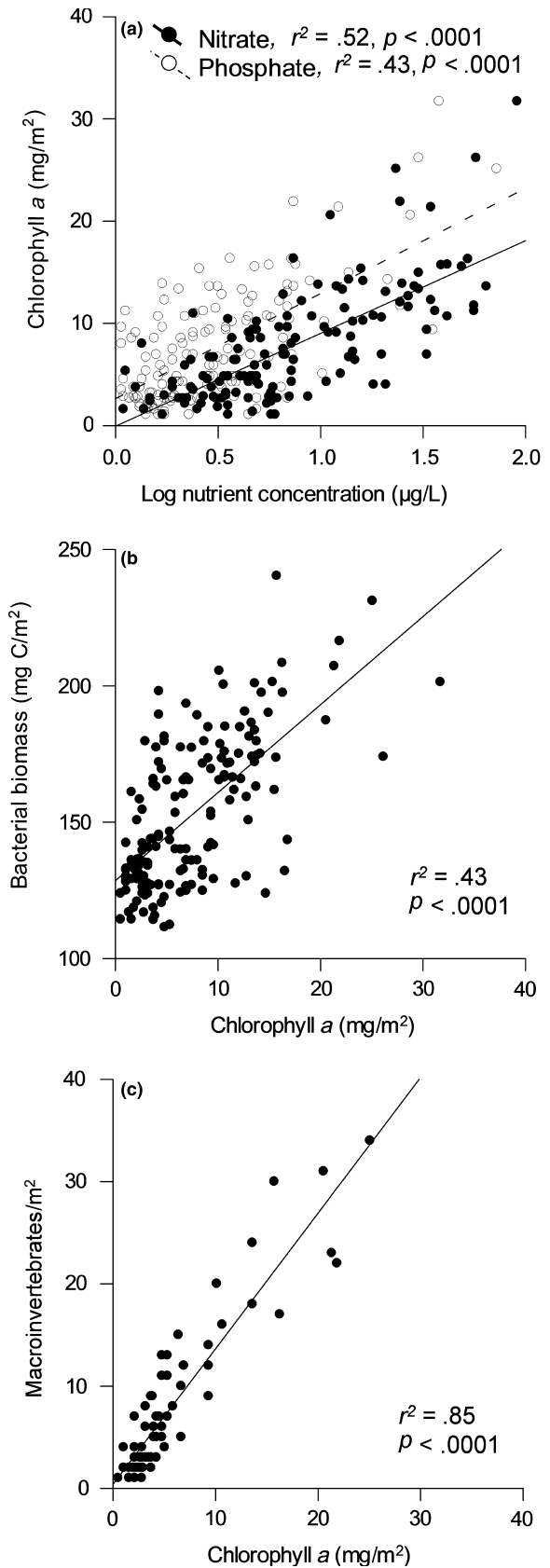
The  $\delta^{13}\text{C}$  signature (mean  $\pm$  SD) of periphyton ( $-32.4 \pm 0.37$ ) showed a large separation (6‰–8‰) from vascular plants ( $-24.4 \pm 0.51$ ), plant detritus ( $-26.0 \pm 0.08$ ) and peat ( $-26.3 \pm 0.19$ ; Figure 6). The  $\delta^{13}\text{C}$  signature for periphyton was depleted by  $\sim 3$ ‰ compared to moss ( $-29.5 \pm 0.05$ ). *Equisetum fluviatile* was more enriched in  $\delta^{15}\text{N}$  ( $4.28 \pm 0.25$ ) than other basal sources, and the  $\delta^{15}\text{N}$  signatures for periphyton ( $1.02 \pm 0.89$ ) and moss ( $0.85 \pm 0.15$ ) were more enriched (1‰–2‰) compared to *C. utriculata* and plant detritus (Figure 6). The  $\delta^{13}\text{C}$  signatures for macroinvertebrates were more similar to periphyton ( $< 1$ ‰ change) than detritus, vascular plants, moss or peat (Figure 6). The  $\delta^{15}\text{N}$  signatures for primary consumers (snails [*Lymnaea*], chironomid larvae, caddisfly [*Limnephilus*] and mosquito [*Culicidae*] larvae) were enriched by 1–6‰ relative to periphyton (Figure 6). The  $\delta^{15}\text{N}$  signatures for predators (dragonfly larvae [Libellulidae, Corduliidae], damselfly larvae [Coenagrionidae], beetle larvae [Dytiscidae] and a leech [Hirudinea]) were enriched 1‰–3‰ relative to primary consumers (Figure 6). According to the SIAR mixing model, primary consumers obtained 79% of their energy from periphyton compared to  $\leq 4.6\%$  from detritus, vascular plants, moss or peat. On average, the energy transferred from primary consumers to predators was 82% of periphyton origin, with the mean of the average predator diet composed of mosquito larvae (56%) and caddisfly larvae (24%).

