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Abstract

We document 134 caddisfly species and their seasonal and habitat affinities based on 93 samples collected from 26 sites throughout the Manistee River watershed in the lower peninsula of Michigan from May through September, 2010. Eleven of these species: *Banksiola dossuaria* (Say), *Cheumatopsyche aphanta* Ross, *Cheumatopsyche pasella* Ross, *Hydroptila xera* Ross, *Ironoquia lyrata* (Ross), *Lepidostoma vernale* (Banks), *Neotrichia vibrans* Ross, *Nyctiophylax affinis* (Banks), *Oxyethira aeola* Ross, *Oxyethira rivicola* Blickle and Morse, and *Polycentropus timesis* (Denning) are reported from Michigan for the first time. More than 85% of species reached peak adult abundance during June or July, although a few species reached peak abundance or emerged exclusively during the other months. Overall species richness reached its peak during early July, with a smaller peak of unique species in September. Caddisfly faunas in lakes, small streams, medium rivers, and large rivers were all distinct from each other, suggesting that the overall watershed is following patterns predicted by the River Continuum Concept. It is likely that the Michigan caddisfly fauna contains considerably more species than what is currently known.

Despite the ecological importance of caddisflies in aquatic ecosystems and their utility in biological monitoring (Allan 1995, Dohet 2002), the faunas of the north central U.S. and southcentral Canada are not well known. Only the Minnesota fauna (Houghton et al. 2001; Houghton 2004a,b; 2007) has been studied extensively. Geographic areas of this state have been delineated into "caddisfly regions" based on similar assemblages, and such assemblages have been correlated to both natural and anthropogenic environmental variables. Having such a framework in place renders future changes to the Minnesota fauna easier to evaluate (Houghton and Hozenthal 2010). For the remainder of the area, basic species checklists have been compiled for the Indiana (Waltz and McCafferty 1983), Manitoba (Flannagan and Flannagan 1982), Michigan (Leonard and Leonard 1949), North Dakota (Harris et al. 1980), Ohio (Huryn and Foote 1983), and Wisconsin (Longridge and Hilsenhoff 1973) caddisflies. All of these studies are >25 years old, and it is difficult to ascertain if changes to the faunas have occurred during the interim.

The caddisflies of Michigan are known primarily from Leonard and Leonard's (1949) checklist. Recently, additional state records have been reported (Bright and Bidlack 1998, Craig and Chriscinske 2007, Houghton et al. 2010), but no comprehensive inventory of the state has occurred. Bright (2010) maintains an online checklist of known species. Prior to the current study, 252 species were reported from the state.

The Manistee River watershed is located in the northwestern portion of the lower peninsula of Michigan (Fig. 1). The mainstem of the Manistee River is 375 km in length and drains a watershed area of approximately 2800 km^2

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Figure 1. The location of the Manistee River watershed in Michigan showing the 26 sampling sites of this study. Site names are in Table 1.

before entering Lake Michigan. High groundwater input with subsequent stable river flow and overall good water quality make the Manistee and its tributaries excellent fisheries for the native brook trout (*Salvelinus fontinalis* Mitchill), as well as steelhead (*Oncorhynchus mykiss* [Walbaum]), brown trout (*Salmo trutta* L.) and other fish (MIDNR 1996). Thus, fishing is one of the most popular uses of the river system. Despite the importance of caddisflies in aquatic ecosystems, no comprehensive inventory has been done on the caddisflies of this watershed. The primary objective of this study, therefore, was to document the caddisfly species of the Manistee River watershed. A secondary objective was to make preliminary assessments on patterns of biological diversity relative to season and habitat type.

Materials and Methods

Site determination. Adult caddisflies were collected from a variety of lakes and streams throughout the watershed (Table 1, Fig. 1) from May through September. The majority of samples were collected during June and July, the typical peak of the adult caddisfly emergence in northern United States temperate environments (Monson 1996, Houghton 2004a). Habitats were chosen to yield a geographically representative sample. Nearly all habitats had official protective status (e.g., state or national forest) and were perceived as minimally disturbed based on observed upstream land use. Four habitats: Rockwell Lake

Table 1. The 26 sampling sites of this study and the number of samples collected from each site. Numbers correspond to those in Figure 1. Stream sizes based on width: small (<3 m), medium (3–15 m), and large (>15 m).

