LIMNOLOGY
and
OCEANOGRAPHY

ASLO

Limnol. Oceanogr. 66, 2021, 1743–1758

doi: 10.1002/lno.11719

Greening of the boreal peatland food web: Periphyton supports secondary production in northern peatlands

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Abstract

Characterizing spatial and temporal variability of food web dynamics is necessary to predict how wetter and more nutrient-rich conditions expected with climate change will influence the fate of organic matter within northern peatlands. The goals of this study were to (1) document spatial and temporal variability in the contribution of periphyton to peatland food webs using isotope analysis (^{13}C and ^{15}N), and (2) quantify the influence of increased nutrient availability on primary and secondary production across a gradient of rich, moderate, and poor fen peatlands common to the northern boreal biome. We established replicate m^2 plots within each fen located in interior Alaska to quantify periphyton (algae and bacteria) and macroinvertebrate biomass with and without nutrient addition throughout a growing season (May–August). Stable isotope analysis showed that periphyton contributed $\bar{x}$ = 65% of organic matter to the food web over time and across fens compared to $\bar{x}$ = 7% from plants or detritus. The transfer of basal resources was reflected in an increase in herbivore biomass as algal biomass increased over time in all fens, followed by an increase in predatory macroinvertebrates during the latter part of the growing season. Furthermore, all measures of periphyton and macroinvertebrate biomass were enhanced by nutrient addition. These data provide insight into patterns of natural variation within the aquatic food web of boreal peatlands and show that basal resources within this ecosystem, which are generally considered to be "detritus-based," are actually driven by periphyton with minimal input from plant detrital pathways.

Food web ecology generally separates basal resources into two separate or alternative pathways, autotrophic (green) and heterotrophic or detrital (brown) (Hairston et al. 1960; Moore et al. 2004). However, more recent studies suggest that organisms frequently consume organic matter from both autotrophic and detrital pathways rather than from either pathway alone (Wolkovich et al. 2014; Buchkowski et al. 2019). For example, in ecosystems where detritus is the primary source of organic matter (i.e., a detrital-based system; Wissinger et al. 2018) animal diets can be supplemented by temporary increases in autotrophic production (i.e., green energy; Crenier et al. 2017). These brief but intense inputs of high-quality green organic matter (e.g., algal production) play a substantial role in sustaining secondary production (Mariash et al. 2014; Vesterinen et al. 2016; Vadeboncoeur and Power 2017), highlighting the importance of understanding the interactions within and between autotrophic and heterotrophic pathways in aquatic ecosystems.

Northern peatland ecosystems have both terrestrial and aquatic phases, both of which can occur at a single location at different points in time (Arsenault et al. 2018). For the most part, studies of peatland food web ecology have focused on the dry phase where plant detritus (i.e., the brown energy pathway) is the primary source of organic matter for animal consumers (van Duinen et al. 2013). Much of this material, which is typically rigid in structure (i.e., recalcitrant), is never consumed leading to the long-term accumulation of organic matter as peat (Gessner et al. 2010). However, during the aquatic phase a very different community emerges with periphyton (i.e., algal biofilm) that forms attached to submerged surfaces serving as the base of the food web (DeColibus et al. 2017). This energy moves up the food web through grazers and predators (i.e., green energy pathway), which may explain why some peatland ecosystems tend to maintain higher than expected rates of secondary production despite low quality dominant detritus resources (van Duinen et al. 2013). However, there is currently too little information

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Author Contribution Statement: K.W. and A.R. conceived the study. E.S., A.M., J.W., A.R., and K.W. performed research. H.F. and A.R. analyzed the data. H.F., K.W., and A.R. wrote the manuscript.

Corrections added on 24 April 2021, after first online publication: Due to a typesetting error, the symbol xc bar has been changed to x bar throughout the article

on the aquatic components of the boreal peatland food web to test this hypothesis.

Rapid environmental change is dramatically altering many of the phenological patterns that influence aquatic community structure and ecosystem function (McMeans et al. 2015; Kendrick et al. 2018). While boreal peatlands are naturally dynamic ecosystems characterized by extreme fluctuations in temperature, daylight, and hydrologic regime, these events tend to be seasonally reoccurring. Regular patterns of variation allow for the colonization of species that are adapted to cope with a range of environmental conditions (McNamara and Houston 2008; Haghkerdar et al. 2019). More recently, ongoing climate change in northern regions has resulted in pronounced increases in growing season length, unprecedented rates of warming, and precipitation swings resulting in either flooding or drought (Woodward et al. 2016). Across the boreal landscape, permafrost thaw, thermakarst slumping, and increasingly dynamic hydrologic conditions are all expected to increase nutrient availability and the expansion of open water areas (Kendrick et al. 2018; Wickland et al. 2018). It is generally accepted that levels of algal production will increase under these wetter, more nutrient-rich conditions (Wyatt et al. 2012; DeColibus et al. 2017). However, it is not yet clear if this shift in resource allocation (i.e., from brown to green energy pathways) will propagate through the peatland food web during periods of surface-water inundation.

The goals of this study were to: (1) document spatial and temporal variability in the contribution of periphyton to peatland food webs using isotope analysis (^{13}C and ^{15}N) and (2) quantify the influence of increased nutrient availability on primary and secondary production across a gradient of rich, moderate, and poor fen peatlands. We anticipated that the underlying differences in the physical and chemical conditions that characterize each fen (i.e., feedbacks between hydrology and biogeochemistry) could influence food web structure and function. We established replicate m^2 plots within each fen and quantified temporal variation in periphyton (algae and bacteria) and macroinvertebrate biomass with and without nutrient addition throughout a growing season (May–August) with sustained inundation. Lastly, because grazing by herbivores can mask the influence of nutrient addition on algal biomass (Rober et al. 2011), we installed grazer exclusion enclosures within enriched and unenriched areas of each peatland to evaluate the influence of herbivory on algal biomass under grazed (ambient) and ungrazed (grazer exclusion) conditions.

Materials and methods

Site description

We conducted this study in three peatlands (a rich, moderate, and poor fen) located within a wetland complex in the Tanana River floodplain just outside the Bonanza Creek Experimental Forest (35 km southeast of Fairbanks) in interior Alaska. The Tanana River valley is 150–250 km south of the Arctic Circle and is part of the circumpolar band of boreal forest. Fens are minerotrophic peatlands that have distinctive vegetation communities and water chemistry (Rydin and Jeglum 2013). Rich fens are the most common boreal peatland type in North America and have concentrations of dissolved minerals that are high enough to support a diversity of vegetation types includes sedges, shrubs, and brown mosses, and have a pH that ranges between 6.8 and 8. Moderate fens are moderately rich in dissolved minerals and vegetation diversity, which include sedges and brown mosses with sparsely distributed *Sphagnum* moss, and have a pH range of 5–7. Fens with extremely low concentrations of dissolved minerals are poor fens that are dominated by *Sphagnum* moss species capable of acidifying the surrounding environment (pH 4–5.5) thereby inhibiting many vascular plants (Rydin and Jeglum 2013). We used natural transitions in vegetation community structure and water chemistry (e.g., pH) to distinguish among the fens selected for this study (Churchill et al. 2015; McPartland et al. 2019). A full description of fen physical and chemical characteristics is presented in Table 1, but briefly the rich fen was dominated by brown moss species (families Amblystegiaceae and Brachytheciaceae) and dense stands of emergent vascular plants (*Carex atherodes*, *Equisetum fluviatile*, and *Potentilla palustris*) with water column pH that ranged from 5.4 to 8.9. The moderate fen had a moss community composed of both brown moss and *Sphagnum* species and was less densely vegetated by *C. atherodes*, *E. fluviatile*, and *P. palustris* with water column pH that ranged from 5.3 to 8.8. The poor fen was primarily composed of *Sphagnum* species with sparsely distributed *E. fluviatile*, *P. palustris*, and *Eriophorum vaginatum* and water column pH ranged from 4.8 to 7.5. All fens in our study were located within ~1 km distance from one another and surrounded by boreal forest, composed of lowland spruce and shrub cover. Each fen site was saturated for the entire growing season. Water depth was at its maximum in each fen immediately following spring snowmelt (May) and declined over time, but remained ≥15 cm above the peat surface by the end of the growing season in August (Table 1).

