

Communities in Freshwater Coastal Rock Pools of Lake Superior, with a Focus  
on Chironomidae (Diptera)

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Alexander Taurus Egan

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Advisor: Leonard C. Ferrington, Jr.

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# **Communities in Freshwater Coastal Rock Pools of Lake Superior, with a Focus on Chironomidae (Diptera)**

## **Abstract**

Exposed freshwater shores have received little ecological attention. At Isle Royale, an archipelago in Lake Superior, coastal areas have a moderated climate due to the large, deep lake. This project was instigated because 1) little was known about coastal ecosystems at Isle Royale, 2) unique aquatic species were expected in this habitat, 3) potentially disastrous impacts from shipping accidents could cause population losses of sensitive species, and 4) long-term shifts in climate could influence communities via warming conditions and erratic precipitation. Focal habitats were pools on the open shore, formed in bedrock depressions from precipitation, ground water, overland flow, and wave wash. The focal study taxon was Chironomidae, a diverse family of aquatic flies, well-known for variable responses to pollution and ecological gradients. Results showed a surprisingly species-rich ( $n = 102$ ) and diverse assemblage. Moderate to extreme range expansions and novel habitat use were documented. Distinct communities were observed between two vertical zones, based on distance from the lake. Differences in seasonal emergence occurred close to the lake, but emerging assemblages were similar across seasons above lake influence. Some evidence supported both biogeographic community variation based on distances between islands and control of emergence events by water temperature. However, there was no evidence that pool depth or potential for desiccation influenced chironomid occupancy. Nutrients (phosphorus, nitrogen, and carbon) were the most important factors driving chironomid assemblage differences.

Pools higher on the shore showed nutrient input from upland habitats, while pools lower on the shore appeared to have nutrients flushed out by wave action and replaced with low-nutrient water. Comprehensive habitat mapping revealed high pool densities, with an extraordinary number on Passage Island, arguably the most threatened locality to shipping pollution. Also, Passage Island had the highest density of *Pseudacris triseriata*, a frog species with a remarkably narrow habitat use at Isle Royale. Overall, a diverse community was revealed in what superficially looks like unremarkable habitat. Apparent similarities to northern and western shores of Lake Superior suggest this study of basic aquatic ecology and physical structure describes reference conditions for coastal management across much of the lake.

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# **CHAPTER I**

## **CHIRONOMIDAE (DIPTERA) IN FRESHWATER COASTAL ROCK POOLS AT ISLE ROYALE, MICHIGAN**

### **Summary**

Chironomid pupal exuviae were collected from coastal rock pools at Isle Royale National Park, Michigan, from April to October in 2009 and 2010. Pools in bedrock depressions were separated into those higher on the shore, where desiccation is likely an important disturbance, and lower on the shore, where wave-wash from Lake Superior is likely a fundamental influence. The 102 species collected represent 42 genera in six subfamilies. The distribution and ecology of each species is summarized. Also included are remarks on species with significant range expansions, either with Palearctic or Nearctic disjunct ranges, or novel habitat use among species that are typically considered lotic but occur in splash zone pools at Isle Royale.

### **Introduction**

Chironomidae are generally ubiquitous, abundant, and diverse components of aquatic ecosystems. Studies on aquatic invertebrate communities regularly report Chironomidae to the family or subfamily level due to identification challenges. This can mask important community dynamics and responses to environmental variables (Rosenberg, 1992). Generic-level identifications can be used to good effect and are often necessary, such as assessing subfossil midge assemblages (e.g., Quinlan et al., 2012). However, within a genus there may be wide species-level differences in habitat use or response to ecological variation. Several comprehensive keys allow efficient identification for Nearctic genera (e.g., Wiederholm, 1986; Ferrington et al., 2008). Species-level identification may be relatively easy when revisionary works include comprehensive keys to immatures, or may be either challenging or impossible in genera for which keys do not exist or do not conform to contemporary taxonomic standards.

Few chironomid studies offer comments and justifications for species lists, which may be based on life stages other than the adult male, or are not confirmed with reared specimens. Major range expansions for chironomids are commonly documented when previously understudied systems are investigated, such as the discovery of new genus records and significant range expansions from a benthic study in Lake Superior (Stroom et al., 2010). Components of the chironomid community in freshwater coastal rock pools are reported, including species not otherwise known from the Nearctic or Great Lakes region, or previously undetected in rock pool habitats.

## **Methods**

Isle Royale National Park (IRNP), Michigan, is a wilderness area consisting of an archipelago of one large (544 km<sup>2</sup>) island surrounded by hundreds of smaller islands in northwestern Lake Superior, with the nearest point to the mainland approximately 19 km. The volume, depth, and surface area of Lake Superior have a considerable buffering influence on local climate, with a cooling effect in summer and warming effect in winter. Study sites were located on exposed, south-facing bedrock shorelines made of basaltic and andesitic lava flows at the east end of the archipelago. Two shoreline zones were differentiated using a typically distinct line between abundant and colorful lichens upslope (the “lichen zone” where pool recharge includes upland inputs) and drab or no lichens downslope (the “splash zone” where wave wash also recharges pools and possibly has an important disturbance influence). Samples were collected from pools in both zones at 18 sites on or near Isle Royale: four on the main island, thirteen on surrounding islands, and one on nearby Passage Island (Figure 1.1).

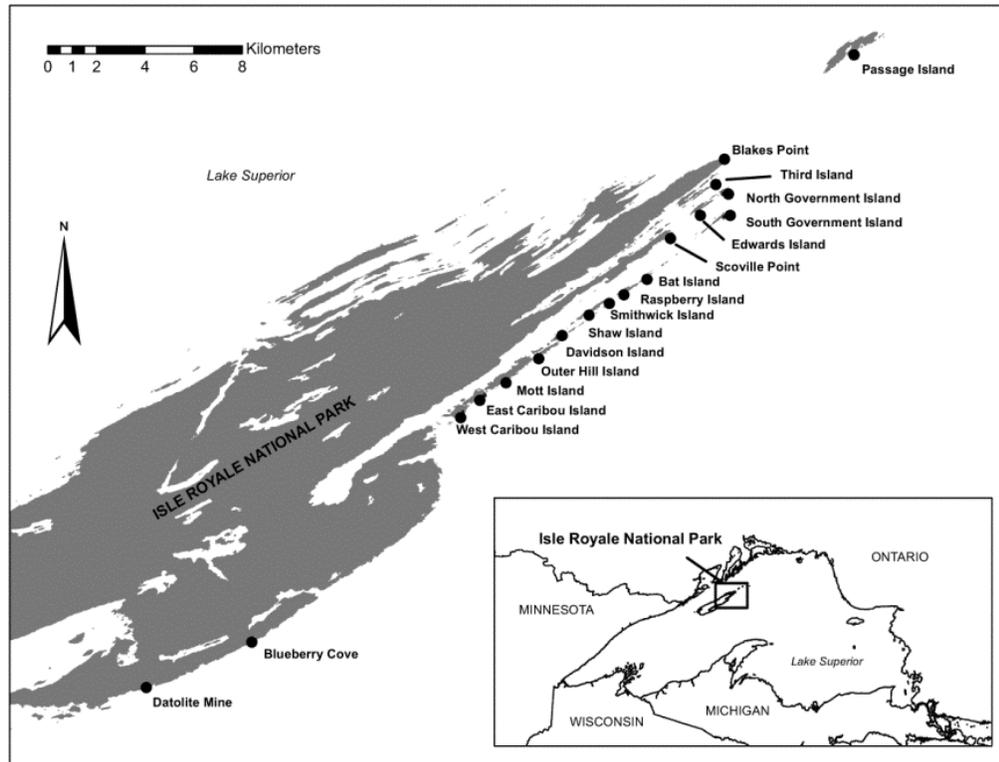
Using techniques modified from Ferrington et al. (1991), surface-floating pupal exuviae were collected from pool surfaces approximately monthly from April to October, in 2009 and 2010. A tray was dipped into the pool to collect water and floating material, poured through a 250 µm sieve, and field-preserved in 80% ethanol. In 2009, samples at each site were separated by zone, with ten minutes of collection occurring in each zone. In 2010, samples were separated both by zone and pool permanence; ten minute

collections occurred for ephemeral pools (likely to dry in drought conditions) in each zone, with an additional five minutes of collecting at each of two permanently established study pools that were likely to retain water regardless of rainfall patterns.

A total of 285 samples were collected. Exuviae were permanently slide mounted in euparal. Generic-level identifications used keys in Wiederholm (1986) and Ferrington et al. (2008). Species-level identifications were generally accomplished using keys listed in each species summary below, with the Palearctic key by Langton (1991) used if no other key existed. The species-level abbreviation “cf.” (latin “confere”) is used to indicate that specimens closely match both original species descriptions and known habitats well, but based on extreme range disjunction they may represent an undescribed Nearctic species. The abbreviation “nr.” indicates specimens that key near a species but do not match any descriptions in the genus. Vouchers are deposited in the University of Minnesota Insect Collection, St. Paul (UMSP), Minnesota, USA.

## **Results**

Chironomidae collected at Isle Royale represented six subfamilies, 42 genera, and 102 species (Table 1.1). Distribution descriptions focus on published Nearctic range. Sixty-two species are known from the western Great Lakes or Nearctic generally, and 19 species were not identifiable due to lack of descriptions of pupal exuviae. Ten species were determined as Palearctic, with no prior confirmation in the Nearctic; some of these may be undescribed, closely-related species, while others represent range expansions of described species. Seven species were known previously from arctic or alpine ranges that are disjunct from the area of Lake Superior, generally northern Canada, with two from western mountains in British Columbia and California. Four species had ranges that include Nearctic locations but IRNP appears to be a range expansion. In addition, at least 13 rheophilic species were collected from splash zone pools, which are all known regionally except *Cricotopus intersectus* with only one other Nearctic record from Manitoba. In the distribution descriptions, the name “Northwest Territories” includes the Canadian province of Nunavut since most sources do not distinguish the two.



**Figure 1.1:** Northeast end of Isle Royale National Park, Michigan, regional context (insert) and locations of sample sites.

**Table 1.1:** Chironomidae collected from coastal rock pools, Isle Royale, 2009-2010.

	Distribution <sup>1</sup>	Ecology	Remarks <sup>2</sup>	Sources
<b>PODONOMINAE</b>				
<i>Parochlus kiefferi</i> (Garrett)	Only known <i>Parochlus</i> in Holarctic. Widely distributed, including Greenland, BC to QC and south to CA, NM, CO, and NY.	Larvae grazers and collector-gatherers. Occupies small, fast-running, cold lotic systems and springs in a temperature range of 0.4 – 8.8 °C.	One IRNP specimen from a lichen zone pool. Species likely cold-stenothermic.	Oliver et al., 1990 Lencioni et al., 2007 Andersen et al., 2013 Langton, 1991
<b>TANYPODINAE</b>				
<i>Ablabesmyia</i> ( <i>Ablabesmyia</i> ) <i>aspera</i> Roback	Widespread but generally northern, from BC to ON and south to CA and FL.	Larvae obligate predators. Recorded in small to large lentic waters, including ditches and possibly caves. <i>Ablabesmyia</i> larvae usually in shallow, mud-bottomed, slow moving areas.	IRNP specimens from lichen zone pools.	Roback, 1985 Saether, 2011
5 <i>Ablabesmyia</i> ( <i>Ablabesmyia</i> ) <i>monilis</i> (L)	Species very widely distributed in the Nearctic, from arctic areas in AK and Canada, to the southwestern U.S. and across to the midwest and northeast. Has also been found in the Carolina's and FL.	Larvae obligate predators and are usually in shallow, muddy-bottomed, slow moving areas of creeks, or in lakes. Species recorded in medium lentic and small-to-medium lotic systems, and in stagnant water. Also in littoral or upper profundal zone of oligotrophic lakes and periphyton substrates.	IRNP specimens from both zones. According to genetic work by Stur and Ekrem, two species may be represented within <i>A. monilis</i> , including <i>A. americana</i> (Fittkau), but a revision is needed.	Roback, 1971 Roback, 1985 Hudson et al., 1990 Langton, 1991 Saether, 2011
<i>Ablabesmyia</i> ( <i>Karelia</i> ) <i>illinoensis</i> (Malloch)	Known from ON, MB and SK, south to most western, plains, and midwestern states; in the east it spans from MA to VA. Material has been noted from the southeast, from the Carolina's to FL, although Epler is skeptical it occurs in the southeast.	Larvae obligate predators, and appear to occur in small lakes and ponds, maybe also marshes, with <i>Karelia</i> species usually in standing water. Genus only rarely in cold, oligotrophic lakes.	IRNP specimens generally from lichen zone pools, but occasionally found in splash zone.	Roback, 1971 Roback, 1985 Hudson et al., 1990 Epler, 2001 Saether, 2011

(Table 1.1 continued)	Distribution	Ecology	Remarks	Sources
<i>Conchapelopia</i> ( <i>Conchapelopia</i> ) <i>fasciata</i> Beck and Beck	From AB to ON and south to KS, Great Lakes states, and FL.	Rivers and creeks, generally small to medium sized shallow streams, and often in places with organic waste. Noted in FL as a vernal species.	IRNP specimens from splash zone pools.	Roback, 1981 Oliver et al., 1990 Beck and Beck, 1966 Simpson and Bode, 1980
<i>Conchapelopia</i> ( <i>Helopelopia</i> ) <i>cornuticaudata</i> (Walley)	Wide distribution in eastern North America, from ON to QC and south to AL and FL.	Creeks and rivers, generally medium sized streams. Genus commonly encountered in riffles of river systems, often in places with organic waste.	IRNP specimens from splash zone pools.	Roback, 1971 Roback, 1981 Hudson et al., 1990 Andersen et al., 2013 Simpson and Bode, 1980
<i>Procladius</i> ( <i>Holotanypus</i> ) <i>abetus</i> Roback	Only known locations are AB, ON, and PA.	<i>Procladius</i> known as predators of zooplankton and small invertebrates, including chironomids. Genus often in muddy littoral and profundal standing water or calm flowing water, and sometimes large, deep lakes.	IRNP specimens from lichen zone pools. Based on known range, may be a northern species. Lichen zone pools fit general habitat type, but not previously reported from bedrock substrate.	Roback, 1971 Roback, 1980 Andersen et al., 2013
<i>Procladius</i> ( <i>Holotanypus</i> ) nr. <i>culiciformis</i> (L)	Not applicable.	See <i>P. abetus</i> for ecology of this genus.	One IRNP specimen from a lichen zone pool. Did not match described species, but appeared to be <i>Holotanypus</i> and morphologically similar to <i>P. culiciformis</i> .	Roback, 1980
<i>Thienemannimyia</i> ( <i>Thienemannimyia</i> ) <i>norena</i> (Roback)	Primarily an eastern Nearctic species, from ON to NH and NJ, but also known from KS and OR.	Genus commonly encountered in rivers, often in places with organic waste, but also habitats including oligotrophic lakes. Species usually in medium sized shallow streams, but also known from rivers and one large lake.	IRNP specimens from splash zone pools.	Roback, 1971 Roback, 1981 Andersen et al., 2013 Simpson and Bode, 1980

(Table 1.1 continued)	Distribution	Ecology	Remarks	Sources
<i>Zavrelimyia</i> cf. <i>melanura</i> (Meigen)	Not previously known in the Nearctic; has Western Palearctic range. Global distribution could not be determined from primary literature.	Species generally found in northern and montane lakes, pools and streams, and <i>Zavrelimyia</i> species are cold stenothermic.	IRNP specimens from lichen zone pools match descriptions of <i>Z. melanura</i> , although this may be an undescribed Nearctic species.	Oliver et al., 1990 Langton, 1991 Andersen et al., 2013
<b>DIAMESINAE</b>				
<i>Diamesa insignipes</i> Kieffer	WY, UT and PA.	Species found in fast-flowing creeks in prairies, plateaus, and flat country generally, but also montane streams and lakes. <i>Diamesa</i> often in northern or alpine habitats and probably often cold-stenothermic.	IRNP specimens from splash zone pools. Hansen considered Nearctic and Palearctic males to be the same species, but many <i>Diamesa</i> not described as pupal exuviae.	Hansen, 1973 Oliver et al., 1990 Pagast, 1947 Langton, 1991 Saether and Andersen, 2013
<i>Pagastia orthogonia</i> Oliver	Wide Nearctic distribution, from AK to ME and south to CA and GA.	Diet probably includes predation of small invertebrates, including chironomids, and collector-gatherer of detritus and diatoms. Usually lotic, but also in lakes and springs.	IRNP specimens from splash zone pools. In Makarchenko and Makarchenko specimens cannot be separated from <i>P. lanceolata</i> , but all clearly the Lake Superior variant described by Caldwell.	Hudson et al., 1990 Oliver et al., 1990 Caldwell, 2007 Makarchenko and Makarchenko, 2000
<i>Potthastia gaedii</i> (Meigen)	Nearctic range includes PA, GA, and NC, with a general eastern U.S. distribution.	Northern and montane lakes and streams, or restricted to streams in southern areas of Europe. <i>Potthastia</i> described for flowing water generally.	IRNP specimens from splash zone pools. Possible that there is a Nearctic-Palearctic difference in species that are currently all labelled <i>P. gaedii</i> .	Hudson et al., 1990 Oliver et al., 1990 Langton, 1991 Andersen et al., 2013 Epler, 2001
<i>Protanypus hamiltoni</i> Saether	BC and NT.	Rivers and lakes from a broad range of depths from 3.5-117 m. <i>Protanypus</i> generally found in oligotrophic lakes.	IRNP specimens from splash zone pools. MI represents a large Nearctic range expansion.	Saether, 1975a Andersen et al., 2013
<i>Protanypus ramosus</i> Saether	ON and MB.	Deep water in large lakes like Lake Huron or in shallow waters of smaller lakes.	IRNP specimens from splash zone pools. <i>P. hamiltoni</i> and <i>P. ramosus</i> thought to be geographically separated, but IRNP data suggest overlap in the Lake Superior region.	Saether, 1975a Oliver et al., 1990

(Table 1.1 continued)	Distribution	Ecology	Remarks	Sources
<i>Pseudodiamesa</i> ( <i>Pseudodiamesa</i> ) <i>branickii</i> (Nowicki)	Wide Holarctic distribution. Rocky Mountains of BC and AB, also NM, PA, OR and Greenland.	Cold running water in montane regions.	IRNP specimens from splash zone pools. While specimens match <i>P. branickii</i> , pupal exuviae can be difficult to separate from <i>P. nivosa</i> , and <i>P. pertinax</i> exuviae not described.	Oliver, 1959 Oliver et al., 1990 Langton, 1991
<b>PRODIAMESINAE</b>				
<i>Monodiamesa</i> <i>tuberculata</i> Saether	BC, NT and across the Canadian prairie provinces to the Great Lakes region.	Sublittoral and profundal zones of oligotrophic lakes, in substrates of sand, silt, organic debris, and clay. At depths of 3-167 m in the Great Lakes and Lake Winnipeg. Appears to require cold water (<18°C) and may be sensitive to low dissolved oxygen.	IRNP specimens from splash zone pools. Saether suggests this is a glacial relict because it occurs mostly in large, deep, oligotrophic lakes.	Saether, 1973 Oliver et al. 1990
<i>Prodiamesa olivacea</i> (Meigen)	Holarctic, with a wide Nearctic range.	Lakes, ponds, rivers and drains. Genus somewhat tolerant of pollution.	One IRNP specimen from a splash zone pool. No source found for the other known Nearctic species, <i>P. cubita</i> (Garrett).	Oliver et al., 1990 Andersen et al., 2013 Langton, 1991 Wirth and Stone (1956)
<b>ORTHOCLADIINAE</b>				
<i>Corynoneura arctica</i> Kieffer	NT and PA.	Montane and northern pools and lakes.	IRNP specimens emerged from both zones, though preference for the splash zone may occur.	Oliver et al., 1990 Langton, 1991
<i>Corynoneura doriceni</i> Makarchenko and Makarchenko	The only Nearctic material is from OH. Species initially known from Russian Far East.	<i>Corynoneura</i> known from very broad habitat types. No habitat described for <i>C. doriceni</i> .	IRNP specimens emerged from both zones.	Fu and Saether, 2012 Andersen et al., 2013
<i>Cricotopus</i> ( <i>Cricotopus</i> ) cf. <i>albiforceps</i> (Kieffer)	Not previously documented with certainty in the Nearctic. Listed from NC, but Epler notes some skepticism about this. Widely known in Europe.	Lakes and slow flowing or stagnant water.	IRNP specimens emerged from lichen zone pools. All exuviae fit <i>C. albiforceps</i> well, though Nearctic uncertainty suggests this may be an undescribed species.	Hudson et al., 1990 Epler, 2001 Hirvenoja 1973 Langton, 1991

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(Table 1.1 continued)	Distribution	Ecology	Remarks	Sources
<i>Cricotopus</i> ( <i>Cricotopus</i> ) <i>annulator</i> Goetghebuer	Labrador to ON and south to CA, NM and the southwest generally, and the Carolinas.	Flowing waters and sometimes northern lakes. As part of the <i>tremulus</i> group, this species may be less abundant with increasing organic or toxic conditions, yet would probably not be eliminated.	IRNP specimens from splash zone pools.	Hirvenoja, 1973 Langton, 1991 Hudson et al., 1990 Epler, 2001 Oliver et al., 1990 LeSage and Harrison, 1980 Simpson and Bode, 1980
<i>Cricotopus</i> ( <i>Cricotopus</i> ) <i>bicinctus</i> (Meigen)	Across Canada from YT to Newfoundland and south to CA and the Gulf Coast states.	Extremely common in lotic systems, yet adaptable to diverse habitats. Apparently tolerant to environmental stress, including oil wastes.	IRNP specimens occupied both zones broadly, reconfirming it as a habitat generalist. Known to become abundant if pollution or toxic conditions exclude other species, <i>C. bicinctus</i> would be useful as an indicator of ecological health during oil spill remediation.	Oliver and Dillon, 1988 Hudson et al., 1990 Hirvenoja, 1973 LeSage and Harrison, 1980 Simpson and Bode, 1980
<i>Cricotopus</i> ( <i>Cricotopus</i> ) <i>curtus</i> Hirvenoja	SK, NY and PA.	Running and stagnant water. See <i>tremulus</i> group notes in <i>C. annulator</i> .	IRNP specimens from the splash zone.	Oliver et al., 1990 Hirvenoja, 1973 Langton, 1991
<i>Cricotopus</i> ( <i>Cricotopus</i> ) <i>cylindraceus</i> group, Sp. 1	Not applicable.	Other species in <i>cylindraceus</i> group occupy broad habitats, including slow flowing or standing water, shorelines of lakes and small water bodies.	IRNP specimens from splash zone pools. Exuviae clearly match the group, but not any species description.	Hirvenoja, 1973 Andersen et al., 2013
<i>Cricotopus</i> ( <i>Cricotopus</i> ) <i>fuscus</i> (Kieffer)	ON, PA and Great Smoky Mountains National Park (NC and TN).	Lakes, flowing water, springs, and rarely in ponds.	IRNP specimens emerged from opposite zones in different years.	Oliver et al., 1990 Epler, 2001 Hirvenoja, 1973
<i>Cricotopus</i> ( <i>Cricotopus</i> ) cf. <i>magus</i> Hirvenoja	Not recorded from the Nearctic.	Lakeshores, rivers and northern streams.	IRNP specimens from splash zone pools. <i>Cricotopus magus</i> is known in Finland, so possibly a closely related undescribed species.	Hirvenoja, 1973 Langton, 1991

(Table 1.1 continued)	Distribution	Ecology	Remarks	Sources
<i>Cricotopus</i> ( <i>Cricotopus</i> ) <i>tremulus</i> (L)	AB, QC and NS, south to OR, OH, GA and eastern and southeastern states generally.	Flowing waters, especially with stones and in mosses.	One IRNP specimen from the lichen zone.	Oliver et al., 1990 Hudson et al., 1990 Epler, 2001 Hirvenoja, 1973
<i>Cricotopus</i> ( <i>Cricotopus</i> ) <i>triannulatus</i> (Macquart)	ON, NY and PA, south to MS and FL.	Flowing waters, lakes, and brackish water. See <i>tremulus</i> group notes in <i>C. annulator</i> .	IRNP specimens from splash zone pools.	LeSage and Harrison, 1980 Hudson et al., 1990 Oliver et al., 1990 Hirvenoja, 1973
<i>Cricotopus</i> ( <i>Cricotopus</i> ) <i>tristis</i> Hirvenoja	YT and NT where range was north of the treeline, but also known from PA.	Small, slow-flowing, meandering streams and a lake above rapids. See <i>tremulus</i> group notes in <i>C. annulator</i> .	IRNP specimens emerged from splash zone pools.	Oliver and Dillon, 1988 Oliver et al., 1990 Hirvenoja, 1973
<i>Cricotopus</i> ( <i>Isocladius</i> ) <i>intersectus</i> (Staeger)	Widespread in Europe, but only one Nearctic citation from MB. Epler discussed larvae from the southeast that may or may not be this species.	Large and medium rivers, sometimes in slow areas with high organic and mild toxic loading, eutrophic and large lakes, and a wide range of dissolved oxygen levels.	IRNP specimens from splash zone pools. Specimens fit description and figures in Hirvenoja very well.	Oliver et al., 1990 Hirvenoja, 1973 Epler, 2001 Simpson and Bode, 1980
<i>Cricotopus</i> ( <i>Isocladius</i> ) <i>sylvestris</i> (F)	Wide Nearctic range, from AK to NT, Newfoundland and south to CA, NY, and broadly in the southeast including the Carolinas.	Standing or slow flowing water, including low dissolved oxygen and on many substrates, but also rivers with moderate to fast flow. Utilizes widespread habitats south of treeline, but only permanent ponds in the arctic. Also found in marine coastal rock pools above high tide line.	Very common at IRNP, clearly a habitat generalist with emergence from a wide range of pool types.	Oliver and Dillon, 1988 Hudson et al., 1990 Oliver et al., 1990 Colbo, 1996 Epler, 2001 Hirvenoja, 1973 Simpson and Bode, 1980 Simpson et al., 1983
<i>Eukiefferiella</i> <i>claripennis</i> (Lundbeck)	Greenland, BC, AB and NT south to NM, PA and the Carolinas.	Northern streams and sometimes lakes. Eurythermic, rheobiotic and mossy areas of swift streams. The <i>claripennis</i> group probably prefers clean water but not excluded from moderately polluted water if dissolved oxygen above 5 ppm.	IRNP specimens from splash zone pools.	Hudson et al., 1990 Oliver et al., 1990 Langton, 1991 Lehman, 1972 Simpson and Bode, 1980

(Table 1.1 continued)	Distribution	Ecology	Remarks	Sources
<i>Eukiefferiella coerulescens</i> Kieffer	Occurs in Europe and North Africa. Although Hudson et al. listed <i>coerulescens</i> for SC, others list Nearctic specimens only as part of the wider <i>coerulescens</i> group.	Northern and montane lakes, and stones and moss in swift streams.	IRNP specimens all from splash zone pools. All key well to <i>E. coerulescens</i> in Langton except small, thin, rounded thoracic horns present. Reiss found similar thoracic horns and Langton noted a "small thin-walled sac-like thoracic horn...present in all the examples I have seen since", suggesting this feature had previously been missed. Some Nearctic material may be misidentified and the cryptic thoracic horn should be looked for.	Lehmann, 1972 Roback, 1985 Bode 1983 Hudson et al., 1990 Langton, 1991
<i>Heterotrissocladius changi</i> Saether	AB to NT and ON, south to the Great Lakes states and CO.	Oligotrophic lakes in the lower littoral and upper profundal zones.	IRNP specimens generally emerged from the splash zone.	Saether, 1975b Oliver et al., 1990
II <i>Heterotrissocladius oliveri</i> Saether	Greenland, NT to BC and ON, south to CA, NY and PA. Populations in large southern lakes, such as Lake Tahoe, Cayuga Lake, and the Great Lakes, occur as relicts.	Strongly cold-stenothermic and ultraoligotrophic.	One IRNP specimen from a splash zone pool. Generally an arctic species, emerging through ice-cracks in summer.	Oliver et al., 1990 Saether, 1975b
<i>Heterotrissocladius</i> Sp. A Saether	Northwest ON and BC, possibly including Vancouver Island.	Oligotrophic lakes, with larvae up to 46 m deep. Some species in this genus found in ponds and puddles.	IRNP specimens from splash zone pools. The species remains undescribed because only pupae and larvae are known.	Saether, 1975b Andersen et al., 2013
<i>Hydrosmittia ruttneri</i> (Strenzke and Thienemann)	AK, NT, YT and MI.	Algal growth on stony substrates of northern and montane lakes and rivers.	INRP specimens from splash zone pools. MI populations may not be as disjunct as distribution records suggest, since the 2011 revision created this as a new genus.	Ferrington and Saether, 2011 Strenzke, 1950

(Table 1.1 continued)	Distribution	Ecology	Remarks	Sources
<i>Hydrosmittia</i> Sp. 1	Not applicable.	Genus typically in aquatic moss and algae, and often cold-stenothermic.	IRNP specimens from splash zone pools. Specimens don't match either <i>Hydrosmittia</i> or <i>Pseudosmittia</i> , but are a mix that appears to represent an undescribed exuviae of a species in <i>Hydrosmittia</i> .	Andersen et al., 2013 Strenzke, 1950 Ferrington and Saether, 2011
<i>Limnophyes carolinensis</i> Saether	ON, MN, SC and TN.	Seeps and wet areas near flowing water.	IRNP specimens almost exclusively from lichen zone pools. Wide variation within <i>Limnophyes</i> , but IRNP specimens have two distinct morphs and one may be an undescribed species that keys to <i>carolinensis</i> .	Saether, 1990
<i>Limnophyes minimus</i> Saether	Broad Nearctic range, from YT, NT and NS south to NE, SD, MI, TN and SC.	Seeps, margins of streams, wet soils, and small rivers. Species is facultatively parthenogenetic.	IRNP specimens from lichen zone pools. Specimens key to <i>minimus</i> but not all traits fit. Saether notes that <i>minimus</i> may represent multiple species.	Saether, 1990
<i>Limnophyes natalensis</i> (Kieffer)	MB, NS, SD and WI.	Rivers, streams, seepages, and sphagnum.	One IRNP specimen from the splash zone.	Saether, 1990 Langton, 1991
<i>Limnophyes pumilio</i> (Holmgren)	Greenland, NT, MB and AB. Generally a northern species, but additional locations include NC, GA and PA.	Littoral zone of lakes.	One IRNP specimen from the splash zone.	Saether, 1990 Langton, 1991 Cranston, 1979 Hudson et al., 1990 Oliver et al., 1990
<i>Limnophyes</i> Sp. 1	Not applicable.	Genus utilizes broad range of habitat types.	IRNP specimens from the lichen zone. Specimens do not key to or match any described <i>Limnophyes</i> .	Andersen et al., 2013 Saether, 1990
<i>Metriocnemus ursinus</i> (Holmgren)	Greenland, NT, northern QC and PA.	Genus has widely variable habitat associations, including coastal rock pools and small habitats like phytotelmata.	IRNP specimens from lichen zone pools.	Oliver et al., 1990 Saether, 1989
<i>Nanocladius (Nanocladius) speniplenus</i> Saether	SK, ON and NB, south to OH, AL, GA and FL.	Apparently rheophilous, possibly from creeks and streams.	One IRNP specimen from the splash zone.	Saether, 1977 Hudson et al., 1990 Oliver et al., 1990

(Table 1.1 continued)	Distribution	Ecology	Remarks	Sources
<i>Nanocladius</i> ( <i>Plecopteracoluthus</i> ) cf. <i>branchicolus</i> Saether	SK, ON and NY.	Generally subgenus phoretic or parasitic on other aquatic insects, so these may emerge from Lake Superior and utilize the abundant stoneflies.	IRNP specimens are from splash zone pools. Saether notes pupae as "easily distinguishable", yet he synonymized similar species that sometimes fit and sometimes contradict IRNP specimens, so determination of <i>N. branchicolus</i> tentative.	Saether, 1977 Andersen et al., 2013
<i>Orthocladius</i> ( <i>Eudactylocladius</i> ) <i>dubitatus</i> Johannsen	From AK, BC, Newfoundland and ON, south to WA, CO, OH and FL.	Wide variety of habitats, including marine coastal rock pools above high tide line.	One of the most common species from IRNP samples, emerging broadly from both zones. A highly variable species, especially pupae.	Oliver et al., 1990 Colbo, 1996 Cranston, 1998
<i>Orthocladius</i> ( <i>Euorthocladius</i> ) <i>rivicola</i> Kieffer	Widely known from AK, Canada, Greenland and south across the U.S.	Generally in lotic systems of various sizes and with wide temperature ranges.	IRNP specimens from splash zone pools. Although <i>rivicola</i> is variable, IRNP specimens match description well except for presence of frontal warts.	Soponis, 1990 Hudson et al., 1990 Oliver et al., 1990
<i>Orthocladius</i> ( <i>Orthocladius</i> ) <i>dorenius</i> (Roback)	YT, NT, ON and NB, south to OR, CO, NM, MN, PA and the Carolinas.	Rivers, creeks and Lake Superior from nearshore at the Gooseberry River.	IRNP specimens from splash zone pools.	Soponis, 1977 Oliver et al., 1990 Roback, 1957
<i>Orthocladius</i> ( <i>Orthocladius</i> ) <i>nigritus</i> Malloch	AB, MB, SK, ON, western Great Lakes states and south to UT, VA and the Carolinas.	Rivers, creeks and lakes.	IRNP specimens from splash zone pools.	Soponis, 1977 Hudson et al., 1990 Oliver et al., 1990
<i>Orthocladius</i> ( <i>Orthocladius</i> ) <i>obumbratus</i> Johannsen	Broad Nearctic distribution south of the arctic.	Larvae consume diatoms, detritus and filamentous algae. Generally in streams and creeks. Apparently sensitive to pollution, but not excluded from polluted sites entirely.	IRNP specimens from splash zone pools.	Soponis, 1977 Hudson et al., 1990 Simpson and Bode, 1980 Roback, 1957
<i>Orthocladius</i> ( <i>Orthocladius</i> ) <i>robacki</i> Soponis	SK, PA, NY and NC.	Creeks.	IRNP specimens from splash zone pools.	Oliver et al., 1990 Hudson et al., 1990 Soponis, 1977