Site #	Site name	Location	Type	Number of samples
1	Harper's Lake	N44.13°, W85.98°	Lentic	1
2	Pine River Oxbow Wetland	N44.23°, W85.91°	Lentic	1
3	Mainstem, Manistee River	N44.28°, W85.86°	Large river	6
4	Arquilla Creek	N44.29°, W85.83°	Medium river	1
5	Slagle Creek	N44.33°, W85.82°	Medium river	1
6	Hinton Creek	N44.28°, W85.79°	Medium river	1
7	Syers Lake	N44.07°, W85.80°	Lentic	1
8	North Branch, Twin Creek	N44.06°, W85.78°	Medium river	1
9	South Branch, Twin Creek	N44.06°, W85.76°	Medium river	1
10	Pine River	N44.13°, W85.69°	Large river	1
11	Lower Little Manistee River	N44.03°, W85.73°	Medium river	6
12	Middle Little Manistee River	N44.03°, W85.68°	Medium river	6
13	Upper Little Manistee River	N44.02°, W85.63°	Medium river	6
14	Rockwell Lake	N44.06°, W85.64°	Lentic	3
15	Lower Fairfield Creek	N44.04°, W85.66°	Small stream	16
16	Middle Fairfield Creek	N44.04°, W85.65°	Small stream	16
17	Upper Fairfield Creek	N44.04°, W85.64°	Small stream	16
18	Coe Creek	N44.10°, W85.55°	Medium river	1
19	Edgett Creek	N44.09°, W85.47°	Medium river	1
20	Beebe Creek	N44.10°, W85.26°	Medium river	1
21	Crocker Creek	N44.10°, W85.24°	Medium river	1
22	North Branch, Manistee River	N44.64°, W85.03°	Medium river	1
23	Big Cannon Creek	N44.50°, W85.00°	Medium river	1
24	Blue Lake	N44.80°, W84.90°	Lentic	1
25	Goose Creek	N44.77°, W85.86°	Medium river	1
26	Upper Manistee River	N44.77°, W84.84°	Medium river	1

(#14), Fairfield Creek (#s 15–17), the Little Manistee River (#s 11–13), and the Manistee River Mainstem (#3) (Fig. 1) were *a priori* considered representative of lakes, small streams (width <3 m), medium rivers (3–15 m), and large rivers (>15 m) respectively, and were sampled on multiple occasions throughout the sampling period. Stream sizes approximated the size divisions of the River Continuum Concept (Vannote et al. 1980), thus inferring ecological information about each site. Samples were taken from multiple sites along a short continuum of both Fairfield Creek and the Little Manistee River.

Sampling. Caddisflies were sampled using ultraviolet light traps, which consisted of an 8-watt portable ultraviolet light placed over a white pan filled with 70% EtOH. Each trap was placed within 2 m of a habitat at dusk and retrieved approximately two hours later. Although the primary purpose of our study was a qualitative assessment of the caddisfly fauna, light traps with a consistent wattage, capture area, and sampling period do allow for quantitative comparisons between sites (Houghton 2004a). To standardize weather conditions, samples were collected only if the peak daytime temperature was >22°C, dusk temperature was >13°C, and there was no noticeable wind or precipitation at dusk. All specimens and their respective locality data were databased using BIOTA software (Colwell 2007) and deposited in the Hillsdale College Insect Collection.

Habitat ordination. All sampling sites were examined for patterns in their caddisfly assemblages with Detrended Correspondence Analysis (DCA) using the program PC-ORD for Windows® (McCune and Grace 2002). DCA is a multivariate gradient analysis that reduces complex patterns inherent in large data sets into several determined axes of ecological interest. Unlike other ordination techniques, such as Principle Components Analysis, DCA does not produce a spurious third axis based on a data arch, and can ordinate species and sampling sites simultaneously. DCA essentially produces a plot of sampling sites in "species-space", which allows visual expression of pure gradients of species assemblages, with distance between sampling sites corresponding to differences in caddisfly faunal composition (McCune and Grace 2002).

Our DCA analysis was performed on a two-dimensional data matrix of sampling sites by species relative abundance values. Relative abundances were determined by counting the number of specimens collected at each site and then coding 0 specimens as '0', 1–10 as '1', 11–100 as '2', 101–1000 as '3', and 1001–10,000 as '4'. Such data coding accounted for variation in specimen abundance between sites and was, therefore, a more powerful measure than simple presence or absence data (Feminella 2000, Houghton 2004a). By coding on a $\log_{10}$ scale, however, the effects of outlier samples often associated with light-trapping data were mitigated, as was the influence of highly abundant species (Cao et al. 1997, Anderson and Vondracek 1999, Dohet 2002, Houghton 2004a). For sites visited more than once, the number of specimens was divided by the number of visits before data coding. All species were weighted equally in the analysis.

Results

A total of 134 species representing 50 genera and 17 families were collected during this study (Table 2). These species were determined based on over 26,000 specimens from 93 different collections (Table 1). Eleven species: *Banksiola dossuaria* (Say) (Phryganeidae), *Cheumatopsyche aphanta* Ross *and C. pasella* Ross (Hydropsychidae), *Ironoquia lyrata* (Ross) (Limnephilidae), *Hydroptila xera* Ross, *Neotrichia vibrans* Ross, *Oxyethira aeola* Ross and *O. rivicola* Blickle and Morse (Hydroptilidae), *Lepidostoma vernale* (Banks) (Lepidostomatidae), and *Nyctiophylax affinis* (Banks) and *Polycentropus timesis* (Denning) (Polycentropodidae) were collected in Michigan for the first time. Of these records, all but *C. aphanta*, *N. vibrans*, and *N. affinis* were found exclusively at the three sites of Fairfield Creek.

