

CHIRONOMIDS SHED LIGHT ON ORGANIC MATTER DYNAMICS IN MACROINVERTEBRATE COMMUNITIES IN PRAIRIE POTHOLE LAKES IN WEST-CENTRAL MINNESOTA, USA

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Abstract

The Prairie Pothole Region (PPR) in North America is characterized by a high density of wetlands that can range from temporary habitats to small lakes. Much of the PPR has been converted to agriculture resulting in outright habitat loss, eutrophication, sedimentation, introduction of agrochemicals, and the introduction of invasive plants and animals. We compared two prairie pothole lakes, Cottonwood Lake and Page Lake, to assess the functional roles and trophic structure of the macroinvertebrate communities in this highly altered landscape. We collected macroinvertebrate samples from littoral and profundal regions of each lake with an Ekman grab sampler in winters of 2007-2008. In fall 2012, 15 samples were collected from the near shore aquatic vegetation of Cottonwood Lake using D-frame nets. Macroinvertebrates, including Chironomidae, were identified to genus or morphospecies and assigned to functional feeding groups (FF-groups). Taxon richness of littoral and profundal samples were comparable in Cottonwood Lake but was significantly lower in the profundal zone of Page Lake. Macroinvertebrate abundance was significantly lower in Page Lake. Chironomidae made up 55% and 38% of the abundance in Cottonwood and Page Lakes, respectively and the similarity in chironomid composition was only 53%. Significantly more shredders, including the chironomid *Glyptotendipes*, occurred in Cottonwood Lake, including in the profundal zone. Macrophytes in Cottonwood Lake support additional taxa and shed light on the importance of near-shore sources of organic matter as a food resource. The FF-group distribution in Cottonwood Lake suggests that macroinvertebrates are taking advantage of a continuum of available organic matter resources that is dominated by coarse particulate organic matter (CPOM) near shore and by fine particulate organic matter (FPOM) in habitats farther from shore. In

contrast, Page Lake had limited sources of organic matter; very few shredders were collected from littoral samples in Page Lake. In profundal samples most taxa were collector gatherers (*Chironomus*) or predators (*Procladius* and other Tanyptodinae). Macroinvertebrates in Page Lake appear to be resource limited suggesting that the extensive algal blooms that characterize this eutrophic lake do not provide a comparable food source to that found in Cottonwood Lake. Analysis of the macroinvertebrate communities allowed us to discern the functional role of macroinvertebrates, including the Chironomidae, in processing organic matter in these highly impacted systems.

Introduction

Macroinvertebrates are diverse and abundant in freshwater habitats where they play critical roles in aquatic food webs and contribute to ecosystem function such as processing of organic matter. Because they exhibit a wide range of preferred environmental conditions and tolerances to anthropogenic impacts including habitat alteration and a variety of pollutants, macroinvertebrates have long been used as bioindicators of the relative health of the habitats in which they occur. This practice is well established in lotic ecosystems where Ephemeroptera, Plecoptera, and Trichoptera, which contain many sensitive species, are common indicators of ecosystem health (e.g. Zweig and Rabeni 2001). While perhaps not as widely used in lakes, macroinvertebrates have shed light on environmental conditions, particularly the trophic state of lentic systems (Sæther 1979, Poikane et al. 2016).

In contrast, evaluating the health of wetland habitats based on macroinvertebrate community composition, particularly in the Prairie Pothole Region (PPR) of North America has proven more challenging (e.g. Tangen et al. 2003, Gleason and Rooney 2017). Part of this challenge stems from

the diversity of habitats that fall under the umbrella of “wetland,” which can range from temporary habitats to small lakes. The PPR is an area spanning several states and Canadian provinces in central North America that is characterized by a particularly high density of depressional wetlands. Much of the PPR has been converted to agricultural land use resulting in loss of 50-90% of wetland habitat since colonization by Europeans (Euliss et al. 2006, Dahl 2014). As smaller wetlands were drained there has been an increase in larger wetlands and lakes (McLean et al. 2016a, McLean et al. 2020, Vanderhoof and Alexander 2016). Besides habitat loss, anthropogenic stressors include eutrophication, sedimentation, introduction of agrochemicals, and the introduction of invasive plants and animals. Even before widespread human impact, this region was naturally subject to extremes in temperature and variable precipitation, so macroinvertebrate communities in the PPR are comprised of resilient species that have physiological, life history, and behavioral adaptations to survive in harsh environments (Euliss et al. 2006).

Another possible hinderance to understanding macroinvertebrates in prairie potholes is that the taxonomic resolution applied to the macroinvertebrate community is inconsistent, particularly when it comes to the Chironomidae. Some studies identify chironomids to genus (e.g. Campbell et al. 2009, Olson et al. 1995), others may treat the predaceous Tanypodinae separately from the rest of the family (e.g. Rennie and Jackson 2005), still others identify chironomid midges only to the family level (e.g. Hentges and Stewart 2010, McLean et al. 2016b). This is unfortunate because chironomids consistently make up a significant portion of aquatic macroinvertebrate abundance and diversity (e.g. Euliss et al. 2006, Oertli 1993, Ferrington et al. 2008, Lemes-Silva et al. 2014). Multiple studies have revealed that the Chironomidae are not a monolithic ecological entity, but rather a lineage that contains species that exhibit a range of environmental tolerances, habitat preferences and trophic strategies (e.g. Belle and Goedkoop 2021) and that occupy different trophic levels in aquatic food chains (Berg 1995). Some authors provide sound arguments that chironomids should not be considered one group in food web studies (Reuss et al. 2013). While the resilient macroinvertebrates that inhabit prairie potholes may not reliably serve as indicators of environmental impact, they may still provide insight into ecosystem function in habitats that are threatened by human activities and even global climate change.