Isotopic analysis

We used isotopic analysis to evaluate trophic structure and the transfer of basal resources through the food web in each of the rich, moderate, and poor fens three times throughout the 2017 growing season beginning immediately after snowmelt until the end of the growing season (early = May 29, middle = July 1, late = August 1). Samples of potential basal resources (periphyton, vascular plants, moss, detritus) and macroinvertebrates were collected from an un-manipulated portion of the peatland to avoid destructively harvesting from within our survey plots (described below). Periphyton was collected from the peat surface using a syringe and scraped from the submersed portions of living plant stems with a

Table 1. The overall growing season (n = 20) mean and standard deviation (SD) for physiochemical characteristics of the rich, moderate, and poor fens in enriched and unenriched treatments. The range represents the minimum and maximum of measurements taken over the growing season. DO, dissolved oxygen; DOC, dissolved organic carbon; PAR, photosynthetically active radiation.

	Rich					
	Enriched			Unenriched		
Characteristic	**Mean**	**SD**	**Range**	**Mean**	**SD**	**Range**
Water depth (cm)	30.4	7.45	21–42	27.5	7.95	20–35
Water temperature (°C)	18.0	2.60	14–21	18.5	2.29	15–21
pH	6.56	1.27	5.6–8.9	6.46	1.29	5.4–8.9
DO (mg L^{-1})	3.84	1.81	1.9–6.8	3.92	1.95	2.0–7.0
Conductivity (μS)	39.2	6.85	29–45	39.0	5.53	31–45
Nitrate (μg NO_3^- L^{-1})	49.0	48.9	9.3–132	7.66	2.14	6.2–8.9
Phosphate (μg PO_4^{3-} L^{-1})	13.4	5.27	8.3–19	8.56	3.40	6.4–14
DOC (mg L^{-1})	30.3	8.40	25–37	32.6	4.32	26–37
PAR (μmol cm^2 s^{-1})	143.2	119.6	70–210	254.4	246.6	38–448
	Moderate					
	Mean	**SD**	**Range**	**Mean**	**SD**	**Range**
Water depth (cm)	30.4	9.75	20–47	34.0	11.4	20–46
Water temperature (°C)	19.0	1.83	17–20	18.0	2.88	14–21
pH	6.51	1.36	5.2–8.8	6.42	1.32	5.3–8.5
DO (mg L^{-1})	5.91	2.07	3.1–8.6	5.71	1.49	4.3–7.8
Conductivity (μS)	26.0	1.95	23–27	25.4	2.69	24–28
Nitrate (μg NO_3^- L^{-1})	25.8	16.4	5.6–52.6	13.2	7.39	7.2–26.0
Phosphate (μg PO_4^{3-} L^{-1})	11.3	4.09	5.9–14.6	7.54	2.95	4.3–10.7
DOC (mg L^{-1})	27.7	2.34	25–31	29.7	3.14	27–35
PAR (μmol cm^2 s^{-1})	300.1	294.8	55–694	266.1	225.1	84–672
	Poor					
	Mean	**SD**	**Range**	**Mean**	**SD**	**Range**
Water depth (cm)	24.8	6.06	18–30	26.6	8.86	16–34
Water temperature (°C)	13.6	3.30	10–18	15.2	3.53	11–20
pH	5.91	0.95	5.0–7.4	5.77	1.03	4.8–7.6
DO (mg L^{-1})	3.40	2.49	1.0–6.5	3.81	2.42	1.0–7.1
Conductivity (μS)	41.2	6.67	35–51	40.8	5.75	34–48
Nitrate (μg NO_3^- L^{-1})	34.8	12.2	21–46	15.8	9.59	7.4–27
Phosphate (μg PO_4^{3-} L^{-1})	32.7	17.5	22–58	20.9	6.21	15–28
DOC (mg L^{-1})	62.3	10.1	52–78	62.4	9.41	51–77
PAR (μmol cm^2 s^{-1})	194.2	185.9	47–463	242.3	207.0	27–484

toothbrush (Rober et al. 2014). The composite sample included autotrophic and heterotrophic components of the periphyton for isotopic analysis. All members of the macroinvertebrate community were collected using three net sweeps (1 m in length) each with a 10 μm plankton net, a 1 mm mesh size hand sieve, and a standard dipnet (Hannigan and Kelly-Quinn 2012). Snails were removed from their shell prior to analysis. When present, emergent winged adult (terrestrial) invertebrates (e.g., dragonfly, damselfly) were collected with a butterfly net. Samples of living vascular plants (*E. fluuviatile*, *C. atherodes*, *P. palustris*), detritus (i.e., dead plant material), moss (composite of *Sphagnum* and brown moss species) were rinsed of sediment and attached algal material in the lab with distilled water. Samples were aggregated and dried at 60°C for 48 h within 48 h of collection. Dried samples were ground into a fine powder, and analyzed for natural abundances of carbon (^{13}C) and nitrogen (^{15}N) with a continuous flow isotopic ratio mass spectrometer (PDZ Europa, Sercon Ltd., Cheshire, UK) 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 $\delta^{13}C$ and atmospheric N for $\delta^{15}N$) where $\delta^{13}C$ or $\delta^{15}N$ = $([R_{sample}/R_{standard}] - 1) \times 1000$, where R is $^{13}C : {}^{12}C$ or $^{15}N : {}^{14}N$. Analytical precision was 0.2% for $\delta^{13}C$ and 0.3% for $\delta^{15}N$.

Experimental design and sampling procedure

To evaluate the influence of nutrient availability on peatland primary and secondary production, we added nutrients to half of each peatland with 30 g m^{-2} granulose slow-release fertilizer (Osmocote, Scotts® Company, Marysville, OH). Nutrients were applied by evenly spreading fertilizer pellets (N : P molar ratio = 16 : 3) with a Broadcast Spreader at the beginning of the growing season. Previous studies have shown that this fertilizer continuously enriches the water column for 6–7 weeks (O'Connor and Donohue 2013) and release nutrients at a rate of approximately 77–123 mmol N m^{-2} d^{-1} and 5–7 mmol P m^{-2} d^{-1} (Heck et al. 2006). The unenriched area of the fen was maintained at ambient nutrient conditions (unenriched). Nutrient exchange from enriched to unenriched sides of each peatland was minimized by naturally poor mixing of the water column and by establishing an approximately 30 m distance between enriched and unenriched sampling plots (described below) to limit potential influence of nutrient diffusion on biomass estimates (Table 1).

Each peatland was sampled every 10–14 d at eight locations (n = 4 enriched and unenriched; 1 m^2 plots) beginning after snowmelt in May until August 2017. Within each plot, we collected loosely attached periphyton from two 25 cm^2 areas of the peat surface (when present) using a plastic syringe and scraped attached periphyton from the submersed portions of eight living plant stems of the dominant emergent macrophyte (Rober et al. 2014). The surface area of the plant stems was measured with a caliper and was accounted for in biomass estimates (Rober et al. 2013). The composite sample was split in half for analysis of algal biomass, which was measured as chlorophyll *a* (Chl *a*), and the remaining sample was preserved with a 2% formalin solution for algal taxonomic composition and bacterial biomass.

We measured algal biomass as Chl *a* (mg cm^{-2}) from a subsample collected on a Whatman glass fiber filter (GF/F; Whatman, Maidstone, UK) with Shimadzu UVmini-1240 spectrophotometer (Shimadzu Corporation, Kyoto, Japan) after extraction with 90% ethanol following standard methods (APHA 1998). We characterized algal taxonomic composition by counting and identifying ≥300 natural units per sample in a Palmer–Maloney nanoplankton counting chamber (Charles et al. 2002). Algae were identified to genus at 400X magnification with a Leica DM 4000 microscope (Leica Microsystems, Wetzlar, Germany) and categorized by division and functional group.

We quantified bacteria cell density by direct counts using epifluorescence microscopy following staining with 4′,6-diamino-2-phenylindole (DAPI) (Porter and Feig 1980). The stained aliquots were filtered onto a 0.2-μm pore-size black filter (OSMONIC INC., Livermore, CA) and a minimum of 300 cells or 25 fields were counted per filter at 1000X magnification using a light microscope with fluorescence (Leica Microsystems model DM 4000, Wetzlar, Germany). Bacterial biomass was calculated by a bacterial abundance per unit biomass conversion factor of 35 fg C $cell^{-1}$ (Theil-Nielsen and Søndergaard 1998).

We collected macroinvertebrates for estimates of biomass (g m^{-2}) and taxonomic composition using methods described above. All samples for estimates of biomass were collected and stored separately from samples collected for isotope analysis. Benthic and planktonic (i.e., zooplankton) invertebrates were separated from detritus and plant material and a reference sample for identification was preserved in 70% ethanol. Benthic macroinvertebrates were counted, identified to family level following Merritt et al. (2008), and categorized into functional feeding groups (i.e., herbivore, predator). Zooplankton samples were counted and identified to order or class level. Macroinvertebrate biomass was determined after drying specimens at 60°C for 24–48 h and weighing to the nearest 0.01 mg.