Oecetis inconspicua (Walker) (Leptoceridae) was the most common species, followed by *Psychomyia flavida* Hagen (Psychomyiidae), *Lepidostoma togatum* (Hagen) (Lepidostomdatidae), and *Banksiola crotchi* Banks (Phryganeidae). *Oecetis inconspicua* was also the most abundant species, followed by *Ceraclea arielles* (Denning) and *Nectopsyche albida* (Walker) (Leptoceridae), and *Lepidostoma bryanti* (Banks) (Lepidostomatidae). The remaining common and abundant species are in Figure 2. These abundant species represented 8% of the total fauna, yet contained nearly 70% of total specimen abundance. In contrast, 40% of the fauna was represented by <10 specimens and 15% was represented by only a single specimen (Fig. 3).

Goera stylata Ross (Goeridae), *Nemotaulius hostilis* (Hagen) (Limnephilidae), and *Parapsyche apicalis* (Banks) (Arctopsychidae) all reached their highest abundance during May (Table 2). Forty-two species reached their highest abundance during June. Seventy-three species reached their highest abundance during July. *Lepidostoma griesum* (Banks) (Lepidostomatidae) reached its highest abundance during August. Ten species, all in the families Limnephilidae and Uenoidae, reached their highest abundance during September. *Limnephilus moestus* Banks (Limnephilidae) had equal peak abundance during June and July. *Lepidostoma bryanti* (Lepidostomatidae) had nearly

Table 2. The 134 caddisfly species collected during this study, including the number of specimens collected per month and per habitat type for each species. Author names excluded for brevity. Sampling effort was greater in June and July than in the other months, and greater in streams than in lakes. Taxa are arranged alphabetically by family and genus. The number of species within each family is listed after each respective family. Species reported from Michigan for the first time are in boldface type.

	Number present					Number present	
Taxon	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Lakes**	**Streams**
ARCTOPSYCHIDAE (1)							
Parapsyche apicalis	33	3	2	0	0	0	38
BRACHYCENTRIDAE (2)							
Brachycentrus americanus	13	459	179	106	0	0	757
Micrasema rusticum	0	111	31	0	0	4	138
GLOSSOSOMATIDAE (5)							
Glossosoma intermedium	0	0	4	0	0	0	4
G. nigrior	5	54	56	14	0	0	129
Protoptila erotica	0	0	4	0	0	0	4
P. maculata	0	0	3	0	0	0	3
P. tenebrosa	0	5	2	0	0	0	7
GOERIDAE (1)							
Goera stylata	48	3	0	0	0	0	51
HELICOPSYCHIDAE (1)							
Helicopsyche borealis	0	345	163	3	0	1	510
HYDROPSYCHIDAE (13)							
Cheumatopsyche aphanta	0	0	37	0	0	0	37
C. campyla	0	10	2	0	0	1	11
C. gracilis	0	0	14	0	0	0	14
C. oxa	3	95	48	1	0	4	143
C. pasella	0	0	1	0	0	0	1
C. pettiti	3	65	43	1	0	6	106
Diplectrona modesta	15	17	51	1	0	0	840
Hydropsyche betteni	4	15	32	0	0	1	50
H. bronta	0	2	13	0	0	0	15
H. morosa	0	0	1	0	0	0	1
H. slossonae	21	64	71	9	2	2	165
H. sparna	40	88	147	28	0	4	299
Potamyia flava	0	0	1	0	0	0	1
HYDROPTILIDAE (25)							
Agraylea multipunctata	3	56	78	11	1	24	125
Hydroptila amoena	0	2	0	0	0	0	2
H. armata	0	0	1	0	0	0	1
H. consimilis	0	5	27	4	0	2	34
H. grandiosa	0	2	0	0	0	0	2
H. hamata	0	0	2	0	0	0	2
H. jackmanni	1	5	16	0	0	0	22
H. metoeca	2	27	41	7	0	0	77
H. spatulata	0	0	1	0	0	0	1
H. waubesiana	0	4	0	0	0	0	4
H. wyomiya	1	4	0	0	0	0	5
H. xera	0	6	0	0	0	0	6
Neotrichia vibrans	0	1	0	0	0	0	1
Ochrotrichia spinosa	0	1	0	0	0	0	1

Table 2. Continued.