We studied the macroinvertebrate community in

two prairie pothole lakes in west-central Minnesota, USA. Though Cottonwood Lake and Page Lake both occur in a landscape dominated by agriculture, adjacent land cover near Cottonwood Lake has more tree-cover. We sought to compare benthic macroinvertebrate communities from littoral and profundal zones of these two lakes. To further evaluate the influence of allochthonous and autochthonous organic matter on the macroinvertebrate community, we sampled macroinvertebrates from near-shore macrophytes and algae.

Materials and Methods

Study Area

Study lakes were in the Northern Glaciated Plains Ecoregion in west-central Minnesota, USA. The landscape was historically dominated by prairie but has largely been converted to row-crop and animal production agriculture. This ecoregion is in the Prairie Pothole Region (PPR), which is characterized by an abundance of depressional wetlands and lakes, i.e. potholes, that formed as the glaciers retreated ca. 14,000 years ago. Most prairie pothole wetlands are naturally fishless and provide valuable habitat for waterfowl and other nongame wildlife.

We studied two prairie pothole lakes, Cottonwood Lake (Grant County) and Page Lake (Stevens County) in west-central Minnesota. Unlike most prairie potholes, these lakes are managed to support piscivorous gamefish, particularly walleye (Percidae: *Sander vitreus*), though several other species, both native and introduced, occur in both lakes (Table 1). Percent tree cover within 50 m of shore was 32% higher at Cottonwood Lake than Page Lake (Table 1). Submerged and emergent macrophytes were common at Cottonwood Lake but were rare in Page Lake (Table 1). Minnesota Department of Natural Resources monitoring suggests that both lakes are eutrophic, though Cottonwood Lake has lower phosphorus levels and higher water clarity than Page Lake (MN DNR LakeFinder; Table 1.)

Data Collection and Analysis

In the winters of 2007 and 2008 benthic macroinvertebrate samples were collected from Page Lake and Cottonwood Lake. Winter sampling ensured a consistent community when no emergence or oviposition was occurring and allowed for undergraduate students to engage in research during the academic year. Samples were collected by lowering an Ekman grab through a hole in the ice and retrieving 0.02 m² of substrate from the bottom of the lake. The volume of grab samples was not

Table 1. Characteristics of Cottonwood Lake and Page Lake, the two prairie pothole lakes located in the Northern Glaciated Plains Ecoregion in west-central Minnesota, USA. Data from Minnesota, Department of Natural Resources LakeFinder, unless noted.

Parameter	Cottonwood Lake	Page Lake
Lake Area (Ha)	103	152
Maximum depth (m)	4.9	3.7
% Tree cover in 50 m buffer*	78	46
10-year-average water clarity (m)	3	2
10-year-average phosphorus (ppb)	161	176
Walleye Stocking	Yes (fingerings)	Yes (fry)
Common Carp	No	Yes
Submerged/emergent macrophytes**	Common	Rare

*ArcGIS10, MN DNR Data Deli

** Field observations

quantified, though seemed comparable between lakes after washing through a 500-micron sieve. From each lake a series of samples from the littoral zone were collected < 50 m from shore. An additional series of samples were collected from the profundal zone > 100 m from shore. Fifteen replicate samples were collected from each habitat in Cottonwood Lake and the profundal zone of Page Lake. Due to weather and ice conditions, only ten samples were collected from the littoral zone in Page Lake.

To assess the association of macroinvertebrates with coarse particulate organic matter (CPOM) in fall 2012, 15 macroinvertebrate samples were systematically collected from the near shore aquatic vegetation of Cottonwood Lake using D-frame nets. Samples were collected from emergent vegetation (primarily *Scirpus*) (N = 6), submerged vegetation, (primarily *Potamogeton* spp.) (N = 6) and filamentous algae (N = 3). Each substrate type was disturbed for 30 seconds and dislodged material, including macroinvertebrates were collected. Near shore aquatic vegetation was extremely rare in Page Lake and was not sampled. Samples from different types of near shore organic matter were not evaluated separately for this analysis.

Both winter benthic samples and samples from near shore vegetation were washed through a 500-micron sieve and preserved in 95% ethanol. Specimens were sorted from sample debris and identified to the lowest possible taxonomic level, typically genus. Functional feeding groups (FF groups) were assigned based on Merritt et al. (2008) and Thorp and Covich (2001).