(Table 1.1 continued)	Distribution	Ecology	Remarks	Sources
<i>Orthocladus</i> ( <i>Pogonocladus</i> ) <i>consobrinus</i> Holmgren	Greenland, NT, ON and PA.	Lakes.	One INRP specimen from the splash zone. Specimen fits the monotypic subgenus <i>Pogonocladus</i> , but not clearly <i>consobrinus</i> . Soponis suggested a review needed, but Saether believed subgenus had no other known species.	Oliver et al., 1990 Langton, 1991 Soponis, 1977 Saether, 2005
<i>Orthocladus</i> ( <i>Symposiocladus</i> ) <i>annectens</i> Saether	NT, BC, ON, MN to NJ and south to MS and FL.	Creeks.	IRNP specimens from splash zone pools.	Saether, 2003 Saether, 2005
<i>Paracladius</i> <i>alpicola</i> (Zetterstedt)	Noted as widespread in the Holarctic, but only three Nearctic places listed in Oliver et al.: NT, Labrador, and PA.	Northern and montane lakes.	One IRNP specimen from the splash zone.	Fu et al., 2010 Andersen et al., 2013 Oliver et al., 1990 Langton, 1991
<i>Paracladius</i> <i>quadrinodosus</i> Hirvenoja	Holarctic, known in Nearctic from Greenland, AK, NT and PA.	Northern lakes.	IRNP specimens from splash zone pools.	Fu et al., 2010 Oliver et al., 1990 Langton, 1991
<i>Parakiefferiella</i> nr. <i>fennica</i> Tuiskunen	Not applicable.	<i>Parakiefferiella fennica</i> favors large oligotrophic northern lakes.	IRNP specimens from the splash zone. Based on large abundance in one sample, species may wash in from Lake Superior. Keys to <i>P. fennica</i> , but differences from descriptions and at least one consistently distinct feature suggest it is a similar, undescribed Nearctic species.	Tuiskunen, 1986 Langton, 1991
<i>Parakiefferiella nigra</i> Brundin	Recorded from an arctic-subarctic range in AK, NT and PA.	Oligohumic, northern lakes.	IRNP specimens from splash zone pools.	Tuiskunen, 1986 Oliver et al., 1990 Langton, 1991
<i>Parakiefferiella</i> cf. <i>scandica</i> Brundin	Known previously only from Finland and Norway.	Standing water, though sometimes lotic in mountain streams, can inhabit barren oligotrophic alpine lakes.	IRNP specimens from splash zone pools. Ecological conditions and descriptions of <i>scandica</i> match IRNP specimens very well.	Tuiskunen, 1986 Langton, 1991

<b>(Table 1.1 continued)</b>	<b>Distribution</b>	<b>Ecology</b>	<b>Remarks</b>	<b>Sources</b>
<i>Parakiefferiella</i> cf. <i>smolandica</i> (Brundin)	Known only from Sweden and Finland.	Clear oligotrophic lakes generally, but occasionally mesohumic lakes and brackish water.	IRNP specimens from splash zone pools. As with <i>P. scandica</i> , ecological conditions and descriptions match <i>smolandica</i> .	Tuiskunen, 1986 Langton, 1991
<i>Parakiefferiella</i> Sp. 1	Not applicable.	Generally this genus is in lentic systems.	One IRNP specimen from splash zone pools. Matches description of <i>P. pyrenaica</i> Moubayed, known from a single cold mountain stream in the western Pyrenees, France. IRNP specimen likely an undescribed species.	Andersen et al., 2013 Langton, 1991 Moubayed, 1991
<i>Parasmittia carinata</i> (Strenzke)	Species is somewhat uncertain in reported range. Originally described from Nova Scotia, also noted from PA and Great Smoky Mountains National Park in NC and TN.	Humus-rich soil of meadows and forests.	IRNP specimens from lichen zone pools, though based on ecology they likely occupied a vegetated hummock near a pool. Specimens match species description well.	Strenzke, 1950 Oliver et al., 1990 Epler, 2001 Andersen et al., 2013
<i>Psectrocladius</i> ( <i>Allopsectrocladius</i> ) <i>pilosus</i> Roback	Broad eastern U.S. range, from ME to FL, also known from SD.	Known from meandering streams, likely acidic with bog influence, although genus in broadly habitat types.	IRNP specimens from lichen zone pools.	Roback, 1957 Epler, 2001 Oliver et al., 1990 Andersen et al., 2013
<i>Psectrocladius</i> ( <i>Allopsectrocladius</i> ) Sp. 1	Not applicable.	Not applicable.	IRNP specimens from lichen zone pools. Traits span different species descriptions. Some traits do not match any descriptions, so likely an undescribed species.	Roback, 1957 Langton, 1991
<i>Psectrocladius</i> ( <i>Psectrocladius</i> ) <i>limbatellus</i> (Holmgren)	Greenland, NT, Lake Winnipeg in MB, SD, and PA.	Ditches, cattle troughs, ponds in southern areas, and lakes in northern areas.	IRNP specimens overwhelmingly from lichen zone pools.	Oliver et al., 1990 Saether and Langton, 2011 Langton, 1991

<b>(Table 1.1 continued)</b>	<b>Distribution</b>	<b>Ecology</b>	<b>Remarks</b>	<b>Sources</b>
<i>Psectrocladius</i> ( <i>Psectrocladius</i> ) cf. <i>sensilipes/dubius</i> Saether and Langton	Saether and Langton list the Lake Winnipeg area for <i>sensilipes</i> , and MB, ON and SC for <i>dubius</i> , reflecting the two subspecies' range.	Both species known from shallow water bodies, including ditches and slow streams, while <i>P. dubius</i> also known from reservoirs.	Very common species at IRNP, the large majority emerged from lichen zone pools, and specimens displayed a wide variety of intergrading traits spanning both species. Molecular work probably needed to separate species in this genus.	Saether and Langton, 2011
<i>Psectrocladius</i> ( <i>Psectrocladius</i> ) <i>subsensilis</i> Saether and Langton	ON and MB.	An oligotrophic lake in Ontario, and Lake Winnipeg.	IRNP specimens from lichen zone pools.	Saether and Langton, 2011
<i>Pseudorthocladius</i> ( <i>Pseudorthocladius</i> ) <i>virgatus</i> group, Sp. 1	Not applicable.	Larvae in genus generally occur in moss, hygropetric areas, acidic streams and areas near springs.	One IRNP specimen from a lichen zone pool. Specimen does not match any described exuviae, but pupae of many species remain unknown. Appears to match " <i>virgatus</i> group", which is distinct enough that it may warrant subgeneric status.	Andersen et al., 2013 Saether and Sublette, 1983
<i>Pseudosmittia</i> Sp. 1	Not applicable.	Generally genus is semiaquatic to semiterrestrial.	One IRNP specimen from a lichen zone pool. Could not be determined to species. Many undescribed pupae in this genus.	Andersen et al., 2013 Ferrington and Saether, 2011
<i>Smittia</i> Sp. 1	Not applicable.	Most <i>Smittia</i> larvae in damp soil or decaying vegetation, though some species aquatic. Very few non-adult stages known.	One IRNP specimen, but from an uncertain zone. Genus determination difficult for terrestrial chironomid genera. Species cannot be determined with exuviae.	Andersen et al., 2013 Ferrington et al., 2008 Langton, 1991 Ferrington and Saether, 2011

(Table 1.1 continued)	Distribution	Ecology	Remarks	Sources
<i>Synorthocladius semivirens</i> (Kieffer)	Widespread in Nearctic, including many southeastern U.S. states.	Swiftly flowing water, in gelatinous tubes with sand grains incorporated. Northern and montane streams, lakes, and pools, and streams in southern localities.	IRNP specimens from splash zone pools. Only known Nearctic <i>Synorthocladius</i> species, although there is probably unknown additional diversity.	Oliver et al., 1990 Hudson et al., 1990 Simpson and Bode 1980 Langton, 1991 Liu and Wang, 2005 Andersen et al., 2013
<i>Thienemanniella lobapodema</i> Hestenes and Saether	ON, MB, OH, St. Lawrence River, Lake Erie and surroundings, and south to AL and FL.	Typically streams, also rivers, and littoral zone of Lake Winnipeg.	Two IRNP specimens from splash zone pools. Genus often abundant when present, suggesting rock pool habitat not ideal.	Hestenes and Saether, 2000 Epler, 2001
<b>CHIRONOMINAE</b>				
<i>Chironomus</i> ( <i>Chironomus</i> ) <i>aberratus</i> Keyl <sup>3</sup>	Species not previously known from the Nearctic.	Cold humus-rich montane pools.	One IRNP specimen from a lichen zone pool. Fits habitat and description in Langton in many important ways, though it is possible this is a Nearctic variant of <i>aberratus</i> .	Langton, 1991
<i>Chironomus</i> ( <i>Chironomus</i> ) <i>anthracinus</i> Zetterstedt	BC, AB, SK, CA and WI to MA.	Moderately eutrophic lakes.	IRNP specimens from lichen zone pools.	Oliver et al., 1990 Langton, 1991
<i>Chironomus</i> ( <i>Chironomus</i> ) Sp. 1	Not applicable.	Chironomus are grazers and filter feeders, usually in sediments of lentic systems, often constructing tubes in or on sediment.	Common at IRNP, with most emergence from lichen zone pools. Variations within this determination may include more than one species.	Andersen et al., 2013 Langton, 1991
<i>Chironomus</i> ( <i>Chironomus</i> ) Sp. 2	Not applicable.	See <i>Chironomus</i> Sp. 1.	IRNP specimens from lichen zone pools. This species may be near <i>C. holomelas</i> or <i>annularius</i> .	Langton, 1991
<i>Chironomus</i> ( <i>Chironomus</i> ) Sp. 3	Not applicable.	See <i>Chironomus</i> Sp. 1.	IRNP specimens from lichen zone pools. These specimens key near Palearctic <i>C. pseudothummi</i> or <i>holomelas</i> .	Langton, 1991

(Table 1.1 continued)	Distribution	Ecology	Remarks	Sources
<i>Chironomus</i> ( <i>Chironomus</i> ) Sp. 4	Not applicable.	See <i>Chironomus</i> Sp. 1.	One IRNP specimen from a lichen zone pool. Possibly <i>C. riparius</i> or similar species.	Langton, 1991
<i>Chironomus</i> ( <i>Chironomus</i> ) Sp. 5	Not applicable.	See <i>Chironomus</i> Sp. 1.	IRNP specimens from lichen zone pools. Keys to near Palearctic <i>C. holomelas</i> , but is not that species.	Langton, 1991
<i>Chironomus</i> ( <i>Lobochironomus</i> ) <i>dorsalis</i> Strenzke	ON and PA.	Ponds.	One IRNP specimen from a splash zone pool. This name has historically complicated use, see Spies and Saether.	Oliver et al., 1990 Langton, 1991 Spies and Saether 2004
<i>Chironomus</i> ( <i>Lobochironomus</i> ) <i>montuosus</i> Ryser, Wulker, and Scholl	Yosemite National Park in CA.	Subgenus in higher altitude lakes and ponds (>1700 m) and arctic areas. Species known in small alpine lakes and ponds up to 2100 m.	IRNP specimens from lichen zone pools. Matches Langton description well, and also generally with Ryser et al.	Ryser et al., 1985 Langton, 1991
<i>Dicrotendipes fumidus</i> (Johannsen)	Known throughout the U.S. and southern Canada.	Larvae feed on algae, detritus, and associated microorganisms.	IRNP specimens from both splash and lichen zone pools.	Epler, 1987 Epler, 1988 Oliver et al., 1990 Hudson et al., 1990
<i>Dicrotendipes modestus</i> (Say)	Widespread in the Nearctic, but not in the U.S. southwest.	Larvae feed on algae, detritus, and associated microorganisms.	IRNP specimens from lichen zone pools. <i>Dicrotendipes modestus</i> and <i>D. neomodestus</i> share considerable overlapping traits, but IRNP specimen measurements trend closest to <i>modestus</i> and one larval exuviae attached to a pupal exuviae also keys to <i>modestus</i> .	Epler, 1987 Hudson et al., 1990 Oliver et al., 1990

(Table 1.1 continued)	Distribution	Ecology	Remarks	Sources
<i>Dicrotendipes nervosus</i> (Staeger)	Wide distribution, from AK, NT to NB, Greenland, and south to CA and FL.	Larvae feed on algae, detritus, and associated microorganisms. Probably in littoral benthos, especially mud, also in reed stems or on algae covered rocks. Usually in slow currents in eutrophic conditions that may be polluted with sewage and low dissolved oxygen, and usually absent in pristine and swift flowing water.	IRNP specimens from both lichen and splash zone pools.	Epler, 1987 Hudson et al., 1990 Oliver et al., 1990 Simpson and Bode, 1980
<i>Endochironomus nigricans</i> (Johannsen)	NT, BC to NS and NB, and south to CA and FL.	Presumably eats algae and diatoms. Generally lentic, sometimes in shallow habitats with vegetation, or found on or in living and dead aquatic macrophyte leaves.	One IRNP specimen from a lichen zone pool.	Grodhaus, 1987 Hudson et al., 1990 Oliver et al., 1990 Andersen et al., 2013
<i>Glyptotendipes</i> ( <i>Phytotendipes</i> ) nr. <i>paripes</i> (Edwards)	Not applicable.	Generally <i>Glyptotendipes</i> species in detritus-rich sediment of standing water.	IRNP specimens from lichen zone pools. Specimens key closest to <i>G. paripes</i> , but <i>G. barbipes</i> also similar. Does not match descriptions of either. Many common Nearctic species are not described as pupae.	Andersen et al., 2013 Langton, 1991 Contreras-Lichtenberg, 1999 Contreras-Lichtenberg, 2001
<i>Micropsectra geminata</i> Oliver and Dillon	A few locations in ON, QC and OH.	Spring runs and pools.	IRNP specimens from lichen zone pools.	Oliver and Dillon, 1994
<i>Micropsectra logani</i> (Johannsen)	AK, YT, MT, CO, NM, UT, and PA.	Varies based on locality, lakes and slow lotic systems, coldwater springs, and profundal areas of lakes.	IRNP specimens from splash zone pools.	Oliver et al., 1990 Stur and Ekrem, 2006

(Table 1.1 continued)	Distribution	Ecology	Remarks	Sources
<i>Micropsectra</i> cf. <i>nana</i> (Meigen)	Not known from Nearctic. Generally found in Central and Eastern Europe.	Cold water habitats, including brooks, pools, small lakes, peat bogs in uplands and mountains.	IRNP specimens from lichen zone pools. Specimens fit descriptions in Anderson et al., but cryptic variation occurs in genus and molecular data may be needed to identify these with certainty (A. Anderson, pers. comm., 17 Oct. 2013).	Gilka and Jazdzweska, 2010 Anderson et al., 2013
<i>Micropsectra</i> nr. <i>sedna</i> Oliver	Not applicable.	Not applicable.	One IRNP specimen from a splash zone pool. Due to the extremely restricted known range of <i>sedna</i> (Char Lake, Cornwallis Island, Northwest Territories; oligotrophic with very limited ice- free season) IRNP specimens likely a closely-related species. One key feature does not agree with reared specimens by Oliver.	Oliver, 1976 Michelutti et al., 2003
<i>Micropsectra</i> <i>subletteorum</i> Anderson, Stur, and Ekrem	Eastern North America, OH, MN, ON and MB.	Small streams fed by groundwater, and other lotic and lentic habitats.	IRNP specimens from splash zone pools.	Anderson et al., 2013
<i>Micropsectra xantha</i> (Roback)	Eastern North America, from QC to FL and west to AB, MN, and MS.	Small, cold lotic systems.	IRNP specimens from splash zone pools.	Anderson et al., 2013 Oliver et al., 1990
<i>Neozavrelia</i> cf. <i>luteola</i> (Goetghebuer)	Uncertain Nearctic distribution. Appears monotypic in the Nearctic. Recent <i>Neozavrelia</i> material from OH, NC and GA.	Montane lakes.	IRNP specimens from splash zone pools. Specimens fit <i>N.</i> <i>luteola</i> , but tergite armament appears distinctive, so may be an undescribed species.	Epler, 2001 Langton, 1991 Goetghebuer and Thienemann, 1942
<i>Parachironomus</i> Pe. 3 Langton	Palaearctic.	Stagnant and slow-flowing water. Larvae cryptic, frequently live in association with aquatic snails (P. Langton, pers. comm., 31 Oct. 2013).	One IRNP specimen from a splash zone pool. Specimen fits important Pe. 3 traits in Langton very well.	Langton, 1991

(Table 1.1 continued)	Distribution	Ecology	Remarks	Sources
<i>Paratanytarsus dimorphis</i> Reiss	Not known from the Nearctic. Described from Europe and Mongolia.	Lakes.	IRNP specimens from splash zone pools. Specimens key very well to <i>dimorphis</i> and match the variability described by Reiss.	Reiss, 1965 Reiss and Sawedal, 1981
<i>Paratanytarsus laccophilus</i> (Edwards)	NC, PA and MB.	Shallow water including ponds, pools, ditches, littoral zone of northern and montane lakes. Usually parthenogenetic.	IRNP specimens generally from lichen zone pools, but some from splash zone.	Oliver et al., 1990 Epler, 2001 Langton, 1991 Reiss and Sawedal, 1981
<i>Paratanytarsus natvigi</i> (Goetghebuer)	Northern Canada, Greenland and PA.	Shallow freshwater ponds, lakes and brackish water.	IRNP specimens from splash zone pools.	Reiss and Sawedal, 1981 Oliver et al., 1990 Langton, 1991
<i>Polypedilum</i> Sp. 1	Not applicable.	Not applicable.	IRNP specimens from lichen zone pools. Specimens appear to be in the subgenus <i>Pentapedilum</i> and possibly near the <i>epleri/tritum</i> group, but subgenus and species cannot be determined with certainty using pupal exuviae morphology. Variation suggests more than one species may be represented.	Saether and Sundal, 1998 Maschwitz and Cook, 2000 Oyewo and Saether, 2008 Saether and Oyewo, 2008 Saether et al., 2010
<i>Sergentia coracina</i> (Zetterstedt)	A northern species, from Greenland, NT, AB, SK, ON and south to OR, MT, MN, IN, OH and PA.	Large lakes, often oligotrophic. Cold stenotherms probably typical of larvae in this genus.	One IRNP specimen from a splash zone pool.	Townes, 1945 Oliver et al., 1990 Wulker et al., 1998 Andersen et al., 2013
<i>Tanytarsus mendax</i> group Sp. 1	Not applicable.	Larvae of this genus known to construct soft tubes on substrate.	IRNP specimens from lichen zone pools. Specimens key to <i>mendax/wirthi</i> , but do not match any described species. Does appear they are in the <i>mendax</i> group.	Ekrem et al., 2003 Andersen et al., 2013

<b>(Table 1.1 continued)</b>	<b>Distribution</b>	<b>Ecology</b>	<b>Remarks</b>	<b>Sources</b>
<i>Tanytarsus wirthi</i> Ekrem, Sublette, Sublette	Broad U.S. distribution, from ID to MN to NY and south to CA, TX, LA and FL.	Broad habitat use, including dams, ponds, creeks, bayou, estuarine marshes, springs, rivers, bogs, and lakes.	One IRNP specimen from a lichen zone pool.	Ekrem et al., 2003

<sup>1</sup> Standard state and provincial abbreviations used for distributions.

<sup>2</sup> IRNP = Isle Royale National Park.

<sup>3</sup> Note on *Chironomus* species: Specimen traits were compared in a spreadsheet, leading to the interpretations reported here. No comprehensive exuviae key exists and there is often much variation in species. In addition, Pinder and Reiss (1986) found that subgenera often cannot be separated, while Ashe (1983) noted that this genus is very confused taxonomically.

## Discussion

Sixty-two of the 102 species found at Isle Royale are known from the western Great Lakes region or the Nearctic generally. Nineteen species have not been described as pupal exuviae, although adult males may be described but not associated with exuviae. With statewide or regional accounts documenting approximately 500-600+ species (Bolton, 2012; Epler, 2001) and Nearctic richness estimated at up to 2000 total species (Ferrington, 2008), coastal pools at Isle Royale may contain 20% of regional species richness and at least 5% of Nearctic richness. Records from the University of Minnesota insect museum (UMSP) revealed between 300-400 chironomid species documented in Minnesota as of 2001. The UMSP diversity can be considered a minimum range since it is an estimate from a single collection, not a family-level review. In aquatic studies where chironomids are identified to species, up to 80-100 species typically occur, with over 100 species occasionally collected (Ferrington et al., 2008), suggesting either that many habitats are undersampled or that Isle Royale coastal pools have a relatively high diversity. Indeed, Bouchard and Ferrington (2011) enumerated 261 taxa from streams in southeastern Minnesota. Intensive and focused sampling for chironomids is likely to reveal a much greater richness in many aquatic habitats.

Of the ten species previously known from the Palearctic, two have tentative accounts from North America (*Cricotopus albiforceps* and *Neozavrelia luteola*), but most represent extreme range expansions (*Zavrelimyia melanura*, *Cricotopus magus*, *Parakiefferiella scandica*, *P. smolandica*, *Chironomus aberratus*, *Parachironomus* Pe. 3 Langton, *Micropsectra nana*, and *Paratanytarsus dimorphus*). These Palearctic disjuncts match published morphology and habitat descriptions very closely. Many studies of aquatic invertebrates identify chironomids to family or subfamily level, with occasional determinations to genus or species level. It is therefore realistic that a great deal of geographic diversity is collected but not identified.

A cold coastal climate at Isle Royale has undoubtedly persisted since the last glacial retreat and the formation of the Great Lakes. Broad occupancy of periglacial

localities by cold-stenothermic species, followed by subsequent glacial retreat, creates a refuge-habitat mechanism for retention of these species in disjunct arctic and alpine habitats (Kubow et al., 2010). Seven Isle Royale species fit this description: *Protanypus hamiltoni*, *Cricotopus tristis*, *Paracladius alpicola*, *P. quadrinodosus*, *Parakiefferiella nigra*, *Chironomus montuosus* and *Paratanytarsus natvigi*. Outside of far northern localities, a number of these were otherwise only noted from Pennsylvania by Oliver et al. (1990). Disjuncts typical of alpine habitats are represented by *C. montuosus*, known in North America only from California, and *P. hamiltoni*, known from British Columbia and Northwest Territories. Non-disjunct species that appear to be glacial relicts in cold habitats include *Monodiamesa tuberculata* and *Heterotrissocladius oliveri* (Saether 1973).

Ranges that are difficult to interpret include: *Corynoneura doriceni*, known from the Russian Far East and Ohio; *Cricotopus intersectus* found in Manitoba; *Eukiefferiella coerulescens* reported in South Carolina; and *Parasmittia carinata*, from Nova Scotia, Pennsylvania, and the Smoky Mountains. Isle Royale represents a broader range in the Nearctic for these species. As previously mentioned, the limited number of studies with species-level chironomid identifications probably contribute to the lack of biogeographic knowledge regarding these species.

Use of pools by taxa typical of stream habitats was first noticed when Hydropsychidae (Trichoptera) larvae were observed in retreats of silk and pebbles wedged into bedrock cracks of the lowest splash zone pools. High dissolved oxygen and slow current of wave splash in pools closest to Lake Superior probably allows occupancy of species usually associated with lotic systems, particularly cold, low-order streams. These “habitat disjuncts” are well-represented in IRNP splash zone pools by at least 13 rheophilic species: *Parochlus kiefferi*, *Conchapelopia fasciata*, *C. cornuticaudata*, *Pseudodiamesa branickii*, *Cricotopus intersectus*, *Limnophyes natalensis*, *Nanocladius speniplus*, *Orthocladius rivicola*, *O. dorenius*, *O. robacki*, *O. annectens*, *Micropsectra subletteorum*, and *M. xantha*.

Chironomidae identifications and access to primary literature can both be challenging and time consuming, which is probably why many studies report taxa only to the family or subfamily level. Results from the current study of rock pools, along with similarly intensive studies (e.g., Bouchard and Ferrington, 2011), indicate that most aquatic habitats are likely to have much greater chironomid species richness than expected. Similarly, a study in the Bahamas that was limited to a small, remote island and a narrow collection timeframe found 3x greater richness than was previously known from across the entire Bahamian archipelago and all but two species were new to the Bahamas (Anderson et al., 2014). Along with these studies, the current work provides insight into how pupal exuviae can be utilized to determine biodiversity and taxonomic breadth of chironomids in many aquatic habitats.

## CHAPTER II

# SPATIAL ARRANGEMENT AND METRICS OF FRESHWATER COASTAL ROCK POOLS APPLIED TO AMPHIBIAN CONSERVATION

### **Summary**

Coastal habitats are an ecotone between aquatic and terrestrial ecosystems. Depressions on volcanic bedrock shores of Lake Superior form small pool habitats that are influenced to various degrees by their spatial context and that relate to differences in mechanisms of disturbance. A total of 71,931 coastal pools were mapped and measured, and amphibian occupants were identified along 48 km of shoreline at Isle Royale National Park, where coastal rock pool habitats were abundant. Generally, mean depth of pools was less than 0.5 m, with a mean surface area of 0.6 m<sup>2</sup>, although maximum measurements were 1.5 m and 378 m<sup>2</sup>, respectively. Two strongly defined zones occurred, with shorelines near the lake having a low slope and more numerous, smaller, and shallower pools, while shorelines near the forest edge had a steeper slope and fewer, larger, and deeper pools. A single offshore location, Passage Island, had nearly 63% of all pool abundance. Two amphibian species were typical of coastal pools, the chorus frog (*Pseudacris triseriata*) and blue-spotted salamander (*Ambystoma laterale*), while spring peeper (*Pseudacris crucifer*) was uncommon and probably incidental to coastal habitats. These three species were significantly more abundant in mid-shore pools. Five other amphibian species were only rarely detected. Both coastal habitat density and chorus frog abundance are highest at localities directly adjacent to an international shipping lane. Consequently, chorus frog should be a species of management concern at Isle Royale, because of an intriguing spatial distribution and the potential to be strongly impacted by coastal pollution.

### **Introduction**

Whereas marine coasts are well studied and have contributed to general ecological theory (e.g., Paine 1966, Berlow 1997), freshwater coasts have received much

less attention, and federal land managers in the Lake Superior region have identified coastal studies as an important gap in knowledge (Lafrancois and Glase 2005). Where open shoreline exists, bedrock morphology can create conditions where small aquatic habitats reside in rock pools formed in depressions fed by snow melt, rainfall, groundwater or overland flow, and wave wash. Many factors influence pool presence and size, including precipitation patterns, evaporation, wave direction and height, distance from shoreline, and spatial arrangements of pools. Similar factors synergistically regulate the water chemistry and character of aquatic communities of inland rock pools (Baron et al. 1998, Jocque et al. 2007, Vanschoenwinkel et al. 2007), and would be expected to do the same in coastal systems.

A common feature of marine coastal habitats worldwide is strong zonation among biotic communities (Little et al. 2009). Lake Superior shores also appear to have distinct community strata, both for macroinvertebrates and amphibians, based in part on summer and winter wave height and evaporation (Smith 1983, Egan et al., in press). Smith's (1983) study of pools on two small islands at Isle Royale National Park (IRNP), Michigan, found that tadpole use and diversity were regulated by wave disturbance in lower pools, odonate predation in forest edge pools, desiccation in shallow pools, and density-dependent competition and food in stable, mid-shore pools. Larval amphibians can influence invertebrate richness and abundance via predation, including zooplankton and Chironomidae (Diptera), along with modifying trophic webs via nutrient processing and excretion (Blaustein et al. 1996, Harding 1997). Egan and Ferrington (in review) found distinct communities of larval chironomids occurring in IRNP pools across vertical strata, including a large proportion of lotic species in lower pools that receive wave wash. As a result, biota at multiple trophic levels appear to be responding to patterns of disturbance, with wave wash a primary influence in pools near the lake, and desiccation important higher on the shore.

Among the many threats to coastal habitats, the two of primary importance at IRNP are shipping pollutants and climate change. A shipping lane from Sault Ste. Marie,

Michigan, to Thunder Bay, Ontario, has between 800-1200 ships passing through park waters annually between Blake's Point and Passage Island (Figure 2.1). These ships primarily haul agricultural products, coal, and road salt (Thunder Bay Port Authority 2013), along with substantial quantities of fuel. While IRNP, in conjunction with the U.S. Coast Guard, has a response strategy in place, little is known about the biota occurring in coastal habitats that are likely to be heavily impacted by a shipping accident. Pre-impact data are crucial for establishing targets for remediation following disturbances. In contrast, climate change is likely to bring more chronic and widespread changes to coastal habitats. Among the primary effects of climate change are warming air and water temperatures and alteration of precipitation patterns (IPCC 2007). Warmer temperatures and less precipitation are expected in the Lake Superior region (Kling et al. 2003), likely leading to reduced ice cover and a feedback of additional solar energy stored in the lake (Austin and Coleman 2007). Rock pool habitats and biota may be able to reveal associations between variation in precipitation and evaporation with ecological repercussions (Hulsmans et al. 2008).

The primary objectives of this chapter were to 1) characterize the spatial arrangement and basic physical properties of coastal rock pool habitats at IRNP and 2) determine distribution of pools as breeding habitat by amphibians. The location, shoreline stratum, size (maximum length, width, and depth), and amphibian presence in coastal rock pools were mapped to assess habitat availability and structure for aquatic organisms. Data from this project have contributed key reference information for understanding how coastal habitats in IRNP operate, assisting managers in identifying sensitive resources and enhancing coastal protection from potential threats.

## **Methods**

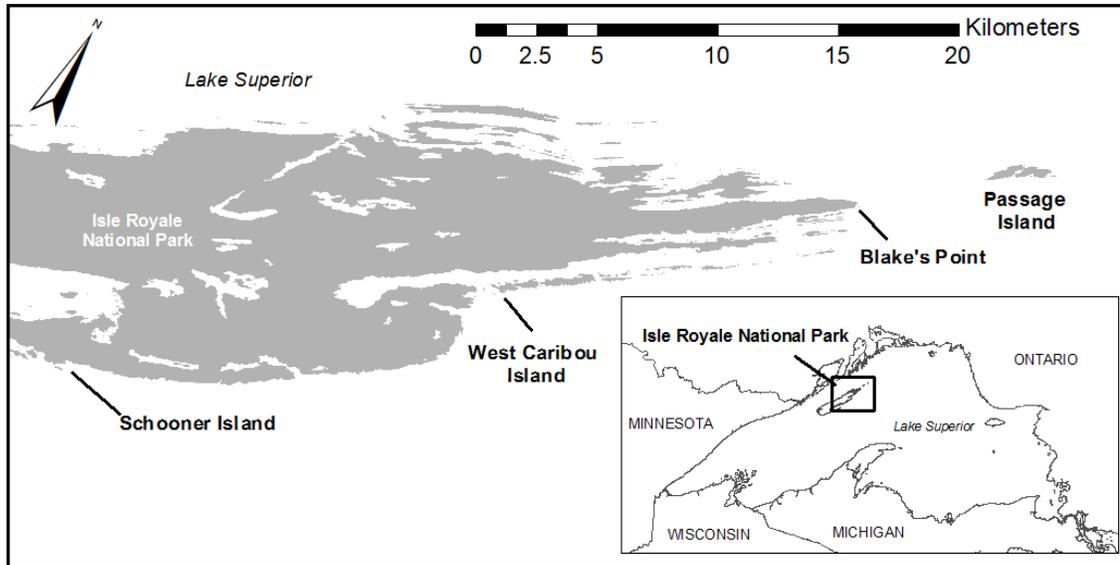
### ***Study Area***

Isle Royale National Park, Michigan, is an archipelago in Lake Superior that comprises one large island (544 km<sup>2</sup>) and hundreds of small islands (Figure 2.1). At its nearest point, the islands are about 19 km from the mainland. Mixed boreal and

hardwood forests dominate the land, with numerous long, narrow wetlands and lakes created from tilted bedrock strata. While the west end of the park has Copper Harbor Conglomerate bedrock, the entire study area at the east end occurs on layers of Portage Lake Volcanics made of numerous basaltic and andesitic lava flows (Thornberry-Ehrlich 2008). The volcanic bedrock, along with gradually sloping shores of the southern side of these islands, creates good conditions for pool formation and retention in bedrock depressions. Precipitation is greatest in summer and fall months with an average (1982-1996) of 8 cm/month (Stottlemeyer et al. 1998).

### ***Data Collection***

In 2011 and 2012, rock pools along exposed areas of the entire southeastern shoreline of IRNP were mapped, from Schooner Island to Blake's Point, and almost all offshore islands including Passage Island. Because of volcanic bedrock and configuration these areas in the park have the densest rock pool habitat. Mapping occurred from June to mid-August because rainfall was expected to keep pools detectable and larval amphibians were active and identifiable. Each pool was visited once, giving a snapshot of pool habitat availability and amphibian occupancy. Mapping did not occur for at least 24 hours following measureable rainfall or moderate-large wave action along the southeastern shoreline to avoid the risk of recording false-positives (i.e., depressions that drain too quickly to be stable aquatic habitat). Areas with dangerous access due to cliffs or slippery conditions (water or loose gravel) were not mapped, but these conditions were rare. Some pools were visible but not directly accessible and were estimated from a nearby location.



**Figure 2.1:** Mapping area, from Schooner Island to Passage Island, Isle Royale National Park, 2011-2012.

Trimble® Juno™ GPS units using TerraSync™ v5.21 software were used for collecting data, with reference datum set to NAD83 (Conus) CORS96. During creation of a new datapoint (i.e., individual pool), a minimum of 10 waypoints were logged while other data were entered. Waypoints were smoothed into a single point feature for increased accuracy. A data dictionary facilitated data entry, while acting as a quality control measure to limit data entry mistakes. The logical scheme for data entry was organized using an entity-relationship model (Chen 1976), with details listed in Table 2.1.

Three ecological zones were defined by proximity to the lake or forest, with the *splash zone* defined by a lack of flora and lichens around pools, the *lichen zone* pools surrounded by crustose or foliose lichens and occasionally with patches of moss or flora along the edges, and *forest transition* pools with an edge adjacent to the vegetation line above bare bedrock and often heavily lined with vegetation. Recharge sources were defined by ecological zones, with seeps indicated by thinly flowing surface water or stains revealing flow through bedrock cracks. Pool dimensions were measured with a

meter-stick or laser rangefinder, depending on size. Based on observations of hydroperiod during 2009-2010 studies, pool permanence was derived from depth data, with ephemeral pools having a maximum depth between 2 – 9.9 cm and permanent pools  $\geq 10$  cm. Distance from a pool to the shoreline used 10 m categories, with Nikon™ laser rangefinders to ensure accuracy. Slope was estimated using a clinometer in the rangefinder or on a Silva® pocket compass. Amphibians were the only biota included in data collection because they were of interest to IRNP managers, generally easy to detect, and identifiable to species in adult and larval stages. A larval amphibian field key was created based on Altig and Ireland (1984), Watermolen and Gilbertson (1996), and Parmelee et al. (2002).

**Table 2.1:** Summary of entities and attributes for coastal rock pool data entry, Isle Royale, 2010-2011.

Entity	Attributes
Ecological zone	Splash Lichen Forest transition
Recharge source	Rain Splash Seep Combination of the above
Pool dimensions (m)	Maximum length Maximum width Maximum depth
Distance to lake (m)	Length
Angle to lake	Slope in degrees
Amphibian taxa observed	Not detected [default] Adults Larvae Eggs Combination of the above
Notes or other observations	[default was empty field]
Date of visit	[auto-filled]
Time of visit	[auto-filled]
Observer initials	[each GPS unit set to default initials]

### *Analyses*

Post-processing of field data included differential correction using Pathfinder® Office software for additional accuracy and creation of .shp files. Daily files were combined into a single .shp file of the entire study area for basic analyses in ESRI®

ArcMap™ 10.1, including enumeration of pools by geographic area, zone, permanence, recharge source and amphibian presence. Surface area (SA) of pools was estimated by assuming surfaces were ellipses, using maximum length and width to calculate the estimated surface:  $SA = \pi ab$ , where  $a = \text{max length}/2$  and  $b = \text{max width}/2$ . During a visual inspection of data using multiple sort functions, 194 pools (0.3%) were removed from measurement analyses due to length, width, or depth data that were not credible. JMP® was used to calculate Spearman's Rho Correlation to assess the relationship between max depth and surface area of pools, including KSL goodness of fit tests to ensure data were normally distributed, and a Tukey-Kramer HSD test to determine means differences.