Physical and chemical characteristics were measured within each plot on each sampling date (Table 1). We measured water depth (cm) with a meter stick, and water temperature (°C), water column pH, dissolved oxygen (DO; mg L^{-1}), and conductivity (μS) with a Hach model 40d multi-probe (Hach Company, Loveland, CO). Water samples for dissolved nutrient analysis and dissolved organic carbon (DOC) were collected from 10 cm below the surface and filtered through a 0.45 μm filter (Millipore Corporation, Bedford, MA, USA) into 60 mL acid-washed polyethylene bottles. Filtered samples were stored on ice in the field and frozen until analysis for DOC (mg L^{-1}) using a Shimadzu TOC-V carbon analyzer (Shimadzu Scientific Instruments, Columbia, MD). A portion of each filtered sample was analyzed for nitrate (μg NO_3^- L^{-1}) and phosphate (μg PO_4^{3-} L^{-1}) using ion chromatography (Dionex Corporation, Sunnyvale, CA). We measured photosynthetically active radiation (PAR; μmol m^{-2} s^{-1}) at approximately 10 cm above the peat surface in each plot using a Li-Cor submersible quantum sensor and LI-250 light meter (Li-Cor, Lincoln, NE) attached to a 1-m pole to prevent disturbance of macrophytes.

Grazer exclusion

Grazer influence on algal biomass was evaluated by installing grazer exclusion enclosures at eight locations (n = 4 enriched and unenriched) within each fen. Exclusion enclosures were constructed of welded wire (25 cm diameter) and wrapped in transparent mesh (2 mm) to allow for water and nutrient exchange but prohibit grazers from accessing periphyton (Rober et al. 2011). Exclusion enclosures were pushed

into the peat so that they extended above the water surface and the enclosed water was in contact with the peat surface. After installation, grazers were manually removed from enclosures and visual inspection during each sampling campaign ensured that the grazer exclusion was maintained (Rober et al. 2011). During the July 1 sampling date, stems were collected from within exclusion enclosures for estimates of algal biomass (as Chl *a*) as described above. We then compared algal biomass within enclosures (ungrazed) to biomass estimates made at the same time in survey plots (grazed) with and without nutrient addition.

Statistical analysis

The percent contribution of basal resources to consumer diet among fens and over time were estimated using the Stable Isotope Analysis in R (SIAR) Bayesian mixing model package (Parnell et al. 2013). We ran separate models for each fen using time (early, middle, late growing season) as a grouping variable and the mean $\delta^{13}C$ and $\delta^{15}N$ for periphyton, *Carex*, *Equisetum*, *Potentilla*, moss, and detritus as basal resources. Only basal resources that were present on all sampling dates within each fen were included in the model. Model targets were comprised of all animal consumers (i.e., combined herbivores and predators) and then run separately for herbivores and predators. We used trophic fractionation factors of $0.47 \pm 1.23\%$ for $\delta^{13}C$ and $3.46 \pm 0.23\%$ for $\delta^{15}N$ according to Vander Zanden and Rasmussen (2001). To evaluate how variation in fractionation factors influenced the results of our mixing models (Gilbert et al. 2019), we re-ran our models using the range of values reported in the literature (-1.3–$1.3 \pm 1\%$ for $\delta^{13}C$; 2.4–$4.4 \pm 1\%$ for $\delta^{15}N$) for aquatic ecosystems by Post (2002). We found that variation in trophic fractionation factors did not produce enough change in the relative contribution of basal resources originally estimated by SIAR models to alter our main findings.

To evaluate spatial (among fens) and temporal (early, middle, late growing season) variation in $\delta^{13}C$ and $\delta^{15}N$, samples were grouped into producer types (periphyton, vascular plants, moss, detritus) or functional feeding groups (herbivores, predators, and omnivores) and analyzed using two-way repeated measures ANOVA (rmANOVA) tests with functional feeding group and fen identity as fixed factors. Tukey's post hoc comparison of means test was used to discriminate between different factor levels. It is important to note that fen identity was not replicated and some caution is warranted due to the lack of true replicates, though we believe that differences associated with fen identity provide the most parsimonious explanation for our findings.

We used two-way rmANOVA to evaluate spatial (i.e., fen identity) and temporal (i.e., sampling date) variation in algal, bacterial, and macroinvertebrate biomass between enriched and unenriched treatments using fen identity and nutrients as fixed factors over repeated sampling events (i.e., time). Repeated measures multivariate ANOVA (rmMANOVA) was used to evaluate differences in algal taxonomic composition among fens over time using fen identity and nutrients as fixed factors over repeated sampling events. A three-way ANOVA was used to evaluate the influence of herbivory (grazed or ungrazed) on algal biomass among fens (rich, moderate, poor) with (enriched), and without (unenriched) nutrient addition (i.e., herbivory×fen identity×nutrient). Chl *a* concentration was log transformed prior to analysis to correct for non-normal distribution and unequal variance among treatments. Tukey's post hoc comparison of means tests were used to discriminate between different factor levels in all ANOVA's. Statistical analyses were performed with SPSS 20 (SPSS Inc., Chicago, IL).

Results

Spatial and temporal variability in the contribution of periphyton to peatland food webs

Stable isotopes showed that there was similar trophic structure among fens and invertebrate $\delta^{13}C$ values reflected differential use of basal resources while differing $\delta^{15}N$ indicated the presence of multiple trophic levels (Fig. 1). Periphyton $\delta^{13}C$ (– 30.5%) was on average 2.77% more depleted than vascular plants (– 27.0%), detritus (– 27.2%), or moss (– 27.7%) across fens. Average $\delta^{13}C$ values for herbivores (– 31.3%) and predators (– 29.9%) were more similar to periphyton ($\leq 0.8\%$ change) than plant material or detritus, but in some instances herbivore $\delta^{13}C$ was more depleted ($\bar{x} = 3.5\%$) than periphyton. Average $\delta^{15}N$ values of herbivores (2.82%) were enriched ~1% relative to periphyton (1.42%) and $\delta^{15}N$ values of predators (4.68%) were enriched ~2% relative to herbivores (Fig. 1).

According to SIAR mixing models, periphyton contributed the greatest proportion of invertebrate diet compared to all other basal resources throughout the growing season in each fen (Fig. 2). Periphyton contributed 71–76% of invertebrate diet (i.e., combined herbivores and predators) in the rich fen over time. All other basal resources (e.g., vascular plants, moss, detritus) contributed ≤12% of invertebrate diet. Similarly, periphyton contributed between 78% and 81% of invertebrate diets in the moderate fen over time, while all other basal resources contributed ≤ 9% to invertebrate diet. In the poor fen, the contribution of periphyton to invertebrate diet increased from 20% in the early growing season to 39% and 65% during the middle and late growing season, respectively. All other basal resources contributed a maximum of 17% of the invertebrate diet early in the growing season and declined to ≤10% by the late growing season.

When analyzed separately, changes in the periphyton contribution to herbivore and predator diets over time reflected patterns of energy transfer through the food web. In the rich fen, the contribution of periphyton to herbivore diet decreased from 52% to 30% over time, but the proportion of periphyton transferred from herbivores to predators increased from 27% to 64%, corresponding with the higher density of