For winter samples, average macroinvertebrate taxon richness and abundance (log x+1) between lakes and habitat zones were compared using a

fully crossed 2-way analysis of variance (ANOVA), followed by the Tukey's multiple comparison of means to evaluate significance of differences among pairs of variables (version 4.4.0, R Core Team 2024). Abundance of shredders, collector gatherers and predators within each habitat zone was compared using 1-way ANOVA followed by the Bonferroni post hoc test. Jaccard's Similarity Index was used to compare the chironomid communities in the two lakes. Organic matter samples, which were collected for a subsequent undergraduate research project, were used to provide a more complete view of the macroinvertebrate community and to help inform hypotheses about organic matter processing in Cottonwood Lake.

Results

Winter Samples

Thirty-five taxa occurred in winter samples, 24 from each of Cottonwood and Page Lakes (Table 2). Seventeen genera (36%) belonged to Chironomidae. Oligochaete worms, and the dipteran lineages Ceratopogonidae, *Chironomus*, and *Procladius*, were the only groups to occur in littoral and profundal samples in both lakes. Both lakes contained 8 unique macroinvertebrate taxa.

Mean taxon richness differed significantly among habitats (2-way ANOVA, $p \ll 0.01$) but not between lakes, though this difference was driven by lower taxon richness in the Page Lake profundal zone (Fig. 1). At Cottonwood Lake, littoral and profundal samples had similar taxon richness (means of 10 and 8, respectively), while at Page Lake littoral and profundal samples had twice the richness of profundal samples (mean 12 and 6, respectively). Overall, the profundal zone in Page Lake had significantly lower taxon richness than all other habitats ($p < 0.01$; Fig. 1).

Table 2. Macroinvertebrate taxa collected from Cottonwood Lake (CW) and Page Lake (PG). Taxa were assigned to functional feeding-groups (FF-Group) based on Merritt et al. (2008) and Thorp and Covich (2001). (Collector-Gatherers = Coll-Gather, Collector Filterers = Coll-Filter). Number of occurrences in near-shore organic samples (CW only) and winter samples (littoral/profundal) from both lakes are reported.

Taxon	FF-Group	CW Organic (N = 15)	CW Winter (N = 15 / 15)	PG Winter (N = 10 / 15)	
Annelida					
	Oligochaeta	Coll-Gather	1	12 / 12	10 / 14
	Hirudinea	Predator	8	0 / 0	2 / 0
Mollusca					
	Gastropod 1	Scraper	10	3 / 0	0 / 0
	Gastropod 2	Scraper	6	1 / 0	0 / 0
	Gastropod 3	Scraper	5	0 / 0	0 / 0
	Bivalve	Coll-Filter	0	0 / 0	1 / 0
Arthropoda					
Arachnida					
	Hydrachnida	Predator	4	4 / 14	0 / 13
Crustacea					
	<i>Orconectes</i>	Shredder	6	0 / 2	0 / 0
	<i>Gammarus</i>	Shredder	4	0 / 0	0 / 0
	<i>Hyalella</i>	Shredder	15	14 / 13	3 / 0
Insecta					
Ephemeroptera					
	<i>Callibaetis</i>	Coll-Gather	8	2 / 1	4 / 0
	<i>Caenis</i>	Coll-Gather	7	7 / 0	7 / 0
	<i>Hexagenia</i>	Coll-Gather	0	0 / 0	6 / 0
Odonata					
	<i>Enallagma</i>	Predator	14	8 / 0	0 / 0
	<i>Anax</i>	Predator	3	0 / 0	0 / 0
Hemiptera					
	<i>Belostoma</i>	Predator	2	0 / 0	0 / 0
	Corixidae		14	1 / 0	5 / 4
	<i>Ranatra</i>	Predator	2	0 / 0	0 / 0
	Notonectidae	Predator	6	0 / 0	0 / 0
	<i>Neoplea</i>	Predator	1	0 / 0	0 / 0
Coleoptera					
	Dytiscidae	Predator	4	0 / 0	0 / 0
	<i>Dubiraphia</i>	Scraper	0	0 / 0	1 / 0
	<i>Peltodytes</i>	Piercer	2	0 / 0	0 / 0
Trichoptera					
	<i>Oecetis</i>	Predator	2	9 / 1	2 / 0
	<i>Phryganea</i>	Shredder	1	0 / 0	0 / 0
	Polycentropodidae	Predator	0	0 / 0	1 / 0
Diptera					
	<i>Chaoborus</i>	Predator	0	1 / 9	0 / 0