### 3.5 | Algal and macroinvertebrate abundance and composition

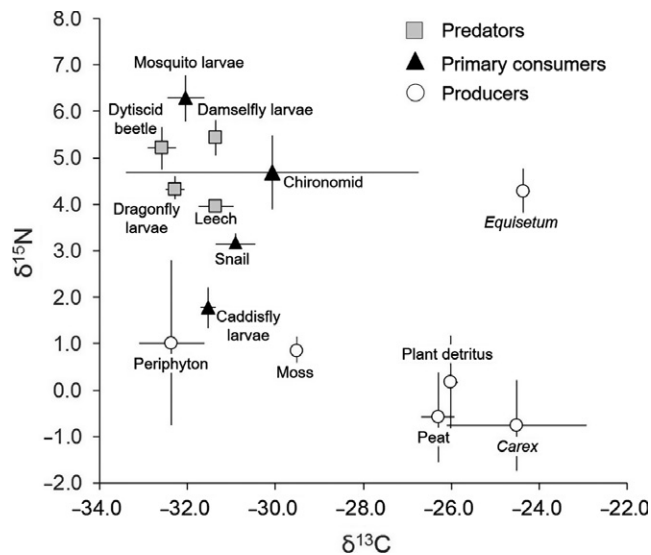
Algal community structure and morphology (i.e., colonial, filamentous) varied with water-table position and resource supply. Filamentous green algae (Chlorophyta) were the most abundant taxonomic group in the lowered water-table treatment during peak algal abundance, comprising 69% of total cell density (RM-MANOVA,  $F_{16,315} = 5.16$ ,  $p < .001$ , Figure 7b), and coccoid and colonial green



**FIGURE 4** Mean ( $\pm 1$  SE;  $n = 6$ ) (a) chl-*a*, (b) bacterial biomass and (c) macroinvertebrate biomass in the control, lowered and raised water-table treatments on each sampling date during the 2013 and 2014 (shaded portion) growing seasons in the APEX fen



**FIGURE 5** Relationships between algal chl-*a* and (a) log-transformed nutrient concentrations, (b) bacterial biomass and (c) macroinvertebrate abundance. Points represent individual measurements across all water-table treatments and sampling dates



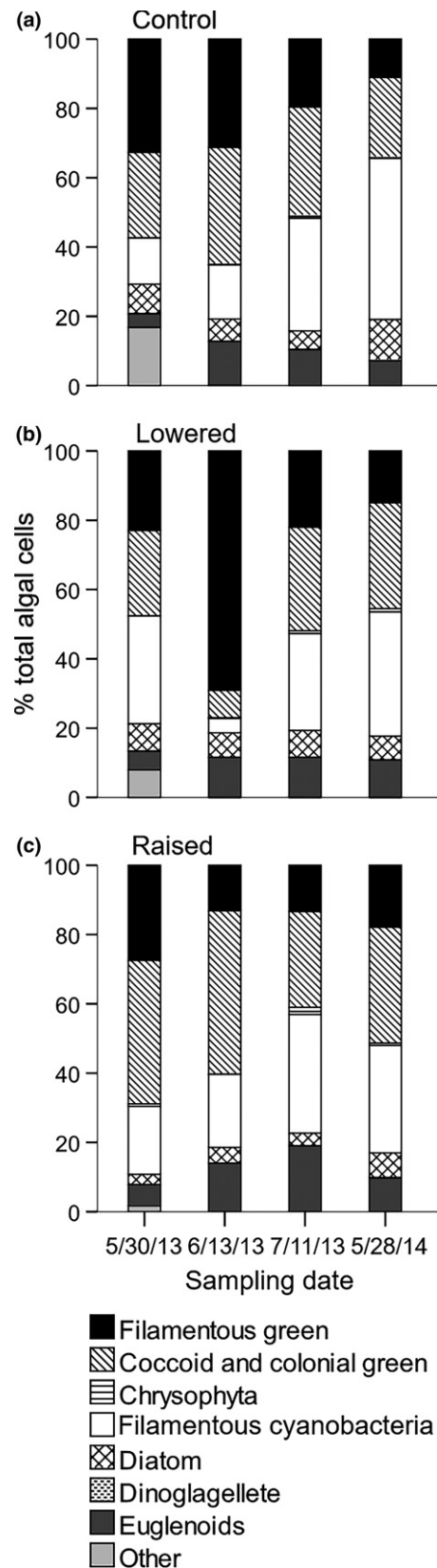
**FIGURE 6** Stable isotope biplot showing mean ( $\pm$  SD) natural abundance  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of producers, primary consumers and predators during peak algal production in the APEX fen following nutrient release from re-wetted peatland sediment

