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COLONIZATION OF LAKE ERIE TRIBUTARIES BY *ALLOCAPNIA RECTA* (CAPNIIDAE)

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ABSTRACT

Plecoptera display a variety of dispersal mechanisms. The most reduced of these, walking, is common for winter stoneflies in the family Capniidae. To examine dispersal in a winter stonefly, *Allocapnia recta*, we sequenced a fragment of the 16s rRNA mitochondrial gene from four adjacent Lake Erie drainages. Nineteen unique haplotypes were obtained from 107 specimens. The four watersheds explained 37% of the haplotype diversity and all pairwise contrasts among streams were statistically significant; not one haplotype was common to all four watersheds. This extreme level of divergence among populations separated briefly in both space and time suggest minimal if any measurable gene flow and therefore the possibility that geological processes may better explain northern colonization to the Great Lakes than may adult migration. One possibility is for post-glacial change in topography, in particular isostatic adjustment to raise land, which led to flow reversal at the headwaters of rivers along what now is Ohio's Northern Divide, separating the Laurentian Great Lakes from the Ohio/Mississippi River system.

Keywords: *Allocapnia recta*, distribution, haplotypes, migration, mtDNA, population structure

INTRODUCTION

Historical dispersal may be inferred by the presence of a species (Hynes 1988; Zwick 2000), but continued movement of individuals is critical to

sustain genetic connectivity within populations, and that may be better measured from genetic markers (Avisé 2000). Directly observing dispersal in aquatic insects is rarely practical (Miller et al.

2009), thus genetic assessment and gene flow provides a useful proxy to assess dispersal in groups of smaller insect species (Finn & Adler 2006; Krosch et al. 2012) including Plecoptera (Kauwe et al. 2004; Schultheis et al. 2012; Pessino et al. 2014). Movement of aquatic invertebrates is expected to be both passive, by downstream drift, or by active flight, but is often limited by habitat (Finn et al. 2006).

Flight in stoneflies can generally be limited by a continuum of extremes in wing size, ranging from full wing and full flight capabilities to apterous, flightless species. In the most rudimentary forms of adult flight, surface skimming may be the primary use of wings (Malmqvist 2000; Winterbourn 2005; Marden 2008). While the adult terrestrial stage in plecopterans is also short lived, some species, like *Pteronarcys californica* Newport (Pteronarcyidae), may possess a wide distribution, suggesting that duration of the adult stage is not necessarily a limit to dispersal (Kauwe et al. 2004). But, what of the many winter emerging species? The Capniidae presently compose 166 species, contributing 23% of the total North American fauna (Stark et al. 2014), and many have small or even rudimentary wings (Briers et al. 2003). A common requirement for cool streams, little silt and generally good water quality (Palma & Figueroa 2008) may further restrict their movement.

Within the winter stoneflies, the distribution of *A. recta* (Claassen) is geographically broad (Stark et al. 2014), and the species is often locally abundant (Grubbs et al. 2012). Yasick et al. (2007) assessed potential physical limits on dispersal by comparing genetic variability between *Allocaupnia recta* and *Leuctra tenuis* (Pictet), a long-winged summer emerging species (Stark et al. 1998). Two populations of *L. tenuis* were more genetically similar than those of *A. recta*, a pattern also found by Watanabe et al. (2010) in Trichoptera. Here we extend that work to test whether genetic variation is correlated most strongly with linear distance along waterways or direct distance overland between watersheds within the glaciated zone. An alternative hypothesis is that geographic distance is not correlated with genetic diversity, a possibility if each stream was colonized separately from the south after glacial retreat.

MATERIALS AND METHODS

Adult specimens of *Allocaupnia recta* (Family Capniidae) were collected from small streams of four Lake Erie drainages (Fig. 1) in northeast Ohio between 2004 to 2007: 1. Rocky River. Summit County, East Branch Rocky River (41.2115, -81.6831); 2. Cuyahoga River. Summit County, tributary Boston Run 1 (41.2314, -81.5086) and Boston Run 2 (41.2335, -81.5021); 3. Chagrin River, Geauga County, tributary East Branch Chagrin River 1 (41.5960, -81.2512) and East Branch Chagrin River 2 (41.6071, -81.2875); 4. Grand River. Lake County, Talcott Creek (41.7217, -81.0830).

Samples were obtained during the peak of annual winter adult emergence between November and February. The best collecting days occurred when temperatures exceeded 0°C with few to no clouds (Yasick, personal obs.). Specimens were collected from tree trunks, on snow and ice, or using a beating sheet on low-lying vegetation within 15 m of the stream. Individual *A. recta* were placed in a 1.5 ml microcentrifuge tube containing 95% ethanol. If a male and female were captured in copula, the mating pair was placed in the same tube.