Taxon	Number present May	Jun	Jul	Aug	Sep	Number present Lakes	Streams
Orthotrichia aegerfasciella	1	7	2	0	0	0	10
O. balduffi	0	5	1	0	0	0	6
O. cristata	0	10	29	5	0	0	44
Oxyethira aeola	0	0	2	0	0	0	2
O. forcipata	0	5	19	0	0	0	24
O. michiganensis	2	13	78	5	0	6	32
O. obtatus	1	0	2	0	0	0	3
O. pallida	0	0	1	0	0	0	1
O. rivicola	0	6	7	0	0	0	13
O. serrata	0	0	1	0	0	0	1
O. zeronia	0	1	7	0	0	0	8
LEPIDOSTOMATIDAE (4)							
Lepidostoma bryanti	237	496	11	453	8	0	1205
L. griseum	0	0	3	8	0	0	11
L. togatum	0	355	479	9	0	2	841
L. vernale	10	16	0	0	0	0	26
LEPTOCERIDAE (26)							
Ceraclea alagma	0	61	194	0	0	120	135
C. arielles	0	3058	6	0	0	41	3017
C. cancellata	0	13	1	0	0	10	4
C. diluta	0	0	3	0	0	3	0
C. tarsipunctata	0	823	62	1	0	845	41
C. transversa	2	3	278	0	0	11	272
Leptocerus americanus	0	332	31	0	0	345	18
Mystacides interjecta	0	12	1	2	0	4	11
M. sepulchralis	0	10	380	0	0	16	374
Nectopsyche albida	0	1545	123	7	0	8	1667
N. exquisita	0	0	3	0	0	0	3
N. pavida	0	4	0	0	0	3	1
Oecetis avara	0	4	0	0	0	0	4
O. cinerascens	0	48	20	0	0	11	57
O. disjuncta	0	0	1	0	0	0	1
O. inconspicua	5	3570	319	67	6	2765	1202
O. osteni	0	102	21	0	0	104	19
O. persimilis	0	86	257	29	0	352	20
Setodes incertus	0	0	6	0	0	0	6
Triaenodes abus	0	3	2	0	0	0	5
T. dipsius	0	2	9	0	0	0	11
T. ignitus	0	1	16	0	0	0	17
T. injustus	0	15	6	0	0	0	21
T. marginatus	0	1	5	0	0	0	6
T. nox	0	15	6	0	0	0	21
T. tardus	1	8	7	4	0	0	20
LIMNEPHILIDAE (20)							
Anabolia bimaculata	0	1	9	0	0	4	5
A. consocia	0	2	2	0	0	1	3
Hesperophylax designatus	2	0	4	0	0	0	6
Hydatophylax argus	2	14	0	0	0	0	16
Ironoquia lyrata	0	0	0	0	3	0	3

Table 2. Continued.

Taxon	Number present May	Jun	Jul	Aug	Sep	Number present Lakes	Streams
I. punctatissima	0	0	0	0	1	0	1
Limnephilus indivisus	1	4	6	1	0	0	12
L. moestus	1	18	18	0	0	0	37
L. ornatus	0	0	4	0	0	1	3
L. rhombicius	0	0	0	0	1	0	1
L. sericeus	0	0	1	0	0	0	1
L. submonifer	0	0	0	1	7	0	8
Nemotaulis hostilis	10	2	2	0	0	0	14
Onocosmoecus unicolor	0	0	0	0	4	0	4
Platycentropus amicus	0	0	1	0	0	0	1
P. radiatus	0	50	17	0	0	12	55
Pycnopsyche antica	0	35	255	123	31	0	444
P. guttifer	0	0	0	0	233	0	233
P. lepida	0	15	19	12	1	22	25
P. subfasciata	0	0	0	0	1	1	0
MOLANNIDAE (3)							
Molanna blenda	0	58	71	18	0	0	147
M. tryphena	0	2	1	0	0	0	3
M. uniophila	0	8	10	0	0	12	6
PHILOPOTAMIDAE (3)							
Chimarra feria	4	25	10	16	0	0	54
C. obscurra	0	344	2	0	0	0	346
Dolophilodes distinctus	0	88	228	41	0	0	357
PHRYGANEIDAE (10)							
Agrypnia improba	1	4	3	0	0	0	8
A. vestita	1	0	3	0	0	0	4
Banksiola crotchi	11	308	188	0	0	35	473
B. dossuaria	2	29	7	0	0	0	38
Hagenella canadensis	0	0	4	0	0	1	3
Phryganea cinerea	0	2	26	10	0	15	23
P. sayi	0	5	12	1	0	0	18
Ptilostomis angustipennis	0	2	5	2	0	0	9
P. ocellifera	0	24	34	2	1	6	55
P. semifasciata	0	4	12	0	0	6	10
PSYCHOMYIIDAE (2)							
Lype diversa	12	52	106	12	0	11	171
Psychomyia flavida	3	708	129	2	0	6	836
POLYCENTROPODIDAE (14)							
Cernotina spicata	0	62	1	0	0	63	0
Neureclipsis crepuscularis	0	16	43	0	0	0	59
Nyctiophylax affinis	0	430	121	0	0	85	456
N. moestus	0	12	78	1	0	14	76
Polycentropus albipunctus	0	1	2	0	0	0	3
P. auroleus	0	1	4	0	0	0	5
P. cinereus	5	11	10	0	0	4	22
P. clinei	0	1	3	0	0	0	4
P. interruptus	1	86	0	0	0	14	72
P. melanae	0	15	0	0	0	0	15
P. pentus	4	39	64	2	0	10	99

Table 2. Continued.