algae (Chlorophyta) were the most abundant taxonomic group in the control (33%) and raised (47%) treatments ( $p = .01$ , Figure 7a,c). Cyanobacteria, particularly  $\text{N}_2$ -fixing taxa (e.g. *Anabaena*, *Hapalosiphon*, *Nostoc*), were most abundant in water-table treatments when nutrient concentrations were low ( $p = .07$ , Figure 7a–c). The proportion of diatoms (Bacillariophyceae), euglenoids, chrysophytes and dinoflagellates remained  $\leq 10\%$  of total cell density among water-table treatments throughout both growing seasons. Algal taxonomic composition was similar among treatments at the end of the 2013 growing season and at the beginning of the 2014 growing season ( $p = .11$ , Figure 7a–c).

Macroinvertebrate abundance was related to algal abundance among water-table treatments and between growing seasons ( $r^2 = .85$ ,  $p < .0001$ , Figure 5c). During the early growing season of both study years when algal biomass was reduced, macroinvertebrate abundance was lower than during periods of increased algal biomass (Figure 8). There was a greater richness of grazers in the presence of elevated algal biomass in the lowered (i.e. drought) treatment (snails, grazing caddisfly larvae and dipteran chironomid and mosquito larvae) compared to the raised and control treatments where snails were the primary grazer ( $p = .002$ ; Figure 8). The composition of predators (e.g. Odonata and Coleoptera larvae, leech) was similar among treatments but the proportion of predators increased with elevated grazer abundance in the lowered water-table treatment (Figure 8b).

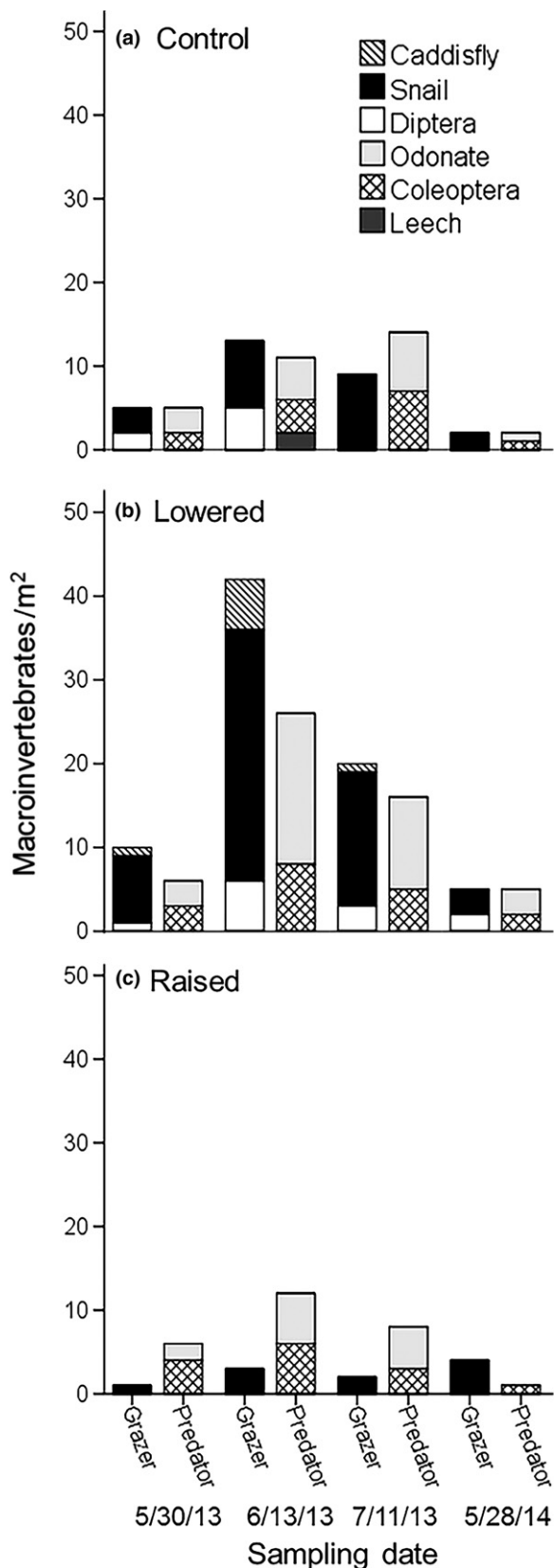
## 4 | DISCUSSION

As temporary aquatic ecosystems, peatlands are sensitive to changes in the frequency and duration of inundation. Yet, we know relatively