Taxon	FF-Group	CW Organic (N = 15)	CW Winter (N = 15 / 15)	PG Winter (N = 10 / 15)
Ceratopogonidae	Predator	0	14 / 8	9 / 15
<i>Chironomus</i>	Coll-Gather	3	9 / 14	4 / 14
<i>Cryptochironomus</i>	Predator	3	12 / 11	4 / 0
<i>Dicrotendipes</i>	Coll-Gather	0	9 / 0	4 / 1
<i>Endochironomus</i>	Coll-Gather	3	0 / 0	0 / 0
<i>Glyptotendipes</i>	Shredder	6	15 / 11	0 / 0
<i>Polypedilum</i>	Coll-Gather	3	3 / 0	10 / 0
<i>Pseudochironomus</i>	Coll-Gather	0	0 / 0	5 / 0
<i>Cladotanytarsus</i>	Coll-Gather	3	9 / 0	4 / 1
<i>Tanytarsus</i>	Coll-Gather	3	1 / 0	1 / 0
<i>Corynoneura</i>	Coll-Gather	1	0 / 0	0 / 0
<i>Cricotopus</i>	Coll-Gather	11	3 / 0	2 / 0
<i>Eukiefferiella</i>	Shredder	0	1 / 0	0 / 0
<i>Tvetenia</i>	Coll-Gather	4	0 / 0	0 / 0
<i>Ablabesmyia</i>	Predator	0	5 / 4	0 / 0
<i>Coelotanypus</i>	Predator	0	0 / 0	1 / 0
<i>Procladius</i>	Predator	0	14 / 15	8 / 14
<i>Tanypus</i>	Predator	0	1 / 0	3 / 1
Empididae	Predator	1	0 / 0	0 / 0
Psychodidae	Coll-Gather	0	0 / 0	1 / 0
Total No. Taxa	47	33	25 (24 / 13)	25 (24 / 9)

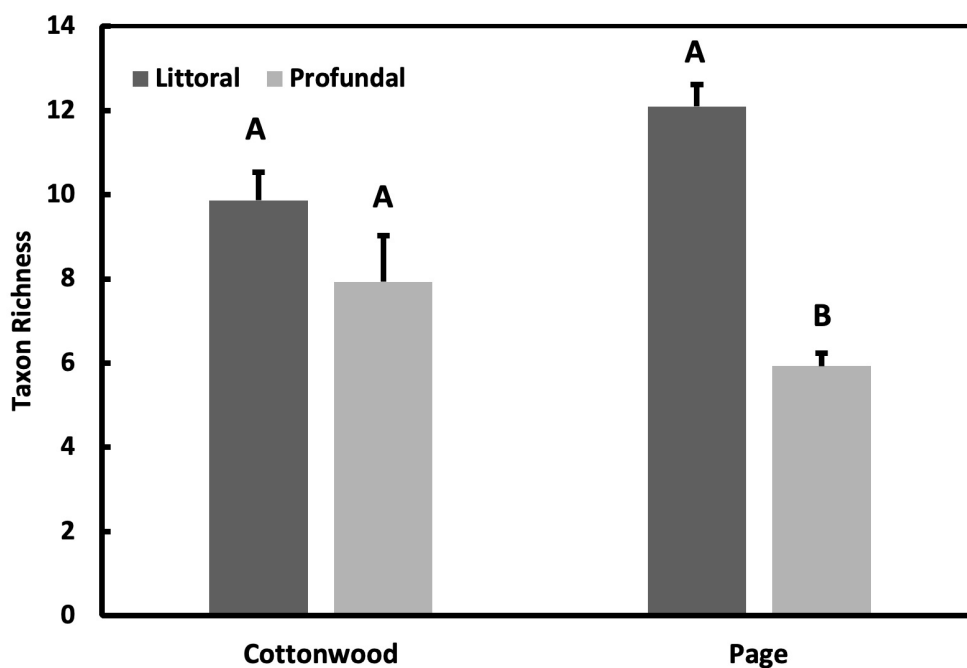


Figure 1. Mean taxon richness (+SE) for littoral and profundal samples from Cottonwood and Page Lake. Taxon richness was compared among lakes and habitats (2-way ANOVA and Tukey's multiple comparison of means test). Different upper-case letters indicate significant differences among habitats.

Macroinvertebrate abundance was significantly greater in Cottonwood Lake (mean 238) than Page Lake (mean 98; $p < 0.01$; Fig. 2). The profundal zone in Page Lake, on average, supported significantly fewer macroinvertebrates than either habitat in Cottonwood Lake, but did not differ in abundance from the Page Lake littoral zone (Fig. 2). The interaction between lake and habitat was marginally statistically significant ($p = 0.07$), driven by lower abundances of macroinvertebrates in the Page Lake profundal zone (mean 73) compared to the Cottonwood Lake profundal (mean 227; $p < 0.01$) and littoral zones (mean 250; $p < 0.01$). The results suggest that the profundal zone in Page Lake, on average, supported significantly fewer macroinvertebrates than either habitat in Cottonwood Lake. However, the difference between mean abundance in Page Lake littoral and profundal zones was not statistically significant ($p = 0.13$; Fig. 2). Chironomidae represented 55% of abundance in Cottonwood Lake and 38% of the abundance in Cottonwood and Page Lakes. Although chironomid richness was comparable between lakes, chironomid communities in the two lakes were not the same (Jaccard Coefficient of Similarity = 0.53).

Shredders were the most abundant functional feeding group in the Cottonwood Lake littoral zone, whereas collector gatherers and predators numeri-

cally dominated in the profundal zone (Fig. 3, Fig. 5). In contrast, few shredders were collected from the littoral zone in Page Lake; no shredders were collected from the profundal zone (Fig. 3). Mean abundance of collector gatherers and predators was similar across all habitats. The trophically diverse Chironomidae contributed to observed patterns in functional feeding group distribution within each lake (Fig. 4). Chironomid shredders were more abundant in the littoral zone of Cottonwood Lake compared to the profundal zone. Chironomid collector gatherers were more abundant farther from shore in profundal samples in Cottonwood Lake. Most chironomids in Page Lake were predators and no chironomid shredders were collected.