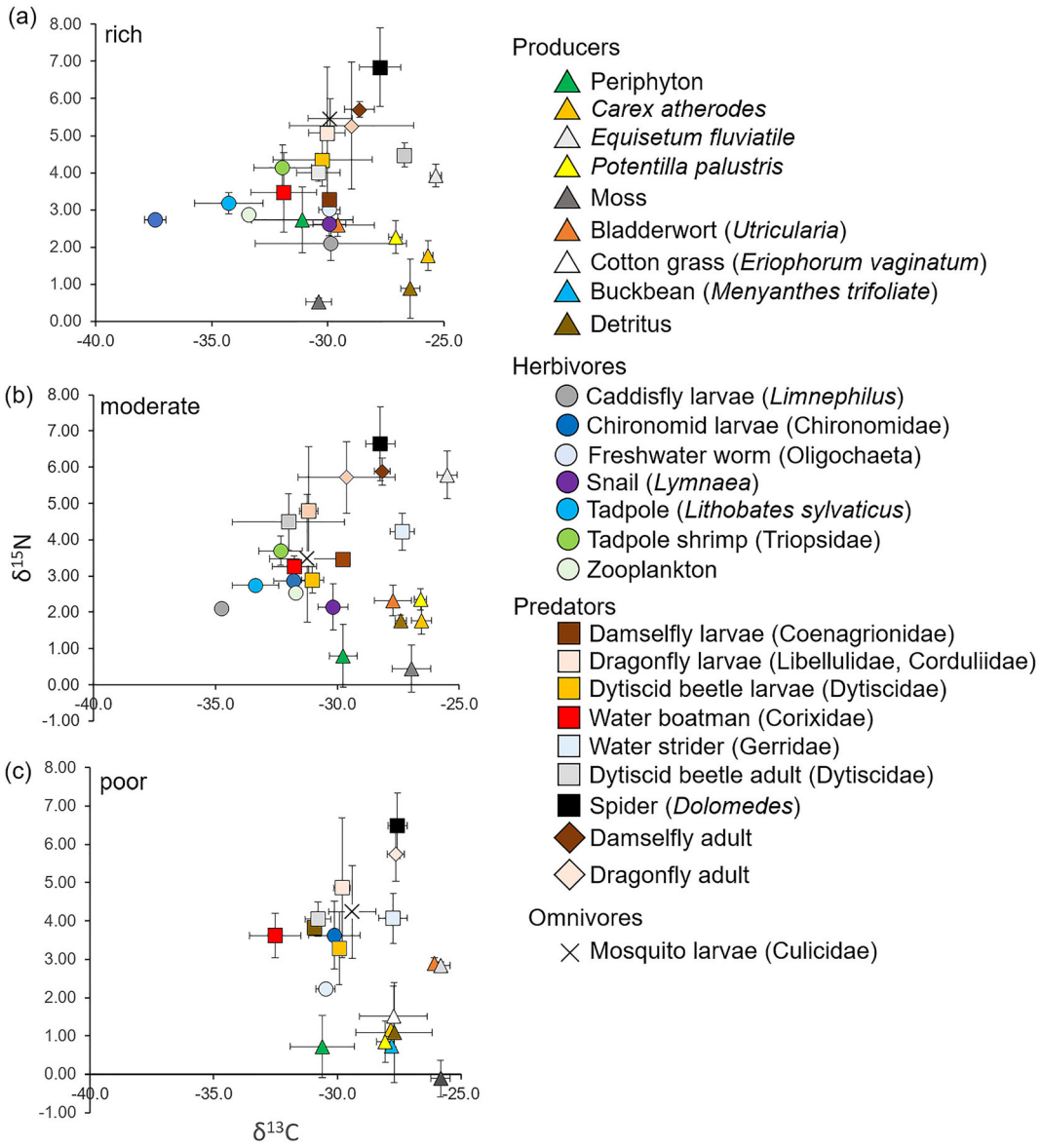

Fig. 1. Natural abundance $\delta^{13}C$ and $\delta^{15}N$ isotopes of producers, herbivores, predators, and omnivores collected from within the rich (**a**), moderate (**b**), and poor (**c**) fen sites. Isotope values are the composite mean ± SD of all three sampling periods (early, middle, late growing season) within each fen.

predators at the end of the growing season and a decrease in herbivore density (Fig. 2). Similarly, in the moderate fen, the contribution of periphyton to herbivore diet decreased from 41% to 28% while the proportion of periphyton transferred from herbivores to predators increased from 59% to 71%. In contrast in the poor fen, the periphyton contribution to herbivore diet increased from 16% to 31% over time whereas the contribution of periphyton transferred from herbivores to predators remained relatively stable over time 22% to 31% (Fig. 2).

Variation in $\delta^{13}C$ and $\delta^{15}N$ values over time reflected changes in organic matter quality and trophic state (Fig. 3). There was little variation in periphyton $\delta^{13}C$ among fens during both early and middle sampling periods (Fig. 3a–c), but the $\delta^{13}C$ value of periphyton was depleted by 4.85% over time in the rich ($F_{2,84}$ = 36.1, $p \leq 0.001$) and by 2.9% in the poor fen ($F_{2,84}$ = 13.3, $p \leq 0.001$), whereas periphyton $\delta^{13}C$ varied little over time (≤ 1.09%) in the moderate fen ($F_{2,84}$ = 0.89, p = 0.41). Herbivore $\delta^{13}C$ also decreased over time in the rich and poor fens ($F_{2,84}$ = 13.1, $p \leq 0.001$), but remained similar over time in the moderate fen ($F_{2,84}$ = 1.57, p = 0.21). Predator $\delta^{13}C$ increased over time in the rich ($F_{2,84}$ = 11.5, $p \leq 0.001$) and moderate ($F_{2,84}$ = 15.3, $p \leq 0.001$) fens, whereas the $\delta^{13}C$ value of predators peaked during the middle sampling period in the poor fen and declined thereafter, though differences were not significant (p = 0.89; Fig. 3a–c). Patterns in the $\delta^{13}C$ value of planktonic consumers (i.e., mosquito larvae and

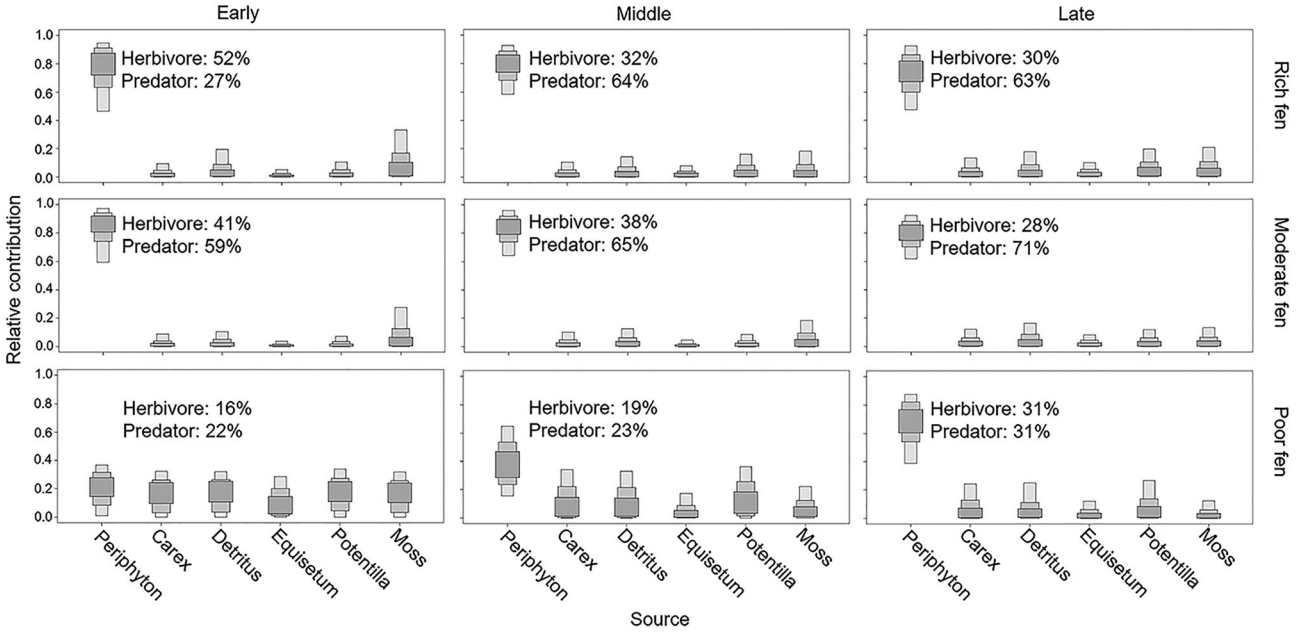

Fig. 2. Relative contribution of periphyton, vascular plants (*Carex*, *Equisetum*, *Potentilla*), moss, and detritus to invertebrate diet (i.e., combined herbivore, predator, omnivore) in the rich, moderate, and poor fens over time (early, middle, and late growing season) as estimated by mixing models. Stacked boxes (shaded dark to light) represent the 25%, 75%, and 95% credible interval levels for mean dietary proportions. Inset percentages indicate the separate contribution of periphyton transferred to herbivores and from herbivores to predators within each fen identity (rows) over time (columns) that were analyzed in separate mixing models.

zooplankton) varied over time within fens (Fig. 3a–c), but the $\delta^{15}N$ values increased from values similar to periphyton early in the growing season to values similar to, or higher than, predator $\delta^{15}N$ by the end of the growing season across fens (Fig. 3d–f). The isotope values of vascular plants, detritus, and moss varied little over time across fens (Fig. 3a–f).