Specimens were identified to species based on the structure of the male genitalia according to Ross and Ricker (1971). The distal portions of the abdomen of specimens were retained as vouchers, while the remainder was used for DNA extraction. Only females captured in copula were used for DNA extraction.

Insect preparation, mtDNA extraction, and amplification methods were conducted as in Yasick et al. (2007) with forward primer (SF_arF) 5'- TCG AAC AGA CCT AAA CTT TG -3' and the reverse primer (SF arR) 5'- AAT AAT TTA AAG TCT GAC CTG C -3'. Samples were sequenced at the Cleveland Clinic Genomic Core Facility initially from the forward primer, which gave a 467 base-pair sequence, reduced slightly from 492 bp in Yasick et al. (2007). Improved sequencing quality has generally eliminated the need for redundant sequencing of most samples, although chromatograms were assessed for any ambiguities by viewing them in Sequencher® (v. 4.10.1, Gene Codes Corp.). Any samples where the haplotype could not be assigned with certainty were sequenced in the reverse direction.

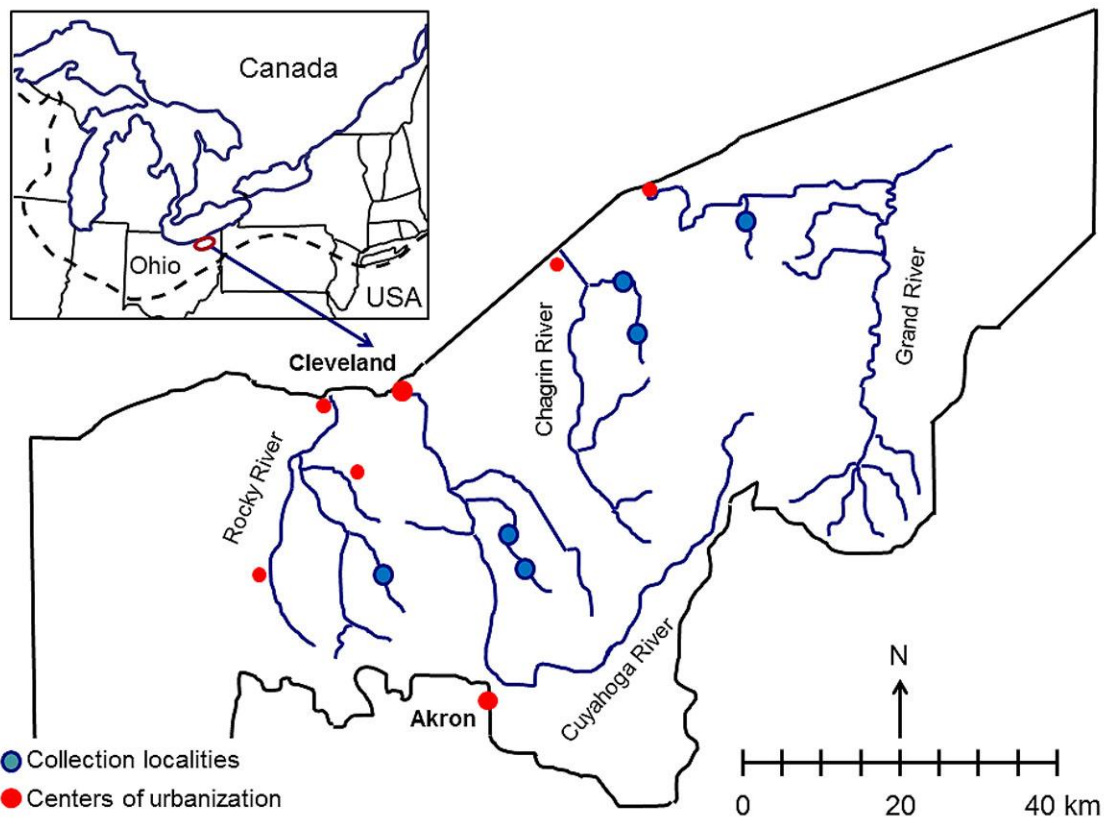


Fig. 1. Collecting sites of *Allocapnia recta* within the Rocky, Cuyahoga, Chagrin, and Grand rivers of northeast Ohio, USA. Inset figure is the Laurentian Great Lakes region of eastern North America, with a line indicating the Wisconsin glacial maximum, approximately 15,000 years ago.