Fall Near-Shore Organic Matter Samples

Near-shore organic matter samples collected from Cottonwood Lake in the fall contained 33 taxa, 14 of which were not collected from littoral or profundal zones in the winter. Most of the unique taxa in organic matter were larger shredders including *Gammarus* (Amphipoda: Gammaridae) and *Phryganea* (Trichoptera: Phryganeidae) or predators that actively swim or crawl among the more complex habitat provided by macrophytes and leaf litter such as *Anax* (Odonata: Aeshnidae) and adult Hemiptera and Coleoptera (Table 2). Chironomids found only in the near-shore organic matter samples (*Corynoneura*, *Tvetenia*, and *Endochirono-*

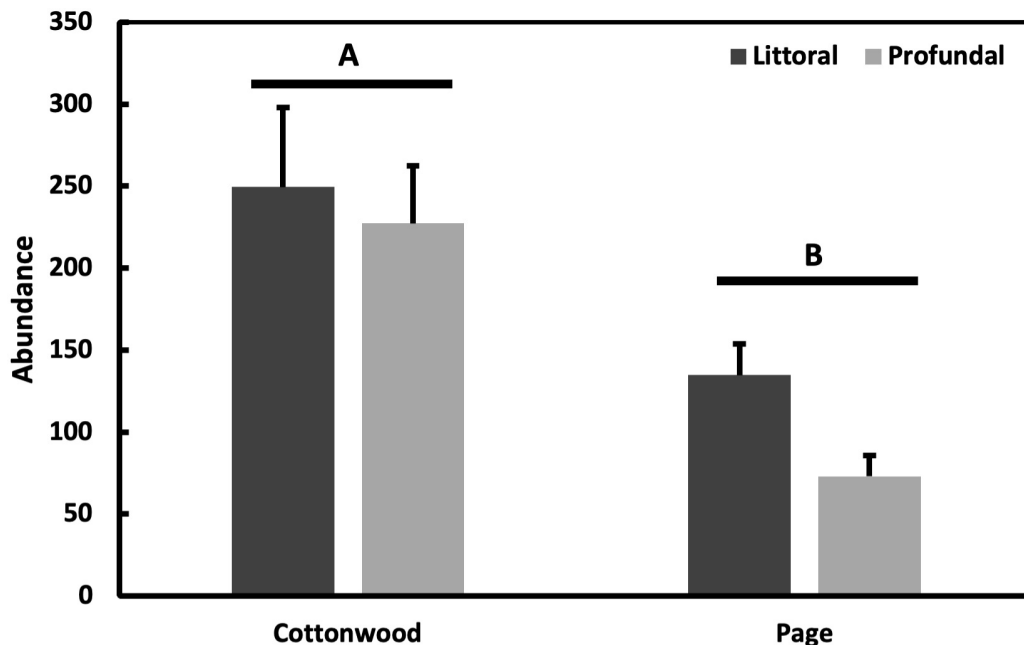


Figure 2. Mean abundance (+SE) of aquatic macroinvertebrates in Ekman grab samples from littoral and profundal samples collected from Cottonwood Lake and Page Lake. Abundance was compared among lakes and habitats (2-way ANOVA and Tukey's multiple comparison of means test). Different upper-case letters indicate significant differences among lakes.