Taxon	Number present May	Jun	Jul	Aug	Sep	Number present Lakes	Streams
P. remotus	1	1	4	0	0	0	6
P. timesis	0	0	1	0	0	0	1
P. weedi	0	0	3	0	0	0	3
RHYACOPHILIDAE (2)							
Rhyacophila fuscula	0	0	1	0	0	0	1
R. vibox	0	5	13	0	0	0	18
UENOIDAE (2)							
Neophylax concinnus	0	0	0	0	9	0	9
N. oligius	0	0	0	0	11	0	11

equal peak abundance during June and August, with minimal abundance during July, suggesting bivoltinism.

Only 11 species exhibited greater abundance in lakes than in streams (Table 2). Eight of these species were in the family Leptoceridae, and 1 each were in the Limnephilidae, Molannidae, and Polycentropodidae. Three of these species: *Ceraclea diluta* (Hagen) (Leptoceridae), *Cernotina spicata* Ross (Polycentropodidae), and *Pycnopsyche subfasciata* (Say) (Limnephilidae) were found exclusively in lakes. In contrast, 87 species were found exclusively in streams.

Although there was substantial variability between individual collections, the number of species caught per collection was low in May, increased throughout June, and peaked in early July. It began declining in August before reaching the lowest point in September (Fig. 4). The largest increase in cumulative species caught occurred during June and July. It leveled off to zero during mid August, and then rose slightly again in September (Fig. 5).

The DCA analysis suggested two axes of ecological interest and four clusters of sampling sites based on caddisfly relative abundance data (Fig. 6). Axes 1 and 2 had eigenvalues of 0.29 and 0.26, respectively, indicating that over half of the variance in the data set was explained by these two axes. Since DCA searches for the maximum possible resolution on the first two axes, it is unlikely that other axes were highly informative in assessing differences in sampling sites (McCune and Grace 2002). Axis 1 corresponded with stream size, with small streams (width < 3m), medium rivers (3–15 m), and large rivers (>15 m) each appearing to constitute distinct groups. Axis 2 corresponded with the change from lotic to lentic habitats, with lakes and wetlands also appearing to constitute a single distinct group.

Discussion

Biological diversity. The primary objective of this study was to document the biological diversity of caddisflies in the Manistee River watershed as a contribution to the overall knowledge of Michigan Trichoptera. A grand total of 263 species have now been reported from the state. Over half of these known Michigan species were collected during the current study. Over 8% of the species collected during the current study were new to the state.

Our rigorous sampling of Fairfield Creek, a first-order stream with a protected watershed, yielded 8 of the 11 new state records. Two of these species: *Banksiola dossuaria* and *Lepidostoma vernale*, were represented by >20 specimens and caught on multiple dates, suggesting that they are fairly abundant and easy to collect at the site. Their previous absence from the documented