Sampling adequacy was tested by rarefaction in PAST 3.0 (Hammer et al. 2001). Diversity indices (H and π) were calculated using Arlequin v. 3.5 (Excoffier & Lischer 2010). Haplotypes were defined and formatted in DnaSP 5.10 (Librado & Rozas 2009) to produce minimum spanning trees in Network v. 4.6 (Röhl 2004). To verify monophyly and species identification of all samples, a maximum likelihood phylogeny was constructed using MEGA V5 (Tamura et al. 2011) comparing *A. recta* to sequences of other Capniidae from Terry (2004) used with permission (GenBank accession numbers EF623127-31) and its sister family, Leuctridae (EF623173-81). Analysis of Molecular Variance (AMOVA) and pairwise F_{ST} analyses were also run in ARLEQUIN, using 30,000 permutations

for tests of significance. Hedrick (2005) and Merimans and Hedrick (2011) propose G'_{ST} as a standardized method of measuring genetic variation between highly variable populations with multiple alleles, as compared to F_{ST} , because a G'_{ST} score of 1 indicates haplotypes frequencies are completely different, while a score of 0 is indicative of identical haplotypes.

RESULTS

Haplotypes were obtained from 107 specimens of *A. recta* from four watersheds in Northeast Ohio; the Grand ($n = 25$), Cuyahoga ($n = 25$; pooled from two sites), Chagrin ($n = 27$; pooled from two sites), and the Rocky River ($n = 30$). Nineteen haplotypes were identified across the four watersheds using a

Table 1. Haplotype frequencies for *Allocapnia recta* in the four watersheds, the Rocky, Cuyahoga, Chagrin and Grand rivers of northeast Ohio.

Sites	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	H12	H16	H17	H19	Minor
Rocky	0	2	3	11	0	0	2	2	2	3	2	0	0	0	3
Cuyahoga	7	3	13	0	0	2	0	0	0	0	0	0	0	0	0
Chagrin	0	2	10	10	3	1	0	0	0	0	0	0	0	0	1
Grand	0	0	0	6	0	0	0	0	0	0	0	3	5	10	1
Sum	7	7	26	27	3	3	2	2	2	3	2	3	5	10	5
Frequency	0,07	0,07	0,24	0,25	0,03	0,03	0,02	0,02	0,02	0,03	0,02	0,03	0,05	0,09	0,05

fragment of the 16S rRNA gene (GenBank accession numbers, KC881036-KC881054). Given a small set of rare haplotypes, rarefaction curves (not shown) indicated sufficient sampling overall, with only one more haplotype expected to be found for

each additional 20 individuals sequenced. Genetic variation, whether measured by the frequency of haplotypes or by π , the amount of nucleotide variation, was not significantly different among rivers (Table 2).

Table 2. Sample size (N), haplotypes, unique haplotypes, gene diversity (H) and nucleotide diversity (π) estimated for the four populations of *A. recta* and overall in the region. SE is one standard error.

Sites	N	H	H (se)	$\pi \times 100$	π (se)
Rocky	30	0,85	0,06	0,37	0,18
Cuyahoga	25	0,66	0,07	0,19	0,12
Chagrin	27	0,73	0,07	0,25	0,14
Grand	25	0,76	0,08	0,32	0,17
Totals	107	0,86	0,02	0,47	0,18

While 14 of the 19 haplotypes occurred in multiple copies within the study, only four haplotypes were shared among watersheds, H2, H3, H4 and H6, and none occurred in all streams sampled (Table 1). The two most common haplotypes were represented by 26 and 27 individuals, respectively, but each was missing from one of the rivers, and each watershed possessed at least one of the 10 private haplotypes, those present only in one watershed and occurring in multiple copies: five in Rocky River, three in the Grand River and one each in the Cuyahoga and Chagrin Rivers. Thus, partitioning genetic differences among the four watersheds explained

37% ($P < 0.05$) of the haplotype diversity (Table 3), and all pairwise contrasts were statistically significant (Table 4). A contrast of the two largest watersheds by area, the Cuyahoga and Grand Rivers, gave a G'_{ST} of 1.0, indicating complete isolation; the two most similar, yet significantly different watersheds, the Rocky and Chagrin Rivers, were not adjacent.

Despite that variation could be significantly partitioned among these four rivers, all 19 haplotypes formed one large monophyletic clade. Geographically, the network supported separation of subgroups within watersheds (Fig. 2), and not just random isolation of different haplotypes.

Table 3. Molecular Analysis of Variance of 16s mtDNA for four populations of *A. recta*.