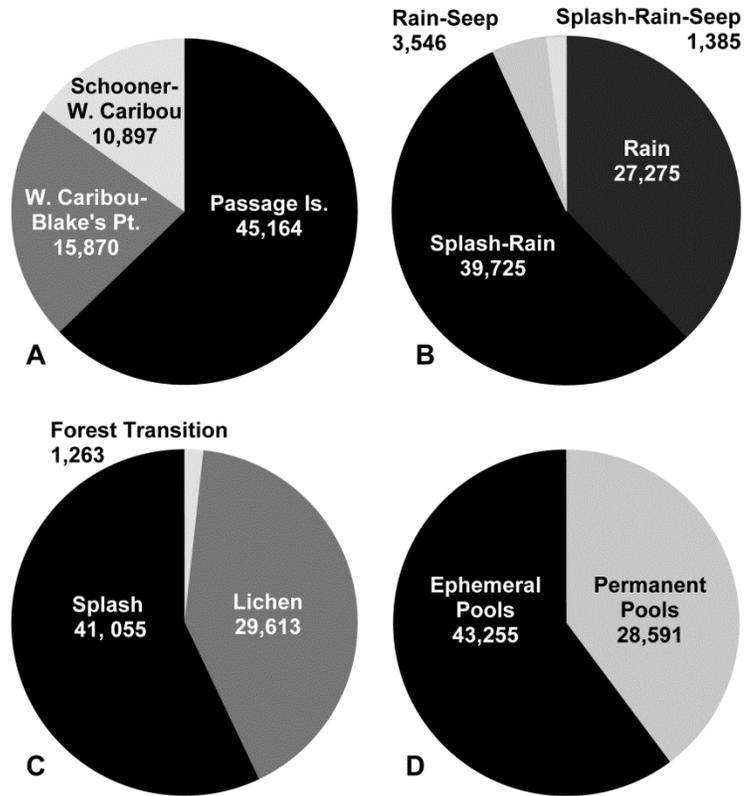
## **Results**

### ***General Pool Arrangement and Mapping Effort***

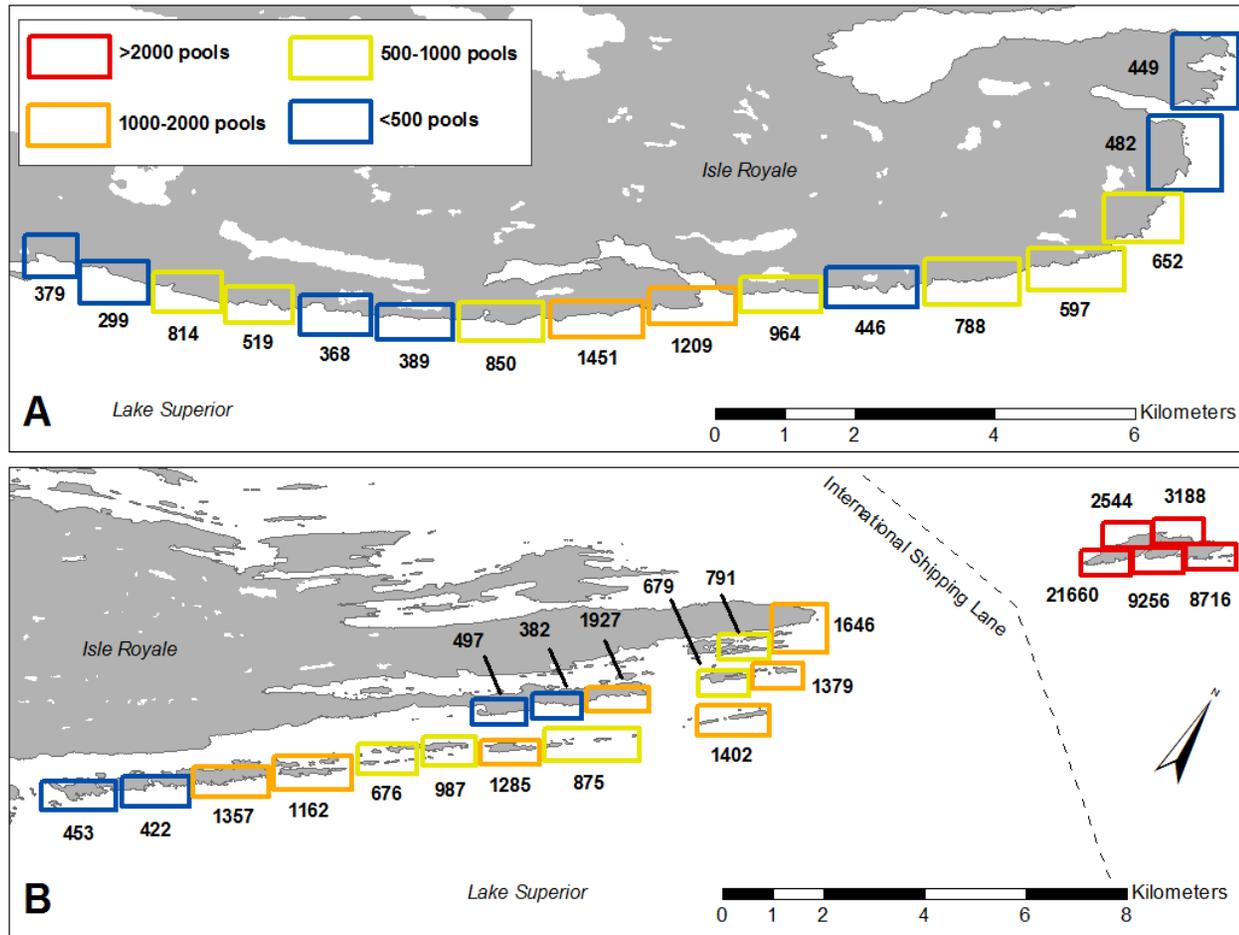
In 2011 and 2012, 48 km (30 mi) of shore were comprehensively mapped, yielding 71,931 pools. Almost 63% (45,164) of pools occurred on Passage Island (Figure 2.2 A). From Blake's Point to West Caribou Island, an area comprising barrier islands and narrow peninsulas, 15,870 pools were mapped, and 10,897 pools were between West Caribou Island and Schooner Island along the south shoreline of Isle Royale. The majority of pools were in the splash zone, recharged with wave splash, and ephemeral. Forest transition pools were rare, and while seep-influenced pools were not common—almost 5,000 fit this description (Figure 2.2 B-D). Numbers for permanent/ephemeral pools in Figure 2.2 D do not add to 71,931 because some pools were removed when outliers lacked credibility (e.g., pool depth of 40 m, a mistake, or 0 m, a forgotten entry). Pool densities in approximately 1 km increments revealed patchy densities on a landscape scale (Figure 2.3).

Following differential correction for each file, the majority of pools (approximately 50-60% per file) were accurate to 1-2 m of the true pool location, with 40-50% between 2-5 m, and few outside these ranges. On average, 790 pools/person/day were mapped, with a range of 35-3,908. Daily distances ranged between 0.07 and 1.75

km per person. It took 61 days to map the entire study area, with Passage Island, the location with the densest collection of pools, taking three people eleven days to cover the roughly 7.29 km of shoreline.



**Figure 2.2:** Characterizations and numbers of pool types, including all pools mapped between Schooner Island and Passage Island, Isle Royale National Park, 2011-2012; density along selected areas (A), recharge sources (B), zone (C), and permanence (D).



**Figure 2.3:** Pool densities along Isle Royale shores, representing the western part of the study area from West Caribou Island to Schooner Island (A) and the eastern part of the study area from West Caribou Island to Passage Island (B), 2010-2011. Boxes represent approximately 1 km of mapped shoreline, not including shoreline irregularities and gaps between islands, and include estimates of pool numbers from GIS software polygons.

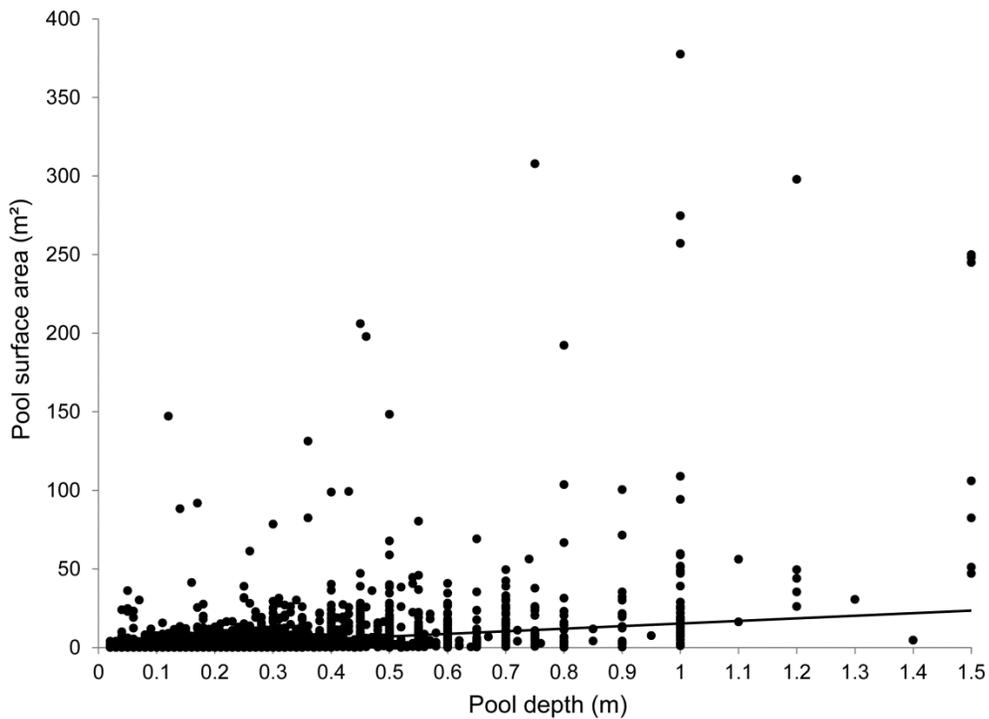
### ***Physical Pool Characteristics***

Maximum pool depth was approximately 1.5 m, although few pools were this deep; 99% of pools were less than 0.5 m, and mean depth was 0.11 m (SE  $\pm$  0.0004). Maximum surface area was 378 m<sup>2</sup>, though 99% of pools were less than 16 m<sup>2</sup>, and mean area was 0.6 m<sup>2</sup> (SE  $\pm$  0.02). Spearman's Rho correlation revealed a significant correlation between max depth and surface area of all pools ( $r = 0.34$ ,  $P < 0.0001$ ; Figure 2.4).

Tukey-Kramer HSD tests showed significant differences in pool sizes across zones (Table 2.2). Forest transition pools were deeper and larger (means  $0.19 \pm 0.003$  m and  $2.82 \pm 0.14$  m<sup>2</sup>, respectively) than the other two zones, and lichen pools deeper and larger (means are  $0.13 \pm 0.0006$  m and  $0.70 \pm 0.03$  m<sup>2</sup>) than splash pools ( $0.09 \pm 0.0005$  m and  $0.49 \pm 0.03$  m<sup>2</sup>). Slope to the lake was also significantly different across zones, with the forest transition zone having a mean 33° slope ( $\pm 0.43$ ), lichen zone having a mean 29° slope ( $\pm 0.09$ ), and splash zone with a mean 15° slope ( $\pm 0.08$ ). Large waves can reach well into the lichen zone, but these conditions are not typical during months with biological activity. Seep-influenced pools typically spanned both zones at the same location.

**Table 2.2:** Results from Tukey-Kramer HSD tests for means differences across zones.

	Zone	Mean $\pm$ S.E.	p-value
Depth	Forest Transition	$0.19 \pm 0.003$ m	<0.0001
	Lichen	$0.13 \pm 0.0006$ m	<0.0001
	Splash	$0.09 \pm 0.0005$ m	<0.0001
Surface Area	Forest Transition	$2.82 \pm 0.14$ m <sup>2</sup>	<0.0001
	Lichen	$0.70 \pm 0.03$ m <sup>2</sup>	<0.0001
	Splash	$0.49 \pm 0.03$ m <sup>2</sup>	<0.0001
Slope	Forest Transition	33° slope $\pm 0.43^\circ$	<0.0001
	Lichen	29° slope $\pm 0.09^\circ$	<0.0001
	Splash	15° slope $\pm 0.08^\circ$	<0.0001



**Figure 2.4:** Relationship between depth and surface area, including linear trend line (correlation significant at  $P < 0.0001$ ), for coastal rock pools ( $n = 71,791$ ) at Isle Royale National Park, Michigan.

### *Amphibian Occupancy*

Amphibian incidence was low overall, with the most common species, chorus frog (*Pseudacris triseriata*), occupying only 3% of pools ( $n = 2,114$ , Table 2.3). The next most common was blue-spotted salamander (*Ambystoma laterale*), occupying 1% of pools ( $n = 945$ ). Spring peeper (*Pseudacris crucifer*) occurred in less than 1% of pools ( $n = 75$ ). Green frogs (*Lithobates clamitans*), wood frogs (*Lithobates sylvatica*), Eastern newts (*Notophthalmus viridescens*), and American toads (*Anaxyrus americanus*) were only rarely encountered and typically detected as adults.

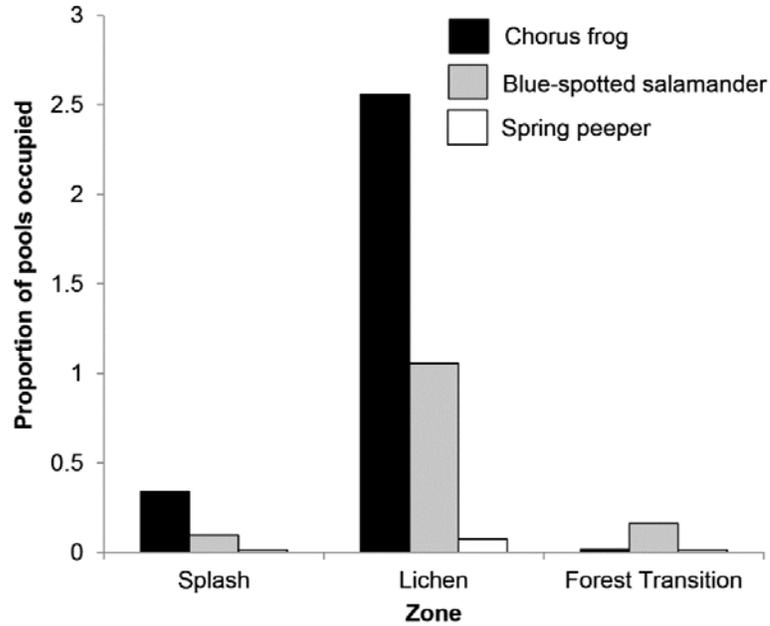
The three most common amphibian species were typically present as larvae and stratified by zone, all favoring the lichen zone (Figure 2.5). In addition, pool occupancy declined strongly for chorus frogs as distance to shoreline increased, but declines were more moderate for the other two species (Figure 2.6). Chi-square tests for zonal

occupancy and distance from shoreline were highly significant for all three species in both tests, revealing a statistical departure from homogeneity across vertical shoreline strata (Table 2.4). There was a strong decline in number of pools as size class increases (Figure 2.7, Table 2.5). Overlaying proportional amphibian occupancy with size class, chorus frog distribution appeared unimodal with a peak at 0.7 m depth and blue-spotted salamanders appeared unimodal with a peak at 0.5 m depth; spring peeper distribution was highest at 0.7 and  $\geq 1$  m classes, with modality difficult to ascertain.

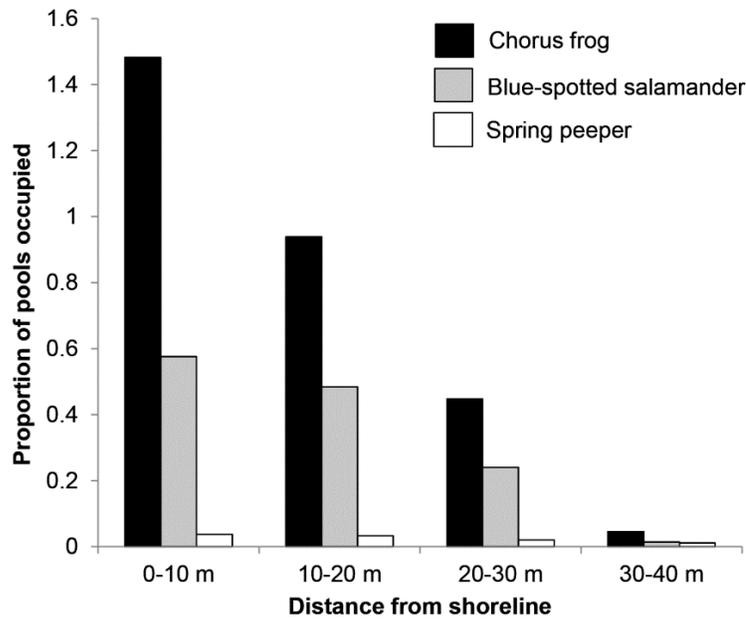
Ranges of the three common species covered the entire study area (Figure 2.8). Chorus frogs had two areas where pool occupancy by larvae was frequent, Passage Island and the small islands south of Blake’s Point, while other populations occurred in disjunct localities west of Davidson Island. Blue-spotted salamander larvae occurred regularly across the entire area, while spring peepers were only irregularly detected.

**Table 2.3:** Amphibian occupancy and proportion of pools occupied at Isle Royale National Park, 2011-2012.

Species	Pools with larvae or eggs	Pools with only adults	Total	Pools occupied
Chorus frog	2098	16	2114	3%
Blue-spotted salamander	945	0	945	1%
Spring peeper	74	1	75	<1%
Green frog	2	22	24	<1%
Wood frog	1	12	13	<1%
Eastern newt	6	7	13	<1%
American toad	2	6	8	<1%



**Figure 2.5:** Amphibian occupancy of total pools by zone, Isle Royale National Park, Michigan, 2011-2012. For each species,  $\chi^2$  differences across zones were a significant departure from homogeneity.



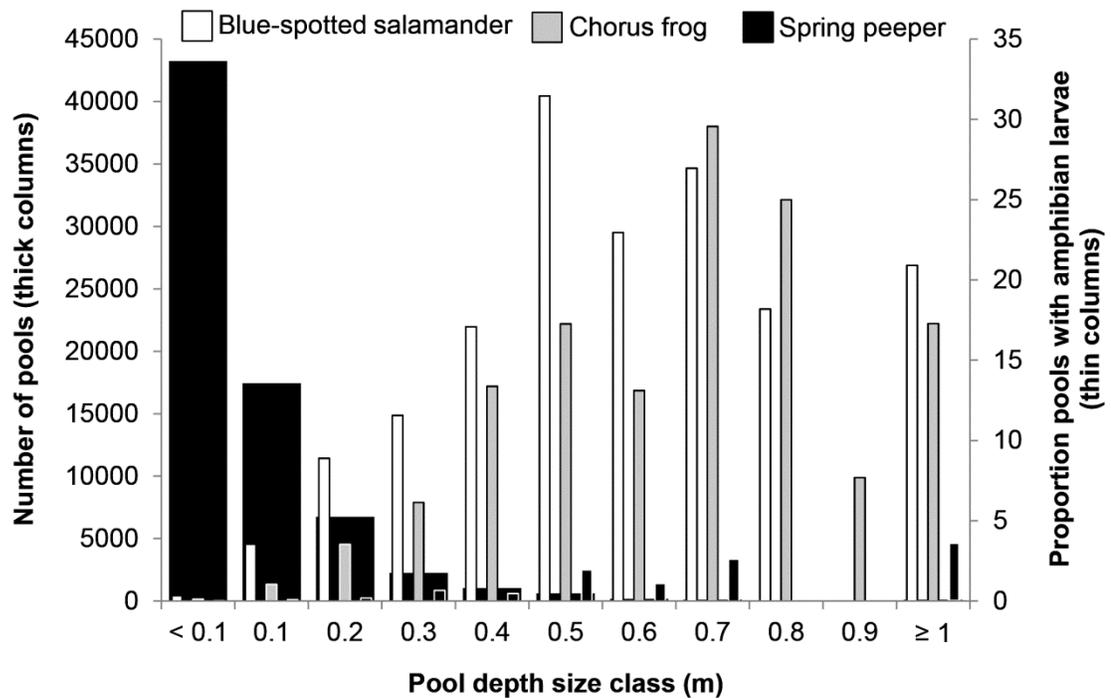
**Figure 2.6:** Amphibian occupancy of total pools by distance from shoreline, Isle Royale National Park, Michigan, 2011-2012. For each species,  $\chi^2$  differences across distance categories were a significant departure from homogeneity.

**Table 2.4:** Results from  $\chi^2$  tests across zones and distances from shoreline.

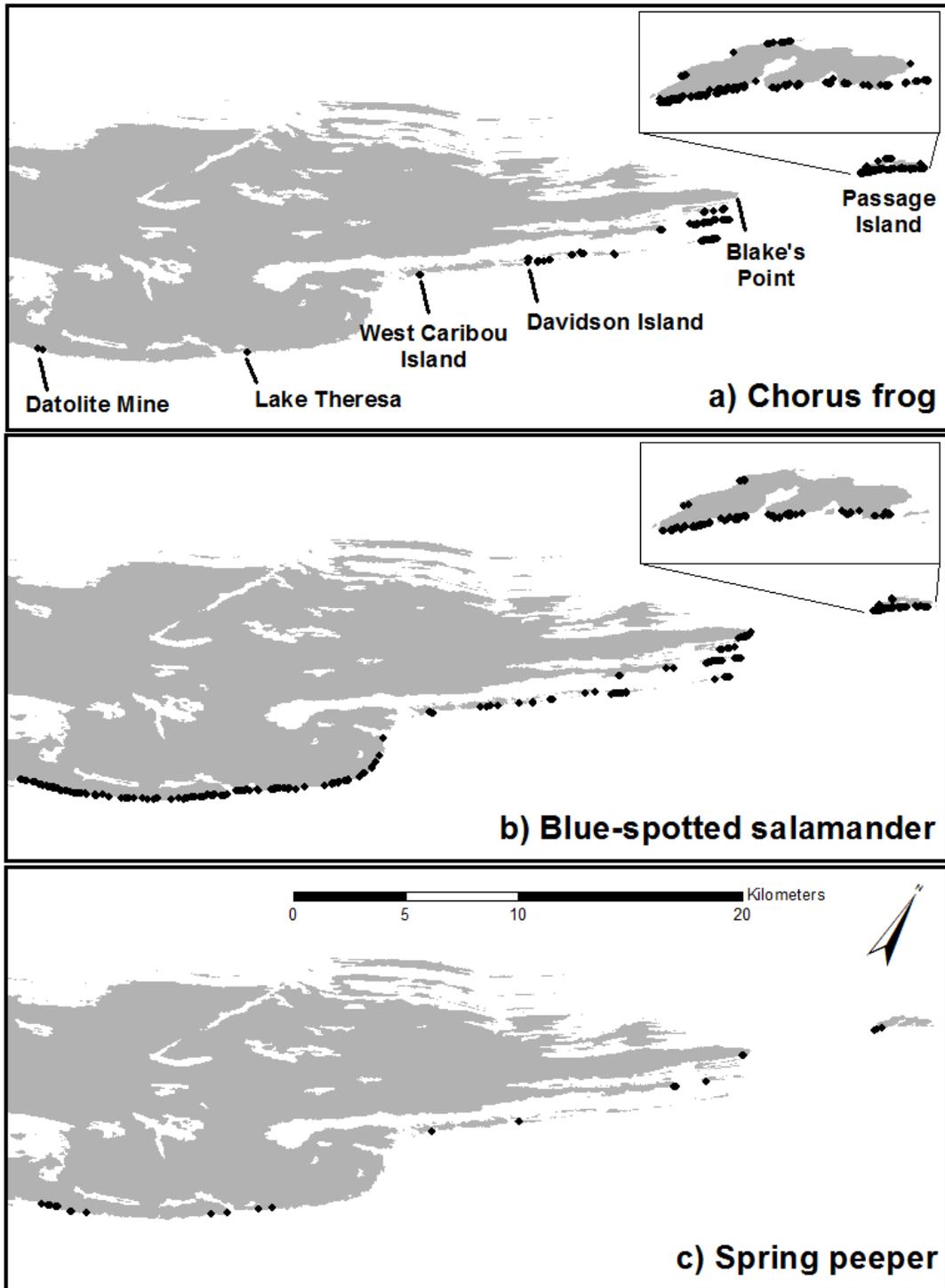
	Zonal occupancy		$\chi^2$ result	d.f.	p-value
	Observed	Expected			
<b>Chorus frog</b>					
Forest Transition	12	699			
Lichen	1840	699			
Splash	244	699	2834	2	<0.0001
<b>Blue-spotted salamander</b>					
Forest Transition	117	315			
Lichen	759	315			
Splash	69	315	942	2	<0.0001
<b>Spring peeper</b>					
Forest Transition	10	25			
Lichen	54	25			
Splash	10	25	52	2	<0.0001
	Distance from shore		$\chi^2$ result	d.f.	p-value
	Observed	Expected			
<b>Chorus frog</b>					
0-10 m	1066	524			
10-20 m	675	524			
20-30 m	322	524			
30-40 m	33	524	1142	3	<0.0001
<b>Blue-spotted salamander</b>					
0-10 m	414	236			
10-20 m	348	236			
20-30 m	173	236			
30-40 m	10	236	420	3	<0.0001
<b>Spring peeper</b>					
0-10 m	27	19			
10-20 m	24	19			
20-30 m	15	19			
30-40 m	8	19	12	3	0.0039

**Table 2.5:** Results from  $\chi^2$  tests across pool depth size classes.

	Depth class occupancy		$\chi^2$ result	d.f.	p-value
	Observed	Expected			
<b>Chorus frog</b>					
< 0.1 m	146	191			
0.1 m	620	191			
0.2 m	600	191			
0.3 m	260	191			
0.4 m	180	191			
0.5 m	195	191			
0.6 m	42	191			
0.7 m	31	191			
0.8 m	8	191			
0.9 m	0	191			
$\geq 1$ m	23	191	2640	10	<0.0001
<b>Blue-spotted salamander</b>					
< 0.1 m	49	86			
0.1 m	182	86			
0.2 m	238	86			
0.3 m	138	86			
0.4 m	141	86			
0.5 m	107	86			
0.6 m	24	86			
0.7 m	34	86			
0.8 m	11	86			
0.9 m	2	86			
$\geq 1$ m	19	86	743	10	<0.0001
<b>Spring peeper</b>					
< 0.1 m	7	7			
0.1 m	14	7			
0.2 m	13	7			
0.3 m	15	7			
0.4 m	5	7			
0.5 m	12	7			
0.6 m	2	7			
0.7 m	3	7			
0.8 m	0	7			
0.9 m	0	7			
$\geq 1$ m	4	7	51.14	10	<0.0001



**Figure 2.7:** Pool count and amphibian occurrence within pool depth size class, Isle Royale National Park, 2011-2012. Classes include all pools within a 0.1 m range (e.g., class 0.4 includes all pools between 0.4 and 0.49 m deep), except the largest class which includes all pools  $\geq 1$  m. Proportion is from pools in respective size classes. For each species,  $\chi^2$  differences across depth classes were a significant departure from homogeneity.



**Figure 2.8:** Pools with larval presence for three primary amphibian occupants of coastal rock pools at Isle Royale, Michigan, 2011-2012.

## **Discussion**

### ***General Pool Arrangement and Mapping Effort***

Open bedrock shores at IRNP generally exist only when sufficient disturbance from Lake Superior removes vegetation and organic material. In protected locations where wave action is limited, there are few or no pools and vegetation is in close proximity to the waterline. Due to bedrock type and orientation, few shoreline areas in this study could be considered depauperate of rock pool habitat. Viewed from the lake, few locations were identifiable as having dense numbers of pools, although high-quality aerial imagery was often, but not always, good at indicating pool densities.

Pool density along broad stretches of shoreline varied considerably. The 71,931 pools were far more than expected, and an astounding habitat density is revealed for some localities. The dominance of Passage Island was surprising, with almost 63% of the habitat occurring on this small, 3 km (1.9 mi) long island. The second densest collection of pools occurred on the small islands south of Blake's Point. The lowest density of pools appears to be the area immediately southwest of West Caribou Island, where a north-south axis shelters the shore from the dominantly western winds and waves, and only 450 pools existed along approximately 3 km of shore, compared to 45,164 on Passage Island.

The number of pools/person/day and distance mapped/day varied widely with observer experience, weather, terrain, pool characteristics, and number of pools available. Our results show an average of 790 pools can be mapped by one observer/day. When pools were extremely dense, thousands were mapped in one day because little walking between pools was needed, while only a few hundred were mapped if terrain was challenging and pools were sparse.

### ***Physical Pool Characteristics***

The majority of pools were very shallow with a small surface area. We were unable to track hydroperiod changes over time, but Smith (1983), in a study on two small islands south of Blake's Point, reported dramatic size fluctuation in a single season with

regular drying events. However, during biotic studies, I found few complete drying events in pools over 0.1 m deep (Egan, unpublished data). Mean pool surface area (0.6 m<sup>2</sup>) was comparable to Smith (0.68 m<sup>2</sup>, 1983), with both datasets highly skewed toward smaller pools, suggesting that general pool structure is similar across the study area and that details from Smith's study could scale up well to other areas at IRNP.

Zonation differences in amphibian occupancy were strong, with both Lake Superior and precipitation patterns undoubtedly having important influences on pools. I expected that a majority of pools would be in the splash zone due to regular recharge by wave wash instead of only irregular rainfall in lichen zone and forest transition pools. This influence was also shown in aquatic invertebrate community and water chemistry differences between zones (Egan et al., in press). The transition from smaller pools on low gradients near the lakeshore, to larger pools on steeper gradients near the forest edge, is sensible considering regular recharge and erosion in the splash zone and increased desiccation of pools fed only by precipitation in the lichen zone. Most pools were observed to have a very small watershed, although this was not measured. The significant relationship between surface area and depth should allow simplification of studies in this habitat, such as measuring only max depth. Slope may have contributed to zonal patterns by limiting formation of pools on steeper slopes. Although means were significantly different, the spread of data shows that pools of all sizes were present in all three zones.

Pools directly influenced by upland or groundwater flow were relatively uncommon (n = 4,931, 7%), and few pools were observed with leaves or wood in the bottom. However, subtle nutrient additions (i.e., phosphorous, nitrogen, and carbon) through bedrock cracks or overland flow during rainfall may be more important than can be detected visually via tannins or allochthonous material (Egan et al., in press).

### ***Amphibian Occupancy***

While all seven amphibian species were detected in larval stages, it was likely that only chorus frogs and blue-spotted salamanders actively sought coastal pools for

breeding, while spring peepers were irregularly present. Coastal pools did not appear important for any other amphibian species at IRNP.

A majority of pools were ephemeral with limited amphibian occupancy. Amphibians were either not typically laying eggs in these pools, eggs were laid but larvae were not surviving, or larvae were present after being washed in from higher pools. Although pools in the range of 0.5-0.7 m deep appeared to be preferred by amphibians, this may have been due to fewer deep pools available. The discrepancy between zonal occupancy differences, with all amphibians favoring the lichen zone, and the steady decline of occupancy as distance from shoreline increases, can be explained by the distance measurements of 10 m increments. Generally, the transition from splash zone to lichen zone occurs within this distance, so that 10 m was too broad to adequately measure preferred pool distances.

Chorus frogs represent an iconic management species at IRNP for two reasons. First, they appear to breed exclusively in coastal rock pools, a novel condition for a species that typically occurs in marshes and meadows, although they are also known to lay eggs in temporary habitats (Harding 1997). Second, long-term studies at IRNP have contributed to important ecological understanding of their populations in the Blake's Point area (Smith 1983, Smith and Van Buskirk 1995). Our study reveals that Passage Island is a major component of the IRNP chorus frog metapopulation, with only steep cliffs along the north shoreline restricting dense habitat use. In addition, intriguing disjuncts occurred in populations along the south shore of the park, with gaps of over 9 km between populations. There were chorus frog breeding populations observed in coastal localities west of Blake's Point, but these were not mapped and the extent of the north shore range remains unknown.

The apparent absence of chorus frogs from inland habitats suggests that this species disperses along the shoreline or in Lake Superior. However, following storms that washed tadpoles out of lower pools, Smith (1983) found no tadpoles in the lake and

assumed there was essentially a 100% mortality rate during these events. In contrast to dispersal events leading to the observed geographic pockets of pool occupancy, a broad coastal presence may have occurred in the past, as observed currently with salamanders, with only a handful of relict chorus frog populations now occurring along the south shore of IRNP. Compared to other western Great Lakes populations, genetic analyses could help determine if there is genetic isolation in IRNP populations. Geographic isolation could be creating genetically distinct populations, even across small spatial scales due to drift and founder effects, as found in deer mouse (*Peromyscus maniculatus*) at IRNP (Vucetich et al. 2001).

Smith and Van Buskirk (1995) and Smith (1983) found a shoreline gradient where spring peepers occupied higher pools and chorus frogs replaced them mid-shore. They proposed this was generally due to *Aeshna* predation and disturbance (waves and desiccation), with no obvious competition effects. Our results support a biologically stratified shoreline, but all three primary coastal species favored the lichen zone, generally within 30 m of shore, and often co-existed in pools, with no obvious replacement zonally. Chorus frogs and salamanders co-occupied 260 pools, chorus frogs and spring peepers co-occupied 8 pools, and salamander and peepers co-occupied 22 pools. Smith and Van Buskirk (1995) noted that it was unclear if spring peepers attained metamorphosis in mid-level pools. IRNP frog surveys showed spring peepers to be abundant in stable pond and marsh habitats, but rare in vernal pools (Egan, unpublished data). Based on irregular habitat occupancy, it seems unlikely that coastal pools or temporary habitats are key habitats for spring peepers at IRNP.

Several years of woodland surveys at IRNP for blue-spotted salamanders, the only salamander species in the park, detected few individuals, although park records suggest an island-wide range (M. Romanski, unpublished data), and habitat use is often associated with woodland pools (Harding 1997). Van Buskirk and Smith (1991) found density-dependent regulation of larvae in coastal pools, and predatory salamander larvae have been shown to have important trophic impacts on invertebrate populations such as

zooplankton and Chironomidae (Blaustein et al. 1996). The current results show coastal pools are commonly utilized by breeding salamanders, suggesting that coastal populations may be more useful in monitoring the species than forest surveys.

Lack of occupation of forest transition pools must be taken with caution because of the limited number of pools in this zone compared to the others. A high occupancy of amphibians within 10 m of the shoreline suggests that summer wave wash large enough to remove tadpoles does not typically reach very high on the shore. Presence of any species in the splash zone is ecologically irrelevant, as no individuals are likely to survive wave disturbance (Smith 1983). Smith (1983) observed that while chorus frogs lay eggs in many pool types few survive in shallow pools, but those that do are usually in predator-free pools.

### *Threats to Coastal Systems*

There are two principal threats to coastal systems at IRNP: pollution from shipping accidents and shifting precipitation patterns due to climate change. High pool density and amphibian occupancy adjacent to a busy shipping lane raises serious concern for spill impacts. Based on proximity of ships to land and reefs, the Passage Island-Blake's Point areas are the most likely part of IRNP to have a grounding occur. The most likely ecologically harmful shipping products are outbound potassium chloride and urea, both used as fertilizers; oil from fuel tanks; or inbound road salt (Thunder Bay Port Authority 2013).