Influence of increased nutrient availability on algal, bacterial, and macroinvertebrate biomass

Chl *a* concentration, a proxy for algal biomass, increased over time in both enriched and unenriched treatments regardless of fen identity ($F_{8,32} = 3.68$, $p = 0.004$; Fig. 4a–c). Under ambient conditions (i.e., unenriched treatment), mean ± SE Chl *a* concentration (0.14 ± 0.03 mg cm^{-2}) was similar among fens at the start of the growing season ($p \geq 0.11$; Fig. 4a–c). Mean Chl *a* concentration increased consistently over time in both the rich and moderate fens and reached a maximum of 0.60 ± 0.03 mg cm^{-2} in the rich fen and 0.41 ± 0.07 mg cm^{-2} in the moderate fen by the end of the growing season (i.e., August; Fig. 4a,b). In contrast, mean Chl *a* concentration in the unenriched treatment in the poor fen peaked in early July (3.06 ± 0.30 mg cm^{-2}) and declined thereafter. Measures of Chl *a* concentration in the unenriched treatment were on average 1.14 ± 0.36 mg cm^{-2} greater in the poor fen ($p < 0.001$; Fig. 4c) relative to the rich and moderate fens where Chl *a* concentration was similar ($p = 0.32$; Fig. 4a,b).

Measures of algal biomass (as Chl *a*) observed within each fen over time were enhanced by nutrient addition ($F_{1,18} = 91.1$, $p < 0.001$; Fig. 4a–c). In the rich fen, nutrient addition resulted in a two-fold increase in Chl *a* concentration (1.22 ± 0.21 mg cm^{-2}) compared to unenriched conditions by the end of the growing season (Fig. 4a). In the moderate fen, Chl *a* concentration in the enriched treatment peaked (1.91 ± 0.45 mg cm^{-2}) 2 weeks earlier and was more than four-fold greater than the unenriched treatment ($p = 0.04$; Fig. 4b). In the poor fen, nutrient addition maintained elevated levels of Chl *a* throughout the growing season compared to the unenriched treatment ($p \leq 0.01$) and elevated levels of Chl *a* in the enriched treatment were sustained 2 weeks longer and were two-fold greater at the maximum than the unenriched treatment (Fig. 4c). Like in unenriched conditions, mean Chl *a* concentration was on average 2.79 ± 0.55 mg cm^{-2} greater in the poor fen compared to the rich or moderate fen ($p < 0.001$).

Measures of bacterial biomass increased over time in both enriched and unenriched treatments regardless of fen identity ($F_{8,32} = 19.1$, $p < 0.001$; Fig. 4d–f). Bacterial biomass was significantly influenced by fen identity ($F_{2,18} = 624.5$, $p < 0.001$), and was on average 20.3 ± 9.57 μg C cm^{-2} greater in the unenriched poor fen compared to the rich or moderate fen ($p \leq 0.001$). Patterns of bacterial biomass were enhanced by nutrient addition ($F_{1,18} = 183.4$, $p < 0.001$) and were consistently greater in the poor fen than the rich or moderate fens ($p \leq 0.02$; Fig. 4d–f).

Macroinvertebrate biomass increased over time with algal biomass in all fens irrespective of nutrient availability ($F_{4,36} = 8.29$, $p < 0.001$; Fig. 4g–i). Although the rich and moderate fens had similar levels of algal biomass in unenriched

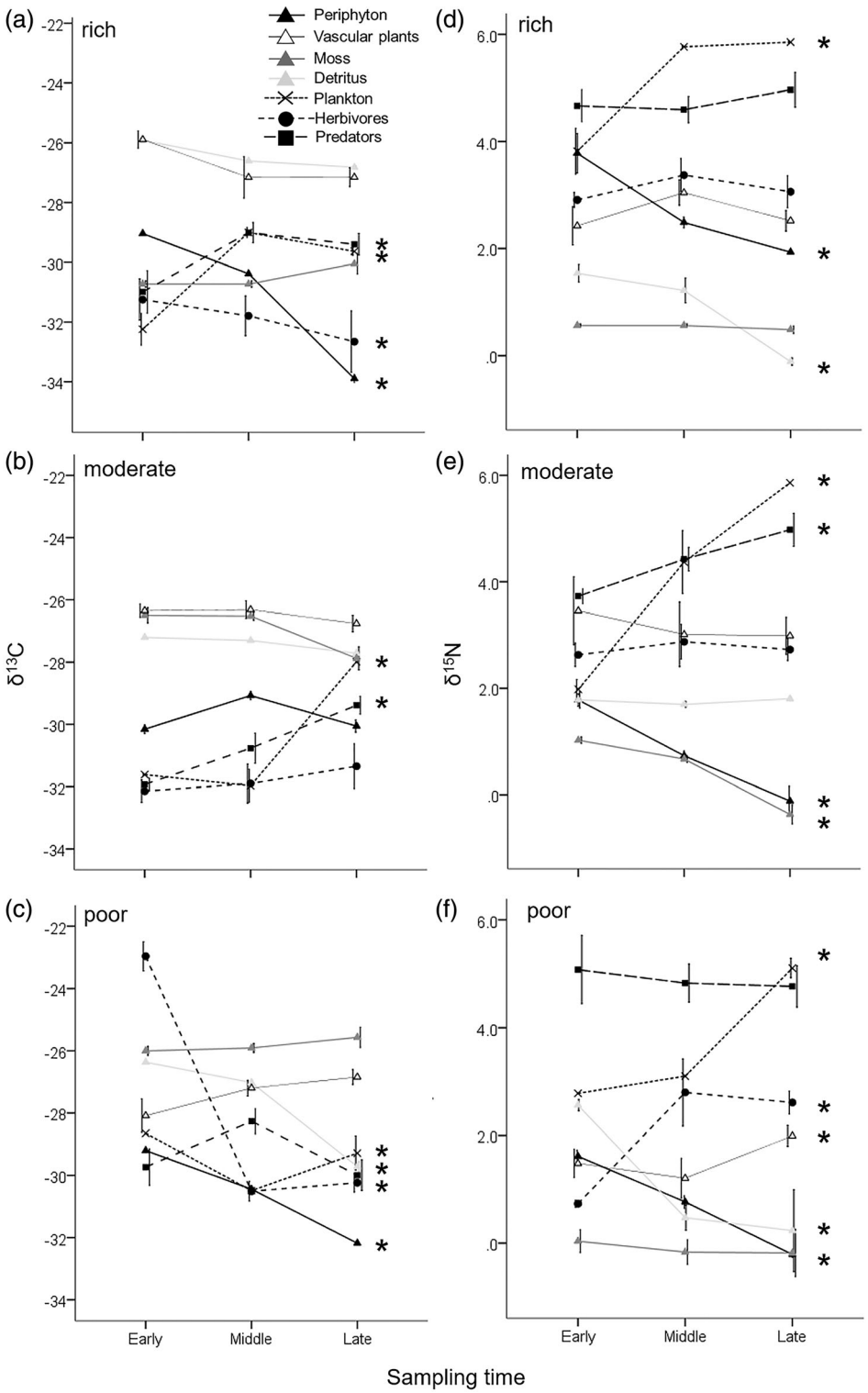

Fig. 3. Change in the natural abundance $\delta^{13}C$ (**a–c**) and $\delta^{15}N$ (**d–f**) isotopes over time (early, middle, late growing season) within the rich, moderate, and poor fen. Symbols represent the mean ± SE of each resource type (periphyton, vascular plants, moss, detritus) or functional feeding group (plankton, herbivores, predators). Significant change over time is indicated by an asterisk ($p < .05$).