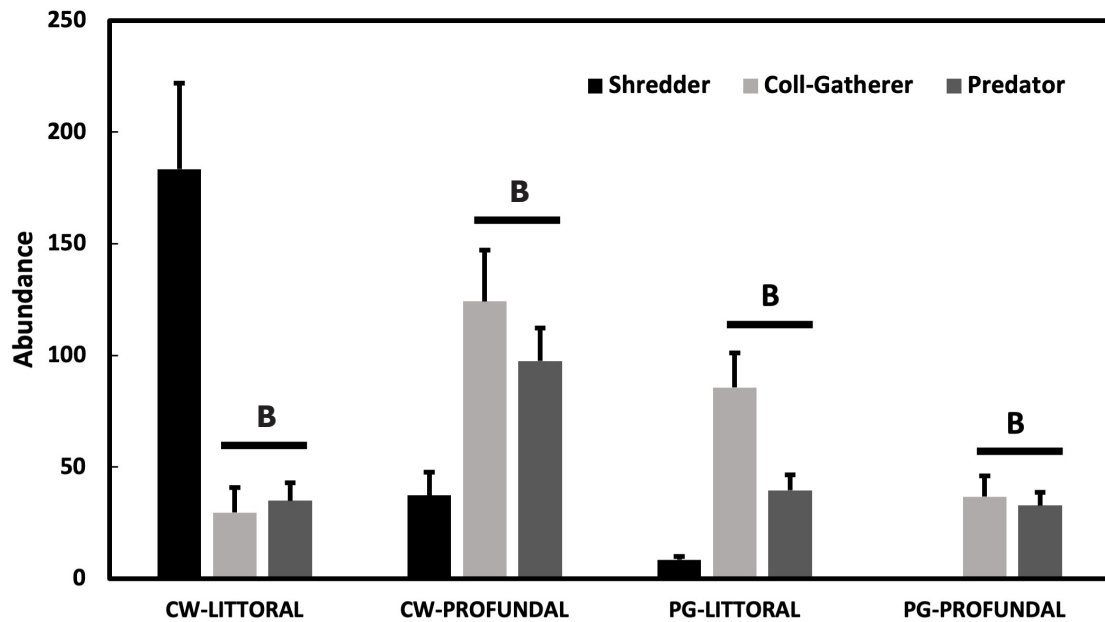


Figure 3. Mean (+SE) abundance of macroinvertebrate shredders, collector gatherers, and predators in Ekman grab samples from littoral and profundal zones from Cottonwood Lake (CW) and Page Lake (PG). Abundances of each FF-group were compared for each habitat (1-way ANOVA and the Bonferroni post-hoc test). Different upper-case letters indicate significant differences in FF-groups within each habitat.

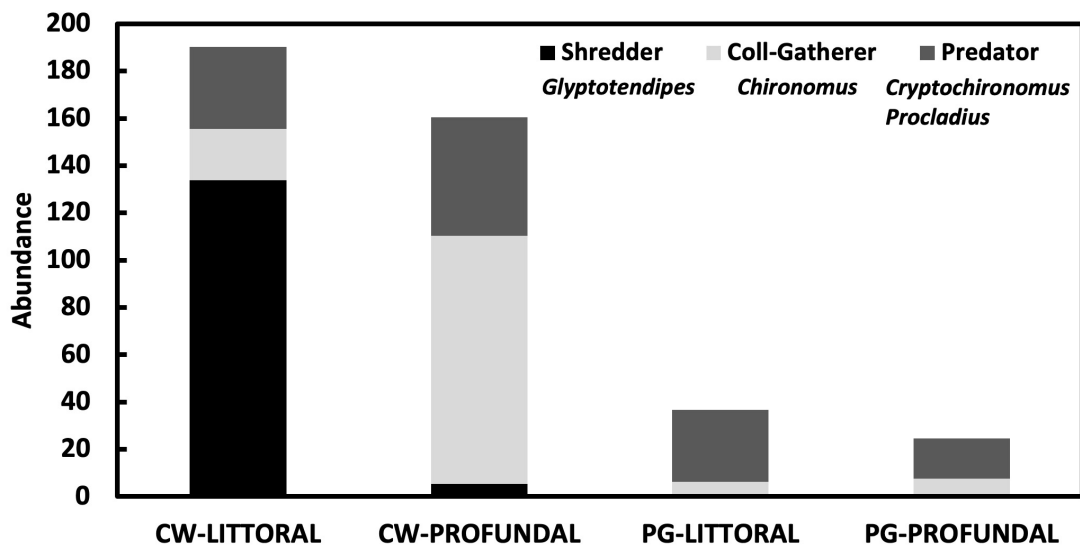


Figure 4. Total abundance of Chironomidae collected in littoral and profundal Ekman grab samples from Cottonwood Lake (CW) and Page Lake (PG). Abundances of chironomid shredders, collector-gatherers (Coll-Gatherer) and predators are indicated. The most common chironomid groups for each functional feeding group are listed.

mus), were all collector gatherers and were infrequently collected. As in littoral samples, shredders were the most abundant functional feeding group (Fig. 5a). Unlike any of the winter samples, scrapers, primarily gastropods, were common in near-shore organic matter (Fig. 5).

Discussion

While both study lakes occur in landscapes dominated by agriculture and are managed to support recreational angling, they exhibit different habitat conditions. Cottonwood Lake has more tree cover within a 50 m buffer, supports abundant submerged and emergent macrophytes, and does not have invasive carp, suggesting it may provide an example