Chorus frog response to potential shipping pollution and climate change should be a key component for amphibian management at IRNP. Habitat impacts are common causes of amphibian extirpations, although local patterns of extinction and recolonization are typical in amphibian metapopulations (Marsh and Trenham 2001). Oil-products are hazardous to amphibians from ingestion and dermal uptake (Brandt et al. 2002). And while removal or degradation of oil products may be reduced to minimal levels within a few years (Brandt et al. 2002), highly localized and apparently static populations such as

IRNP chorus frogs may not be able to recover. Impacts from road salt or fertilizers (via a breached ship hull) would probably have a very limited spatial and temporal effect, yet onshore movement from large waves could have a strong local effect by reducing amphibian survival or causing malformations (Karraker and Ruthing 2009).

Expected and documented changes in weather patterns are likely to impact coastal pool habitats. Reduced winter ice cover (Austin and Colman 2007) may increase shipping traffic with an increased risk of grounding, while greater wave height (Austin and Colman 2007) could increase the amount of shoreline fouled with pollutants in the event of a spill. Increased wave height would also change the dynamics of wave disturbance and recharge. Also, reduced summer rainfall during biologically active summer months would result in more pool desiccation events and possibly greater pool temperatures from solar radiation, impacting larval amphibians and other biota.

Climatic impacts to biota in pools are not easy to predict. Chorus frogs are known to successfully utilize temporary pools where drying can be a threat to tadpoles, but avoidance of predators is apparently worth the risk (Skelly 1995). Thermal stress due to reduced cloud cover and recharge may not be problematic for chorus frogs, which have been shown to have plasticity in thermal tolerances, surviving temperatures up to 38.8°C, and would presumably be more susceptible to more rapid desiccation (Hoppe 1978). In addition, numerous studies suggest that chorus frogs are relatively tolerant of variable chemical conditions, such as changes in pH, ammonium, and dissolved oxygen as water levels change (Gerlanc and Kaufman 2005). Climate patterns of reduced rainfall may be positive for the chorus frog population overall, which have been shown to respond positively to lower predator densities during drought, provided there was still connectivity to breeding habitat (Werner et al. 2009).

## **Conclusions**

Coastal rock pools were abundant and widespread at the east end of IRNP, particularly on Passage Island. The Minnesota shoreline also has high densities of pool

habitat in many locations, including occupancy of amphibians and macroinvertebrates similar to IRNP (A. Egan, unpublished data), and I expect that other volcanic bedrock-dominated shorelines in the Great Lakes have much higher abundance of pool habitats than is generally recognized.

Most pools were relatively shallow with a small surface area. In addition, a gradient occurred with smaller pools on low slopes near the lake and larger pools on steeper slopes occurred near the forest edge. Mid-shore preference for amphibian occupancy across the entire study area was similar to results previously found by Smith (1983), suggesting that patterns and mechanisms influencing amphibians in IRNP coastal pools are consistent across spatial scales. Chorus frogs and blue-spotted salamanders were the most common and widespread species occupying pools, with chorus frogs having a patchy geographic range and salamanders regularly distributed along shores.

High levels of chorus frog tadpole inhabitation in Passage Island pools, along with the proximity to shipping traffic, makes this location among the most critical areas of IRNP shoreline to protect from shipping pollutants or habitat degradation. Isolated populations may reflect challenges to dispersal and colonization, even of nearby habitats (Marsh and Trenham 2001), which would bode ill for chorus frogs following local extirpation. I believe that additional work on chorus frogs at IRNP to monitor broader populations and habitat use, better understand diversity, and investigate mechanisms of dispersal and the reasons behind range limitations will help managers understand this unique population.

## **CHAPTER III**

# **CHIRONOMIDAE (DIPTERA) OCCURRENCE AND EMERGENCE IN FRESHWATER COASTAL ROCK POOLS OF LAKE SUPERIOR**

### **Summary**

Chironomidae communities were sampled in freshwater coastal rock pools at Isle Royale National Park, Michigan, an archipelago in northwestern Lake Superior. The large surface area and thermal mass of the lake strongly moderates coastal climate and creates important disturbance conditions via wave action. Pools occupy depressions in volcanic bedrock and were differentiated into vertical zones based on predicted influence of recharge sources from rainfall in the upper zone and wave splash in the lower zone. Community richness, abundances, and structure were assessed, along with stratification by zone, season, and island geography. The chironomid community was more species rich than expected, consisting of a few very abundant species and many rare ones. Zonation differences were clear, but seasonal variation in species emergence was not, and distinctions across geographic area appeared to occur in overlapping but ecologically coherent clusters. Except for the most abundant species, which were clearly habitat generalists, an interacting mosaic of sub-communities occurs across the study area. Results lay the groundwork for understanding coastal aquatic communities of Lake Superior and will assist land managers in responding to key risks such as pollution from shipping spills.

### **Introduction**

Coastal shorelines are at the transition of disparate systems, aquatic and terrestrial, and are often subjected to challenging physical stressors such as wave action and desiccation. Along the shorelines of Lake Superior in the Great Lakes, there are wide areas of volcanic bedrock exposed to these demanding physical conditions that create

freshwater pool habitats. Marine tidal pools have been well-studied worldwide and have led to understanding key principles in ecological theory (e.g. Paine 1966), while freshwater pools have very different communities and have received much less attention. However, recent studies of inland pools on rock outcrops have begun to bridge this gap in knowledge (Baron et al. 1998, Jocque et al. 2010, Vanshoenwinkel et al. 2009). On the shores of Lake Superior, Isle Royale National Park (IRNP), Michigan, offers a well-defined setting similar to, yet ecologically between, the typically studied rock pool habitats along marine coasts and inland outcrops.

Defining characteristics of rock pools include recharge source, hydroperiod, and disturbance (Wiggins et al. 1980, Jocque et al. 2010). Recharge sources along Lake Superior shores consist of precipitation, overland flow and groundwater seepage through bedrock cracks, and wave wash, with variable influences on susceptibility to drying (Figure 3.1). Similar to marine shores, lower pools are impacted regularly by ice scour and wave action, while higher pools more often experience disturbances such as drying and extreme temperature fluctuations (Little et al. 2009). The importance of vertical position above the shoreline, with variable disturbance from summer and winter wave height, has been shown in microhabitat distribution of tadpoles and dragonfly larvae at IRNP (Smith and Van Buskirk 1995). In addition, coastal areas of Lake Superior have a moderated climate due to the lake's large surface area and thermal mass, with colder summer temperatures allowing rare, cold-tolerant disjunct taxa to exist in near-shore habitats (Judziewicz 2004).

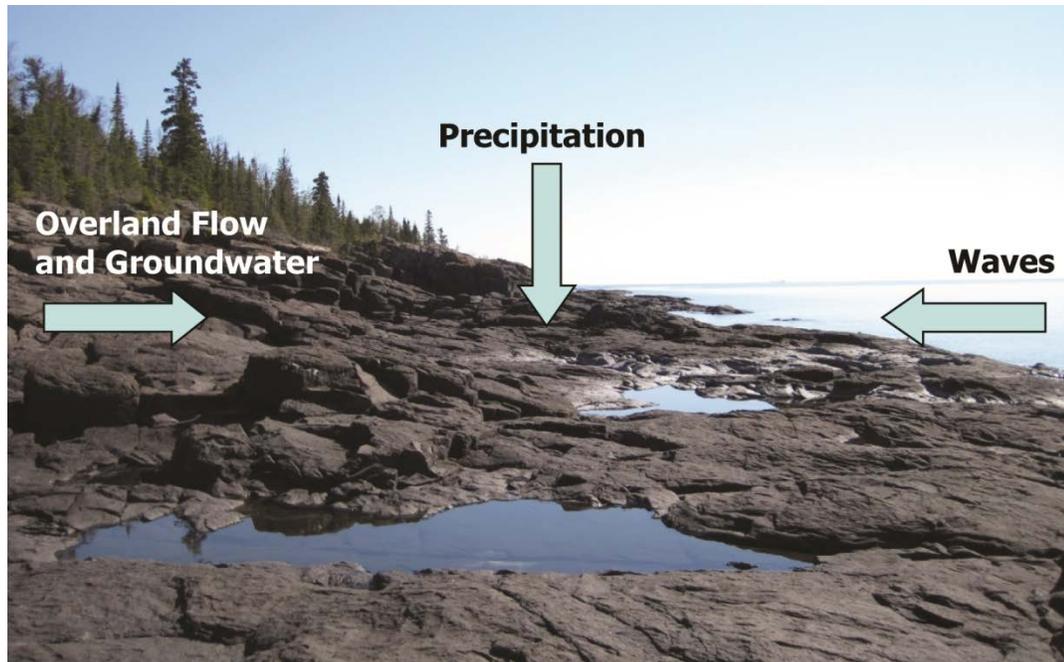
Invertebrates are often understudied components of ecological systems. At IRNP, studies on *Aeshna juncea* (Odonata), a larval predator in rock pools, are the only extensive investigations (Van Buskirk 1993). Chironomidae (Diptera) communities of rock pool habitats are rarely studied and essentially unknown along coastlines of the Great Lakes. Typically, chironomids are abundant and diverse in aquatic habitats globally, yet only 38 species have recently been identified from rock pool habitats worldwide (Jocque et al. 2010). In addition to characteristics listed above, other

fundamental influences expected to regulate Chironomidae in pools include habitat and trophic structure (Srivastava 2006), prey selectivity by chironomid predators (Dillon 1985), availability of nutrients (Brooks et al. 2001), and chemical conditions such as salinity and dissolved oxygen (Baron et al. 1998).

Two fundamental threats exist for coastal habitats in Lake Superior: pollutants from shipping spills and climate change. As a consequence of devastating accidents internationally, coastal land managers have become aware of variable ecosystem responses to spills and the importance of baseline data on coastal resources (Diez et al. 2009). Multiple shipping lanes cross the lake, including one passing through Isle Royale waters. IRNP has strategies in place to respond to shipping accidents, which may involve substantial volumes of fuel or oil. These strategies stress that critical habitats be identified and strategically protected based on known criteria, yet response plans typically have no data on invertebrate populations and consider rocky shores low priority (Schaefer et al. 2004). Rosenberg and Wiens (1976) showed that chironomid responses to oil products may not cause a collapse of the community, but highly variable responses are likely depending on species. Likewise, rock pool communities have a potentially valuable role as sentinels in determining regional effects of global climate change, linking variations in precipitation and evaporation with ecological repercussions (Hulsmans et al. 2008). Because of its ability to store solar energy, Lake Superior surface water temperatures have been increasing at a faster rate than regional air temperatures (Austin and Coleman 2007). Near-shore warming has the potential to influence extirpation of cold stenothermic species and greater domination by invasive species preferring moderate temperatures. Warmer surface temperatures, creating increased turbulence and wave heights, may increase recharge and disturbance to lower pools.

I characterize basic ecological conditions of Chironomidae in coastal pool habitats at IRNP, including 1) estimates of community richness, abundance and structure; 2) whether communities stratify zonally based on hydrogeographic grouping, as occurs with

invertebrates on marine rocky shores; 3) the extent of geographic clustering of communities; and 4) seasonal variation in emergences.



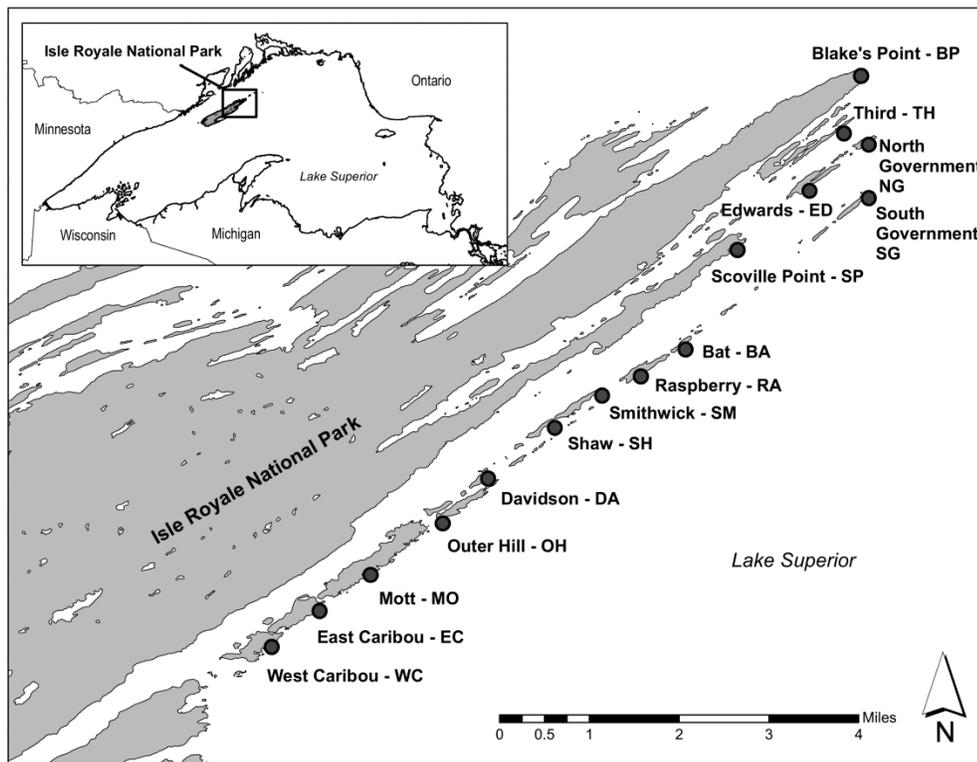
**Figure 3.1:** General setting and recharge sources for coastal rock pools at Isle Royale National Park; Raspberry Island study site shown.

## Methods

### *Study site*

Isle Royale National Park, Michigan, is located in the northwest corner of Lake Superior, the largest and deepest of the Great Lakes (Figure 3.2). Isle Royale is an archipelago of one large (544 km<sup>2</sup>/210 mi<sup>2</sup>) island surrounded by hundreds of small islands, with the nearest point to the mainland approximately 19 km (12 mi) distant. Study sites were located on exposed volcanic bedrock, made of numerous basaltic and andesitic lava flows, along the northeast shores of the archipelago (Thornberry-Ehrlich 2008). This area of the park has shorelines that are generally composed of lower-gradient slopes, which creates good conditions for pool formation. The western half of the park has conglomerate bedrock and the north shore generally has steep cliff slopes, both limiting pool formation. While some pools are part of a series fed by upland flow from

forest habitats, the tilted bedrock of the barrier islands and peninsulas at the east end of Isle Royale generally gives pools a strongly restricted watershed. Fifteen sites were chosen based on regular spacing, so sites could not be adjacent to each other yet on different islands, in the island chain from West Caribou Island to Blake’s Point, a span of about 18 km, with one site per island (except Isle Royale, which included sites on two points).



**Figure 3.2:** Isle Royale National Park and 2009 study sites, including regional context. All sites are on separate islands except Scoville Point and Blake’s Point.

***Data collection***

Five sample rounds occurred approximately monthly between 24 April and 13 October, 2009, yielding a total of 142 samples. This timeframe spanned the entire period the park was accessible. In each round, two samples were collected from each site, with each sample representing a zone termed splash or lichen. The “splash zone”, where wave wash from Lake Superior was expected to have a dominant influence, was identified by

lack of lichens or only black-grey crustose lichens. The “lichen zone” was above the area of regular wave splash and generally had abundant, colorful, foliose or crustose lichens covering the bedrock. An exception was for Outer Hill and East Caribou Islands where pools could not be adequately distinguished into zones following the first sample round and all samples from these sites were therefore considered lichen zone.

Chironomidae, or non-biting midges, are often ubiquitous and diverse in aquatic habitats during immature life stages. When the pharate adult is ready to eclose, it floats to the waters’ surface where the adult emerges and the pupal exuviae remains. The exuviae will float for a day to a week, depending on temperature, decomposer activity and mechanical disturbance (Kavanaugh 1988). Consequently, collections were not made for 24+ hours following rainfall or moderate-large wave action and, based on typical cold summer shoreline conditions, I expected samples to represent emergences from the previous 1-7 days. Pupal exuviae were sampled using a technique developed by Ferrington et al. (1991), which is efficient, effectively targets the waterbody of interest (Verneaux and Aleya 1999), allows for species-level resolution using slide mounted specimens, and limits impacts to pool communities by not removing live larvae or pupae from the community.

To collect exuviae, a tray was dipped slightly beneath the surface of a pool, allowing water and surface material to flow into the tray, and then poured into a 125 $\mu$ m mesh sieve. Collections were made for ten minutes in each zone and included as many pools as could be accessed during this time. The entire edge of larger pools was sampled, or the entire surface of smaller pools, with sample materials concentrated in jars and preserved with 80% ethanol. In the laboratory, exuviae were picked and sorted under a dissecting microscope. Subsampling occurred with material placed in a tray of water with a 4x4 grid, swirled to evenly distribute the sample, and if the summed material in four randomly selected squares was >20 specimens then half of the material (every other square) was removed for slide mounting. In addition, after removals, a brief visual inspection determined if any remaining specimens appeared unique from those removed,

which were added to picked material to detect diversity of rare species present in samples (Courtemanch 1996; Vinson and Hawkins 1996). Voucher specimens will be integrated and curated in the University of Minnesota Insect Collection (UMSP).

### *Statistical analyses*

EstimateS 9.1.0© (Colwell 2013) was used to calculate an estimate of the true chironomid community richness. The Chao1 estimator performs well with datasets including many rarities (singletons and doubletons), and the Chao1 Classic (not the bias-corrected estimator) was used based on a coefficient of variation of 0.516 (details in Colwell 2013). Colwell and Coddington (1994) noted that all estimators used in EstimateS gave adequate bias reduction when there were over 50 samples. See Colwell (2013) for equations of Chao1 and Chao1 95% confidence interval.

I calculated two tests for beta and alpha diversity to assess influence of abundant or rare species. Beta diversity tests scale from 0 (no community similarity) to 1 (complete similarity) and were used to examine compositional similarity across shoreline zones and seasons. Jaccard's coefficient of community index (JCC, also called "classic" Jaccard) utilizes only presence/absence and is thus sensitive to rarities, thereby often underestimating similarity (Chao et al. 2005). Significance values for JCC coefficients are based on N species (Real 1999). Whittaker's Percent Similarity (WPS) incorporates abundances and is sensitive to the most abundant species. WPS summarizes the minimum percent of shared indices of all species (equation 7.48 in Legendre and Legendre 2012). No formal significance test could be found for WPS, so I considered a result  $\leq 0.05$  to be significantly dissimilar and  $\geq 0.95$  significantly similar. To limit the biases of these tests, I removed the three most abundant species (based on abundance distributions, Figure 3.3), along with singletons and doubletons, from beta diversity calculations. Otherwise, WPS results may have homogenized due to presence of the most abundant species in all or nearly all seasons and in both zones, while JCC results may have become dominated by singletons occupying only a single zone or season. Seasonal beta diversity was arranged by collection round into five "seasons": early spring (24 April – 7 May), late spring (12

May – 3 June), early summer (8 June – 6 July), late summer (9 July – 14 August), and fall (1 September – 13 October). Seasonality in zones was analyzed separately and the three most abundant, along with singletons and doubletons, were also removed from seasonal beta analyses.

Simpson (the inverse form) and Shannon (using natural log) diversity indexes were also calculated in EstimateS and were reported as the means of 100 randomizations without replacement, which stabilized results and therefore all species were included in the calculations. The stabilization is important because both tests, particularly Simpson, are abundance-influenced and a single species may otherwise strongly influence the result. Shannon is more sensitive to rare species and will therefore more closely match species richness. Both equations can be found in Magurran (2004) and were used to assess diversity differences across sampling sites.

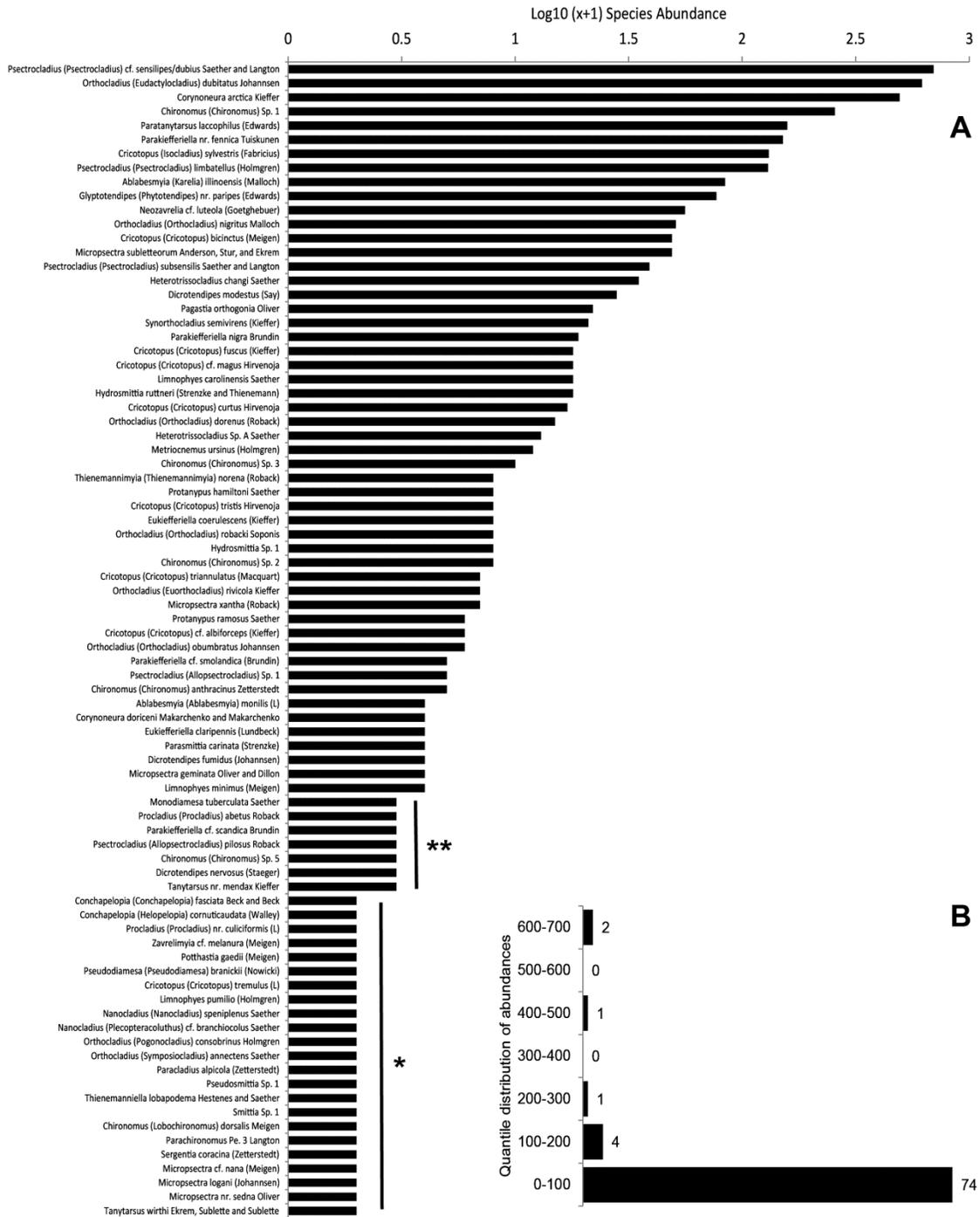
To explore potential geographic differentiation of community components I used clustering techniques. Legendre and Legendre (2012) suggested comparing among multiple clustering methods to obtain the most robust solution based on commonalities, which should represent valid clusters. Cluster analyses were done in JMP® 10, using four methods: average linkage, centroid, Ward's minimum variance, and single linkage (see SAS 2012 for details). All analyses used hierarchical/agglomerative and unweighted techniques, with the actual joining distance shown in dendrograms. Analysis of variance (ANOVA) for seasonal and zonal diversity was also calculated in JMP.

## **Results**

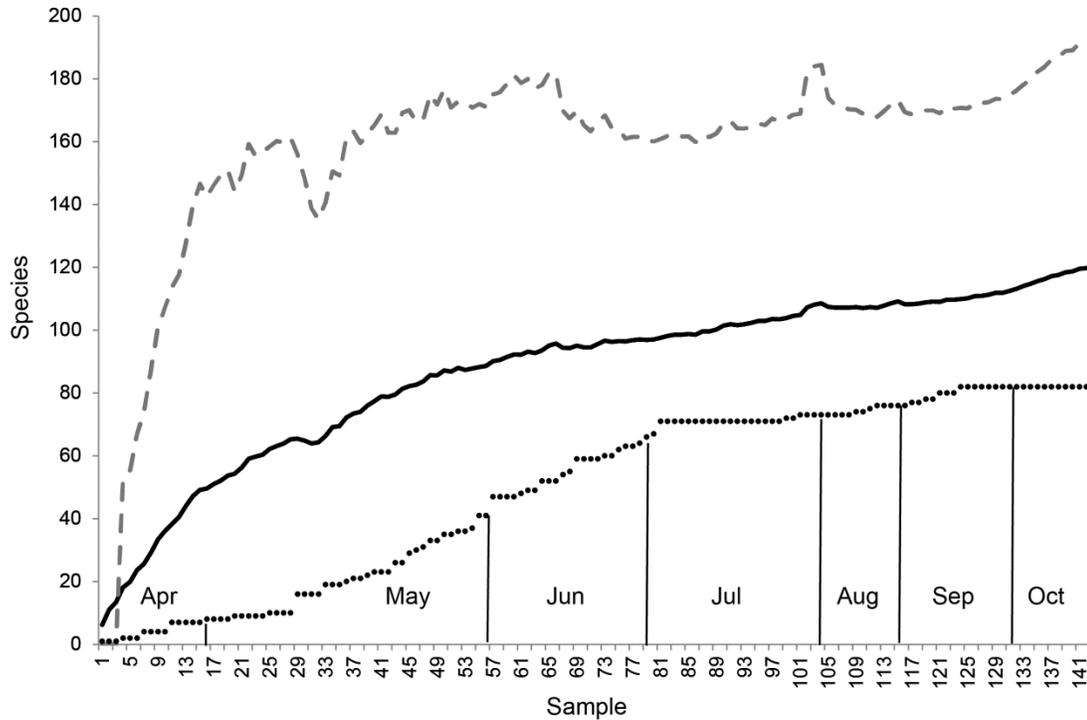
Eighty-two species were identified from 3427 individuals (see supplementary tables 1 and 2 for details). Three species dominated community abundance, occurring at most sites and both zones, while the large majority of species occurred at very low abundance (Figure 3.3A). Using the Chao 1 richness estimator, there were approximately 120 species predicted to be in the community, with an upper 95% confidence interval of 192 species (Figure 3.4). Chao noted that the estimate should be considered the minimum

value, thus the lower confidence value was not reported. The species accumulation curve indicates up to 68% of the estimated true community richness was detected in 2009. Twenty-four species were found only in lichen zone pools and 44 species were found only in splash zone pools.

For beta diversity analyses (both zonal and seasonal), the three most abundant species were considered overly-influential to calculations: *Psectrocladius* cf. *sensilipes/dubius* Saether and Langton, *Orthocladius dubitatus* Johannsen, and *Corynoneura arctica* Kieffer (Figure 3.3B). These three were removed from beta diversity analyses to avoid bias in the abundance-influenced WPS test, along with removal of all singletons and doubletons to avoid bias in the rarity-influenced JCC test and because singletons can only occupy one zone. This left 48 species for refined beta diversity analyses. In addition, three sites (WC, EC, OH) were not included in zonal beta analyses because zonation could not be clearly assessed through the entire season and study pools generally appeared to be in the lichen zone.



**Figure 3.3:** Distribution of abundances for chironomid species on a  $\log_{10}(x+1)$  scale (A), singletons (\*) and doubletons (\*\*) also noted, and number of species per quantile categories (B), Isle Royale, 2009.



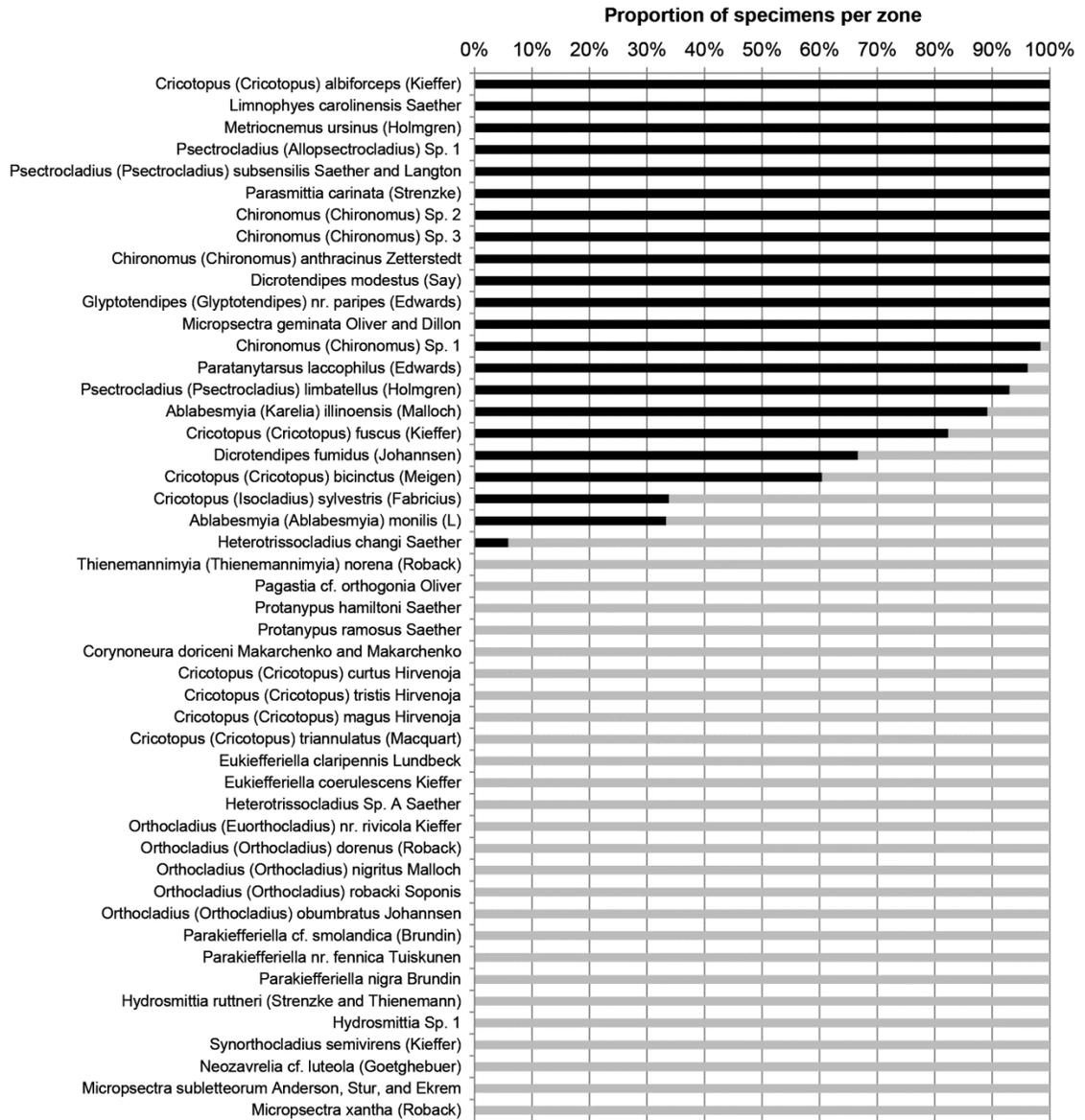
**Figure 3.4:** Accumulation of chironomid species between 24 April (sample 1) and 13 October (sample 142), with 82 species detected, Isle Royale, 2009. Dots represent sample-based accumulation, solid dark line is the Chao 1 estimate of richness, and gray dashed line is the Chao 1 95% upper confidence interval.

Jaccard's coefficient generally supported a pattern of community zonation, with significantly different ( $JCC = 20.83$ ,  $\alpha = 0.05$ ) communities occurring in each zone across the entire study area. However, communities at individual sites did not always show differences. Six sites showed significant differences, one site was not different but nearly so, and five sites were clearly not different between zones (Table 3.1). Similar statistics in Table 3.1 (e.g., Mott and Bat both 0.09) varied in significance due to sample size differences per site (Real 1999). Using WPS as a comparative statistic, there is general agreement regarding community differences, and at no sites were zones statistically similar. Proportional results for species used in beta analyses revealed how each species utilized zones (Figure 3.5).

**Table 3.1:** Ranked Jaccard's coefficient of community and Whittaker's Percent Similarity zonal beta diversity results for 12 sites, Isle Royale, 2009. Dark cells indicate significant results of dissimilar emerging communities across zones (Real 1999) and '‡' shows sites with matching ranks.

Site	JCC (Rank)	WPS (Rank)
Third ‡	0.00 (1)	0.00 (1)
Smithwick	0.05 (2)	0.18 (11)
Shaw ‡	0.07 (3)	0.04 (3)
North Government ‡	0.08 (4)	0.05 (4)
Davidson	0.08 (5)	0.09 (8)
Mott	0.09 (6)	0.03 (2)
South Government	0.09 (7)	0.07 (6)
Bat	0.09 (8)	0.15 (10)
Edwards	0.10 (9)	0.05 (5)
Blake's	0.16 (10)	0.07 (7)
Raspberry	0.19 (11)	0.11 (9)
Scoville ‡	0.24 (12)	0.29 (12)

For the lichen zone, there was no indication that emerging components of the community were different across seasons (Table 3.2). In fact, between late spring and late summer, two of three seasonal transitions showed a significantly similar community emerging (results nearing 1), with all other seasons showing no departure from chance. For the splash zone, early spring was statistically dissimilar from all other time periods except late summer, yet it must be noted that following removal of abundant species only one remained for early spring. Both JCC and WPS were in strong agreement, and WPS also suggested (based on results  $\leq 0.05$ ) that in the splash zone additional differences occurred between late spring and both late summer and fall. Seasonal species richness was highest in early summer and lowest in early spring, while numbers of exuviae collected exhibited peaks in late spring and was lowest in fall (Figure 3.6). Zonal distinction was further supported by a one-way ANOVA revealing that JCC rankings of seasonal communities were significantly different between zones ( $F = 8.62$ ;  $P = 0.0088$ ;  $\alpha = 0.05$ ;  $df = 1, 18$ ). Proportional emergences for species used in beta analyses illustrate across-season variation in emergences (Figure 3.7).