**FIGURE 7** Per cent of total algal cells in algal functional groups in the (a) control, (b) lowered and (c) raised water-table treatments on sampling dates during the 2013 and 2014 growing seasons in the APEX fen





**FIGURE 8** Abundance and taxonomic composition of macroinvertebrate grazers and predators in the (a) control, (b) lowered and (c) raised water-table treatments on sampling dates during the 2013 and 2014 growing seasons in the APEX fen

little about how variation in the desiccation-inundation cycle influences aquatic communities in northern peatlands. The natural flooding event over experimental plots at the APEX fen beginning in 2013 disrupted the experimental manipulation but provided a unique opportunity to evaluate how rewetting of previously dried sediments influences nutrient dynamics and energy transfer through a peatland food web compared to more stable hydrologic conditions. Overall, our hypothesis that hydrologic regime influences aquatic community structure and energy flow in northern boreal peatlands was supported. Specifically, we found that elevated nutrient levels in conditions of more variable hydrology in the lowered water-table treatment promoted algal production with increased energy transfer to higher trophic levels. Conversely, higher trophic levels were nearly absent in conditions of sustained flooding where low nutrient concentrations constrained algal biomass accumulation.

Similar to responses observed in other ecosystems with intermittent hydrology (Ardón, Morse, Montenari, Doyle, & Bernhardt, 2010; Kinsman-Costello, O'Brien, & Hamilton, 2014; Steinman et al., 2012), rewetting of previously dried sediments promoted elevated nutrient concentrations in the water column above the peat surface, especially in the drought treatment. Owing to seasonal drawdown that commonly occurs during the growing season (Churchill et al., 2015), water table was below the peat surface in all experimental plots during the growing season prior to our study, but was 15 cm lower in the drought treatment compared to the raised and control treatments. Since water table was above the peat surface (and at similar depths) in all plots during the natural flooding event, elevated nutrients in the lowered water-table treatment were likely associated with the deeper drying depth during the previous growing season. Specifically, the greater drying intensity (i.e. oxygenation of sediments) may have accelerated the extent of electron acceptor regeneration in the lowered water-table treatment and the resulting buildup of redox products moved into solution with rewetting (Estop-Aragónés, Knorr, & Blodau, 2013). In contrast to the response following antecedent drought, there was no increase in nutrient levels following the spring thaw in 2014, which was preceded by a growing season with constant inundation (i.e. in 2013). A lack of elevated nutrient levels after one growing season of constant inundation is noteworthy as it indicates that the carry-over or legacy effects associated with antecedent drought were short-lived and a growing season of constant inundation resets the ecosystem to conditions prior to manipulation.

Algae responded positively to elevated nutrient levels associated with variable hydrology. Algae accumulated on the peat surface shortly following the spike in nutrient levels (upon rewetting) in the lowered water-table treatment and nutrient concentrations declined following the increase in algal production. Nutrient concentrations and algal biomass remained at reduced levels under continuously saturated soil conditions following the spring thaw in 2014. These results may help to explain why peatlands within the region with stable hydrology (i.e. permanent pools) tend to have minimal levels of algal production (Rober et al., 2014). Conversely, algae may play a larger role in overall primary production in conditions of elevated

nutrient availability associated with more variable hydrology (e.g. more frequent desiccation-inundation cycle) expected for northern peatlands with ongoing climate change (Osterkamp et al., 2009; Schuur et al., 2013).

The biomass of heterotrophic bacteria was elevated simultaneously with algal production. It is well established that algae and heterotrophic bacteria grow in close association within benthic biofilms (Battin et al., 2007), where they exchange resources (Kuehn, Francoeur, Findlay, & Neely, 2014). In a concurrent experiment within the fen complex (Wyatt & Turetsky, 2015), we demonstrated that: (1) nutrient enrichment alone (experimental conditions in the dark to eliminate algae) had no stimulatory effect on bacterial growth without the simultaneous addition of a carbon source (glucose) and (2) elevated algal productivity (in the presence of nutrient enrichment in the light) stimulated heterotrophic bacteria similar in magnitude to that of glucose enrichment. Therefore, the observed increase in bacterial biomass following rewetting of dry sediments in the drought treatment was likely associated with an increase in the availability of more labile carbon sources in the presence of elevated algal production. Considering that heterotrophic metabolism in peatlands is typically limited by the availability of labile organic matter, elevated levels of labile carbon from algae sources may become increasingly important for energy transfer and organic matter turnover in conditions of ongoing climate change in northern peatlands.