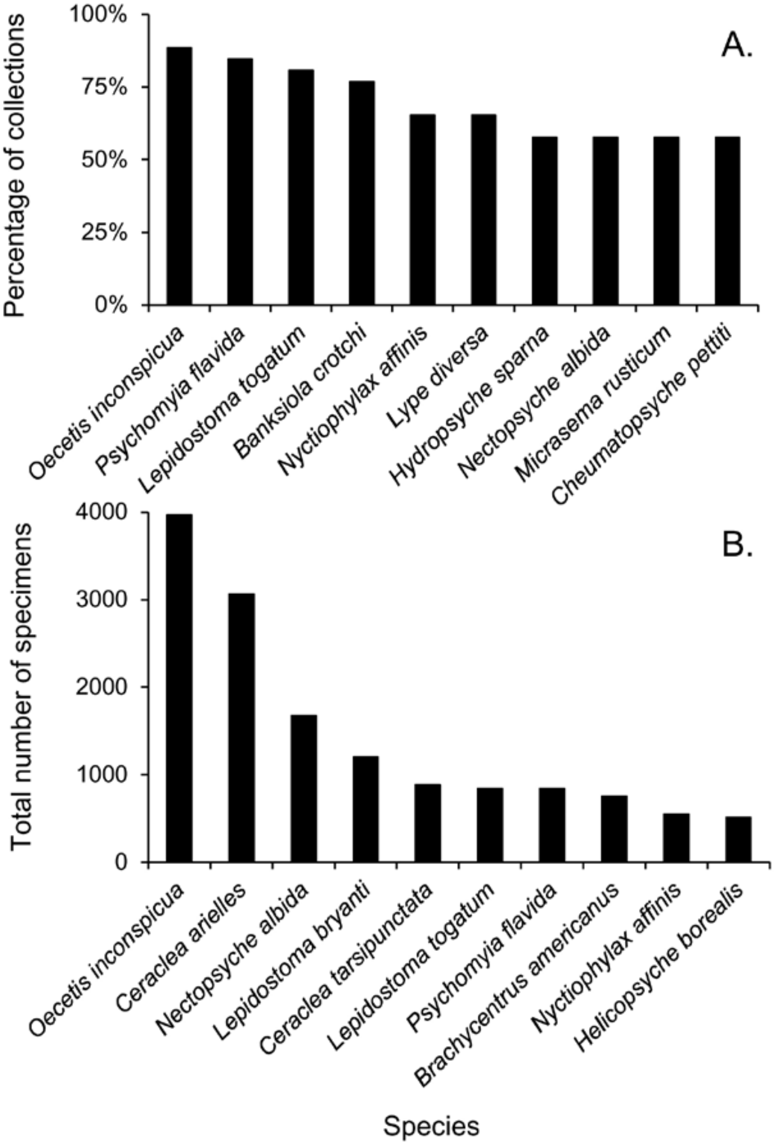

Figure 2. The top 10 most widespread (A) and most abundant (B) caddisfly species of the Manistee River watershed based on our sampling.

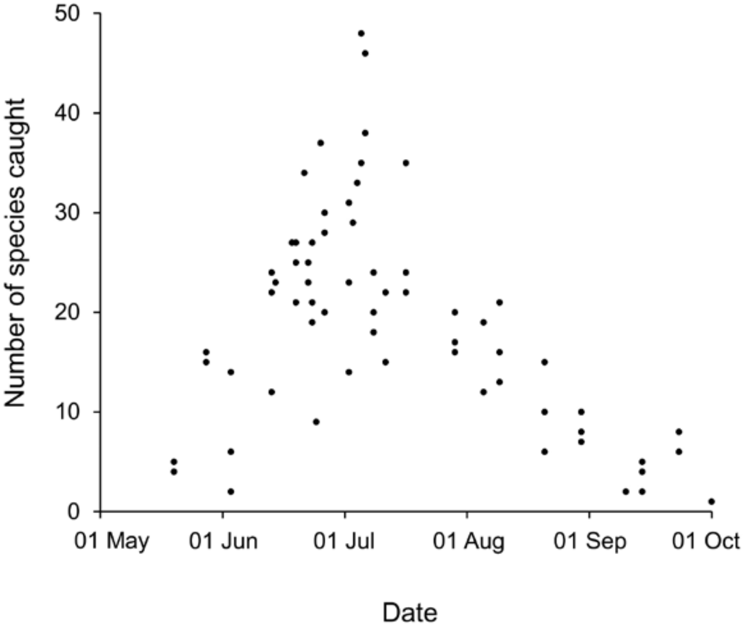

Figure 3. The number of caddisfly species caught per date. Each point represents one sample on a respective date. Overlap occurs between points.

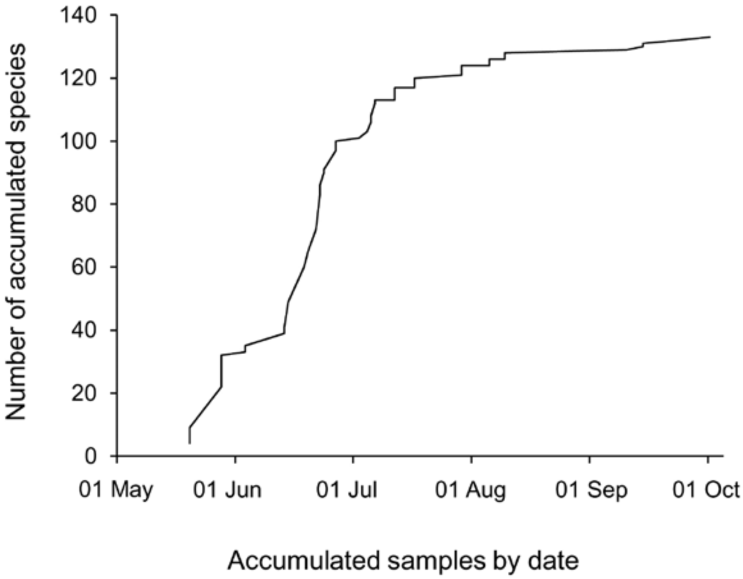

Figure 4. The accumulated number of species caught based on accumulated samples and corresponding dates.