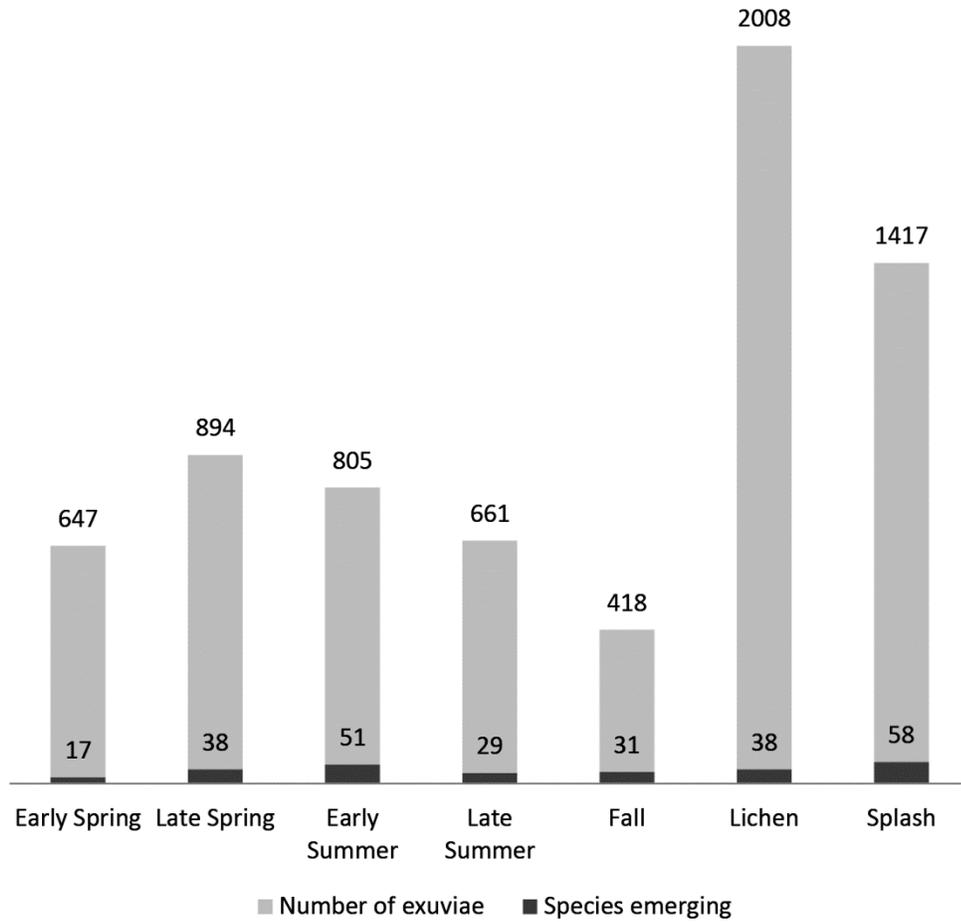


**Figure 3.5:** Proportional emergence of species (n = 48) used in beta diversity analyses, by zone, Isle Royale, 2009. Black bars = lichen zone, gray bars = splash zone.

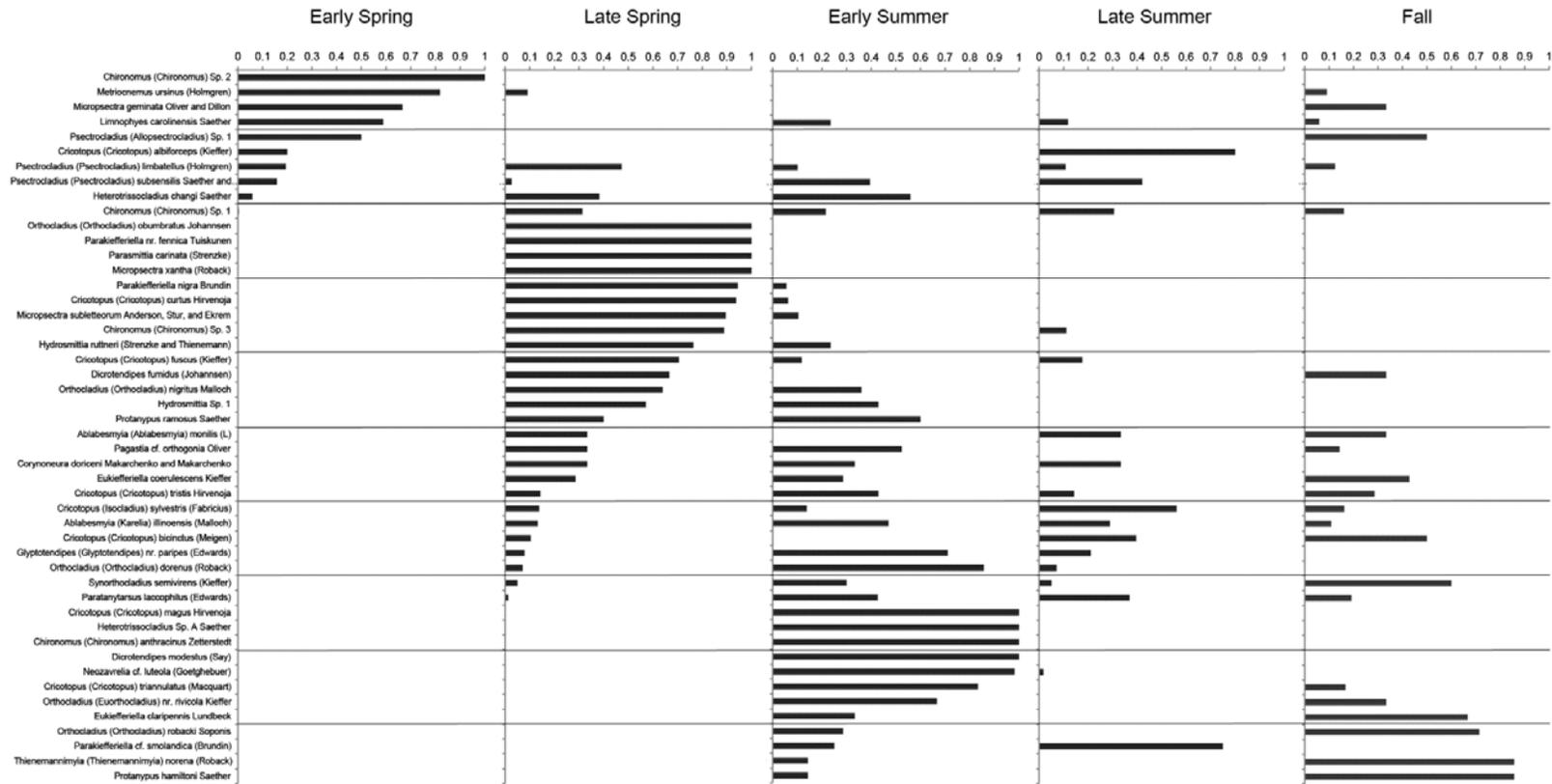
**Table 3.2:** Seasonal results for Jaccard's (top number in each pair) and Whittaker's (bottom number) across five collection periods, Isle Royale, 2009. Dark cells indicate significant results (*similar* emerging communities in the lichen zone, *dissimilar* emerging communities in the splash zone). As noted by "†", early spring splash zone comparisons must be viewed with caution.

		Late Spring	Early Summer	Late Summer	Fall
LICHEN ZONE	Early Spring	0.20 0.31	0.25 0.13	0.24 0.16	0.46 0.20
	Late Spring		0.44 0.38	0.69 0.56	0.39 0.64
	Early Summer			0.64 0.71	0.40 0.56
	Late Summer				0.47 0.76
	Early Spring†	0.05 0.01	0.00 0.00	0.08 0.01	0.00 0.00
SPLASH ZONE	Late Spring		0.47 0.26	0.27 0.03	0.19 0.04
	Early Summer			0.28 0.88	0.41 0.19
	Late Summer				0.27 0.34

A range of 7-30 species were collected at each site (with zones combined), so between 9-37% of the detected community was present at a given site. Typically, sites with high density of habitat had greater richness, but some splash zone sites contradicted this (North Government and Edwards, Figure 3.8). Simpson and Shannon indexes generally tracked each other (Figure 3.9). However, when using species richness as an unbiased baseline, diversity indexes were similar in the lichen zone, but more volatile in the splash zone. Lichen zone diversity was generally higher in the eastern portion of the study area, from Raspberry to Blake's Point, while there appeared to be no geographic relationship to diversity in the splash zone (Figure 3.8). Three fewer sites were compared in the splash zone because stratification could not be clearly assessed and field notes suggested that pools were likely in the lichen zone at these sites. Means testing of site richness between zones, using a one-way ANOVA, did not give a significant result ( $F = 3.414$ ;  $P = 0.0765$ ;  $\alpha = 0.05$ ;  $df = 1, 25$ ), but the trend was toward greater richness in the splash zone.

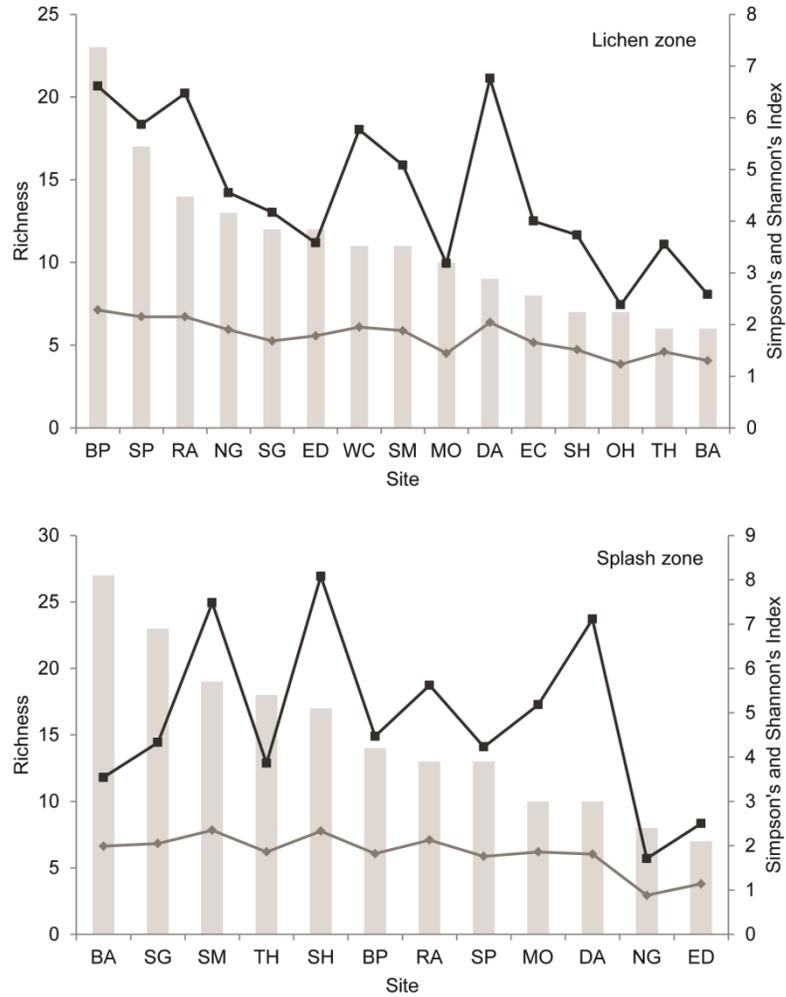


**Figure 3.6:** Exuviae abundance (tall, light columns) and number of chironomid species (short, dark columns) emerging by season and zone from coastal rock pools at Isle Royale, 2009.

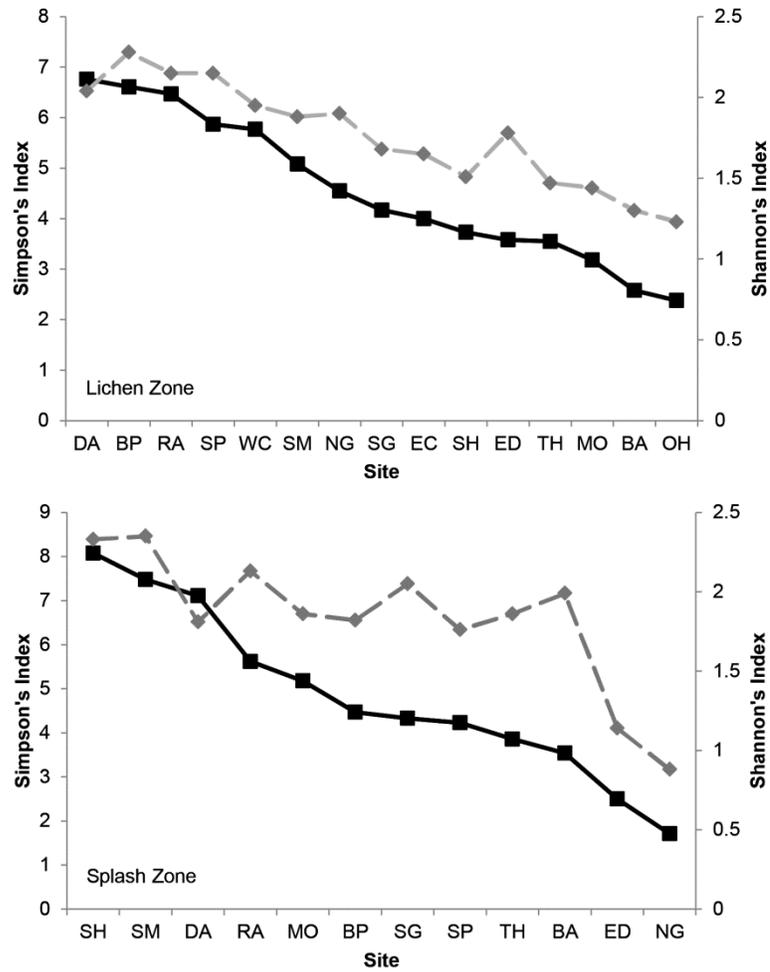


**Figure 3.7:** Proportional emergence of species (n = 48) used in beta diversity analyses, by season, Isle Royale, 2009.

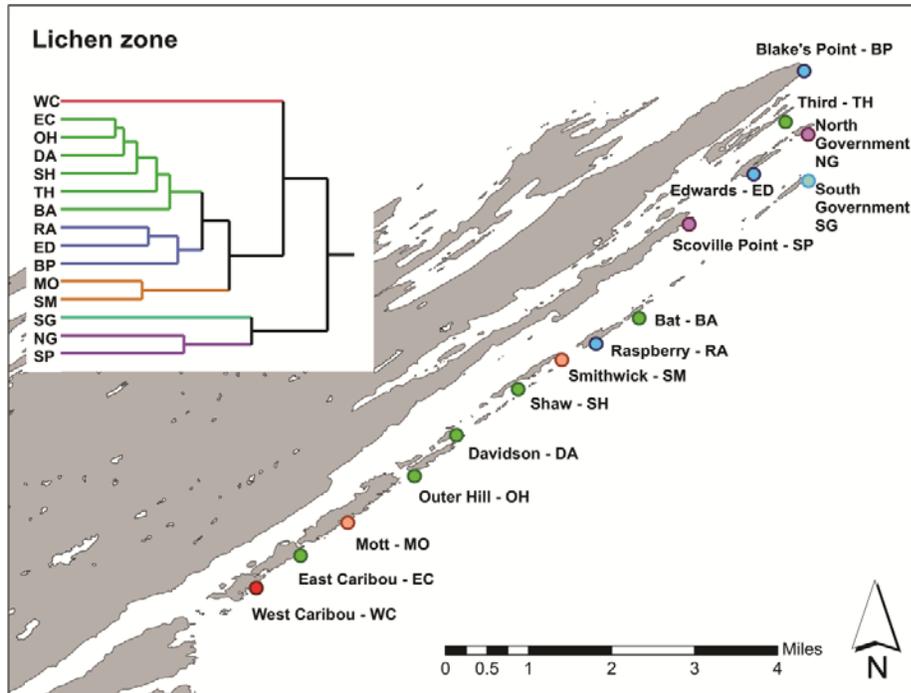
Cluster analyses appeared consistent in all four methods. Although overlap in clusters occurred, they did span sensible geographic boundaries (Figures 3.10 and 3.11). Two community boundaries appeared to exist based on consistent similarities between clustering methods, with three to four relatively distinct assemblages in the study area. In the lichen zone, a large cluster between East Caribou and Bat occurred, with two overlapping clusters to the northeast (BP-ED-RA and NG-SG-SP) and West Caribou distinct from all other sites. In the splash zone, similar clustering existed with three clades representing analogous geographic boundaries. One of the few inconsistent results is South Government in the lichen zone, which often did not cluster with any other sites. Dendrograms for each zone display representative results of stable clustering from all four methods. Overall, sites in the western portion of the study area generally clustered separately from eastern sites, while eastern sites either formed two overlapping clusters (lichen zone) or one cluster with otherwise mixed results (splash zone).



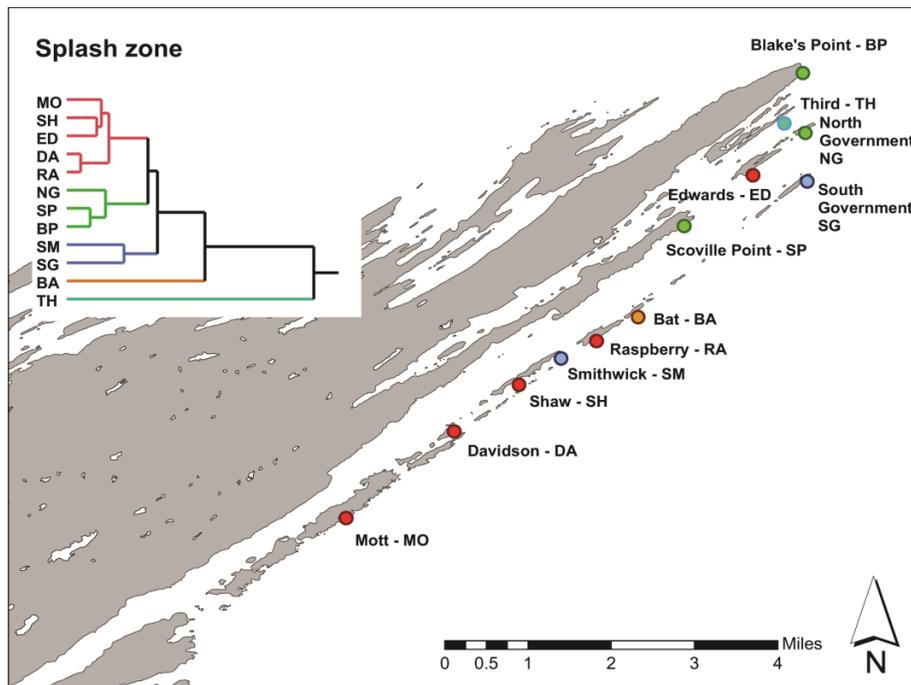
**Figure 3.8:** Chironomid alpha diversity results, arranged by species richness (bars), including Simpson's (dark lines) and Shannon's (light lines) indexes in the lichen zone (top) and splash zone (bottom) pools, Isle Royale, 2009.



**Figure 3.9:** Simpson's (dark lines with squares) and Shannon's (dashed light lines with diamonds) index relationships in the lichen zone (top) and splash zone (bottom), Isle Royale, 2009.



**Figure 3.10:** Cluster analysis (average link method shown) of chironomid communities in lichen zone pools, Isle Royale, 2009.



**Figure 3.11:** Cluster analysis (Ward's minimum variance method shown) of chironomid communities in splash zone pools, Isle Royale, 2009.

## Discussion

The 82 chironomid species accounted for a higher richness than expected, given the generally small pool sizes, restricted watersheds, and apparently limited habitat variation and nutrient inputs. Additionally, the 120 estimated species should be considered a minimum likely value (Colwell 2013), which suggests that either IRNP coastal rock pools have an unusually high diversity or the family is often undersampled in other habitats. Marine pools have also shown high taxon diversity, though with very different biological communities, probably due to a very dynamic series of disturbances such as tides (Little et al. 2009). In comparison, Colbo (1996) found only 14 freshwater chironomid species in coastal rock pools at 14 sites along the Labrador coast, Canada. The current chironomid richness was over double the taxa previously known in reviewed rock pool studies worldwide (n=38, Jocque et al. 2010), although important sources, including Colbo (1996), were not included in the review for unknown reasons. Therefore, I can infer that greater niche and resource availability occurs in our rock pool habitats than anticipated. The high number of species detected from only one or two exuviae (n = 31, 38%) suggests that numerous species are yet to be detected, and the lack of an asymptote for community richness, as in the Chao 1 estimate, is common in arthropod datasets (Gotelli and Colwell 2001). Between 38 and 110 species remain undetected and, at best, 68% of the community was identified in 2009. The remainder of the community is likely composed of either rarities or species that emerge in a narrow timeframe.

Beta diversity showed a significant difference between communities occupying each zone, which was reflected at half the individual study sites. Site-by-site discrepancies were likely due to low statistical power based on limited richness. However, spatial-scale effects may also be important, with local mixing of patchy community components, which has been shown in marine coastal habitats where highly variable components occur (Little et al. 2009). I would consequently expect strong inter-annual variation of community components to occur at a given site, yet general zonal stratification to be consistent over time. The three most abundant species occurred in both zones, although *P. sensilipes/dubius* seemed to favor the lichen zone while *C. arctica*

seemed to prefer the splash zone. Along with *O. dubitatus*, these were generalists, occupying both zones, occurring at most sites, and often abundant when present.

Seasonal emergence patterns presented an opposing depiction of community structure between zones. In the lichen zone, the significantly similar emerging species from late spring to late summer, and remaining results not diverging from random chance, revealed a lack of seasonality for emergences. So in the lichen zone future studies could accomplish surveys in late spring and early summer, when both abundance and diversity are highest, and expect to detect much of the true richness. In contrast, the splash zone had strong seasonal shifts between early spring and other seasons. However, these results were not reliable because only four species were identified in early spring; three of these were the abundant species removed from beta analyses, leaving only a single species to represent early spring. Interestingly, if the abundant species were not removed, early spring continued to have significant differences from early summer and fall. So the seasonal shift detected in the splash zone is due to the lack of emerging species in early spring, not a shift to different species. Splash zone differences between late spring and late summer-fall were not significant using JCC, but abundance-influenced WPS suggested differences between these seasons, presumably the result of highly variable relative abundance of species present across seasons.

A general seasonal pattern was observed for many individual species, with peak emergence occurring either in a single season or adjacent seasons. With few exceptions, even species that emerged across most or all seasons had a peak emergence. Emergences did not allow for a clear assessment of voltinism, with most species either low in abundance or occurring across multiple seasons. The greatest richness of emergence occurs in early summer, making it a good season for detecting the greatest diversity possible. Early spring richness is low and represents few unique species, while fall had moderate richness and the lowest exuviae numbers, with no unique species collected. I expected a distinct fall emergence, or potentially a spring-fall similarity based on climatic conditions, but these did not occur. Given the detection of many cold-stenothermic

species (Chapter 1), the limited warm-season along the coast of IRNP, and apparently limited predation pressure in most pools (Egan et al., in press), I suspect that there is no advantage to emergence in early spring and fall. Biological conditions in pools therefore appear aestival, yet climatic moderation from the lake probably allows for broader seasonal activity for larvae.

Generally, sites with more available habitat had higher richness and diversity, particularly in the lichen zone. In the splash zone, Davidson and Bat both had limited habitat yet high diversity, which I interpret as an artifact of diversity calculations in the case of Davidson and potentially detection of Lake Superior species washed in at Bat. For unknown reasons, other sites (e.g., North Government) had low diversity regardless of abundant habitat. Alpha diversity suggests the most productive sites for sampling include Blake's Point, South Government, and Smithwick, though several others would be good if a particular zone was targeted. Randomized means reduced the chances for spurious results in alpha diversity calculations, and both indexes, with a few exceptions, matched species richness. So richness is likely the simplest statistic for assessing alpha diversity, although without a clear asymptote in species accumulation it must be used with some caution (Gotelli and Colwell 2001).

Chironomid diversity is known to be relatively high in littoral habitats and limited in profundal habitats of large lakes, including Lake Superior (Vadeboncoeur et al. 2011). An important consideration was whether exuviae were washing into splash zone pools from Lake Superior. Two lines of evidence suggested that washed in exuviae influenced results. First would be if the abundance-influenced Simpson's index were to contradict Shannon's index and species richness due to large numbers of exuviae washing into pools from the much greater available nearshore habitat. While contradictory results for the lichen zone occurred at Davidson and West Caribou, both indexes ranked sites similarly, as expected. Yet in the splash zone contradictory index rankings occurred at almost half the sites (5 of 12), giving support to lake additions. Second, there would be a higher richness in the splash zone because species from both splash pools and Lake Superior

would be collected in the same samples. It has been observed that splash zone pools are colder with fewer nutrients (Egan et al., in press), so a more diverse community was predicted in the lichen zone. Comparing richness means between zones did not reveal a statistical difference, but the results were close enough to suggest a difference occurs with the splash zone showing a distinct trend toward higher richness, again supporting lake additions. While it appeared possible that Lake Superior exuviae were being washed into splash zone pools, it remains uncertain whether washed in larvae would be able to complete a lifecycle; this is a reasonable consideration, based on strong similarities in temperature and water chemistry (Egan et al., in press).

Geographic clustering of approximately three community assemblages was implied for both zones, although clean spatial breaks did not occur. Assemblage boundaries made sense from an ecological perspective, with margins between West Caribou and the rest of the study area, and Raspberry-Bat islands where sites to the northeast and southwest of this area were generally distinct from each other. West Caribou, as the western-most island in the chain having substantial pool habitats, potentially represented a location where barrier-island community components intergraded with main-island communities of the peninsula to the southwest. The second boundary, around Raspberry-Bat, may have represented a transition between two clusters of islands. Within each cluster, islands were probably close enough to each other that short-range dispersal could occur easily (Armitage 1995), yet between clusters were larger gaps where prevailing winds down the long, southwest-northeast oriented harbors could have hindered dispersal events from one side of the harbor to the other.

While broad clusters appeared to exist, regular dispersal between sites may have mixed community components consistently enough that some points within a cluster were more representative of an adjacent cluster. For example, in the splash zone, Edwards clustered with sites in the Mott-Raspberry chain, while Blake's Point, North Government, and Scoville Point clustered, but sites between were not similar enough to join them. This model has been shown to apply on marine shores, where large geographic

areas had stable community components, but smaller scales revealed regular community turnover based on disturbance and competition (Little et al. 2009). With between 7-30 species occurring at a given IRNP site, only 12-37% of the community was present at any single location from spring to fall. The outliers for Third and Bat in the splash zone may have been due to input from Lake Superior, representing species that may or may not utilize pools to complete development. Clustering indicated that future studies should consider island groups and gap distance, and that one site over time may be representative of other sites in a cluster.

### ***Potential Threats and Stressors***

The most likely direct habitat threats at IRNP, and coastal areas in Lake Superior generally, are oil pollution from ship groundings and climate change. Trends in reduction of ice cover (Austin and Colman 2007), with a potential increase in shipping traffic, increase the probability for accidents. While grains constitute most cargo passing through IRNP waters, 145-235 thousand tonnes of inbound petroleum products and chemicals have been shipped to Thunder Bay annually since 2000, along with contents of ships' fuel tanks (Thunder Bay Port Authority 2013). Acute pollution events may result in loss of rare chironomid species, which represented the bulk of pool richness at IRNP. A few generalist species that occurred in both lichen and splash zones are known to be tolerant of oil pollution, such as *Cricotopus bicinctus* (Meigen) (Rosenberg and Wiens 1976). However, zonal stratification of chironomid communities indicated that the lichen zone would not generally be a refuge for splash zone taxa, limiting splash zone recolonization from nearby sources in the event of severe coastal pollution.

The U.S. Coast Guard and Environmental Protection Agency categorize rocky shores as low priority during spill responses, but this rests on inaccurate assumptions that underestimate the diversity, susceptibility and rarity of community components occupying rocky shores. For IRNP, results from coastal pool studies can assist in identifying areas that may deserve higher priority for protective actions and those that can remain low priority for protection in the event of coastal pollution. For example, pool

densities (Chapter 2) and diversity results, along with possibly distinct communities within island clusters, suggest that pools along Third Island and South Government Island would be good to protect in the northeast island clusters. In addition, the Smithwick-Shaw Islands in the central part of the study area, and Mott Island to the west, would be good candidates for protection efforts during spill responses.

Climate change is generally expected to cause important habitat modifications and subsequent species extinctions (Thomas et al. 2004). Local community patchiness in IRNP pools may limit diversity losses in the event of a major acute impact, but persistent changes in patterns of rainfall, wind, and lake temperature are likely to modify habitats that impact diversity across the entire archipelago. A number of IRNP chironomid species that are cold-adapted, have highly disjunct ranges to arctic, alpine or Palearctic populations, or cannot tolerate modifications to hydrology (e.g., pool drying or modified wave action) or water chemistry may consequently be extirpated permanently.

## **Conclusions**

Overall, the chironomid community of rock pool habitats at Isle Royale was composed of a handful of very common species that were generalists in terms of site occupation, habitat stratification, and season, combined with a large proportion of rare species. The rare species were likely detected by chance, and the undetected species predicted to be part of the community were likely to be rarities or have a very narrow temporal emergence. Communities were different between zones, but seasonal variation was mixed, with some significant similarities in the lichen zone and dissimilar assemblages emerging from the splash zone. Clustering across sites was based on logical habitat connections and considered gap width between islands, where distance and wind may create challenges for dispersal. Zonal, seasonal, and geographic emergence patterns demonstrated preferable localities and timeframes by which further investigations could target collections for particular taxa of interest. These results should be applicable in a wider context to Lake Superior generally, particularly the north shore where bedrock and rock pool habitats appear structurally similar (Egan, unpublished data).

## CHAPTER IV

# PHYSICAL, CHEMICAL AND SPATIAL REGULATION OF CHIRONOMIDAE (DIPTERA) IN FRESHWATER POOLS

### **Summary**

Previous chapters have revealed a relatively species-rich chironomid community with unique components, such as disjunct populations and novel habitat use, and clear zonal differences in species assemblages. Geographic community differences appeared to occur in relation to gap distance between islands, and seasonal emergences had different patterns between the lichen and splash zones. In 2010 new study sites were selected from a wider geographic range, a new stratum of pool depth, as an indicator of desiccation potential, was taken into account, and water chemistry data from 16 permanent pools was collected across three seasons. Seventy species were identified in 2010, with a total of 102 in both years, but only 49 species were shared between the two years. Diversity results reconfirm many of the findings from 2009, although geographic cluster analyses were inconclusive. Numerous species preferred particular habitat niches, which could allow them to be used as indicators either individually or collectively. Ordination revealed nutrients to be important in regulating community assemblages, with mesotrophic pools higher on the shoreline that are influenced by upland forest inputs and primary production, and oligotrophic pools near Lake Superior where low-nutrient conditions are maintained by wave disturbance. Surprisingly, pool temperatures were very similar between zones, potentially reaching thermal maxima for some species and showing distinct spring-summer-fall transitions that could partially control voltinism and development. Overall, chironomid communities on shores of Lake Superior appear to be regulated by nutrients and wave disturbance, while a mosaic of geographic assemblage patterns and a high-incidence of rare species with narrow emergence times probably influence sampling results.

## **Introduction**

Rocky shores have long been model habitats for studying community responses to environmental gradients (Platt and Connell 2003, Denny 1995, Menge et al. 2002). Historically, studies of rock pool ecosystems have focused on marine shores, while inland studies have had a narrow spatial scope in isolated inland freshwater systems, and only recently have inland habitats received more comprehensive attention (Brendonck et al. 2010). The current study was unique because it included coastal pools of a large freshwater lake where habitats experienced physical conditions similar to marine shores, yet without complicating factors such as large tidal fluctuations and salt spray.

Studies of Isle Royale National Park (IRNP) rock pools have revealed a chironomid community comprised not only of species that may be anticipated in pool habitats of the central Nearctic, but also novel habitat associations and significant expansions from disjunct ranges across the Holarctic (Chapter 1). While individual habitats are small, the sheer number of pools across the coastal landscape yields an impressive amount of available habitat, particularly at Passage Island, and physical configuration of the shoreline appears to determine traits and arrangement of both pools and biota within them (Chapter 2). Chironomidae were the focus for biotic studies, based on well-known patterns of abundance and diversity in virtually all freshwater habitats worldwide (Ferrington 2008). Zonal, seasonal, and geographic stratifications of community diversity were observed in the chain of barrier islands and peninsulas in the northeast end of the park (Chapter 3).

The goals of 2010 sampling, as illustrated in the current chapter, were to build on 2009 work by considering spatial, hydroperiodical, and chemical factors. Questions posed in 2010 were: Do zonal, seasonal, and geographic differences continue to be important when considering additional sites along the south shoreline of Isle Royale, where habitat patches more closely adjoin each other without gaps between islands, and Passage Island, which is small and remote? Does desiccation potential influence community assemblages? And can water chemistry help determine important

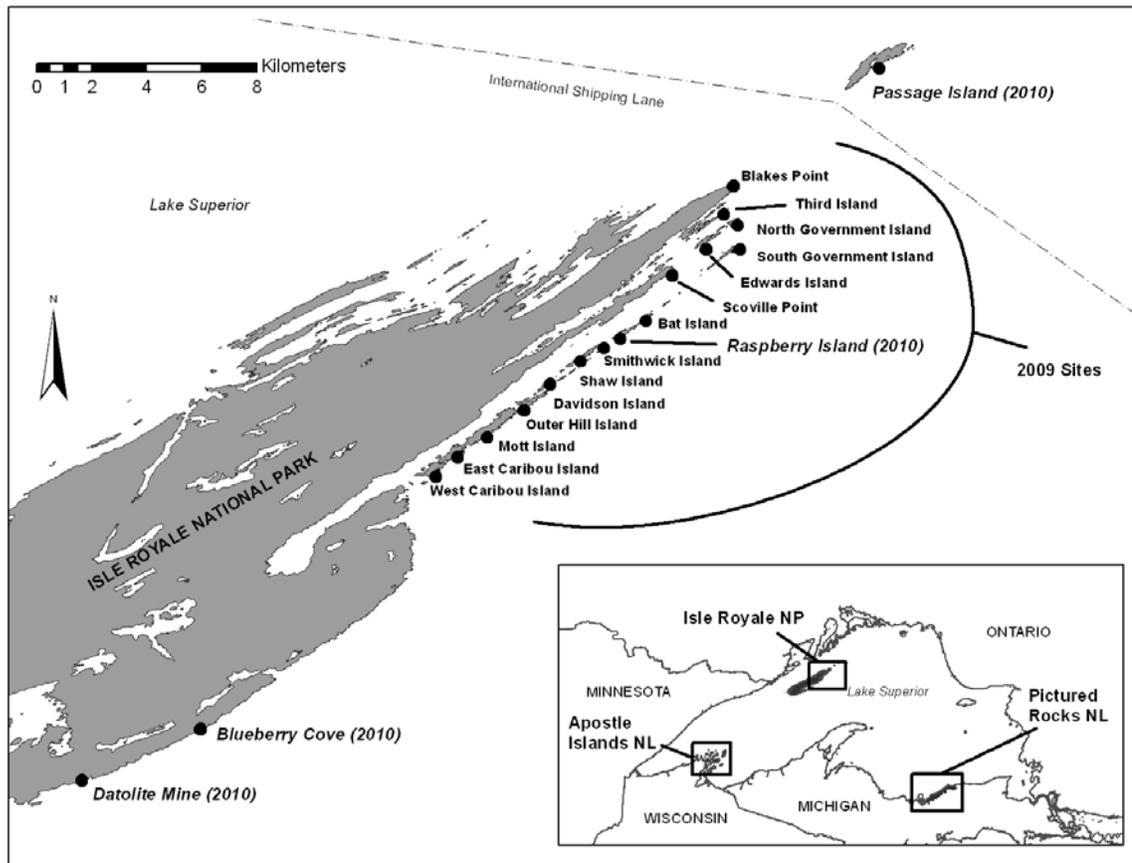
mechanisms driving the organization of chironomid assemblages (Wazbinski and Quinlan 2013, Brooks and Birks 2004)?