Source of variation	Df	Sum of squares	Variance component	% Variation
Among populations	3	58,9	0,69***	36,7
Within population	103	122,9	1,19	63,3
Total	106	181,7	1,88	

*** P<0.001

Table 4. Pairwise population differences based on location from west to east in the region presenting both Fst (above the diagonal) and G'st (below the diagonal).

	Rocky	Cuyahoga	Chagrin	Grand
Rocky	-----	0,47 ***	0,07 *	0,34 ***
Cuyahoga	0,86	-----	0,35 **	0,62 ***
Chagrin	0,31	0,45	-----	0,29 ***
Grand	0,68	1	0,72	-----

* P<0.05, ** P<0.01, *** P<0.001

DISCUSSION

The initial hypothesis stated that dispersal distance drives patterns of intraspecific variation in *A. recta* across neighboring watersheds. That expectation was only partly supported, because whether watersheds were adjacent or distant (up to 75 km away), levels of differences were similarly large. No single haplotype was found in all four watersheds, and haplotypes from the two largest rivers were completely different (G'_{ST} of 1.0). Thus, little connectivity among populations, or conversely, little gene flow, even between neighboring watersheds, was observed. Concurrently, similar levels of genetic diversity were present in each of the four rivers, but this diversity arises from different sets of haplotypes. One plausible cause is that many haplotypes arrived during initial colonization events within the region, and genetic drift has led to some haplotype losses. The Capniidae lineage appears very diverse for haplotypes, yet members of the family present some of the shortest 16S rRNA gene branch lengths (Terry, 2004). That result is

consistent with high levels of within-species variation and incomplete lineage sorting, leading to poor differentiation among species for any one gene (Kutschera et al. 2014). Such an outcome is theoretically more likely in lineages where population sizes have been historically large (van Velzen et al. 2012).

At present, migration in *A. recta* appears to be slow, as males of *A. recta* are brachypterous, the species emerges in winter, and females tend to remain in the natal stream to oviposit (Malmquist 2000; Alp et al. 2012). Furthermore, the current distribution of *A. recta* regionally suggests that this is not a vagile species. This stonefly inhabits cool streams from the highlands of Alabama and Georgia, northeast to Maine, largely within the range of the Appalachian Mountains (Earle 2009). From this historic base, *A. recta* has only sporadically dispersed into regions once covered by the Wisconsin glacial lobes (Ross & Ricker 1971); the species does not occur in Michigan (Stark et al. 1986; Grubbs et al. 2012) and inhabits mainly the unglaciated regions of Illinois and Indiana