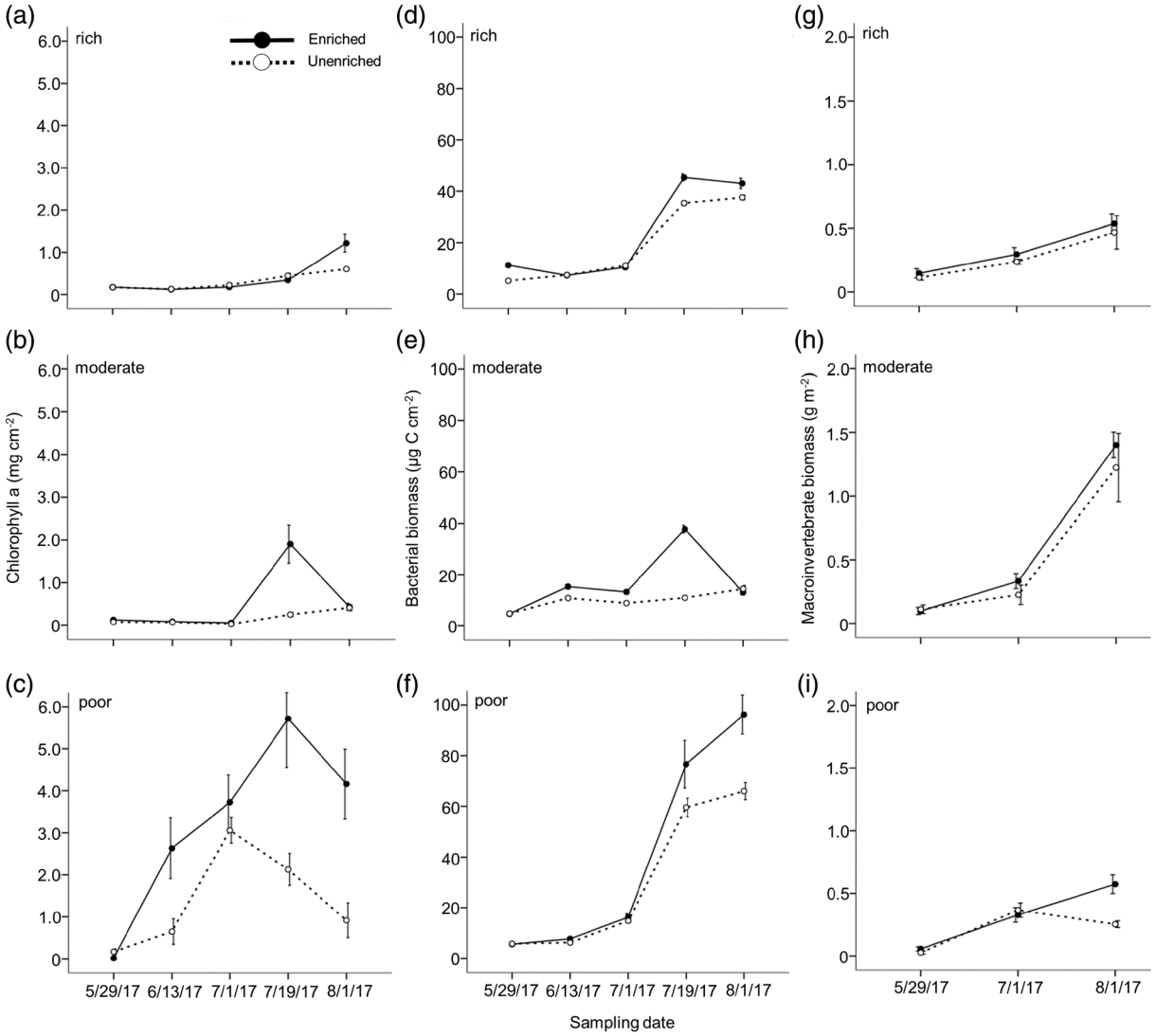

Fig. 4. Measures (mean ± 1 SE; n = 4) of algal biomass as Chl *a* (**a**–**c**), bacterial biomass (**d**–**f**), and macroinvertebrate biomass (**g**–**i**) within the rich, moderate, and poor fen between enriched and unenriched treatments over the growing season. Note that axes have different units.

conditions, macroinvertebrate biomass was greatest in the moderate fen after increasing 13-fold over the growing season compared to four-fold in the rich fen ($F_{2,18}$ = 28.8, $p < 0.001$). Macroinvertebrate biomass in the poor fen peaked after a 14-fold increase in the middle of the growing season to levels that were similar to the rich and moderate fen ($p \geq 0.17$) before declining at the end of the growing season, a pattern that was consistent with changes in algal biomass in the poor fen (Fig. 4i).

Spatial and temporal variation in aquatic community structure

The proportion of macroinvertebrate biomass made up of herbivore, predator, and planktonic (i.e., zooplankton) consumers varied over time and reflected increases in energy flow through the food web (Fig. 5a–c). In both the rich and moderate fens, herbivores contributed the greatest proportion (rich: 40.0%, moderate: 63.8%) to total macroinvertebrate biomass in the unenriched treatment at the start of the growing season. Although the total amount of herbivore biomass remained similar over time, the fraction of total biomass comprised of herbivores declined over time to <8% as total macroinvertebrate biomass increased (Fig. 5a,b). Simultaneously, the proportion of macroinvertebrate biomass comprised of predatory taxa increased in both the unenriched rich and moderate fens from 17.4% and 30.8% in the early growing season to 69.1% and 90.8% in the late growing season, respectively (Fig. 5a,b). In the poor fen, herbivores and predators comprised roughly equal proportions of total biomass at the middle sampling date, but the proportion herbivore biomass decreased two-fold while a similar proportion of predator biomass was maintained late in the growing season (Fig. 5c).

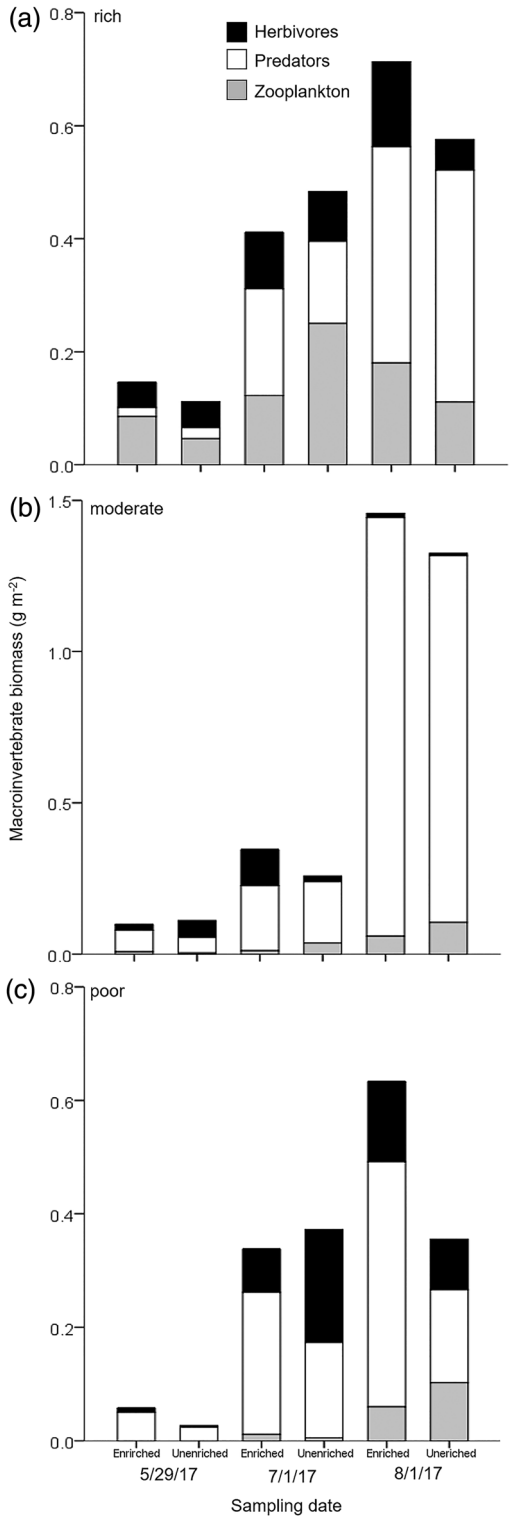

Fig. 5. Proportion of macroinvertebrate biomass (g m^{-2}) comprised of benthic herbivore and predator taxa and zooplankton between enriched and unenriched treatments within the rich (**a**), moderate (**b**), and poor (**c**) fen over the growing season. Note that axes have different scales.

The proportion of macroinvertebrate biomass comprised of zooplankton was consistently greater in the rich fen compared to the moderate or poor fens irrespective of nutrient addition (Fig. 5a), and the zooplankton contribution to total biomass varied from a maximum of 46.4–22.1% across fens (Fig. 5a–c). The zooplankton community was comprised of cladocera, copepoda, and water mites in all fens (data not shown).

The effect of nutrient addition on the proportion of herbivore, predator and zooplankton taxa that comprised macroinvertebrate biomass was minimal (Fig. 5a–c). However, nutrient addition tended to support a greater proportion of herbivorous biomass in the rich fen, whereas predatory taxa were favored by enrichment in the moderate and poor fens. In moderate and poor fens, enrichment decreased the proportion of zooplankton taxa, while the proportion in rich fens was similar irrespective of nutrient addition.

Algal community structure was significantly influenced by the interaction between fen identity and time ($F_{72,712}$ = 1.99, $p < 0.001$) but was not significantly influenced by nutrients alone ($p = 0.28$) or in combination with either fen identity or time ($p \geq 0.24$). Therefore, algal community structure in enriched and unenriched treatments were combined to illustrate shifts in community structure within each fen over time (Fig. 6). Within each fen, algal community structure was dominated by diatoms (20–36%) and colonial green algae (28–37%) early growing season each fen. By the end of the growing season, N-fixing cyanobacteria (e.g., *Anabaena*, *Haplosiphon*, *Nostoc*) comprised 61% of the community in the rich fen, 66% in the moderate fen, and 80% in the poor fen.