## **Methods**

### ***Study Sites***

Descriptions of Isle Royale National Park (IRNP) and the general study area can be found in Chapters 2 and 3. Based on a perceived need for study design improvements during 2009 sampling, along with a broader protocol that included collecting water chemistry samples, zooplankton, and diatoms for collaborating studies (which also included Apostle Islands and Pictured Rocks National Lakeshores), sites in 2010 were not the same as 2009 (except for Raspberry Island). Using high-definition aerial photography provided by the National Park Service, 2010 sites were chosen using a stratified-random regime for selecting both the locality and individual pools. Based on anticipated biotic response to geographic differences, at least one site was required from each of three categories: 1) Passage Island, representing a distant offshore island; 2) the barrier islands near Isle Royale between West Caribou Island and Blake's Point; and 3) Isle Royale shoreline between West Caribou Island and the Datolite Mine area (Figure 4.1).

Sites were to be rejected if 1) access or sampling would not be safe or feasible, 2) limited habitat was available (i.e., too few pools), and 3) visits would disturb sensitive resources such as nesting wildlife. No sites were rejected on the first criterion and only one site was rejected based on the last two, which lacked extensive lichen zone pools and had a gull colony. At each site a general area for sampling was randomly selected if pool density was abundant (e.g., Passage Island was subdivided into multiple sections, of which one small area was randomly chosen), and during initial site visits four permanent pools, two in each zone, were randomly selected using dice. From 16 sites where aerial images showed a moderate-to-high pool density, four were randomly selected: Passage Island (PA), Raspberry Island (RS), Blueberry Cove (BL), and Datolite Mine (DM).



**Figure 4.1:** Rock pool study sites at Isle Royale, including both 2009 and 2010. Inset shows Isle Royale in a regional context with other Lake Superior parks.

### *Data Collection*

In 2010, six sampling rounds occurred, each clustered within a 3-9 day period generally separated by one month (except for April-May with a two week gap due to park opening times, and August-October with a two month gap due to timing of other duties). Chironomidae sampling occurred in each round, while water chemistry collections were in May, July, and October (Table 4.1). Although biweekly sampling would have been ideal, monthly sampling was deemed likely to yield acceptable taxonomic and compositional data and the April-October timeframe was expected to detect the majority of richness (Bouchard and Ferrington 2011). Justification and methods for collection, processing, and identification of chironomid pupal exuviae are in Chapters 1 and 3 (Raunio et al. 2011, Verneaux and Aleya 1999, Coffman 1973).

**Table 4.1:** Coastal rock pool sample dates, Isle Royale National Park, 2010.

	Round 1 <i>22–28 April</i>	Round 2 <i>9–17 May</i>	Round 3 <i>3–8 June</i>	Round 4 <i>3–9 July</i>	Round 5 <i>3–6 Aug</i>	Round 6 <i>2–4 Oct</i>
Macroinvertebrates	x	x	x	x	x	x
Water chemistry		x		x		x

Six chironomid pupal exuviae samples were collected at each site in each round of sampling, resulting in 143 total samples (one less than expected due to dry pools at DM on 3 June, following several weeks with little rain). Of these six, one sample was from each of the permanent pools (two in each zone, four total) and one combined sample was from ephemeral pools in each zone. Ephemeral pools were defined as one to four inches deep, based on observed water levels during sampling. Permanent pools were defined as having over four inches of water, but the 16 pools tracked during the entire summer were purposely  $\geq 6$  inches deep to avoid including an ephemeral pool inadvertently. Based on 2009 sampling, it appeared that pools  $>4$  inches deep retained water even during dry periods, while pools  $<1$  inch deep were likely to dry within a few days after recharge or offer no structural refuge during wave action. Therefore, the ephemeral pools were expected to retain enough water for biological development with regular precipitation and wave wash, yet have the potential to desiccate without regular recharge.

During water chemistry sampling, a set of field measurements and a bulk water sample were taken to characterize each permanent pool. Lake Superior samples were taken from nearshore sites on the same dates as other water samples. A Hydrolab sonde, calibrated daily, was used to measure pH, electrical conductivity ( $\mu\text{S}/\text{cm}$ ), and dissolved oxygen ( $\text{mg}/\text{L}$  and % saturation). For water quality, three acid-washed 1-L amber polypropylene bottles were filled with pool water by immersion in the center of the pool, capped, and placed on ice for transport to the field laboratory at Davidson Island. Chlorophyll-a was filtered onto a GF/C filter, stored in foil, and kept frozen. Nutrient samples for total phosphorous (TP) and total nitrogen (TN) were stored in a 60 mL bottle and frozen. Dissolved inorganic and organic carbon (DIC/DOC) samples were filtered with a  $\text{CuSO}_4$  (copper sulfate) solution, sealed in amber vials without air, and refrigerated

(see Egan et al, in press, for details). Samples were analyzed at the Science Museum of Minnesota's St. Croix Watershed Research Station. All laboratory analyses included field duplicates, lab duplicates, lab spikes, and blanks as appropriate. In addition, eight thermistors were placed in permanent pools, one per zone at each site, and set to log hourly water temperature.

### ***Statistical Analyses***

To assess community structure, EstimateS 9.1.0© (Colwell 2013) was used for calculation of chironomid community richness estimates and alpha diversity indexes. For community richness, the Chao1 Classic estimator with 95% confidence intervals was chosen because it works well when datasets have many rarities (see Colwell 2013 for details and equations). Simpson's inverse form and Shannon's natural log indexes were calculated using the means of 100 randomizations without replacement to stabilize results. Simpson's index can be influenced strongly by the relative abundance of species, while Shannon's index better integrates the evenness across abundances (Magurran 2004). Indexes were compared to understand interactions between the dominance of individual species abundances and evenness in the community. In addition, rank-abundance plots were calculated to assess differences between dominance and evenness (Magurran 2004).

Beta diversity testing, on a scale from 0 (no similarity) to 1 (complete similarity), was used to examine the similarity of community composition across shoreline zones, pool permanence, and seasons. Jaccard's coefficient of community index (JCC) incorporated presence or absence of species, with a bias toward rarities and consequently a potential for underestimating similarity (Chao et al. 2005). JCC significance values were based on N species to test for similarity or dissimilarity (Real 1999). Whittaker's Percent Similarity (WPS) index incorporates abundances and can be biased toward highly abundant species. WPS is a summary of minimum percentages, on a species-by-species basis, for all species shared between samples (Legendre and Legendre 2012). To limit the beta diversity biases, the single dominant species collected in 2010 was removed,

*Orthocladius dubitatus* Johannsen, along with all species where only one individual was collected (n=18), leaving 51 species for beta analyses. Removals reduced the chance for WPS to homogenize results or for species collected only once to drive JCC comparisons across multiple samples. Mean body length was also compared using Analysis of Variance (ANOVA) for exuviae to test if species were selecting zones based on development times or voltinism, as indicated by body size.

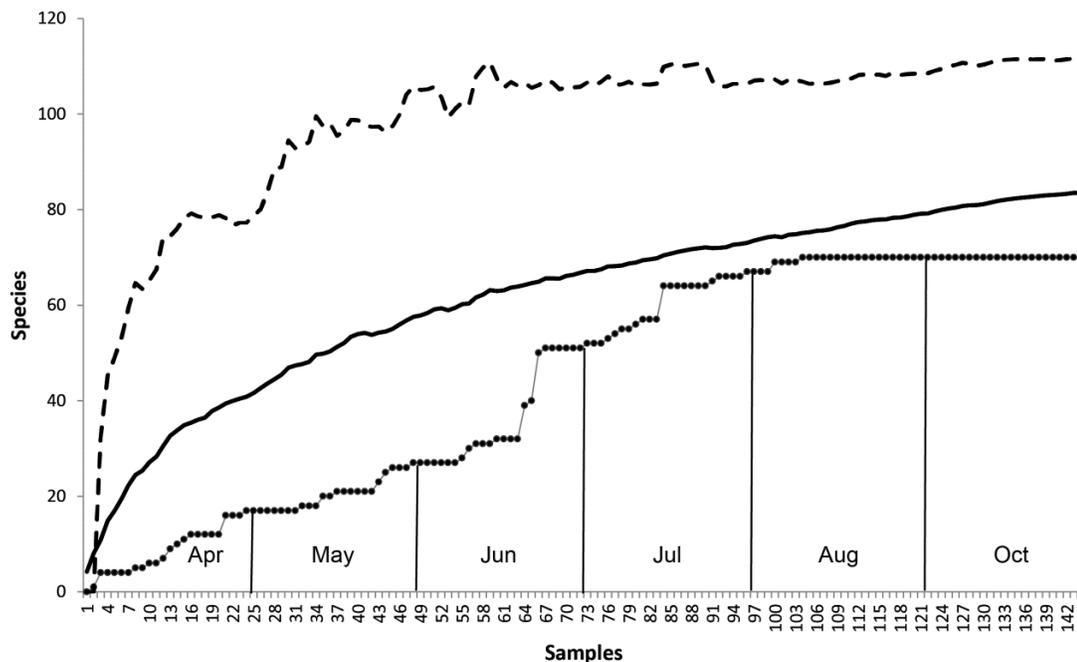
Geographic differentiation across sites was explored using clustering techniques in JMP® 10. As suggested by Legendre and Legendre (2012), multiple methods were compared to assess the most robust solution based on commonalities representing valid clusters. Using hierarchical, agglomerative and unweighted techniques, with actual joining distance shown in dendrograms, four methods were employed: average linkage, centroid, Ward's minimum variance, and single linkage (see SAS 2012 for details). All ANOVA and Spearman rank tests were also calculated in JMP.

To test chironomid community responses to water chemistry gradients, ordination was accomplished in CANOCO 5. Ordinations aligned species and samples along chemical gradients and was used to assess ecological relationships, optimal conditions, and expected frequencies of occurrence (Lepš and Šmilauer 2003). Using 46 species (24 species from ephemeral pools were not included because no chemistry data was collected), water chemistry variables from all 16 permanent pools were analyzed to explore potential explanations for community variability. Detrended correspondence analysis (DCA, unimodal based on a 4.0 standard deviation gradient) and constrained correspondence analysis (CCA) were run, including log-transformed species data, Monte Carlo testing (499 permutations), and forward selection as advised in Lepš and Šmilauer (2003). DCA is an unconstrained ordination that shows basic compositional gradients, with variables tested independently and providing an optimal fit from regressions. CCA is constrained, using linear gradients from the measured data instead of an optimal fit. Lepš and Šmilauer (2003) advised calculating both ordinations and comparing results.

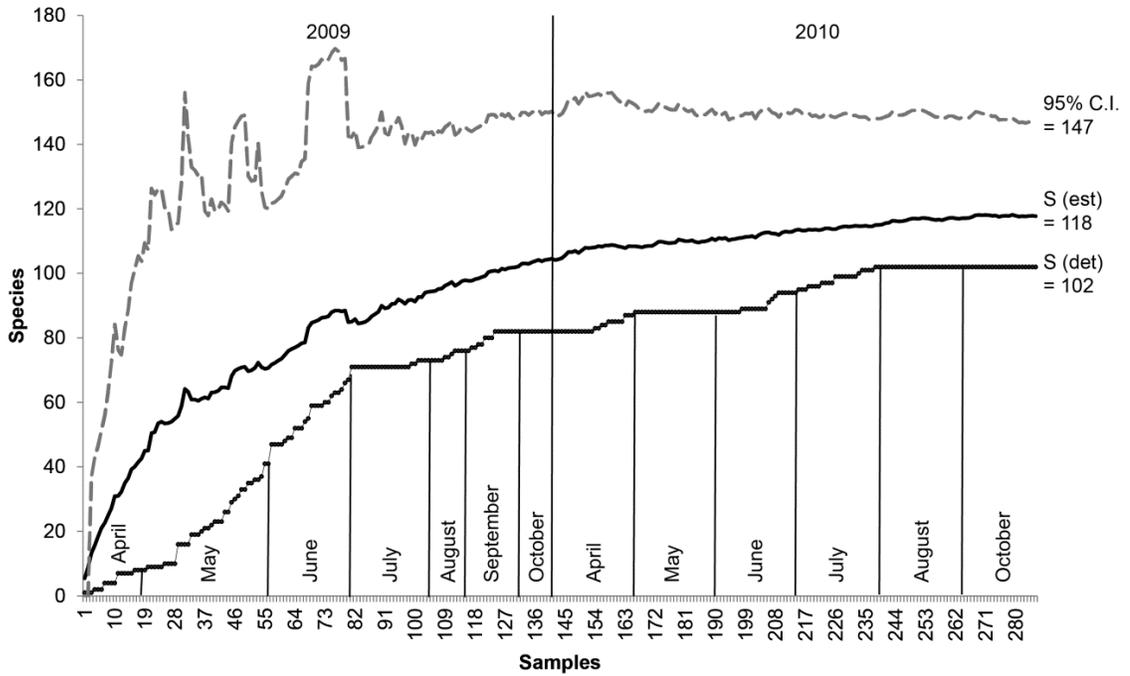
## Results

### *Chao richness estimator and general reporting on overall community richness*

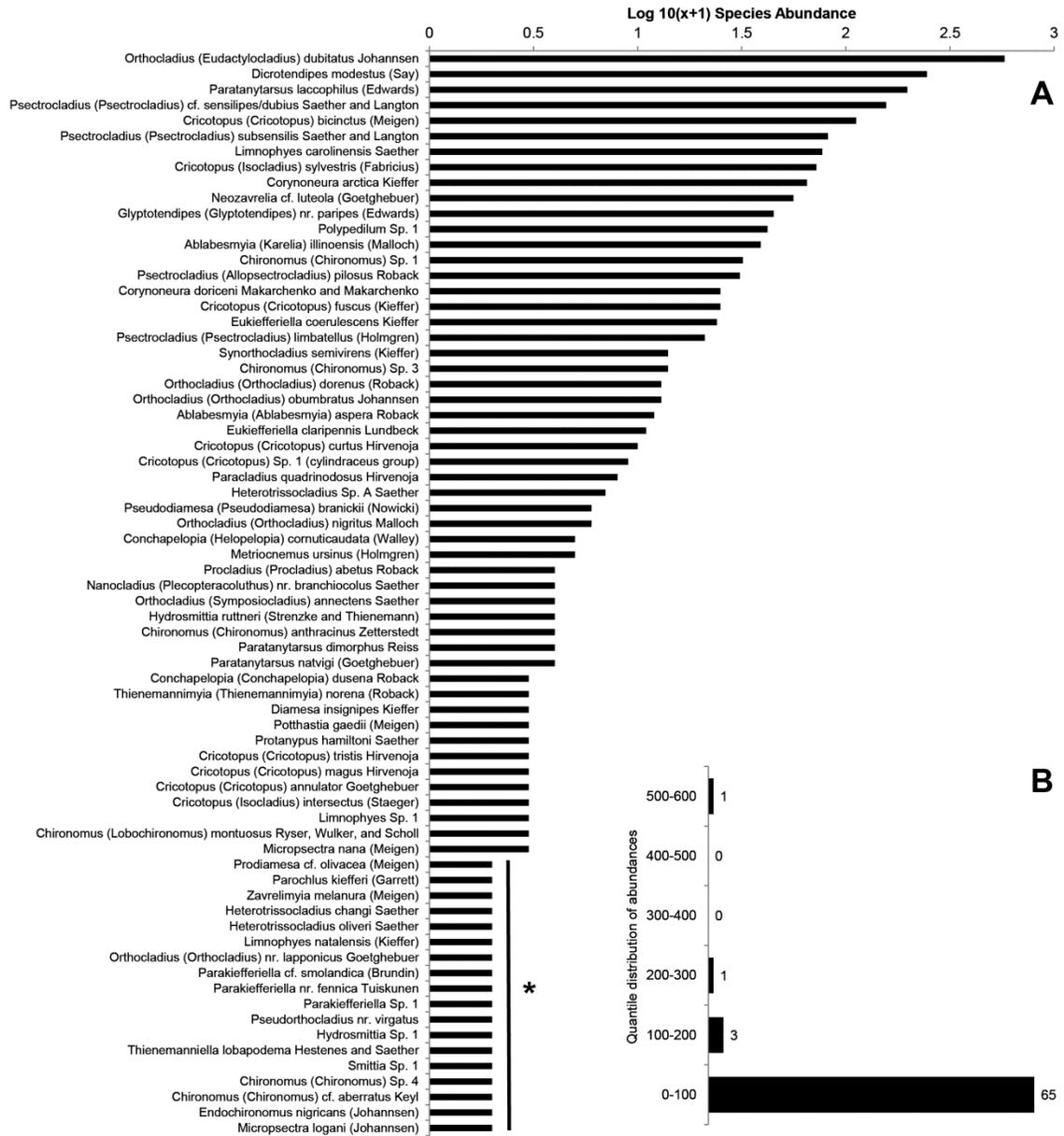
From 2,090 individuals, 70 chironomid species were identified from rock pools in 2010. The 2010 Chao 1 community richness estimate was 83, with a 95% upper confidence interval of 111 species (Figure 4.2). A combined accumulation curve for 2009-2010 gave an estimated richness of 118 and a 95% upper confidence interval of 147 (Figure 4.3). One species, *Orthocladius dubitatus* Johannsen, was dominant ( $n = 577$ , 28%) and four others had between 100 and 250 individuals (with a range of 5-12% each). The large majority of species ( $n = 65$ ) had fewer than 100 individuals, and there was a long tail of species ( $n = 46$ ) with 10 or fewer individuals collected (Figure 4.4). Comparing the two years of collections, 82 species occurred in 2009 and 70 in 2010. Forty-nine species were shared between the years, with 33 only occurring in 2009 and 21 only in 2010 (see Appendixes for details).



**Figure 4.2:** Accumulation by month of chironomid species from 22 April (sample 1) to 4 October 2010 (sample 144), Isle Royale. Dots represent sample-based accumulation of species detected ( $n = 70$ ), solid line is the Chao 1 richness estimate (83), dashed line is Chao 1 95% upper confidence interval (111).



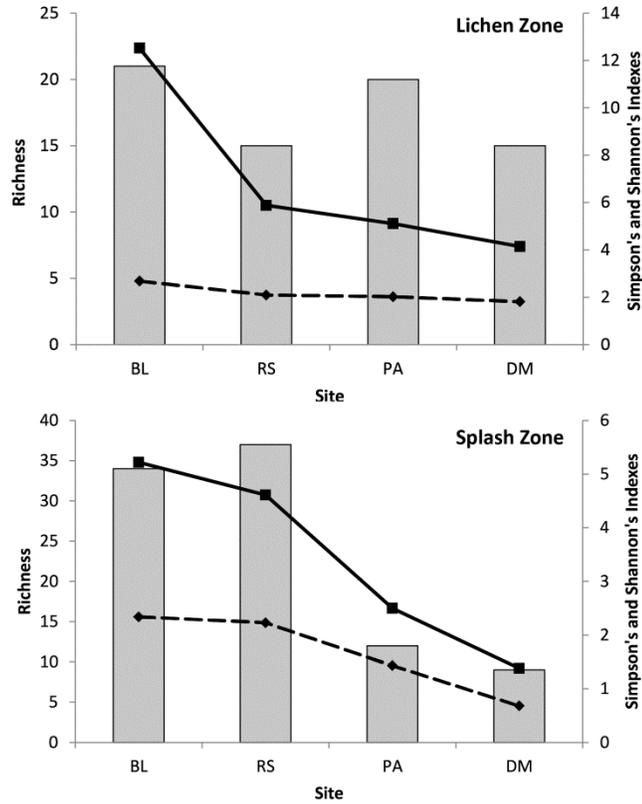
**Figure 4.3:** Combined sample-based species accumulation for 2009 and 2010, including detected species (102), estimated species richness (118), and 95% upper confidence interval (147).



**Figure 4.4:** Distribution of abundances for chironomid species on a log10 (x+1) scale (A), singletons (\*) noted, and number of species per quantile categories (B), Isle Royale, 2010.

### *Alpha diversity – Simpson and Shannon Indexes, and Site Richness*

As in 2009 (Chapter 3), species richness and Simpson's and Shannon's indexes provided generally equivalent results at each site (Figure 4.5). Species richness in the lichen zone was stable among the four sites with between 15 and 21 species. Richness among sites in the splash zone was sharply variable, with one cluster of 34 and 37 species, and another with nine and 12 species. This variability can be seen in the slopes from rank-abundance plots of log-transformed abundances, where shallower slopes indicate greater evenness in the assemblage and steep slopes indicate dominance by individual species (Figure 4.6, Tables 4.2 and 4.3). Lichen zone pools have variable but moderated slopes and show greater evenness at Blueberry Cove and Passage Island. Splash zone pools have a greater evenness at Blueberry Cove and Raspberry Island than in the lichen zone, and the steep slopes for Passage Island and Datolite Mine indicate dominance by a single abundant species. One-way ANOVAs (all at  $\alpha = 0.05$ ,  $df = 1, 6$ ) between zones were not significant for richness ( $F = 0.50$ ,  $P = 0.51$ ), Shannon's ( $F = 1.25$ ,  $P = 0.31$ ) or Simpson's ( $F = 2.74$ ,  $P = 0.15$ ). The only exception was Blueberry Cove lichen pools, where Simpson's index was much higher based on a lack of both dominant species or a tail of rare species, and conformed to the standard concept for this statistic as a probability of drawing two different species from the same community.

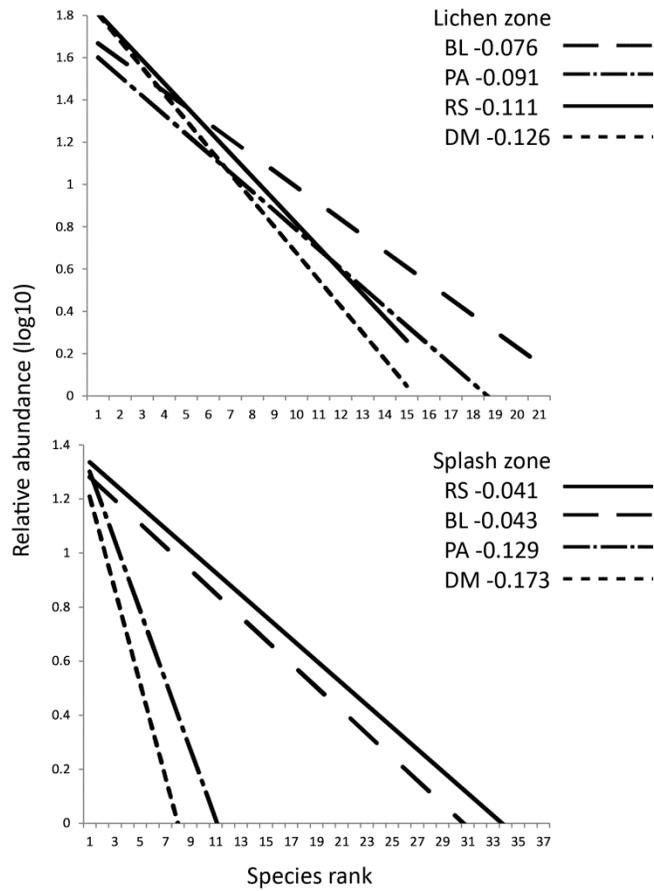


**Figure 4.5:** Chironomidae species richness (bars), Simpson's Index (solid lines) and Shannon's Index (dashed lines) by zone and site, Isle Royale, 2010.

### *Beta Diversity*

Beta diversity tested community similarity across zones and seasons. For the entire study area, 41 of the 51 beta-analyzed species (80%) exclusively occupied a single zone, while 46 (90%) occupied zones at an absolute abundance of  $\geq 90\%$  and were considered to prefer a zone (Figure 4.7). Similarity indices give mixed results (Table 4.4). Communities across the entire study area were significantly dissimilar between the two zones (JAC = 0.196,  $P = 0.05$ ; WPS = 0.146), while at individual sites only Raspberry Island had significant dissimilarity of communities as a function of zone (JAC = 0.167,  $P = 0.05$ ; WPS = 0.088). No zonal results showed statistically significant similarity. Species mean body length was not significantly different between zones ( $F = 2.52$ ,  $P = 0.119$ ,  $\alpha = 0.05$ ,  $df = 1, 44$ ), although splash zone species trended smaller as expected.

In seasonal analyses the two zones responded in opposite ways. Lichen zone communities generally had no clear results, except that significant JAC similarity occurred between May-August and July-August (Table 4.5). WPS supported July-August similarity, but also suggests a seasonal difference between April-June. In contrast, the splash zone had clear seasonal JCC and WPS differences with no indication of similarities. April and May were distinct from June and July, while June and July were also distinct from October. ANOVA results indicate significant mean differences in monthly JAC results between zones ( $F = 13.62$ ,  $P = 0.001$ ,  $\alpha = 0.05$ ,  $df = 1, 28$ ), supporting zonal differences. Proportional emergences by month reveal a small number of unique species emerging in April, July, and August, with a larger assemblage of species unique to June and no unique species emerging in October (Figure 4.8).



**Figure 4.6:** Slopes of species ranks and log-transformed relative abundance ( $\log_{10}(x+0.5)$ ) for two chironomid assemblages separated by zone, including ranked slopes for each site, Isle Royale, 2010. Raspberry Island (RS) solid lines, Blueberry Cove (BL) long dashed lines, Passage Island (PA) dash-dot lines, and Datoilite Mine (DM) short dashed lines. Note scale changes for each axis. See Tables 4.2 and 4.3 for data.

When comparing permanent and ephemeral pools across the entire study area, there was a significantly similar relationship between pool types (JAC = 0.529, P = 0.01; WPS = 0.387). Twenty-four species (47%) exclusively occupied either permanent or ephemeral pools. Analyses from each study site yielded no results departing from randomness, except that Blueberry Cove split results, with lichen zone permanent and ephemeral pools significantly similar (JAC = 0.647, n = 17, P = 0.01) and splash zone pools significantly different (JAC = 0.129, n = 31, P = 0.01). There was no difference in mean species body length between the two pool types (F = 0.56, P = 0.46,  $\alpha$  = 0.05, df = 1, 30).

**Table 4.2:** Ranked species abundances per site in the lichen zone, including log<sub>10</sub> (n+0.5) transformations, Isle Royale, 2010.

PA species	log <sub>10</sub> (n+0.5)	RS species	log <sub>10</sub> (n+0.5)	BL species	log <sub>10</sub> (n+0.5)	DM species	log <sub>10</sub> (n+0.5)
94	1.98	89	1.95	32	1.51	131	2.12
63	1.80	63	1.80	32	1.51	62	1.80
41	1.62	50	1.70	29	1.47	49	1.69
24	1.39	31	1.50	24	1.39	26	1.42
18	1.27	16	1.22	20	1.31	9	0.98
7	0.88	11	1.06	19	1.29	9	0.98
7	0.88	10	1.02	17	1.24	8	0.93
5	0.74	9	0.98	16	1.22	6	0.81
3	0.54	6	0.81	13	1.13	5	0.74
3	0.54	6	0.81	12	1.10	4	0.65
3	0.54	4	0.65	11	1.06	2	0.40
3	0.54	4	0.65	11	1.06	2	0.40
2	0.40	4	0.65	7	0.88	2	0.40
2	0.40	3	0.54	6	0.81	2	0.40
2	0.40	1	0.18	4	0.65	1	0.18
1	0.18			2	0.40		
1	0.18			2	0.40		
1	0.18			1	0.18		
1	0.18			1	0.18		
1	0.18			1	0.18		
1	0.18			1	0.18		

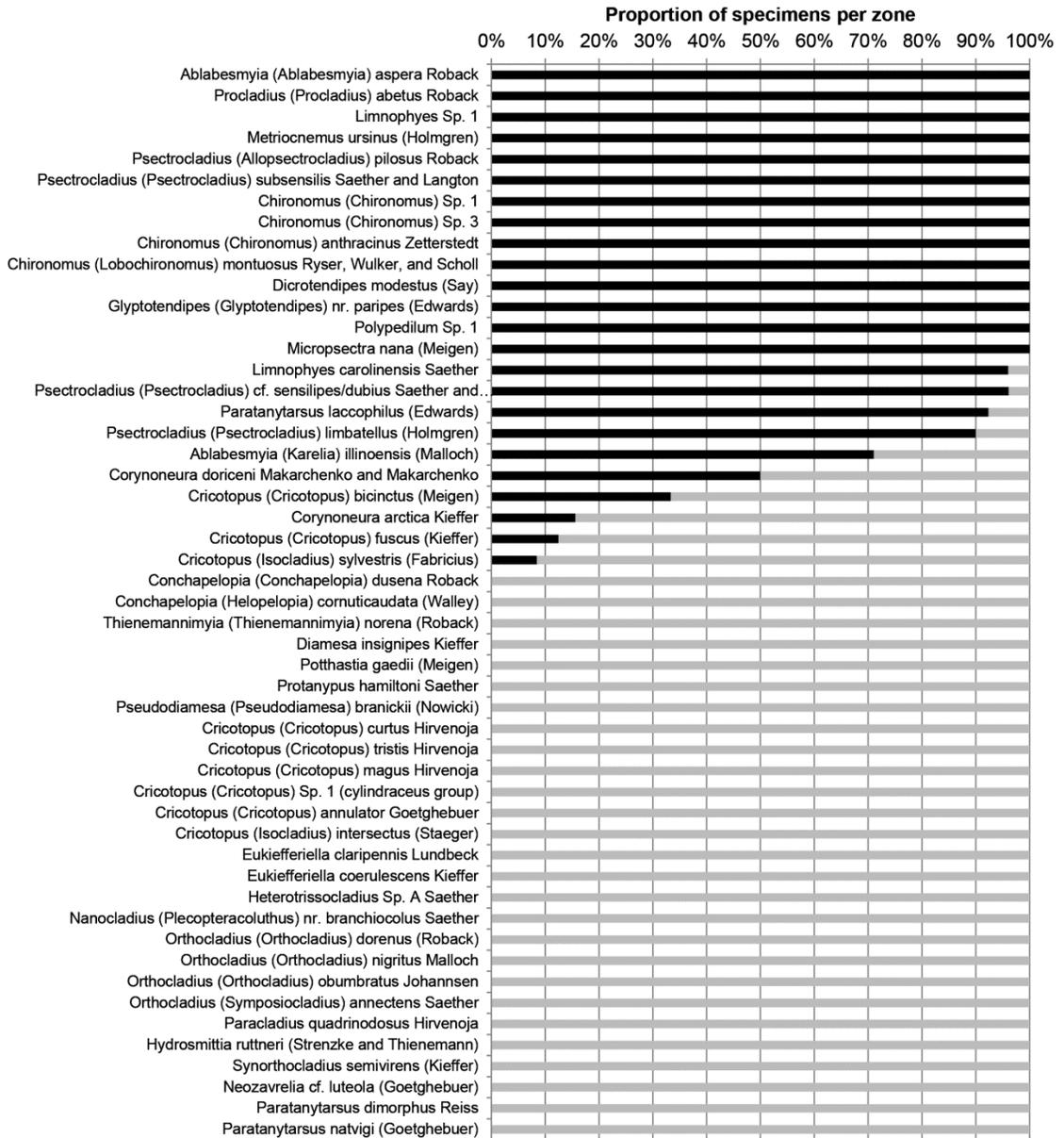


**Table 4.4:** Ranked Jaccard's and Whittaker's zonal beta diversity results for individual sites and the entire study area, Isle Royale, 2010. Dark cells indicate significant dissimilar results of emerging communities across zones, "\*" indicates likely ecologically important result for WPS.

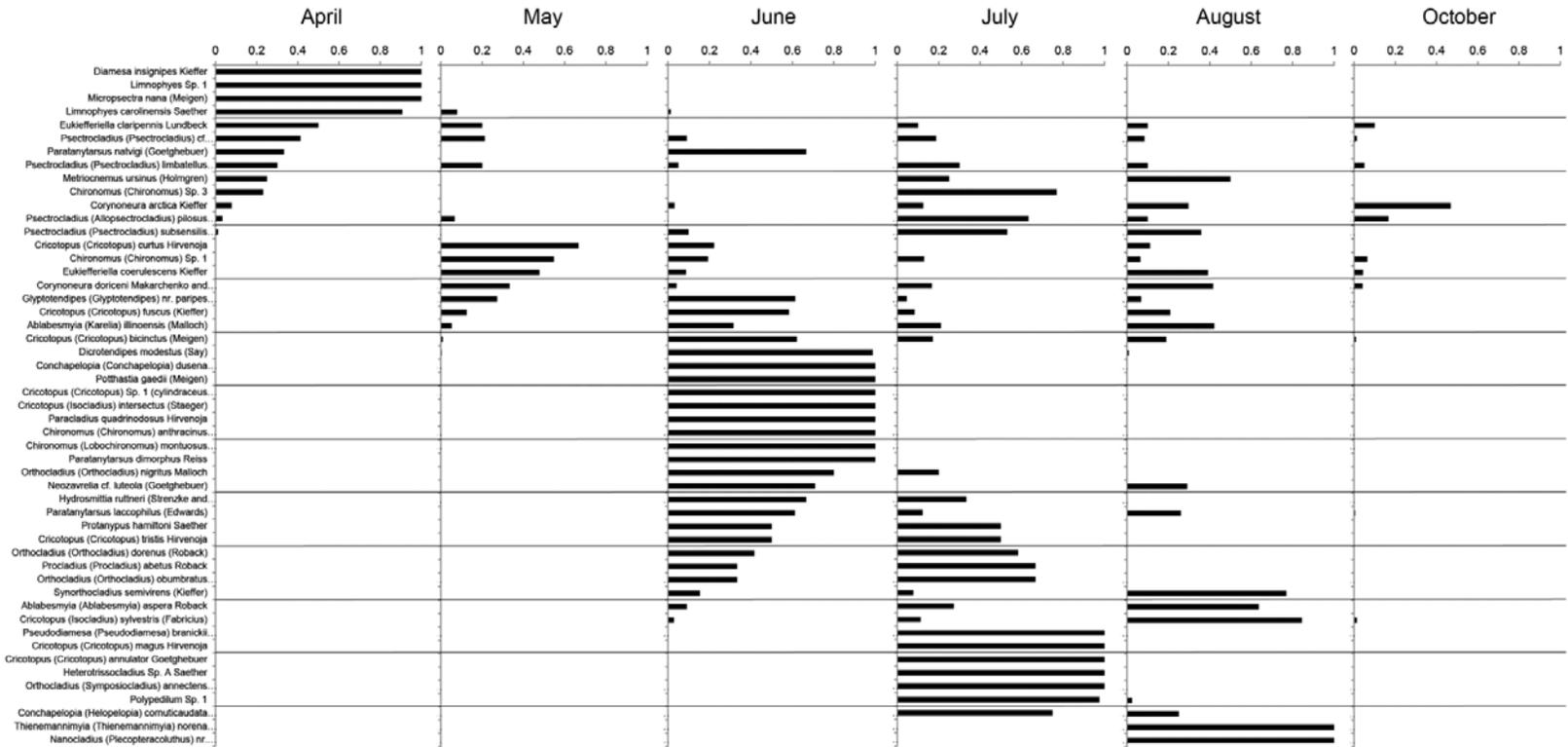
Site	JCC (Rank)	WPS (Rank)
Raspberry Island	0.167 (1)	*0.088 (1)
Blueberry Cove	0.231 (2)	0.253 (4)
Datolite Mine	0.250 (3)	0.115 (3)
Passage Island	0.286 (4)	0.110 (2)
Entire Study Area	0.196	0.146

**Table 4.5:** Seasonal comparisons for Jaccard's (top number in each pair) and Whittaker's (bottom number) across six months, Isle Royale, 2010. Dark cells indicate significant results (*similar* emerging communities in the lichen zone, *dissimilar* emerging communities in the splash zone), "\*" indicates likely ecologically important results for WPS.