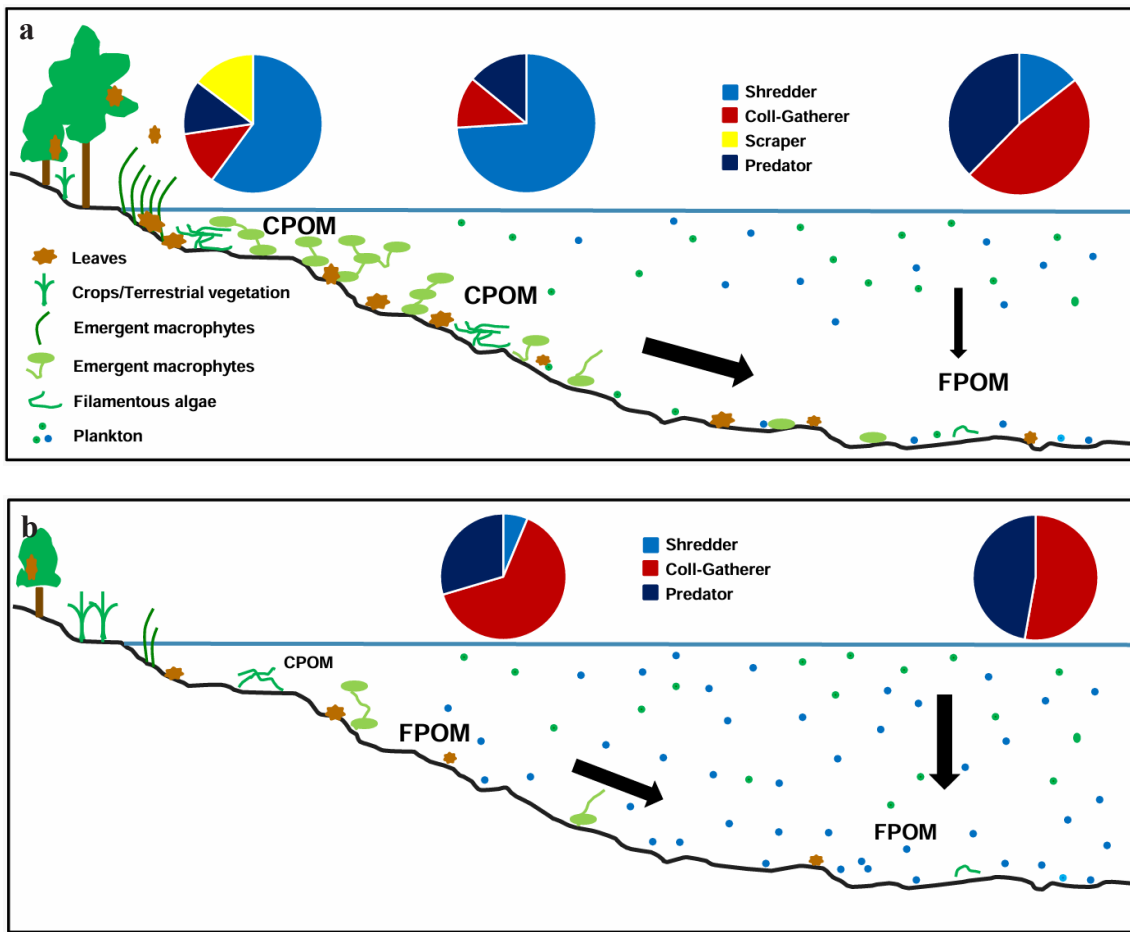


Figure 5. Schematic view of the distribution of particulate organic matter source in a) Cottonwood Lake and b) Page Lake based on relative abundance of macroinvertebrate functional-feeding groups in winter samples from littoral and profundal regions of both lakes and from near-shore organic matter (Cottonwood Lake only). Size of font of indicates relative amounts of coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) hypothesized in each region of the lake.

of relatively high-quality conditions in this highly altered landscape. In contrast, Page Lake has invasive carp, few macrophytes and lower water clarity, thus exhibiting many of the environmental challenges that plague lakes in the area. Analysis of the macroinvertebrate communities in each lake also reveal differences between the two lakes.

Macroinvertebrate communities from Cottonwood Lake and Page Lake are consistent with what has been reported from other prairie pothole lakes and wetlands — Chironomidae were the most abundant and diverse macroinvertebrates in littoral and profundal samples from both lakes and relatively few mayflies and caddisflies were collected (Euliss et al. 2006, Oertli 1993, Ferrington et al. 2008, Lemes-Silva et al. 2014). Taxa in both lakes are well adapted to live in the harsh conditions that typify the PPR, particularly benthic anoxia (sensu Euliss et al. 2006). For example, oligochaete worms and midges, especially *Chironomus* and

Procladius, which are often found in low oxygen conditions (Hershey and Lamberti 2001), were frequently collected in littoral and profundal samples in both lakes (Table 2). Additionally, many adult Coleoptera and Hemiptera, which use atmospheric oxygen and can disperse among habitats, occurred in organic matter samples from Cottonwood Lake.

Taxon richness in winter samples did not differ significantly between the two lakes. While there was insufficient macrophyte cover to collect meaningful samples in these habitats at Page Lake, the widespread occurrence of submerged and emergent macrophytes in Cottonwood Lake yielded 14 additional taxa in fall sampling, suggesting that Cottonwood Lake has the potential to support higher abundance and greater richness of macroinvertebrates than Page Lake.

Winter macroinvertebrate abundances further suggest that Cottonwood Lake provides better habitat for macroinvertebrate communities. Mean mac-

roinvertebrate abundance in Cottonwood Lake was comparable in littoral and profundal environments and was significantly greater than mean abundance in Page Lake. The greater abundance of macroinvertebrates throughout Cottonwood Lake indicates that this lake provides relatively favorable environmental conditions for freshwater organisms even in a highly altered landscape.

By identifying chironomids to the level of genus, we were able to discern meaningful differences in functional feeding groups between the two lakes (Fig. 3). In Cottonwood Lake shredders were significantly more abundant than collector gatherers and predators in the littoral zone but were the least abundant FF-group in the profundal zone, which was dominated by collector-gatherers and predators. Most chironomids in the littoral region of Cottonwood Lake were shredders, which feed in/on coarse particulate organic matter. Shredders including *Glyptotendipes* (and the amphipod, *Hyalella* sp.) also occurred in profundal samples, though in lower numbers. Conversely, collector-gatherers, such as *Chironomus*, comprised a small part of the midge community in the littoral region, but were very abundant in profundal samples.