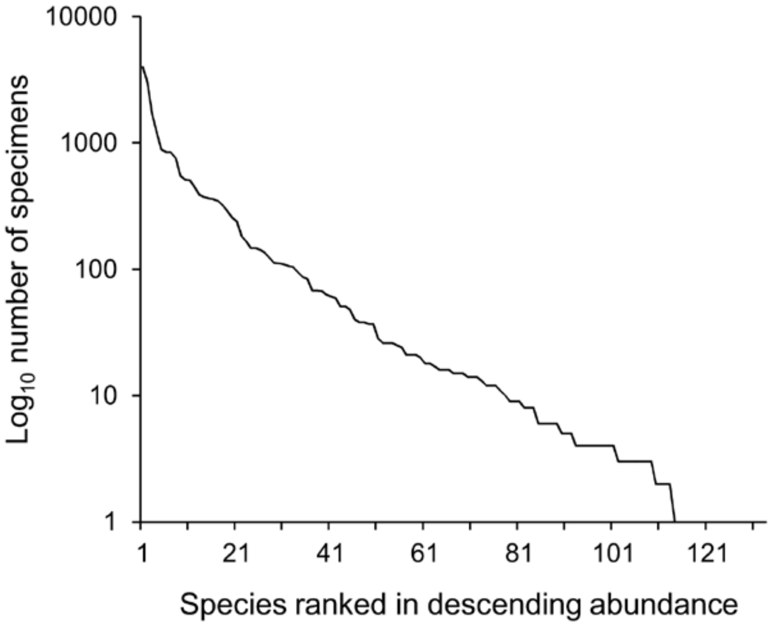

Figure 5. The number of caddisfly specimens for each species collected from the Manistee River watershed.

Michigan fauna probably reflects a lack of collecting in small, protected woodland streams. Such streams are becoming increasingly rare in the lower peninsula of Michigan and elsewhere (Houghton 2007, Wang et al. 2008). Another species collected from Fairfield Creek: *Polycentropus timesis*, was known previously only from Massachusetts and New Hampshire (Weaver 1995). The Fairfield Creek population is separated from the others by >800 km. This fact may also indicate the rarity of protected small streams in the northcentral US and the difficulty of locating such habitats.

It is likely that the actual number of caddisflies occurring in Michigan remains considerably higher than has been reported. The neighboring state of Minnesota, for example, has been collected extensively since the 1890s, including rigorous sampling of nearly all of its 58 watersheds (Houghton 2004a, Houghton and Holzenthal 2010). Despite the greater collecting effort, the Minnesota fauna contains only 277 species. The new state records and unique species collected during our limited study suggest that the Michigan fauna would likely be larger than that of Minnesota with a comparable collecting effort.

Limitations of sampling. Our sampling strategy was designed with our primary objective in mind. Thus, we sampled with greater effort during the high-emergence months of June and July instead of with an equal effort during all months. Likewise, we were more interested in sampling throughout the watershed area and collecting as many species as possible, than in sampling all habitat types with equal effort. Our sampling, therefore, included many medium rivers and fewer of other habitat types. Large rivers, for example, are not abundant within a single watershed. Small streams typically contain fewer species than medium rivers and are more difficult to find (Houghton 2004a). The one small stream that we did sample, Fairfield Creek, was visited several times