Negative effects of herbivory on algal biomass

Comparison of algal biomass between grazer exclusion treatments (ungrazed) and ambient conditions (grazed) showed that herbivory had a negative effect on algal biomass ($F_{1,36}$ = 6.08, p = 0.02; Fig. 7). The effects of herbivory were more pronounced in enriched compared to unenriched treatments ($F_{2,36}$ = 3.74, p = 0.03). However, the interactive effects of herbivory, nutrients, and fen identity were only weakly significant ($F_{5,36}$ = 2.10, p = 0.09). Differences in algal biomass between grazed and ungrazed treatments were greatest in the poor fen compared to the rich or moderate fens ($p < 0.001$), but differences between grazed and ungrazed algal biomass within the poor fen were only significant in the enriched treatment (p = 0.001).

Discussion

Our stable isotope analyses indicated that boreal fens rely primarily on green energy pathways (i.e., periphyton), and that secondary producers gained minimal support from detrital pathways. We found that when averaged across all fens and time, periphyton contributed the largest fraction of organic matter ($\bar{x}$ = 65%) to the peatland food web. This level

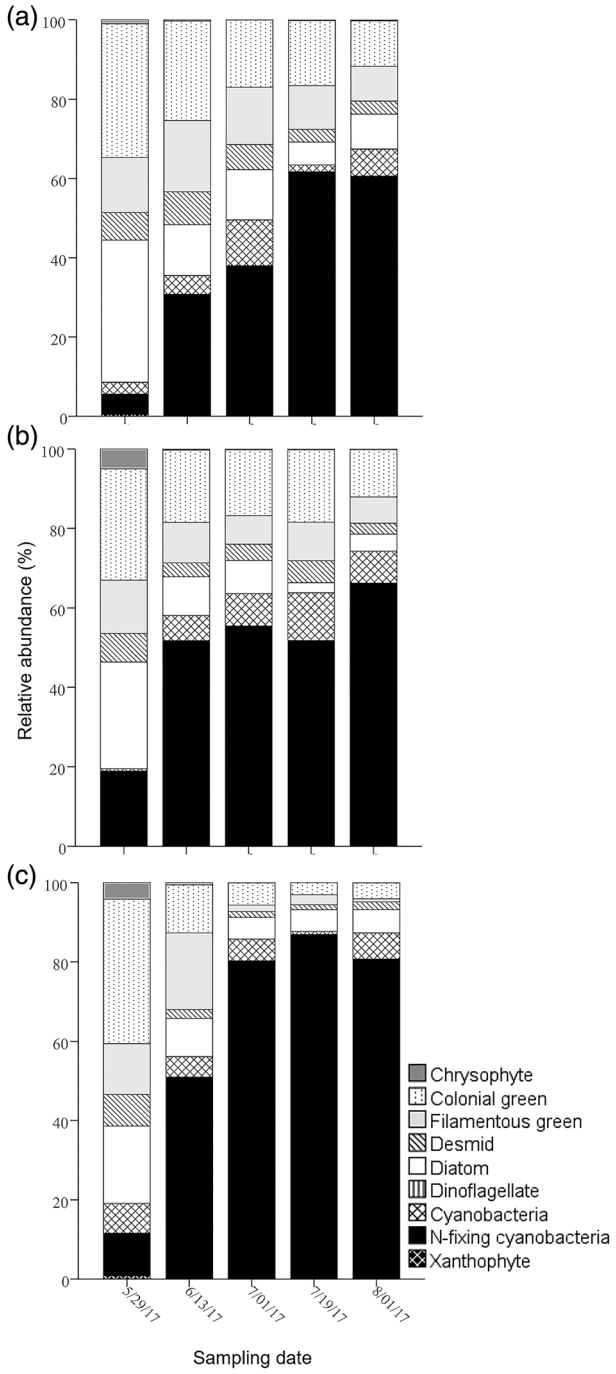

Fig. 6. Algal taxonomic composition as relative abundance of functional groups among the rich (**a**), moderate (**b**), and poor (**c**) fens over the growing season. Bars are the mean of eight replicates (combined enriched and unenriched).

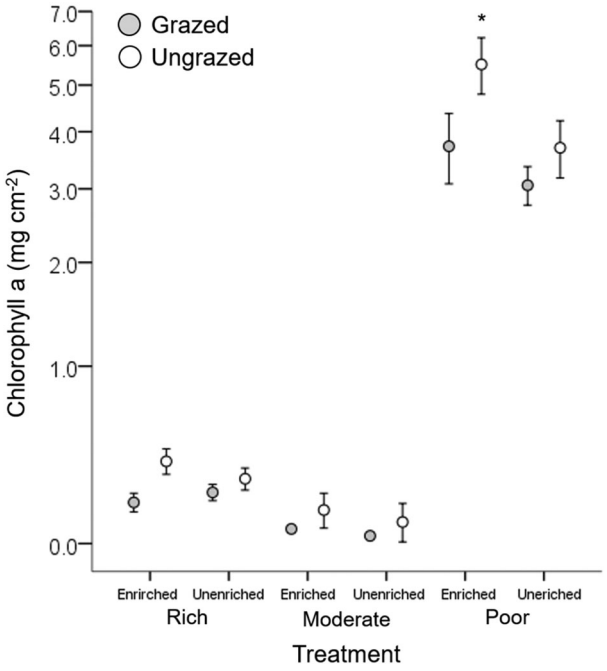

Fig. 7. Algal biomass measured as Chl *a* concentration in grazed and ungrazed treatments with (enriched) or without nutrients (unenriched) within the rich, moderate, and poor fen. Dots are the mean of four replicates ± 1 SE. Significant differences between grazed and ungrazed treatments are indicated by an asterisk ($p < 0.05$).

of algal contribution to the food web is consistent with previous stable isotope analysis conducted during a single sampling event within a rich fen which found that 79% of carbon in secondary producers was derived from algal sources (DeColibus et al. 2017). Our current study also shows that the algal energy pathway persisted across the growing season in three fens that span the range of peatlands that occur within the boreal landscape. Specifically, we found that periphyton contributed more to invertebrate diet over the growing season (71–76% in rich, 78–81% in moderate, and 20–65% in poor) compared to all other possible sources of carbon combined (e.g., bryophytes, vascular plants, or detritus), which contribute less than 17% in the poor fen and less than 9% in moderate and rich fens. These findings add to a growing body of literature challenging the notion that primary production by algae is of minor importance to peatland energy flow (van Duinen et al. 2013; Mieczan et al. 2015; Vesterinen et al. 2016; DeColibus et al. 2017). It is also noteworthy that some herbivores had lower $\delta^{13}C$ than periphyton, which could reflect the inclusion of highly ^{13}C-depleted heterotrophic bacteria (e.g., methane-oxidizing bacteria) as another source of dietary carbon (van Duinen et al. 2013). Similar findings have been reported from ecosystems where high DOC concentrations serve as the primary source of organic matter for heterotrophic bacteria, resulting in strongly depleted ^{13}C values that are transferred through the food web (Vesterinen et al. 2016; Kendrick et al. 2018).

Variation in the amount of biomass at each trophic level reflected the progressive movement of periphyton-derived organic matter to higher trophic levels (from grazers to predators) over time. Evidence for this trend was the coupling of algal and macroinvertebrate biomass throughout the growing

season and across the fen gradient, irrespective of nutrient addition. The transfer of algal biomass up the food chain was reflected in the greater proportion of herbivore biomass early in the growing season, followed by an increase in the relative abundance of predatory macroinvertebrates during the latter part of the growing season. Further evidence for this trend was apparent from SIAR mixing models where the relative contribution of periphyton to herbivore diet was more elevated early in the growing season and declined over time, whereas the contribution transferred from herbivores to predators increased over time in each fen. These findings are consistent with research demonstrating that high quality algal food sources play a significant role in sustaining secondary production in detritus-based ecosystems (Crenier et al. 2017; Vadeboncoeur and Power 2017). Our findings also provide insight as to why some peatlands maintain higher than expected rates of secondary production despite the potential for poor nutrient conditions to limit energy flow (van Duinen et al. 2013).