In Page Lake there were very few shredders and the relative distribution of FF-groups was similar to that of the Cottonwood Lake profundal zone. The relative abundance of predators and collector gatherers were similar the littoral and profundal zones of Page Lake, indicating limited differentiation in community structure and function in these two “habitats.” In contrast, Cottonwood Lake had greater abundance of collector-gatherers in the profundal zone than in the littoral zone, suggesting clear differentiation in FF-groups by habitat. The observed patterns in distribution of FF-groups were discernable because chironomids were identified to genus, which allowed us to recognize different feeding strategies found within this diverse family (Ferrington, et al. 2008; Fig. 4).

The FF-group distribution in Cottonwood Lake suggests that macroinvertebrates are taking advantage of a continuum of available organic matter resources that is dominated by coarse particulate organic matter (CPOM) in the littoral region of the lake and by fine particulate organic matter (FPOM) deeper habitats that are farther from shore. As reported for other ecosystems, particularly streams, it is likely that littoral macroinvertebrates facilitate the breakdown of CPOM into FPOM and that macroinvertebrates are distributed in a way to take advantage of the resources they are best adapted to exploit (e.g. Vannote et al. 1980, Dieterich et al. 1997). The low number of shredders in the Page

Lake littoral zone and their complete absence in profundal samples suggest there is less CPOM available near shore and consequently less FPOM available in the profundal zone. This is consistent with the observed paucity of macrophytes and relatively low tree-cover within 50 m of the shoreline, compared to Cottonwood Lake (Table 1).

Macroinvertebrate samples from near-shore sources of organic matter in Cottonwood Lake provide a more complete picture of trophic dynamics in the macroinvertebrate community. As expected, organic matter samples were dominated by shredders, including larger organisms such as crayfish and phryganeid caddisflies. Scrapers, collector-gatherers, and predators occurred in approximately equal numbers (Fig 5a). CPOM, whether it originates from the adjacent landscape (i.e. leaf litter) or in-lake primary productivity (i.e. submerged and emergent macrophytes), is a valuable resource for many macroinvertebrates and seems to ultimately support benthic production throughout the lake (e.g. Batzer 1998). Whether due to feeding and production of feces by shredders, breakdown by microbes, or other physical means, CPOM contributes to the pool of FPOM, which serves as a food resource for collector-gatherers. Page Lake had fewer potential sources of CPOM (i.e. few macrophytes, less tree cover) (Fig. 5b) and supported fewer shredders that would facilitate processing of organic matter required by collector-gatherers. The relatively small inputs of CPOM and low abundance of benthic macroinvertebrates suggest that higher trophic levels may be food limited in Page Lake.

It seems counter-intuitive that organisms in a eutrophic lake could be food limited, but much of the productivity in Page Lake is in the form of dense annual blooms of phytoplankton, dominated by cyanobacteria. The combination of low water clarity due to phytoplankton and benthic disturbance by common carp paired with possible effects of allelopathic chemicals produced by cyanobacteria (Mohammed 2017) create an environment that is unfavorable for macrophyte growth. As in other systems, habitat simplification and lack of physical structure provided by submerged and emergent macrophytes influences the diversity and abundance of macroinvertebrates that the system can support (e.g. Olson et al. 1995). Cyanobacteria and other phytoplankton, which senesce and enter the benthic detrital pool in late summer/early fall do not provide a sufficient food resource to support robust macroinvertebrate populations. In contrast, systems with food originating from either the adjacent landscape or emergent and submergent mac-

rophytes provide a variety of food resources to sustain macroinvertebrate communities following the senescence of planktonic primary producers. While some studies have shown that cyanobacteria may be consumed by zooplankton and benthic macroinvertebrates (Yu et al. 2013), invertebrates commonly avoid or reject cyanobacteria as a food source (Vanderploeg et al. 2001) and cyanotoxins are toxic to many macroinvertebrates (Fadel et al. 2023, Stephanian et al. 2020). Determining if and how benthic macroinvertebrates use detrital cyanobacteria and whether this food resource is sufficient to support macroinvertebrates throughout the winter should be further investigated.

Prairie pothole lakes are consistently subjected to human impacts due to agricultural practices that alter the natural vegetation and hydrology of the landscape, augment nutrient availability, deposit other agrochemicals, and aid the establishment of invasive plants and animals (Euliss et al. 2006), all of which may be exacerbated by changing temperature and precipitation patterns associated with climate change (McLean et al. 2020). Despite this plethora of stressors, hardy macroinvertebrate communities of prairie pothole lakes and wetlands continue to play critical functional roles in organic matter processing and the food webs in these highly impacted systems

Our analysis suggests that organic matter deriving from either autochthonous or allochthonous sources near shore provide a critical resource for benthic macroinvertebrates throughout the lake. This conclusion is consistent with theoretical models for processing organic matter in streams (Vannote et al. 1980). Recognizing different feeding strategies of the Chironomidae, which are frequently all lumped together as collector-gatherers made this interpretation of organic matter dynamics in prairie pothole lakes possible. More detailed analysis of detrital food resources, gut content analysis of benthic macroinvertebrates, and the consumption of macroinvertebrates by fish and other vertebrate predators will provide more insight into the trophic dynamics of these environments.

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