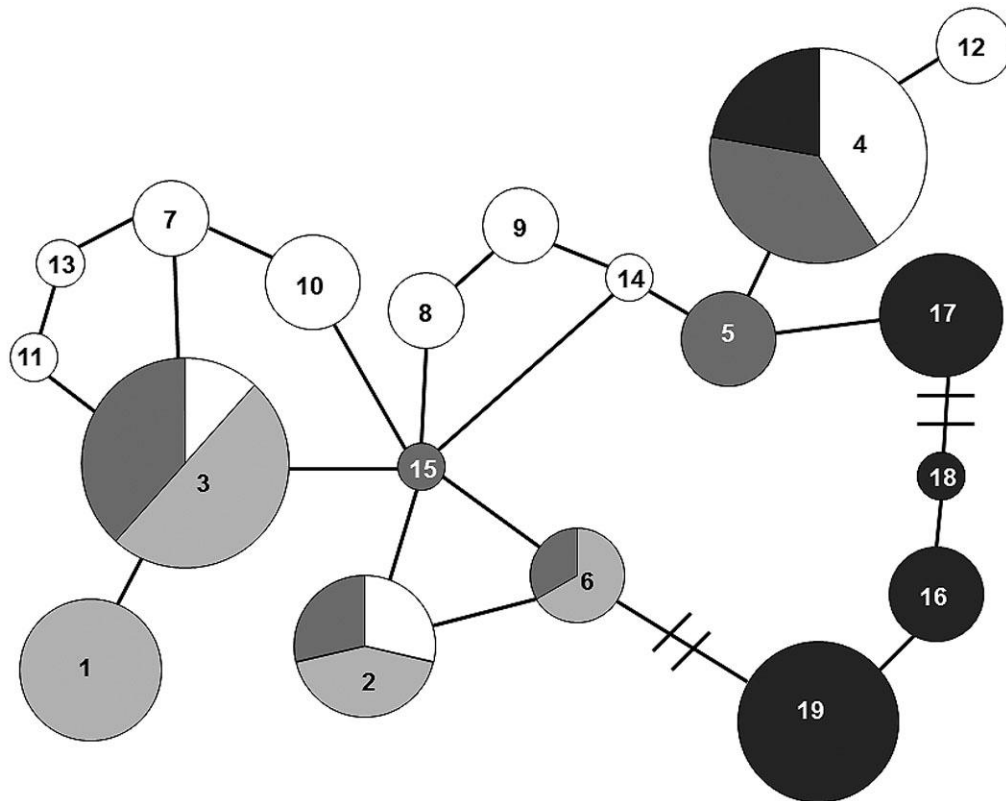


Fig. 2. A network of 16S mt rRNA haplotypes for *Allocapnia recta* collected in four watersheds of NE Ohio, USA. The diameter of each circle is proportional to haplotype frequency and levels of shading denote location increasing in shading level from west to east: Rocky River (white), Cuyahoga River (light grey), Chagrin River (dark grey) and Grand River (black). Numbers denote haplotypes and hash marks indicate base changes where more than one nucleotide difference separates the connected haplotypes.

(DeWalt & Grubbs 2011) where a dispersal route was formed by the Ohio River watershed.

This distributional limit is important for considering colonization into the Laurentian Great Lakes region. One important path for many aquatic species after the last glacial retreat 15,000 years ago was the Wabash River (Teller 2004), which drains extensive plains before entering the Ohio River near its confluence with the Mississippi River. Prior to the opening of the St. Lawrence river, a developing Lake Erie would have covered the lake plains of NW Ohio (White & Totten 1982). After a northern outlet opened, flow reversed to create a slow warm-water river, the modern Maumee

(Lewis et al. 2012), the largest tributary of Lake Erie. This environment favored migration of amphibians, fish, and molluscs into Lake Erie (Mandrak & Crossman 1992; Austin et al. 2002; Graf 2002, Borden & Krebs 2009), but failed to provide habitat for silt sensitive cold-water species like *A. recta* (Meador & Goldstein 2003; Allan 2004). A failure to collect this species along the Maumee River or in the lake itself (Grubbs et al. 2012; DeWalt et al. 2012) is suggestive of a physiological barrier that limits or slows dispersal. That cool streams flowing from the escarpment of northeastern Ohio provide habitat (Szabo et al. 1988; DeWalt et al. 2012) may implicate

temperature effects, but several related species, like *A. granulata*, *A. pygmaea* and *A. minima* also colonized glacial areas (Frison 1942; DeWalt & Grubbs 2011; Stark et al. 2014). The extensive southern distribution of the species in highlands [note the removal of *A. recta* from taxa lists for Mississippi (Nations et al. 2007)] may suggest that sediment composition is a more important factor (Pessino et al. 2014).

Ross & Ricker (1971) recorded *A. recta* along the boundary of the once-glaciated region of Ohio, and DeWalt et al. (2012) extended records to include the counties along Lake Erie for which we report genetic data, as well as the neighboring counties to the south. These provide a link for *A. recta* to the Lake Erie watershed by stream capture following isostatic rebounding (Coffey 1958; Bishop 1995), which was also proposed to explain the disjunct distribution of genetic variants above waterfalls in NE Ohio streams for two unionid mussels, *Pyganodon grandis* (Krebs 2004) and *Lampsilis siliquoidea* (Krebs et al. 2013), as well as smallmouth bass, *Micropterus dolomieu* (Borden & Krebs 2009). The high levels of mtDNA haplotype diversity strengthens support for a geological cause of observed patterns rather than a biological one, because waves of rare adult dispersal are likely to reduce variation to few or even single haplotypes in founding populations (Theissinger et al. 2013; Krebs et al. 2015).

As the glacial ice melted, re-colonization by *A. recta* may have occurred first into the Rocky River, and expanded eastward. This post-glacial population dynamic may explain why specimens of *A. recta* collected from the Rocky River are the most diverse, and why only some haplotypes are shared among watersheds. Similar limits are predicted for caddisflies (Lehrian et al. 2010). By contrast, a long-winged warm-weather species like *Acroneuria frisoni* shows low levels of divergence in nearby watersheds in comparisons made across its range (Pessino et al. 2014), as similarly reported for *Leuctra tenuis* between the Chagrin and Grand rivers (Yasick et al. 2007). However, all three of these species, *A. frisoni*, *L. tenuis* and *A. recta*, are characterized by high haplotype diversity in the region north of the Ohio River. Variation within streams may historically have been even higher,

with genetic drift creating the differences observed today. Current gene flow in *A. recta* remains minimal, while levels of movement even along streams remain unknown. A prime region in which to extend this research are streams draining south from Ohio's northern divide.

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