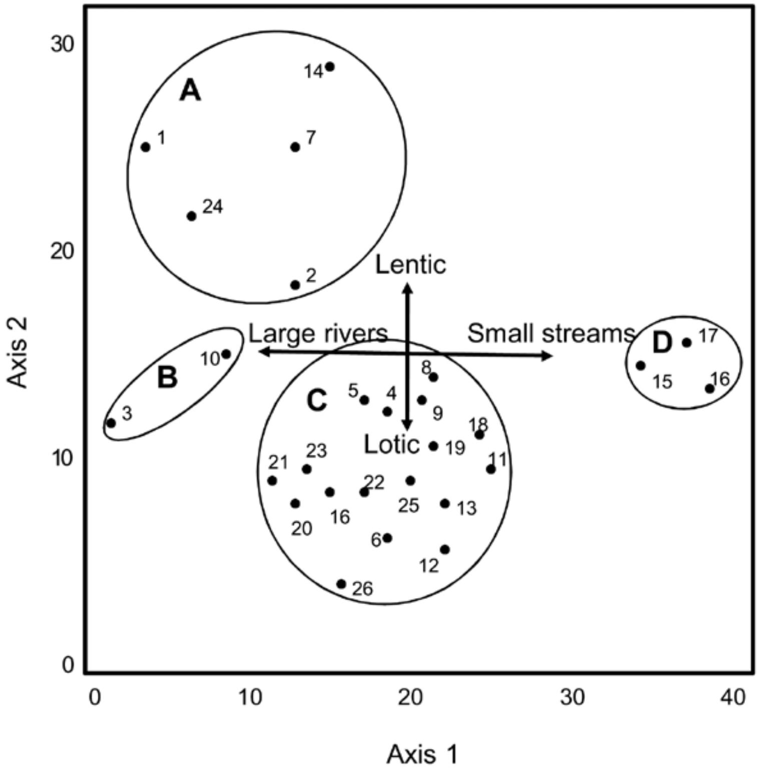

Figure 6. Detrended correspondence analysis ordination of 26 sampling sites based on the relative abundance of 134 caddisfly species and suggesting four distinct types of habitats within the watershed. A: lakes and wetlands, B: large (>15 m width) rivers, C: medium (3–15 m) rivers, and small (<3 m) streams. Numbers correspond to sites names in Table 1. Arrows indicate correlations between site characteristics and determined ecological axes.

to represent small streams of the watershed. Further, our sampling effort was higher overall in streams than in lakes, which may explain in part the greater abundance in streams for >90% of the fauna (Table 2). Due to these limitations in sampling, our conclusions about faunal differences between seasons or habitat types should be viewed as preliminary. Despite these limitations, our data do suggest some trends worth noting.

Seasonal periodicity. Many studies assume a peak flight period during late June and early July for sampling purposes. One result of our study—a definite peak in species richness in early July—certainly appears to corroborate this assumption. Sampling exclusively during July would have yielded 84% of the total species caught (Table 2).

Our data suggest some other trends worth noting about sampling and season. First of all, a distinction should be made between emergence and adult flight period. Many species in our study reached peak abundance in June or July and then decreased in later weeks and months (Table 2). We suspect that the highest abundance of a species probably occurred immediately after the adult emergence, and that later adult presence probably reflected individuals that had already mated but not yet senesced. This suspicion would explain why August has higher species richness than September, despite the fact that the latter month had 10 species unique to it, whereas August had only 1. Likewise, our species accumulation curve (Fig. 5) indicated that the number of species caught for the first time remained unchanged throughout most of August, and then increased again in September as additional species began emerging.

Sampling in both July and September may, therefore, be the best approach to capture the greatest species richness without an exhaustive effort. In our study, 80% of all species were caught by sampling 5 sites during the first 2 weeks of July and 2 during the second week of September. Obviously, weather would also need to be taken into consideration when planning such a specific sampling regime, but these two periods collectively appear to be the most productive for sampling caddisflies of the Manistee River watershed.

Habitat differences. There appears to be a distinct difference in the overall caddisfly faunas of small streams, medium rivers, large rivers, and lentic habitats (Fig. 6). The River Continuum Concept (RCC) (Vannote et al. 1980) predicts distinct changes in the aquatic insect fauna of a river system from headwaters, to middle reaches, to lower reaches due to changes in stream morphology and interaction with the riparian corridor. In watersheds disturbed by agriculture or deforestation on a landscape level, however, different habitat types often become "homogenized" due, in large part, to a loss of coarse allochthonous input and the increase in fine particulate organic matter (Quinn 2000, Zweig and Rabeni 2001, Baker and Richards 2003, Nord and Lanyon 2003). In such disturbed watersheds, all habitat types have a similar aquatic insect fauna—a high abundance of pollution tolerant fine-particle filtering collectors—regardless of stream type, and all sites cluster together regardless of habitat type in DCA analyses (Houghton 2006, 2007).

The distinct differences observed in the caddisfly faunas of different-sized streams and of lentic systems suggest that the Manistee River watershed is functioning as predicted by the RCC. Such a conclusion would be enhanced with a greater sampling effort and an exploration of changes in trophic functional groups between different habitat types. The latter, however, is beyond the scope of this study. Further, Houghton (2007) found that in agriculturally disturbed watersheds in Minnesota, virtually all small and medium streams had the caddisfly faunal composition of large rivers. Thus, even our small sample size should have been able to detect some homogenized small and medium streams if they were present. Instead, all of our medium stream sites, and the sites of our single small stream, clustered in groups of their own habitat type distinct from other types. Such a result suggests that the Manistee River watershed, although possibly disturbed in portions, is a relatively "healthy" (Karr and Chu 1999) watershed throughout much of its area. Houghton (2007) found a similar result for watersheds of northern Minnesota, an area similar to the Manistee River watershed in habitat and land use (USGS 2007).

Future research. The asymptotic shape of our species accumulation curve (Fig. 5) suggests that the majority of the caddisfly biological diversity in the Manistee River watershed was discovered during our study. Despite this observation, the fact that 15% of all species caught were represented by a single specimen suggests that additional species remain undiscovered in the watershed, particularly in habitats that are difficult to access such as small woodland streams and vernal wetlands. To representatively inventory the Trichoptera of the entire state will, obviously, take a concerted effort. Such an effort, however, is important and will allow for the evaluations of future changes to the fauna with greater precision.

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