	May	June	July	August	October	
LICHEN ZONE	April	0.24	0.24	0.35	0.29	0.21
		0.48	*0.04	0.21	0.11	0.17
	May		0.50	0.40	0.56	0.29
			0.16	0.26	0.21	0.32
	June			0.50	0.57	0.28
				0.23	0.39	0.13
	July				0.79	0.41
					0.61	0.41
	August					0.41
						0.28
SPLASH ZONE	April	0.22	0.11	0.13	0.16	0.22
		0.17	*0.03	0.11	0.14	0.20
	May		0.11	0.08	0.24	0.25
			*0.09	*0.05	*0.10	*0.06
	June			0.44	0.37	0.11
				0.20	0.25	*0.02
	July				0.37	0.13
					0.33	0.13
August					0.31	
					0.20	



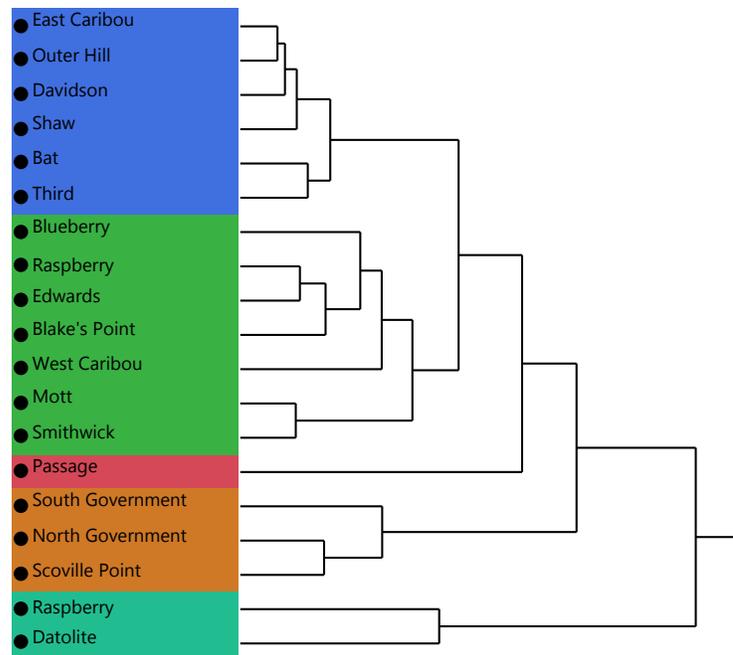
**Figure 4.7:** Proportional emergence of species (n = 51) used in beta diversity analyses, by zone, Isle Royale, 2010. Black bars = lichen zone, gray bars = splash zone.



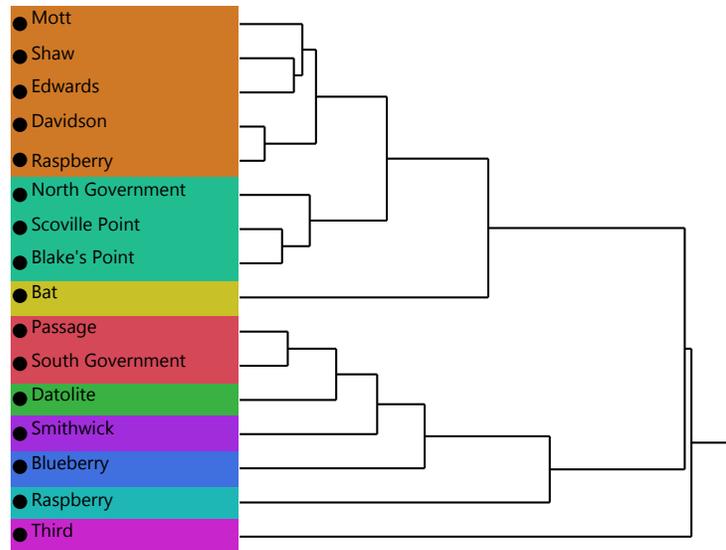
**Figure 4.8:** Proportional emergence of all species (n = 51) used in beta diversity analyses, by season, Isle Royale, 2010.

### *Cluster Analysis*

Clustering for lichen zone pools was inconsistent, with varying relationships between sites in each method, combined with long scalar distances. Splash zone pools had high consistency in relationships and scalar distances, but no sensible or realistic ecological relationships were discovered. As a result, no separate 2010 results are presented. However, in an exploratory analysis, 2009-2010 data were combined (Figures 4.9 and 4.10). Although the varying methods between years makes this particularly tentative, combined results yielded three notable points: 1) the basic east-west distinction in communities from 2009 data (Chapter 3) were retained essentially unchanged for both zones, 2) Raspberry Island samples between years did not cluster together in either zone, creating an interesting spatial conundrum, and 3) the Passage Island lichen zone community was potentially unique.



**Figure 4.9:** Hierarchical clustering (Ward's minimum variance shown) of chironomid communities in lichen zone pools, with combined 2009 and 2010 results, Isle Royale.



**Figure 4.10:** Hierarchical clustering (Ward's minimum variance shown) of chironomid communities in splash zone pools, with combined 2009 and 2010 results, Isle Royale.

### *Habitat Preferences by Species*

The above results focused on community-wide assemblages. For management purposes and future research, identification of species showing either exclusive or preferential occupancy in a habitat ( $\geq 90\%$  occupancy) would be useful. Twenty-five species were detected at abundances (ten or more exuviae per species in 2010) that may be valuable for management actions such as monitoring. Four species can be considered generalists in coastal habitats at IRNP: *Ablabesmyia (Karelia) illinoensis* (Malloch), *Corynoneura arctica* Kieffer, *Cricotopus (C.) fuscus* (Kieffer), and *Orthocladius (Eudactylocladius) dubitatus* Johanssen (details in Chapter 1). Species with exclusive or preferential occupancy of a habitat type are listed in Table 4.6. Five of these species can be considered permanent pool lichen zone occupants, one an ephemeral pool lichen zone occupant and six others representing the lichen zone with no pool type favored. For the splash zone, only one species was typical of permanent pools and one of ephemeral pools, with five additional species favoring the splash zone generally. Finally, two species favored permanent pools regardless of zone.

**Table 4.6:** Chironomidae showing exclusive or preferential ( $\geq 90\%$ ) occupancy of specific shoreline zone or pool type, Isle Royale, 2010. Only species with  $\geq 10$  individuals collected are shown.

Species	Zone		Pool type	
	Lichen	Splash	Permanent	Ephemeral
<i>Ablabesmyia (Ablabesmyia) aspera</i> Roback	X		X	
<i>Psectrocladius (Allopsectrocladius) pilosus</i> Roback	X		X	
<i>Psectrocladius (Psectrocladius) subsensilis</i> Saether and Langton	X		X	
<i>Dicrotendipes modestus</i> (Say)	X		X	
<i>Polypedilum</i> Sp. 1	X		X	
<i>Limnophyes carolinensis</i> Saether	X			X
<i>Chironomus (Chironomus)</i> Sp. 1	X			
<i>Chironomus (Chironomus)</i> Sp. 3	X			
<i>Glyptotendipes (Glyptotendipes) nr. paripes</i> (Edwards)	X			
<i>Paratanytarsus laccophilus</i> (Edwards)	X			
<i>Psectrocladius (Psectrocladius) limbatellus</i> (Holmgren)	X			
<i>Psectrocladius (Psectrocladius) cf. sensilipes/dubius</i> Saether and Langton	X			
<i>Neozavrelia cf. luteola</i> (Goetghebuer)		X	X	
<i>Orthocladius (Orthocladius) obumbratus</i> Johannsen		X		X
<i>Eukiefferiella claripennis</i> Lundbeck		X		
<i>Eukiefferiella coerulescens</i> Kieffer		X		
<i>Orthocladius (Orthocladius) dorenius</i> (Roback)		X		
<i>Synorthocladius semivirens</i> (Kieffer)		X		
<i>Cricotopus (Isocladius) sylvestris</i> (Fabricius)		X		
<i>Corynoneura doriceni</i> Makarchenko and Makarchenko			X	
<i>Cricotopus (Cricotopus) bicinctus</i> (Meigen)			X	

## *Ordination*

Ordination of community composition and water chemistry was used to determine likely chemical mechanisms for variation observed in community assemblages.

Chemistry data included as environmental variables in ordinations, arranged by pool, are shown in Table 4.7, and ordination results in Table 4.8. Chemical parameters included conductivity, total phosphorous, total nitrogen, dissolved organic carbon, dissolved inorganic carbon, chlorophyll-a maximum and mean, ratio of TN:TP, pH (log-transformed for analysis), and  $\text{NO}_3^-$ .

DCA results showed pools from each zone clustering together, with splash pools along axis 1 and lichen pools along axis 2 (Figure 4.11). Species that favored pool types (from Table 4.6) strongly associated with pool clusters while generalist species occurred between the two. Axis one appeared to be a nutrient gradient, centering on phosphorous, nitrogen, and both organic and inorganic carbon resources. Axis two was much weaker, related to either chlorophyll-a or pH. Eigenvalues also showed axis 1 strongly correlated with nutrients, explaining 29% of community variability, and axis 2 was less dominant yet still important, explaining 10% of variability (Table 4.8).

CCA results supported the DCA, with nutrients along axis one and pH and chlorophyll-a most oriented with axis two (Figure 4.12). As suggested by Lepš and Šmilauer (2003), a forward selection was run to limit the number of linked explanatory variables in the final model, using Monte Carlo testing at 599 runs. The simple (marginal) effects, including all linked variables separately, showed nutrients or nutrient-related factors as all significantly important to explaining taxonomic variation, pH also significant, and chlorophyll-a not significant (Table 4.9). The conditional effects showed TN:TP ratio as the most important factor, with pH the second most important, though the “non-significant” factors in this test must be taken with caution because when related to the first factor they tend to strongly drop in significance. No P-value corrections were used during CCA forward selection, but the three options (False Discovery Rate, Holm’s

correction, and Bonferroni correction) all returned similar results (though with varying values of P).

Additional exploratory analyses were done to assess whether other physical or chemical factors were important (not shown in ordinations). Using forward selection and including pool depth, estimated surface area, and dissolved oxygen (mg/L), the same two chemical factors were most important (TN:TP explained 26% of variability,  $P = 0.002$ ; pH explained 10% of variability,  $P = 0.008$ ), with neither depth nor surface area significantly contributing to community variability and dissolved oxygen as potentially defining a third significant axis (7.5% explanation,  $P = 0.032$ ). An important cautionary note for all CCA analyses was that small sample size (number of pools) made significance values potentially unreliable. Nonetheless, since CCA closely matched DCA the results were likely valid and forward selection remains insightful.

Spearman's rank correlations of chemical and physical data, including species richness and abundance and nitrate ( $\text{NO}_3^-$ ) (Table 4.10), illustrated the high degree of linked productivity variables. Significant positive and negative correlations can be observed in Figures 4.10 and 4.11, with positively or negatively clustered arrows. Nutrients (P, N, and DOC) were all significantly positively correlated. Depth and surface area were correlated with each other, as expected from linear regression (Chapter 2), but not to any chemical factor. Species richness and species abundance were also positively correlated only to each other.

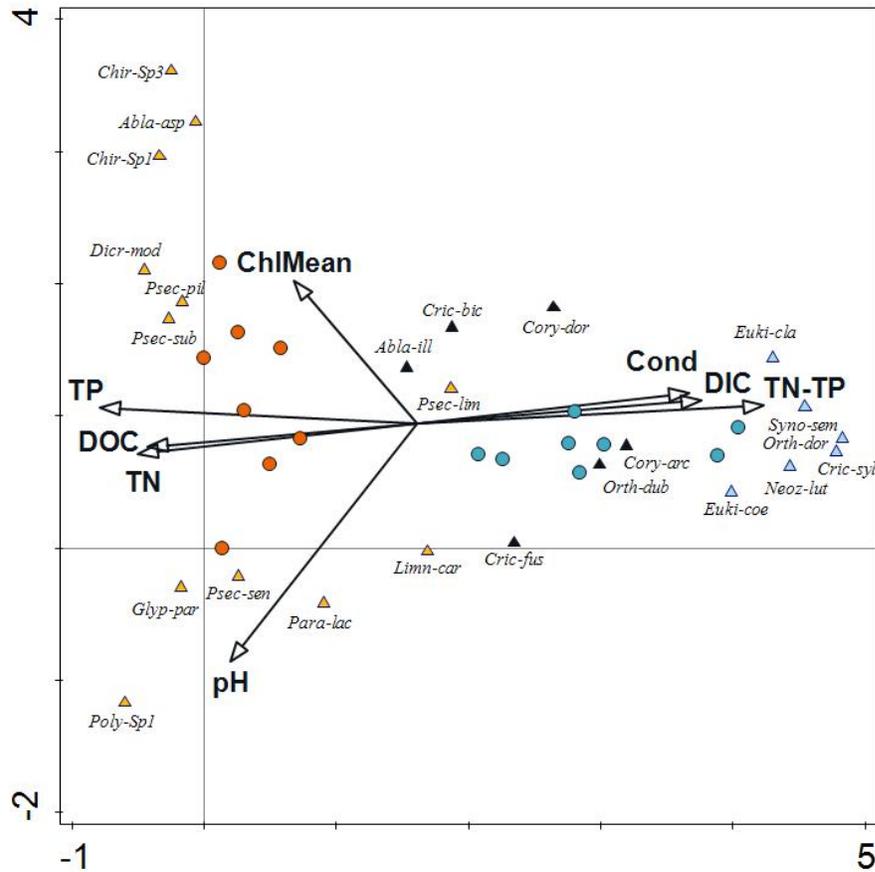
**Table 4.7:** Chemical, physical, and community variables used in ordination analyses. Pools abbreviated by site (Passage, Blueberry, Raspberry, and DatoLite), zone (lichen [shaded rows] or splash), and pool number (permanent pool 1 or 2). All results are mean values from three samples (May, July, October) except chlorophyll-a (Chl) maximum and TN:TP ratio. Lake Superior values (Lk\_Sup) and rainfall values (MI97) included for comparison.

	Cond (mS/cm) <sup>1</sup>	TP <sup>2</sup> (µg/L)	TN (mg/L)	DOC (ppm)	DIC (mg/L)	ChlMax (µg/L)	ChlMean (µg/L)	TN:TP	pH	NO3- (µg/g)	Depth (m)	SurArea (m <sup>2</sup> )	Species Abund.	Species Rich.
PA_L1	0.039	28.04	0.8567	25.64	3.47	0.439	0.362	70.73	7.18	0.199	0.52	1.51	63	10
PA_L2	0.038	28.22	0.6767	25.72	3.54	0.677	0.3913	53.17	6.9	0.016	0.47	5.78	135	14
PA_S1	0.0932	12.12	0.4567	5.127	8.83	1.161	0.573	92.53	8.53	0.095	0.27	0.604	11	5
PA_S2	0.0981	7.26	0.3733	4.58	9.55	0.404	0.2957	131.5	8.49	0.181	0.6	10.8	19	6
RS_L1	0.0394	36.42	0.7233	10.68	4.29	4.263	2.287	43.7	8.02	0.015	0.28	1.13	58	12
RS_L2	0.0305	38.21	0.75	10.28	2.983	2.259	1.98	46.4	7.90	0.007	0.28	3.52	181	9
RS_S1	0.0973	4.89	0.4133	4.14	9.747	0.871	0.5563	191.6	8.15	0.244	0.63	21.4	139	21
RS_S2	0.0971	6.52	0.42	5.56	10.15	0.886	0.6293	167.6	8.23	0.271	0.39	13.6	92	11
DM_L1	0.0171	19.72	0.4767	8.557	1.443	5.18	2.126	51.73	7.82	0.003	0.4	26.9	28	7
DM_L2	0.1093	47.36	0.4667	13.91	10.91	0.337	0.2643	45.63	8.32	0.003	0.63	14.3	138	5
DM_S1	0.1381	11.55	0.375	6.915	10.3	4.016	2.13	114.2	8.84	0.204	0.23	1.42	47	4
DM_S2	0.0673	24.24	0.5933	7.197	7.23	1.145	0.685	115.4	8.2	0.084	0.17	0.864	11	3
BL_L1	0.0707	25.08	0.7367	29.61	6.433	2.495	1.025	65.2	8.15	0.012	0.44	108	34	8
BL_L2	0.0271	36.05	0.6767	23.13	2.293	11.49	4.466	44.53	7.57	0.001	0.42	7.69	110	16
BL_S1	0.0828	8.23	0.3267	7.77	8.923	0.57	0.3173	100	8.66	0.137	0.5	17.1	66	14
BL_S2	0.0969	8.27	0.3733	5.337	9.067	3.91	1.788	128.2	8.89	0.096	0.32	2.11	91	8
Lk_Sup	0.0988	6.22	0.4275	4.379	9.783	0.867	0.5678	172.2	8.02	0.318	--	--	--	--
MI97 <sup>3</sup>	--	--	0.4558	0.8876	--	--	--	--	5.17	--	--	--	--	--

<sup>1</sup> Unit abbreviations: mS/cm = milli-Siemens/centimeter, µg/L = micrograms/liter, µg/g = micrograms/gram, mg/L = milligrams/liter, ppm = parts per million, m = meters.

<sup>2</sup> TP reported in molar units.

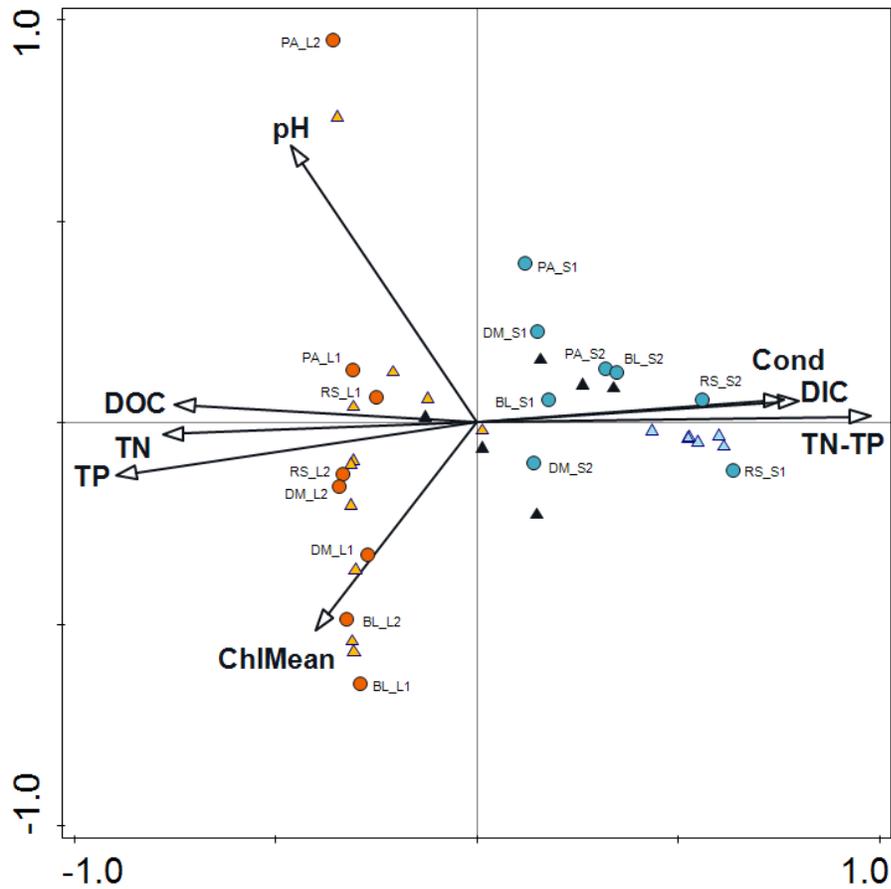
<sup>3</sup> MI97 is a National Atmospheric Deposition Program chemical precipitation station located at Isle Royale; values are means from summer months of 2005-2006 (recent data not available).



**Figure 4.11:** Detrended correspondence analysis results. Arrows are environmental factors, circles are permanent pools (orange = lichen zone [all are left of chemistry origin], blue = splash zone [all are right of origin]), and triangles are chironomid species (colors same as associated pools, black = “generalist” species).

**Table 4.8:** Results of detrended correspondence analysis and constrained correspondence analysis.

		Axis 1	Axis 2	Axis 3	Axis 4
DCA	Eigenvalues	0.7521	0.2677	0.1523	0.0547
	Explained variation ( <i>cumulative</i> )	28.71	38.93	44.74	46.83
	Gradient length	4.04	2.16	2.23	1.32
	Pseudo-canonical correlation	0.9736	0.5656	0.4712	0.7581
CCA	Eigenvalues	0.7143	0.2908	0.2579	0.1769
	Explained variation ( <i>cumulative</i> )	27.26	38.37	48.21	54.96
	Pseudo-canonical correlation	0.9771	0.9874	0.9098	0.9199
	Explained fitted variation ( <i>cumulative</i> )	40.58	57.10	71.75	81.80



**Figure 4.12:** Canonical correspondence analysis results. Arrows are environmental factors, circles are permanent pools (orange = lichen zone [all are left of origin], blue = splash zone [all are right of origin]), and triangles are chironomid species (colors same as associated pools, black = “generalist” species).

**Table 4.9:** Results of CCA forward selection using Monte Carlo testing at 599 runs. Shaded results represent likely significant environmental factors.

	Name	Explains %	pseudo-F	P
Simple (Marginal) Effects	TN:TP	26.4	5.0	0.002
	TP	22.8	4.1	0.002
	DIC	18.9	3.3	0.002
	TN	18.2	3.1	0.002
	DOC	18.1	3.1	0.002
	Cond	17.8	3.0	0.002
	pH	13.9	2.3	0.05
	ChlMean	9.3	1.4	0.158
Conditional Effects	TN:TP	26.4	5.0	0.002
	pH	10.4	2.1	0.006
	DOC	6.3	1.3	0.192
	TP	5.5	1.2	0.24
	Cond	4.8	1.0	0.432
	TN	5.0	1.1	0.364
	ChlMean	4.1	0.9	0.544
	DIC	4.5	1.0	0.486

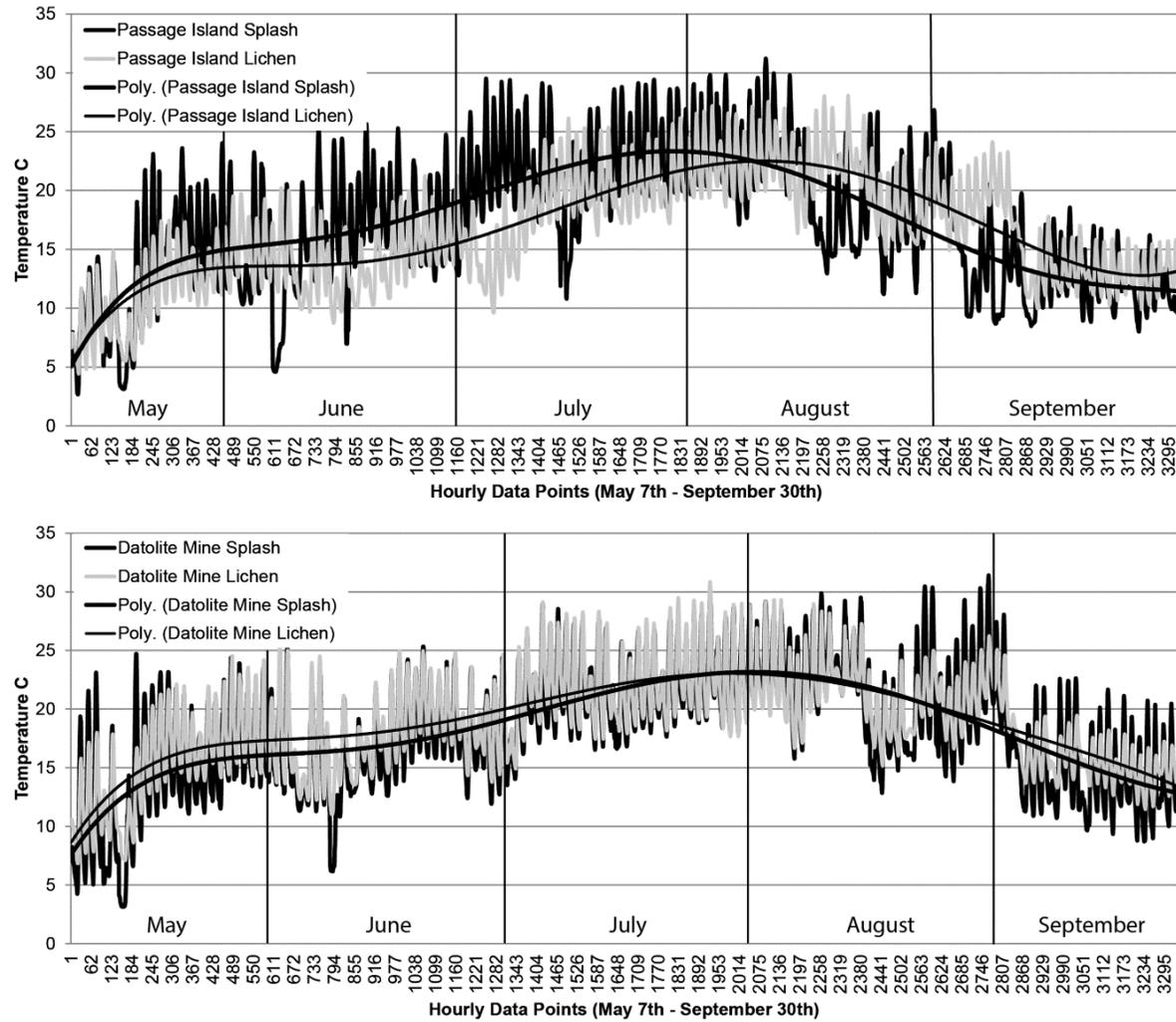
### *Temperature patterns*

Hourly temperatures were logged using thermistors placed in eight of the permanent study pools, four in the lichen zone and four in the splash zone. Peak temperatures were between 27.9-31.3 °C for the lichen zone, and 31.2-31.4 °C for the splash. Minimum temperatures were 4.6-7.1 °C lichen, and 2.7-3.2 °C splash. Overlaying temperature patterns for both zones, Passage and Datolite showed strong mean temperature changes in spring and fall, with peak temperatures generally in late July and early August (Figure 4.13). Lichen zone pools showed a moderated daily fluctuation. Splash zone pools had an exaggerated daily fluctuation and extreme troughs, presumably due to wave inputs. Limiting the timeframe, late May to mid-July illustrated at least two distinct warming trends in pools. Two sampling dates where sharp increases in species accumulation were detected from the splash zone pools at Raspberry and Blueberry appeared to coincide with plateaus following the warming trends (Figure 4.14).

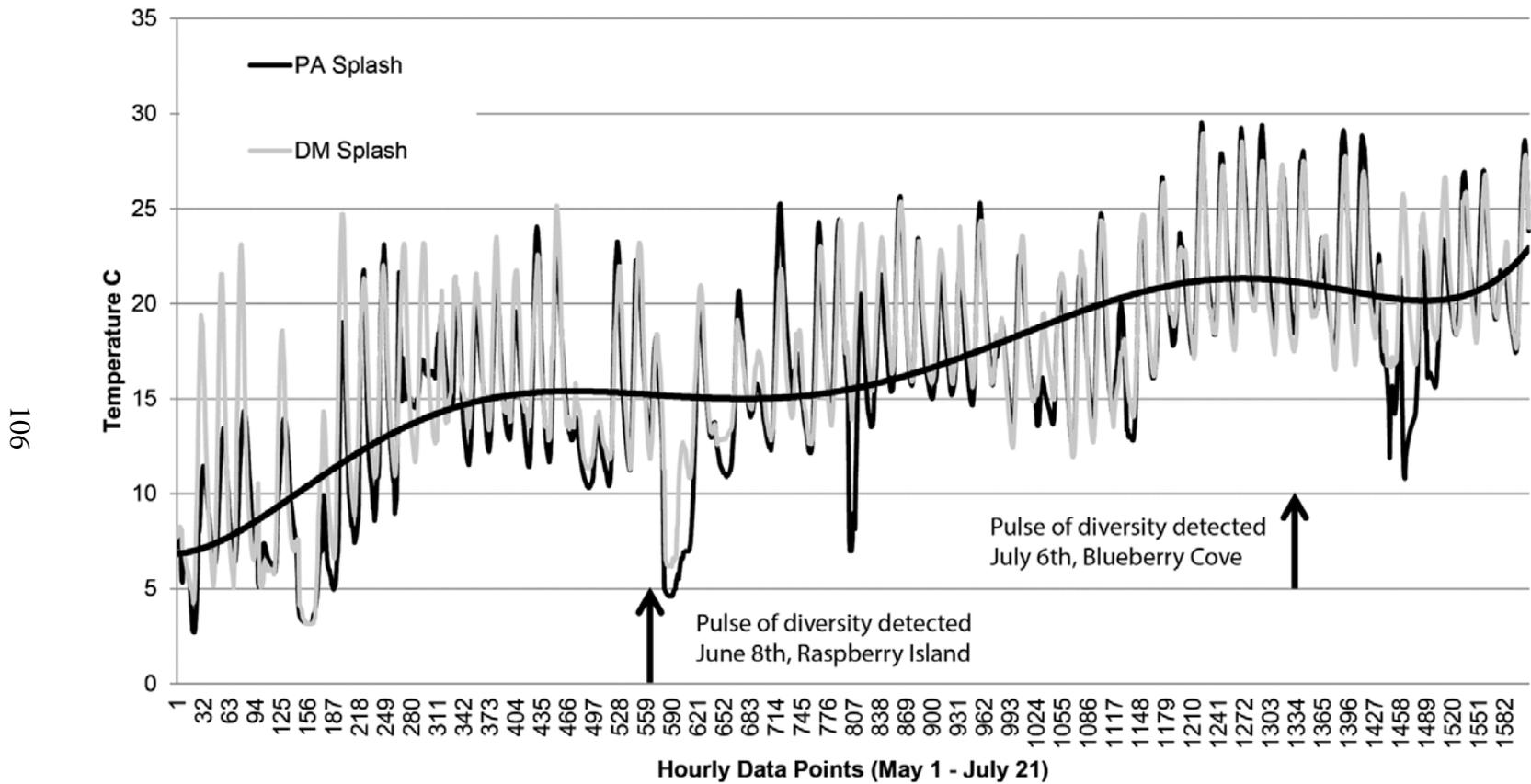
**Table 4.10:** Spearman's Rho rank order calculations for chemical (conductivity, total phosphorous, total nitrogen, dissolved organic/inorganic carbon, chlorophyll-a mean, total nitrogen:total phosphorous ratio, nitrate, pH) and physical properties (max depth, estimated surface area, total species abundance, species richness) of coastal rock pools, Isle Royale National Park, 2010. Shaded correlations are significant at  $P \leq 0.05$ .

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	Cond	TP	TN	DOC	DIC	Chl mean	TN:TP	NO <sub>3</sub> -	pH	Depth	Sur Area	Sp Abun	Sp Rich
Cond	1.00												
TP	-0.50	1.00											
TN	-0.68	0.76	1.00										
DOC	-0.57	0.78	0.76	1.00									
DIC	0.98	-0.49	-0.69	-0.55	1.00								
Chl mean	-0.42	0.22	0.29	0.13	-0.44	1.00							
TN:TP	0.60	-0.91	-0.65	-0.75	0.59	-0.35	1.00						
NO <sub>3</sub> -	0.592	-0.783	-0.500	-0.600	0.578	-0.336	0.8477	1.00					
pH	-0.79	0.54	0.82	0.67	-0.77	0.18	-0.54	-0.428	1.00				
Depth	0.17	-0.09	-0.10	0.14	0.16	-0.67	0.06	0.060	0.19	1.00			
SurArea	0.02	-0.21	-0.15	0.14	0.05	-0.23	0.05	-0.125	0.13	0.67	1.00		
Sp Abun	-0.04	0.24	0.12	0.20	0.05	-0.07	-0.17	-0.081	0.26	0.41	0.30	1.00	
Sp Rich	-0.34	-0.05	0.13	0.20	-0.28	0.04	-0.10	0.058	0.45	0.43	0.34	0.62	1.00



**Figure 4.13:** Daily water temperature variation in splash (black line) and lichen (gray line) zone pools, with 6<sup>th</sup> order polynomial trend lines (from lichen zone pools), at Passage Island and Datolite Mine, Isle Royale, 2010.



**Figure 4.14:** Daily water temperature variation detail with 6<sup>th</sup> order polynomial trend line in splash zone pools at Passage Island and Datoilite Mine, Isle Royale, 2010. The two sample dates with sharp increases of species accumulation are noted.

## **Discussion**

### ***Chao and overall richness***

Seventy species collected in 2010 was less than the 82 species in 2009 (Chapter 3). Although the collection methods were somewhat different between years, and the number of study sites and focal areas of the park were substantially different, the combined accumulation curve results of 118-147 appear to be a good representation of estimated true community richness. These numbers were similar to 2009 accumulation (Chapter 3), but with the important benefits of a Chao 1 estimate that was stabilizing around 120 species and an upper 95% confidence interval converging toward the estimate. Consequently, it appears about 20-40 chironomid species remain to be detected in this habitat.

Forty-nine species were shared between years, while 33 species were only identified in 2009 and 21 only in 2010. Eight of the new 2010 species were found at the only site shared between years, Raspberry Island, suggesting that some of the inter-annual variation is due to shifting local community mosaics. Of species not shared between years, all were very low in abundance except a few with higher numbers detected, presumably during an emergence event.

### ***Alpha diversity***

While simple richness can be a useful indicator of community response to environmental conditions, such as low richness in polluted systems, indexes are also employed to include abundance as an analytical factor (Mason 2002). At IRNP, Chironomidae abundance patterns, with many rare and a few abundant species, were similar at different spatial scales, from the entire study area (gamma diversity) to individual sites (alpha diversity). These patterns followed predictable ecological arrangement in many taxonomically rich communities, including chironomids (Tokeshi 1995). Clear dominance of a single species in 2010 was interesting, with over 1/4 of individuals accounted for by *O. dubitatus* alone, whereas three species were dominant in 2009.

The incompleteness of the known community required caution for species-abundance distributions, but data appeared to fit a truncated log-normal curve at both community and site scales. This curve is typical of many communities, and meta-analyses with matching curves at different scales have been interpreted as showing consistency in the ecological processes that influence communities at both alpha and gamma levels (Ulrich et al. 2010). Results suggest that abundant species are not entirely dominant and the community is relatively stable, particularly in the lichen zone, and that competition may be of limited importance. However, in the splash zone both Passage and Datalogite pools had low richness and were dominated by a single species that was likely outcompeting others (Magurran 2004). The effects of richness on community variability is not consistent across ecological studies (e.g., Lehman and Tilman 2000), but invertebrate communities in coastal pools of Jamaica have shown less variability as richness increases (Romanuk and Kolasa 2002). Notably higher Simpson's index for Blueberry Cove lichen pools probably resulted from groundwater inputs from upland habitats, with tannin-staining observed in one permanent pool from this site. Proportionally few (7%) coastal pools had obvious groundwater sources (Chapter 2), yet these may accommodate distinctly higher diversity and nutrient inputs were not always visually apparent.