Given the low nutrient conditions and poor nutritional quality of the dominant peatland plants, higher trophic levels in peatlands are likely to be constrained by available resources (van Duinen et al., 2013). Our data show that grazers and predators were abundant when water was present at the peat surface and tended to increase with algal abundance, owing to increasing nutrient availability and the release of bottom-up constraints on energy flow. Isotopic analysis provided support for this hypothesis, suggesting that elevated algal production contributed to grazer abundance directly as a food source and indirectly by promoting heterotrophic bacteria within the periphyton matrix (which are also consumed by grazers). Elevated predator density coincided with elevated grazer abundance in the lowered water-table treatment, which is consistent with food web theory (Hansson, 1992) where a sufficient increase in resource availability allows for predators to invade the system. In contrast, the presence of grazers and predators was reduced within experimental plots, including the lowered water-table treatment, when algal biomass was limited by low nutrient levels during the second year of sustained flooding over all plots.

In addition to the effects of algae on the movement of energy to higher trophic levels within the food web, it is possible that consumption of algal material by grazers may have altered the size and composition of the algal community (Rober, Stevenson, & Wyatt, 2015; Steinman, Mulholland, & Hill, 1992). In particular, selective grazing of coccoid and colonial green algae in the lowered water-table treatment may have promoted the increase in filamentous green algae observed during the same time. Owing in part to mechanical constraints of the feeding structures of grazing macroinvertebrates, both filamentous green algae and cyanobacteria are

generally considered to be less edible than smaller coccoid and colonial green algae and diatoms (Agrawal, 1998; Guo et al., 2016). We used this size and growth-form dichotomy to infer edibility (Bell, 2002) and observed a decrease (from 40% to 10%) in the proportion of edible taxa and a simultaneous increase (from 60% to 90%) in less-edible taxa during peak grazer abundance. Further evidence for selective grazing was demonstrated by the disproportionate abundance of coccoid and colonial green algae and a similar proportion of edible (40%) and inedible (60%) taxa in the control and raised treatments where grazers were lower in abundance. It is also important to note that dense growths of filamentous algae can provide refuge for macroinvertebrates and reduce the negative effects of predators (Liston, Newman, & Trexler, 2008; Tonkin, Death, & Barquín, 2014). It is possible that, in addition to resource provisioning, biofilm architecture had a supporting role in the development of the macroinvertebrate community during peak algal biomass.

Compared to their terrestrial counterpart, the open water areas of northern peatlands are relatively understudied. As a consequence, our knowledge of food web ecology in peatland pools is lagging behind other aspects of peatland ecology. Peatland pools are largely intermittent and the paucity of information on these ecosystems may reflect the inherent difficulty of studying such environments. It was only in the presence of a long-term study site that we had access to hydrologic data from a single fen during both wet and dry phases. This is notable as our results show that the legacy effects of hydrologic regime regulate aquatic community structure when water covers the peat surface. Within a predictive context, our findings indicate that more stable hydrology will limit energy transfer within these ecosystems while more variable hydrologic conditions expected with ongoing climate change (e.g. wetting and drying of peatland pools) will promote energy flow to higher trophic levels by releasing nutrient constraints on labile basal resources in surface waters. With that said, it is not possible to rule out the potential for repeated drying and rewetting to deplete redox-sensitive nutrients over time (Dieter, Herzog, & Hupfer, 2015). Yet, if nutrient availability is sustained, there is a potential for elevated aquatic production to transfer to higher trophic levels, including the migratory waterfowl, which use northern wetlands as a summer nursery and stop-over habitat (DesGranges & Gagnon, 1994; Lewis, Lindberg, Schmutz, & Bertram, 2014). Given the importance of species composition for determining the flux and transformation of carbon and nutrients in both terrestrial and aquatic environments (e.g. Amundrud & Srivastava, 2016; Atwood et al., 2015; Strickland, Hawlena, Reese, Bradford, & Schmitz, 2013), trophic interactions may play a greater role in regulating ecosystem function in the presence of a more variable hydrologic regime associated with climate change in northern peatlands.

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