Despite having similar trophic structure, the efficiency of biomass transferred through the food web varied among fens. In particular, the highest levels of algal biomass in the poor fen did not translate to the most invertebrate biomass. Although periphyton was the dominant basal resource in the poor fen, it consistently comprised a lower proportion of invertebrate diet than in the rich or moderate fens. Further, the relative contribution of periphyton to invertebrate diet was at its maximum at the end of the growing season as opposed to early in the growing season in the rich and moderate fens. Together these results point to a slower or less efficient rate of biomass transfer in the poor fen compared to the other fen types (Müller-Navarra et al. 2000). Similar findings have been attributed to a change in food quality associated with shifts in periphyton community composition and subsequently $\delta^{13}C$ (Spivak 2015). When we examined the carbon : nitrogen (C : N) ratio of periphyton as an indicator of food quality, we found that periphyton in the poor fen had the highest C : N (lowest quality) compared to the rich or moderate fen (data not shown), providing evidence that lower periphyton quality slowed biomass transfer to higher trophic levels (Guo et al. 2016). Yet, the C : N of periphyton decreased over time from 16.9 to 7.97 in the poor fen which is suggestive of increasing food quality and may explain the greater proportion of periphyton in invertebrate diets later in the growing season. In contrast to the poor fen, invertebrate biomass in the moderate fen was three-fold greater by the end of the growing season despite comparatively lower levels of algal biomass than the rich or poor fens, possibly indicative of a higher food quality or more efficient transfer of resources (Crenier et al. 2017). Consistent with these expectations, the C : N of periphyton in the moderate fen was lower (higher quality) than in either the rich or poor fen, and showed little variation (10.2–10.6) over time. Taken together, these findings suggest that periphyton remained a qualitatively important food source to animal diet throughout the growing season but the underlying differences in the physical and chemical conditions that characterize each fen (i.e., feedbacks between hydrology and biogeochemistry) likely influenced the quality of basal resources with consequences for energy transfer (Buchkowski et al. 2019).

In addition to serving as the primary basal resource for benthic macroinvertebrates, periphyton also appeared to be subsidizing planktonic consumers (i.e., zooplankton; Vadeboncoeur et al. 2003; Mariash et al. 2014), particularly in the rich fen. The presence of planktonic consumers in a peatland food web is noteworthy given that zooplankton are traditionally studied in limnetic food webs whereas the aquatic phase of boreal peatlands has largely been ignored. The dynamic environmental conditions that characterize the aquatic phase of boreal peatlands favor animal populations with short life histories, such as zooplankton, that can take advantage of high-quality food sources available during the short summer growing season (Rautio et al. 2011; Mariash et al. 2014; Mieczan et al. 2015). The shallow nature of peatland pools with a well-lit photic zone and an abundance of submerged substrata (e.g., erect plant stems) facilitates periphyton development throughout the entire water column, enabling access for both benthic and planktonic consumers. Previous research from high latitude lakes and ponds has shown that benthic primary production often provides the basis for zooplankton diets, particularly under low nutrient conditions (Rautio et al. 2011; Mariash et al. 2014). Consistent with previous work, we found that zooplankton $\delta^{13}C$ was more similar to periphyton than any of the other potential basal resources (e.g., detritus). These findings suggest that the periphyton that forms attached to submerged surfaces during periods of inundation provides an important link between benthic and planktonic habitats in boreal peatlands (Mieczan et al. 2015).

Results from this study demonstrated both bottom-up and top-down regulation of algal biomass in boreal fens. Food web theory predicts that nutrient poor ecosystems contain only primary producers that are resource limited (Hairston et al. 1960). When bottom-up regulation is alleviated, the potential for top-down regulation via consumers exists (Hanson 1992). We found that nutrient addition increased biomass at all trophic levels in each of our study sites suggesting underlying bottom-up regulation. Collectively, these findings are noteworthy given that enhanced nutrient availability associated with climate change is expected to alleviate bottom-up constraints on aquatic primary production (Wyatt et al. 2012; Lougheed et al. 2015), with anticipated consequences for energy flow to higher trophic levels (DeColibus et al. 2017). Furthermore, we found that increased consumer biomass following nutrient addition was adequate to exert top-down regulation of algal biomass. Decreases in algal biomass as a result of grazing were only evident in our

grazer exclusion experiment, suggesting that herbivory was masking the effect of nutrient addition on algal biomass (Rober et al. 2011).

Contrary to expectations of strong top-down regulation from herbivory, algal biomass continued to increase over time in all fens. This trend may be explained by the observed shift in algal community structure from one dominated by more edible algae (e.g., diatoms) to N-fixing cyanobacteria (e.g., *Anabaena*, *Nostoc*), which have a thick mucilaginous sheath that is difficult to consume (Müller-Navarra et al. 2000). Herbivores can selectively consume algae based on size and growth form and this differential consumption of more edible prey can in turn promote an increase in inedible prey (Bell 2002). Consequently, the algal community may have become less edible over time thereby preventing the overexploitation of resources that would otherwise occur with strong top-down control of an edible community (McMeans et al. 2015). These findings are consistent with a previous study in a boreal peatland showing an increase in the proportion of inedible algae in the presence of elevated herbivore biomass (DeColibus et al. 2017).

Overall, our data provide insight into patterns of natural variation within the aquatic food web of boreal peatlands and support our hypothesis that periphyton sustains secondary production during periods of inundation. Boreal peatlands are naturally dynamic and can be inundated with water for all or part of a growing season (Arsenault et al. 2018). The frequency and duration of inundation determines the spatial distribution of habitats as well as aquatic community structure (Kneitel 2014; Mazumder et al. 2017; Nelson et al. 2019). Although periods of inundation have become increasingly common in boreal regions over the past decade, more variable precipitation regimes are also expected intensify the intermittent nature of peatland hydrology (Euskirchen et al. 2019). While we expect periods of drought to restrict the development of an aquatic food web (Kneitel 2014; Mazumder et al. 2017), biogeochemical cycling is enhanced at the interface of wet and dry phases (Wyatt et al. 2012). Our previous work has shown that alternating drought and flooding promotes nutrient availability in the water column and thereby increased algal production and resource availability for higher trophic levels (DeColibus et al. 2017). While variable hydroperiods have been linked to accelerated carbon dioxide (CO_2) efflux from other temporary aquatic ecosystems via enhanced microbial decomposition (i.e., brown energy pathways; DelVecchia et al. 2019), research from our study sites has shown that elevated algal production (green energy pathway) can offset increases in CO_2 efflux during periods of inundation (Kane et al. 2021). Further, we have recently demonstrated that predatory macroinvertebrates can substantially reduce CO_2 emissions by limiting herbivore access to algal biomass, resulting in greater primary productivity and CO_2 uptake in peatlands (Wyatt et al. 2021). Collectively, these findings suggest that the presence or absence of an algal-based food web has consequences for carbon cycling in temporary aquatic ecosystems.

Conclusion

A critical challenge to predicting ecosystem resilience in the face of global change is characterizing spatial and temporal variability in food web dynamics (McMeans et al. 2015). This paucity of information is particularly acute in boreal peatlands where the variable nature of the aquatic phase is a primary control on nutrient availability as well as sources of production, making peatland food webs difficult to evaluate over time. Here, we have documented spatial and temporal variation in how individual taxa function in the peatland food web and how the biomass at each trophic level changes over time. Our findings demonstrate that despite having annual primary production that is dominated by mosses and vascular plants, periphyton are central to supporting invertebrate production during periods of inundation in boreal peatlands. These findings challenge the prevailing view in peatland ecology that energy flow is detritus-based (Moore et al. 2004; van Duinen et al. 2013). Further, we found similar trophic structure among fens but strong seasonal dynamics in biomass at all trophic levels that were enhanced by nutrient addition. These findings suggest that accelerated nutrient mineralization and transport from terrestrial to aquatic ecosystems as a result of ongoing climate change (Wickland et al. 2018), will alleviate bottom-up constraints on aquatic primary production and subsequently increase resource availability for higher trophic levels (Kendrick et al. 2018). Given that the majority of macroinvertebrates in boreal peatlands are aquatic as larvae but emerge as adults into the surrounding terrestrial environment, increased resource availability for higher trophic levels may provide an important link between aquatic and terrestrial phases of boreal peatland ecosystems.

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Acknowledgments

This research was supported by the National Science Foundation (DEB-1651195) and the Bonanza Creek Long-Term Ecological Research Program (USDA Forest Service, Pacific Northwest Research Station grant

number RJVA-PNW-01-JV-11261952-231 and National Science Foundation grant number DEB-1636476).

Conflict of Interest

None declared.

Submitted 27 July 2020
Revised 07 January 2021
Accepted 18 January 2021

Associate editor: Robert O. Hall, Jr