In contrast, individual splash zone pools showed volatility in diversity, probably due to patterns of disturbance from wave wash, basin complexity, nutrient limitations, or a combination of these. Particularly low diversity for Datalogite splash pools probably reflected their limited size and complexity, reduced refuge during wave disturbance, and oligotrophic status (Egan et al. in press). Steep relative abundance slopes for Datalogite and Passage suggested those pools had a more disturbed and unstable condition, while shallower slopes at Raspberry and Blueberry indicated greater stability and presumably less disturbance impact due to greater physical complexity for microhabitat refuge (Ulrich et al. 2010). With diversity indices typically employed to measure stressors in and across environments (Mason 2002), it seemed that chironomid communities in both zones

were responding in similar ways, though probably to very different stressors. Richness and abundance varied across sites, but alpha diversity generally supported the idea that chironomid communities were structured and responding to environmental factors similarly on both local and landscape scales.

### ***Beta diversity***

Zonal beta analyses were inconsistent at different spatial scales. JAC showed a clear dissimilarity of communities between zones overall. The site-by-site calculations revealed only Raspberry to have dissimilar zonal communities, but the overall results were probably a better predictor of communities since low richness at some sites negatively influenced statistical power. Contrary to abundance slopes, which suggested a relatively even and stable community at most sites, WPS revealed that one or a few species, typically abundant generalists spanning both zones, could strongly influence results. When *O. dubitatus* was removed from analyses, WPS results dropped considerably, yet no distinct change occurred to JAC. Size differences were also expected between zones, with smaller species that have shorter generation times predicted from the splash zone due to greater disturbance from waves and a reduced development time in response. Many IRNP species were smaller in pupal length than published means, which may be due to population-level variation based on cold lakeshore conditions. However, no significant size differences occurred, though the trend was indeed toward larger body size in the lichen zone.

Seasonal environmental cues, such as photoperiod and temperature, are known to trigger pupation and emergence during optimal conditions (Tokeshi 1995, Pinder 1986). Seasonal emergence patterns were different between the two zones, with stability in the lichen zone and volatility in the splash zone. Beta diversity revealed no lichen zone variation in emergences across seasons, and in the primary biologically active months of May to August assemblages were generally similar. In the splash zone there were three distinct emergence assemblages, roughly following seasonal patterns. Individual species trends showed an intriguing pattern where many species emerging in spring continued to

emerge across all months, yet a large proportion of species were found to emerge only in June and July. This created a unique summer community not due to lack of spring and fall species but addition of many new species. Only a few species were unique to either spring or late summer.

Significant similarity between permanent and ephemeral pools was unexpected since desiccation disturbance is a critical determinant in habitat occupancy for many aquatic invertebrates (Wiggins et al. 1980). With up to 47% of species occupying a single pool type this similarity was even more surprising. As with zonal analyses, low statistical power for site-level analyses was problematic, so the study-wide result was probably more stable and realistic for describing occupancy of pool types. Experimentally comparing a culicid and a chironomid, Arav and Blauenstein (2006) found that neither species was able to detect pool depth and subsequently numerous larvae died upon desiccation. However, the culicid was able to detect and avoid pools with notonectid (Hemiptera) predators and the chironomid was suspected of being unaffected by notonectid predation. A study of rock pools in Utah also determined no particular community response to hydrologic extremes (Baron et al. 1998). Predator avoidance may therefore be more important to chironomids than the risks of pool desiccation. Pool permanence at IRNP also had no clear influence on body size, and although smaller species were expected in ephemeral habitats, these pools had a slight tendency toward longer body length. Ultimately, beta diversity continued to support the 2009 results showing both distinct zonal communities and mixed seasonal assemblages.

### *Cluster Analysis*

Geographic clustering based on chironomid communities for 2010 sites was inconclusive. Results for the lichen zone differed in each method and scalar distances between sites on the dendrograms were generally long, suggesting weak clustering tendencies and no site-to-site relationships (Romesburg 2004). Lack of ecologically reasonable clustering in either zone was probably due to the large distances between sites

and the small number of sites, preventing spatial analysis from revealing potential similarities.

As an exploratory exercise, 2009 and 2010 clustering data were combined. Previous 2009 clusters remained virtually unchanged in both zones and interpretation can remain the same as in Chapter 3. The 2010 splash zone sites generally clustered together, creating an awkward spatial similarity where distant sites showed more similarity than nearby sites (e.g., in the lichen zone Passage Island and Datolite Mine were more similar than Passage Island and Blake's Point). Beyond supporting 2009 clusters, only two results from 2010 are worth mentioning. First, in neither zone did Raspberry, the only site sampled in both years, cluster together, signaling that community turnover occurred in approximately the same pools. Second, for lichen zone pools, Passage Island showed some indication of hosting a unique community by consistently forming its own cluster of one object, yet it remained nested between other clusters.

It is generally thought that chironomid dispersal is passive, with swarms or habitat-seeking gravid females moved by wind, but there is also some evidence for directed oviposition flights of up to 850 m (Armitage 1995). This distance is enough to "island-hop" along the chain of islands formed by submerged ridges at IRNP, but not enough to effectively cross the wider channels where wind is stronger, and far too short for directed flight to Passage Island.

### ***Habitat Preferences by Species***

Ecological generalists tend to occupy temporary habitats, with high tolerances for variable conditions (Wiggins et al. 1980), and the most abundant IRNP species followed this pattern. Of the species collected in suitable numbers, many are known as habitat generalists, occupants of small, standing water bodies, or are found in oligotrophic lakes (Chapter 1). While many species were too rare for confident classification by habitat, some categorizations appeared reliable. Four species in 2010 were habitat generalists: *Ablabesmyia illinoensis* is a predator of invertebrates, though this genus can feed on

detritus, algae and diatoms when necessary (Vallenduuk and Moller Pillot 2007), found in broad habitats, and widely distributed in the Nearctic (Roback 1971, Roback 1985). *Corynoneura arctica* is found in northern and alpine pools and lakes, and not commonly collected in the Nearctic (Oliver et al. 1990). *Cricotopus fuscus* is known from the eastern Great Lakes and is typical of lotic systems or lakes (Hirvenoja 1973). *Orthocladius dubitatus* has a very broad habitat and geographic range, including marine coastal pools (Oliver et al. 1990, Cranston 1998, Colbo 1996).

Any future targeted monitoring or sampling could utilize species that were known to occupy particular subsets of habitat. Of species preferring the lichen zone, only five were also permanent pool occupants (*Ablabesmyia aspera*, *Psectrocladius pilosus*, *P. subsensilis*, *Dicrotendipes modestus*, and *Polypedilum* Sp. 1), and six had no preference for pool type (*Chironomus* Sp. 1, *C.* Sp. 3, *Glyptotendipes* nr. *paripes*, *Paratanytarsus laccophilus*, *Psectrocladius* cf. *sensilipes/dubius*, and *P. limbatellus*). Likewise, six species preferred the splash zone (*Orthocladius obumbratus*, *O. dorenius*, *Eukiefferiella claripennis*, *E. coerulescens*, *Synorthocladius semivirens*, and *Cricotopus sylvestris*), with one more also preferring permanent pools (*Neozavrellia luteola*). Only two species preferred ephemeral habitats, with both *Limnophyes carolinensis* and *Orthocladius obumbratus* typical of seeps or wet margins of lotic systems (Saether 1990, Simpson and Bode 1980). Slow-flowing seeps are somewhat common along IRNP shores and may host additional niche-specific taxa. All of these species are good candidates for intensive studies on ecological responses by particular taxa. These may also act as successful indicator species for detecting community changes over time, but given the limited number of abundant chironomid species it may be more useful to collectively track species by habitat category. This would stabilize assessments and could be incorporated into a biotic index.

Regardless of zonal occupancy, nearly all chironomid species can be considered collector-gatherers or scrapers of some type (Berg 1995). Predators in pools did not seem either diverse or common. Odonata, Dytiscidae, Notonectidae, predaceous Chironomidae

(including *Ablabesmyia* spp. listed above), and possibly predaceous Corixidae were present, though in very low abundance and absent in the majority of pools (Egan et al., in press). Odonates may be important in controlling chironomid populations in a limited subset of pools (Van Buskirk 1992). Diving beetles have been observed moving between pools, but chironomids, tadpoles, and zooplankton can often escape predation pressure in pool habitats.

### ***Ordination and Water Chemistry***

Water chemistry is determined by a suite of complex and interacting factors. Chemical composition of permanent rock pools was related to chironomid community responses (no chemistry data were collected from ephemeral pools). Lake Superior appeared to have a strong influence on pools in the splash zone, particularly in terms of nutrients and ions, and was clearly a primary driver of biotic variation.

Both DCA and CCA results suggested nutrients were primarily responsible for the arrangement of chironomid communities, with oligotrophic conditions in splash zone pools and mesotrophic conditions in the lichen zone. These results fit well with clustering of lichen versus splash pools along axis one of the ordinations. In addition, pools arrayed along axis two suggested weathered ions were retained in lichen pools and washed out of splash pools. There was a lack of correlation between pool size and chemistry, providing additional strength to diversity data that shows significant similarity between permanent and ephemeral pools. Spearman's rank testing showed depth and surface area were significantly correlated, supporting regression from the entire study area (Chapter 2). In studies that find depth as the primary factor in community arrangement, a focus on strictly ephemeral pools indicate they may not be directly comparable to the current study (Vanshoenwinkel et al. 2010).

Saether (1979) found chironomid assemblages in lakes to correlate to both phosphorous and chlorophyll, with the availability of food the primary mechanism determining chironomid distribution patterns. Chlorophyll-a also showed that splash

pools were oligotrophic and lichen zone pools spanned oligotrophic-to-mesotrophic conditions, and the chl-a relationship to ordination axis one supported the idea that lichen zone pools were driven by biological processes. Total nitrogen to total phosphorous ratios are often used to indicate which of these key nutrients is limiting to productivity. Generally if the molar ratio exceeds 35:1 phosphorous is considered the limiting factor (Mason 2002). For IRNP samples, all molar ratios were well above this number (range 77 – 625, mean 236) except one reading in July from a Datolite lichen zone pool of 24. Total phosphorous for that pool was 50 ug/L, far above other readings, and it was one of the few pools in our study that received consistent upland inputs directly from overland flow. Phosphorous correlations with productivity were not as simple as either single or mean readings, but based on consistently P-poor conditions. Highest readings of P and N generally occurred in July, yet both were in low amounts as expected in pools with typically very small watersheds. Wave inputs from Lake Superior, which like many large lakes has low phosphorous availability relative to nitrogen (Finlay et al. 2013), were likely driving community changes via water replacement. In addition, reduced nitrogen availability from the lake may be due to summer plankton uptake, though the offshore drawdown is relatively small (Kumar et al. 2011). Chironomid communities have often been linked to trophic status and nutrient ranges (e.g., Luoto 2011), and IRNP rock pools showed similar patterns with nitrogen, phosphorous, and chlorophyll.

Readings of pool pH were either neutral or basic (range 6.65 – 9.02), and in a range of healthy levels for aquatic biota. While ordination suggested pH was the second most important factor, there was no apparent relationship between nutrients and pH in the ordination. However, pH was correlated positively with nutrients and negatively with DIC in Spearman's rank test. This suggests that pH was influenced by photosynthetic activity instead of ions from the weathering of volcanic, andesitic bedrock. Dissolved inorganic carbon, a source of carbon for photosynthesis, is closely related to pH and acts as an important buffering agent. DIC is typically homogenous across Lake Superior, with changes related to photosynthetic depletion (Zigah et al. 2012), as shown in lower DIC in lichen zone pools. Dissolved organic carbon was the closest chemical metric related to

pH in ordinations, probably based on addition of nutrients, increased primary productivity, and thus contribution to photosynthetic reductions of H<sup>+</sup> ions. Higher DOC in lichen pools again showed upland influence, which was only visibly apparent via tannin staining in some pools, and lower DOC in splash pools indicated wave wash influence. Conductivity indirectly measures ions and thus trophic levels. Weathering processes from bedrock are likely the most influential to conductivity levels, though temperature changes and pool drying are also important. Conductivity readings were low, particularly in splash pools, mirroring other trophic indicators like N and P.

All nutrients were also significantly positively correlated with pH, but were negatively correlated with conductivity and DIC. These contradictory correlations suggested primary productivity was responsible for pH variation, and significant negative correlation of pH to conductivity and DIC supported this by suggesting that weathering was not influential to pH.

Overall, pool chemistry suggested a gradient from relatively nutrient and DOC-rich pools higher on the shoreline, to low-nutrient controls in pools near the lakeshore due to frequent inputs of highly oligotrophic water from Lake Superior. In addition to nutrient poor conditions, near shore pools were highly disturbed by waves and may have been more influenced by UV solar radiation because of low DOC concentrations. Influential factors appeared to include degree of connection to upland nutrient sources, photosynthetic processing of carbon, and proximity to wave disturbance. Wave influences presumably acted via a combination of removal of higher nutrient water and addition of low nutrient water. Chemical factors in IRNP pools fell within ranges of clean water for healthy ecosystem functioning.

### ***Temperature Patterns***

Temperature is a key factor in determining chironomid growth and development, and is probably a key environmental trigger for developmental responses (Wiggins et al. 1980). Changing water temperature is often not a problem for macroinvertebrates (Mason

2002), which can usually seek better conditions, yet pools do not allow chironomids to move when conditions change. Unexpectedly, splash zone pools from two sites were as warm as or warmer than lichen zone pools, even though regular input of waves and direct adjacency to the cold lake were expected to keep splash pools colder, particularly at a windy location like Passage Island. Lichen zone pools had a moderated daily fluctuation, while splash zone pools had much stronger fluctuation, perhaps due to lower overnight bedrock temperatures in proximity to the lake. A species such as *Eukiefferiella claripennis*, exclusive to splash zone pools and known to be eurythermic, may be a good indicator of the widely fluctuating daily temperature regime.

Temperature peaks of 31°C were high and may reach thermal maxima for some chironomids, though this may vary for different life stages (Eggermont and Heiri 2012). Elevated temperatures influence physiological stress responses, such as producing heat shock proteins, shifting metabolic activity away from growth and feeding, or increasing respiration behaviors (Dahlhoff et al. 2002, Eggermont and Heiri 2012). Failure of chironomid eggs to hatch is known from about 30-35 °C, and some larvae may enter diapause or aestivation to avoid warm summer temperatures (Tokeshi 1995). High temperatures were clearly related to small volumes of water in pools heated by solar radiation in unshaded habitat. Distinct splash zone temperature drops were likely related to windy days when large waves mixed surface waters of the lake and washed it into pools, but daily temperature means were unexpectedly similar between zones and suggested only irregular lake input.

Spring warming at IRNP is typically slow and often weeks behind mainland and inland areas. Steadily rising pool temperatures could be observed throughout the summer, and a strong, distinct transition to cold autumn weather patterns regularly occurs within days to a week (Egan, personal observation). Lake Superior water temperature patterns show a deeply mixed condition until May, with stratification occurring from June to October (Kumar et al. 2011). Limited diversity and abundances emerging in spring and fall were likely due to distinctly colder water temperatures, limiting primary production

and signaling a need for organisms to prepare for winter conditions. Chironomids in cold habitats where the breeding season is short, like IRNP coasts, may overwinter as prepupae, quickly emerging after a spring temperature cue (Armitage 1995).

Chironomid diversity is often higher in oligotrophic bodies of water when compared to eutrophic systems, though biomass is lower (Luoto 2011), and although this pattern is not universal it did occur in IRNP pools. Detection of species richness pulses in splash zone pools was previously suspected as indicative of exuviae inputs by wave action (Chapter 3). Bulk exuviae additions had been observed on windy days, although study design avoided this problem by not sampling after windy weather. Diversity pulses in 2010 followed several days of calm conditions following increasing temperature trends. Under these conditions, exuviae can be expected to neither wash into nor out of pools, limiting false or missed detections. Chironomids are known to respond to increased temperatures with faster growth and development (Pinder 1986). As a result, water warming trends could have allowed more rapid development, along with signals to chironomid larvae that meteorological conditions were improving for emergence and swarming (Armitage 1995), thus increased diversity detected at emergence. This pattern has also been noted for emerging chironomids in lotic systems of Pennsylvania (Coffman 1973) and Kansas (L. C. Ferrington, unpublished data). Emergence during calm periods has the added benefit of reducing problems associated with mating and egg laying in windy conditions. Additional evidence suggesting a lack of sample pollution from wave wash was that of the three genera known to inhabit Lake Superior in the vicinity of Isle Royale (Cook 1975), only *Heterotrissocladius* was detected in splash zone pools and only in very low numbers. Finally, pool chemistry is significantly similar to Lake Superior (Egan et al. in press), removing a potential problem for washed-in larvae that may survive and finish development in warmer pools even if eggs or larvae had been in Lake Superior.

### ***Community Responses to Non-natural Disturbance***

The two human-influenced factors expected to be of greatest influence on rock pool habitats are pollution and climate change (see general discussion in Chapter 3). Basically, relatively short-term and localized impacts can be expected to follow spills, but climate is likely to permanently shift entire communities due to fundamental environmental changes and biotic responses (Woodward et al. 2010).

For oil spills, hazardous material would cause acute coastal problems across a limited range in calm weather, while in stormy conditions impacts could be widespread and difficult to manage. Rebound of communities is uncertain, but chronic problems may be limited by easy pollutant transportation into Lake Superior and subsequent collection or dilution, though sublethal effects may persist (Mason 2002). Unexpected responses occur following pollution events, such as reduced predator numbers due to reduced prey, or tolerant organisms increasing in relative abundance with a lack of competition, but generally communities are expected to become more simple (Mason 2002). Of species detected in 2010 that are influenced by pollution, four are known to be tolerant of pollutants and oil wastes, including *Cricotopus bicinctus*, *C. intersectus*, *Prodiamesa olivacea* and *Dicrotendipes nervosus* (Oliver and Dillon 1988, Simpson and Bode 1980, Andersen et al. 2013). *Chironomus* species may also fall into this category, increasing following spill impacts. Most other species are likely to be negatively impacted by spills, either via direct mortality or indirectly due to impacts on food resources like algae and diatoms. Rare species with disjunct ranges would be at particular risk for extirpation.

Changes due to trends in climate may have a more fundamental impact on coastal pool communities. Due to variable hydroperiod and temperature, which could include lethal temperatures for many species, energetic costs may become higher under warmer conditions (Little et al. 2009). Although lake levels have always fluctuated naturally, anthropogenic climate change and increased water usage may contribute to much lower levels (Larson and Schaetzl 2001), while other studies suggest only moderate annual fluctuations (Mackay and Seglenieks 2013). Factors leading to community variability

across zones may compromise resilience to or rebound from intensive disturbances. Based on known ecological niches (Chapter 1), many cold stenothermic species detected in IRNP pools may be lost under a warmer temperature regime where mean temperatures are notably higher, and new generalist species may establish. Therriault and Kolasa (2001) found that regular desiccation of pools had reduced community variability, presumably due to specialized species taking advantage of fast generation times and high colonization rates, though at the cost of lower overall diversity. Consequently, less predictable precipitation patterns may not lead to loss of temporary pool specialists. A number of chironomid genera are able to survive larval desiccation, reviving within hours or days of rewetting, though not all individuals survive (Grodhaus et al. 1983). The current results showed only two chironomid species (*Limnophyes carolinensis* and *Orthocladius obumbratus*) at IRNP apparently having the strong r-selected traits to take advantage of pools likely to become dry.

Chemically, expected changes in climate could modify ratios of carbon, phosphorous, and nitrogen in food sources, leading to shifting competitive interactions. For example, rising CO<sub>2</sub> could increase C storage in allochthonous material, reducing the nutrients available and causing shifts toward different food sources (Woodward et al. 2010). It has also been shown experimentally that chironomid emergence will advance by weeks if temperatures are elevated (Armitage 1995).

The impetus for coastal studies was a perception among federal managers that specific threats to coastal systems were underappreciated and habitat dynamics were not well understood (Lafrancois and Glase 2005). Of the three threats identified, climate change and pollution from shipping spills have been considered in previous chapters, while increased visitor traffic was not included since direct visitor impacts at IRNP are likely to remain minimal regardless of visitation numbers. For addressing direct human threats, studies would be productive in state parks along the Minnesota shore, where bedrock and habitat arrangement are very similar to IRNP and access is easy with high summer visitation (Egan, personal observation).

## **Concluding Remarks - Descriptive Models for Observed Community Patterns**

Several hypotheses may be invoked to shed light on rock pool community structure: 1) resource availability, where basal resources influence energy transfer and predator diversity; 2) stability, where intensity and frequency of disturbance changes food chain length; and 3) ecosystem scale, where spatial bounds are related to variable community complexity (Sabo et al. 2009).

### ***Productivity and Nutrients***

Among the many theories explaining patterns of freshwater biodiversity, current results suggest that a nutrient-based model may describe much of the community variability for rock pool Chironomidae (Stendera et al. 2012). Increasing nutrients should lead to increased growth and productivity in both consumers and predators (Menge et al. 2002). IRNP pools have highly oligotrophic conditions in the splash zone and somewhat mesotrophic conditions in the lichen zone, along with uncommon predator occupancy. Therefore, nutrients are low, restricting consumer productivity and limiting the ability for a diverse and abundant predator community to thrive. Certainly there are pools with a more developed food web, generally those fed directly by upland sources, but the majority of pools appear to be regulated by a nutrient model and probably resemble a simple food chain (Sabo et al. 2009).

For additional clarity on food webs, stable isotopes of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) could be used to determine the origin of nutrients and the trophic position of top predators (Sabo et al. 2009). Most pools should show short, bottom-up food chains, but mesotrophic pools with stable upland inputs may show complex interactions of primary producers, diverse consumers, and multiple predators exerting some top-down control. Clarifying the food webs of different pool types would be useful in understanding communities and pursuing more detailed studies (Little et al. 2009). For example, greater nutrient availability in lichen pools may allow larvae to grow faster and avoid small predators, when they are present, while slow growth in splash pools should be less

important in the absence of predators (Tokeshi 1995). Splash pool occupancy by consumers should be a way to spatially avoid predation pressure.

### ***Environmental Stress***

Environmental stress is a commonly observed factor in coastal community dynamics, although most disturbances are not extreme enough to cause species loss or high mortality (Platt and Connell 2003). Stress from disturbance, both mechanical from wave wash and hydrological from desiccation, were expected to be crucial factors in arrangement of chironomid communities. No strong indication was observed for desiccation in controlling community patterns, even though two species may indeed be ephemeral pool specialists, and creation of drought-resistant cocoons is known in many genera (Wiggins et al. 1980). When it comes to wave action, larval collections to verify genera occupying the splash zone revealed that individuals occupied refugia such as cracks and often enhanced natural refuges by creating silk retreats, which probably reduces predation pressure and dislodgement risk (Berg 1995). In general, waves may be more important by controlling nutrients or chemistry, instead of directly impacting occupancy. Storms that bring stronger mechanical scouring appear to be limited to fall and winter months when pool occupants are likely in winter refugia or ice cover protects pools. Mechanically stressful conditions may limit free-living predators, with consequently limited controls on prey (Menge et al. 2002).

A stress factor that may be broadly important is temperature. Measurements revealed peak temperatures reaching close to lethal temperatures for some aquatic organisms, or at least levels where stress responses should lead to sublethal effects. A method for measuring this would be to use a combination of heat shock proteins (HSPs) and RNA:DNA ratios for organisms in the same pools (Menge et al. 2002). Theoretically, HSPs should be high in pools across both zones (due to similar daily temperature peaks), but experimental shading could determine if lower HSP production occurred, and additional HSP production may occur in pools with the additional stressor of wave action. RNA:DNA can measure short-term growth as an indicator of nutrient availability. Direct

measurements of wave energy, both on the rock face near pools and in deep parts of pools, could help determine if wave action is an important disturbance factor or if it only delivers cold, low-nutrient water to pools, thus changing the nutrient regime during biotically active months (Denny 1995, Murray et al. 2002). Except for irregular events, water temperature patterns suggest that the lake is only occasionally exerting a strong physical influence during summer months. Stable air leads to lower wave conditions in spring (Austin and Coleman 2007), and in winter pools are likely frozen, a typical condition in Minnesota shorelines with similar bedrock context (personal observation). Autumn storms probably have the strongest physical exertion on coastal pools, and macroinvertebrates that have not taken refuge may be significantly impacted.

### *Spatial Arrangement*

Ecological systems often form a mosaic defined by spatial scales, with constantly mixing local community components over time within a larger spatial framework that remains temporally stable (Little et al. 2009, Lehman and Tilman 2000). Consideration of smaller scale population structure is likely to increase understanding of influential mechanisms (Hanski and Gilpin 1991). Individual habitat patches with different mechanisms may range from having stable long term conditions to unstable conditions that continuously reset the successional clock (Denny 1995, Berlow 1997). Individual samples may show high variability while stability occurs across a broader landscape. Results from coastal rock pools in Jamaica suggest this pattern, with greater stability at a community scale as richness increases and populations respond to local environmental factors (Romanuk and Kolasa 2002).

Alpha and beta diversity both support a mosaic model, with variable results across sites and between years. Geography is suspected of playing an important role at IRNP. Short-range distances are often not problematic for dispersing aquatic organisms, with local environmental variables, such as water chemistry, effectively determining assemblages (Vanschoenwinkel et al. 2007). Yet there was indication that dispersal across windy channels or gaps between islands limits colonization to strong dispersers or

stochastic events (Chapter 3). In addition, intermediate spatial patterns for communities are known to be inconsistent (Fraschetti et al. 2005). Raspberry Island, with similar pools sampled in both years, had different communities between years in both zones, indicating that variable assemblages occurred in the same pools across years. Initially, it was suspected that the warmer, more protected conditions on the Isle Royale shores, where dispersal could occur along shorelines, would lead to very different species assemblages compared to Passage Island, which is small, distant from mainland populations, and presumably challenging to disperse to. Unfortunately, 2010 sample size was too small and distances between sites too large to adequately detect meaningful geographic variation.

### ***Rarity and Abundance***

A substantial proportion of diversity consisted of rare species that were probably collected randomly, and a large proportion of relative abundance was represented by a handful of species. With twenty-two new species collected in 2010 and an estimated large amount of undetected diversity overall, additional sampling would be needed to determine a pattern of either continuing species accumulation or a tapering of new detections. However, for species newly encountered at Raspberry Island in 2010, fewer than seven individuals were collected, so that these uncommon or rare species may have been present but undetected in 2009, supporting abundance-based detectability for most species. Similar to Raspberry Island, the other species newly detected in 2010 were also rare ( $\leq 3$  individuals), except for *Ablabesmyia aspera* Roback with 11 individuals, and *Polypedilum* Sp. 1 with 41 individuals that were nearly all from a single emergence event. Targeted sampling of habitat niches or expanded sampling to detect univoltine species with narrow emergence times may overcome some of the challenge in detecting rare species.

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## **APPENDICES**

**Appendix A:** Full names for Chironomidae described in text: Genus (subgenus) species and Authority. Authority name in parentheses if original description was in a different genus; L = Linnaeus, F = Fabricius. Cf. = compare to named species, but with current evidence material cannot be confirmed as that species; nr. = keys to or near named species, but is not that species based on the original description.

<b>PODONOMINAE</b>	<b>2009</b>	<b>2010</b>
Parochlus kiefferi (Garrett)		X
<b>TANYPODINAE</b>		
Ablabesmyia (Ablabesmyia) aspera Roback		X
Ablabesmyia (Ablabesmyia) monilis (L)	X	
Ablabesmyia (Karelia) illinoensis (Malloch)	X	X
Conchapelopia (Conchapelopia) fasciata Beck and Beck	X	X
Conchapelopia (Helopelopia) cornuticaudata (Walley)	X	X
Procladius (Holotanypus) abetus Roback	X	X
Procladius (Holotanypus) nr. culiciformis (L)	X	
Thienemannimyia (Thienemannimyia) norena (Roback)	X	X
Zavrelimyia cf. melanura (Meigen)	X	X
<b>DIAMESINAE</b>		
Diamesa insignipes Kieffer		X
Pagastia orthogonia Oliver	X	
Pothastia gaedii (Meigen)	X	X
Protanypus hamiltoni Saether	X	X
Protanypus ramosus Saether	X	
Pseudodiamesa (Pseudodiamesa) branickii (Nowicki)	X	X
<b>PRODIAMESINAE</b>		
Monodiamesa tuberculata Saether	X	
Prodiamesa olivacea (Meigen)		X
<b>ORTHOCLADIINAE</b>		
Corynoneura arctica Kieffer	X	X
Corynoneura doriceni Makarchenko and Makarchenko	X	X
Cricotopus (Cricotopus) cf. albiforceps (Kieffer)	X	
Cricotopus (Cricotopus) annulator Goetghebuer		X
Cricotopus (Cricotopus) bicinctus (Meigen)	X	X
Cricotopus (Cricotopus) curtus Hirvenoja	X	X
Cricotopus (Cricotopus) cylindraceus group, Sp. 1		X
Cricotopus (Cricotopus) fuscus (Kieffer)	X	X
Cricotopus (Cricotopus) cf. magus Hirvenoja	X	X
Cricotopus (Cricotopus) tremulus (L)	X	
Cricotopus (Cricotopus) triannulatus (Macquart)	X	
Cricotopus (Cricotopus) tristis Hirvenoja	X	X
Cricotopus (Isocladius) intersectus (Staeger)		X
Cricotopus (Isocladius) sylvestris (F)	X	X
Eukiefferiella claripennis (Lundbeck)	X	X
Eukiefferiella coerulescens Kieffer	X	X
Heterotrissocladius changi Saether	X	X
Heterotrissocladius oliveri Saether		X
Heterotrissocladius Sp. A Saether	X	X
Hydrosmittia ruttneri (Strenzke and Thienemann)	X	X
Hydrosmittia Sp. 1	X	X
Limnophyes carolinensis Saether	X	X
Limnophyes minimus Saether	X	
Limnophyes natalensis (Kieffer)		X
Limnophyes pumilio (Holmgren)	X	
Limnophyes Sp. 1		X
Metriocnemus ursinus (Holmgren)	X	X
Nanocladius (Nanocladius) speniplus Saether	X	
Nanocladius (Plecopteracoluthus) cf. branchiocolus Saether	X	X
Orthocladius (Eudactylocladius) dubitatus Johannsen	X	X
Orthocladius (Euorthocladius) rivicola Kieffer	X	
Orthocladius (Orthocladius) dorenius (Roback)	X	X
Orthocladius (Orthocladius) nigrilus Malloch	X	X
Orthocladius (Orthocladius) obumbratus Johannsen	X	X
Orthocladius (Orthocladius) robacki Sponis	X	
Orthocladius (Pogonocladius) consobrinus Holmgren	X	
Orthocladius (Symposiocladius) annectens Saether	X	X

<b>ORTHOCLADIINAE (continued)</b>	<b>2009</b>	<b>2010</b>
<i>Paracladius alpicola</i> (Zetterstedt)	X	
<i>Paracladius quadrinodosus</i> Hirvenoja		X
<i>Parakiefferiella</i> nr. <i>fennica</i> Tuiskunen	X	X
<i>Parakiefferiella nigra</i> Brundin	X	
<i>Parakiefferiella</i> cf. <i>scandica</i> Brundin	X	
<i>Parakiefferiella</i> cf. <i>smolandica</i> (Brundin)	X	X
<i>Parakiefferiella</i> Sp. 1		X
<i>Parasmittia carinata</i> (Strenzke)	X	
<i>Psectrocladius</i> ( <i>Allopsectrocladius</i> ) <i>pilosus</i> Roback	X	X
<i>Psectrocladius</i> ( <i>Allopsectrocladius</i> ) Sp. 1	X	
<i>Psectrocladius</i> ( <i>Psectrocladius</i> ) <i>limbatellus</i> (Holmgren)	X	X
<i>Psectrocladius</i> ( <i>Psectrocladius</i> ) cf. <i>sensilipes/dubius</i> Saether and Langton	X	X
<i>Psectrocladius</i> ( <i>Psectrocladius</i> ) <i>subsensilis</i> Saether and Langton	X	X
<i>Pseudorthocladius</i> ( <i>Pseudorthocladius</i> ) <i>virgatus</i> group, Sp. 1		X
<i>Pseudosmittia</i> Sp. 1	X	
<i>Smittia</i> Sp. 1	X	X
<i>Synorthocladius semivirens</i> (Kieffer)	X	X
<i>Thienemanniella lobapodema</i> Hestenes and Saether	X	X
<b>CHIRONOMINAE</b>		
<i>Chironomus</i> ( <i>Chironomus</i> ) <i>aberratus</i> Keyl		X
<i>Chironomus</i> ( <i>Chironomus</i> ) <i>anthracinus</i> Zetterstedt	X	X
<i>Chironomus</i> ( <i>Chironomus</i> ) Sp. 1	X	X
<i>Chironomus</i> ( <i>Chironomus</i> ) Sp. 2	X	
<i>Chironomus</i> ( <i>Chironomus</i> ) Sp. 3	X	X
<i>Chironomus</i> ( <i>Chironomus</i> ) Sp. 4		X
<i>Chironomus</i> ( <i>Chironomus</i> ) Sp. 5	X	
<i>Chironomus</i> ( <i>Lobochironomus</i> ) <i>dorsalis</i> Strenzke	X	
<i>Chironomus</i> ( <i>Lobochironomus</i> ) <i>montuosus</i> Ryser, Wulker, and Scholl		X
<i>Dicrotendipes fumidus</i> (Johannsen)	X	
<i>Dicrotendipes modestus</i> (Say)	X	X
<i>Dicrotendipes nervosus</i> (Staeger)	X	
<i>Endochironomus nigricans</i> (Johannsen)		X
<i>Glyptotendipes</i> ( <i>Phytotendipes</i> ) nr. <i>paripes</i> (Edwards)	X	X
<i>Micropsectra geminata</i> Oliver and Dillon	X	
<i>Micropsectra logani</i> (Johannsen)	X	X
<i>Micropsectra</i> cf. <i>nana</i> (Meigen)	X	X
<i>Micropsectra</i> nr. <i>sedna</i> Oliver	X	
<i>Micropsectra subletteorum</i> Anderson, Stur, and Ekrem	X	
<i>Micropsectra xantha</i> (Roback)	X	
<i>Neozavrelia</i> cf. <i>luteola</i> (Goetghebuer)	X	X
<i>Parachironomus</i> Pe. 3 Langton	X	
<i>Paratanytarsus dimorphis</i> Reiss		X
<i>Paratanytarsus laccophilus</i> (Edwards)	X	X
<i>Paratanytarsus natvigi</i> (Goetghebuer)		X
<i>Polypedilum</i> Sp. 1		X
<i>Sergentia coracina</i> (Zetterstedt)	X	
<i>Tanytarsus mendax</i> group Sp. 1	X	
<i>Tanytarsus wirthi</i> Ekrem, Sublette, Sublette	X	

**Appendix B:** Chironomidae presence and abundance per site, generally west-to-east, Isle Royale National Park, 2009. General abundances: no fill  $\leq 10$  specimens, light gray 11-25, medium gray with white text 26-50, dark gray with white text  $> 50$  specimens collected. In each cell, abundances are given as lichen/splash zone occupancy, with a dash if no splash zone was distinguished.

TAXA	Site															TOTAL
	WC	EC	MO	OH	DA	SH	SM	RA	BA	SG	NG	SP	ED	TH	BP	
<b>TANYPODINAE</b>																
Ablabesmyia monilis									0/1			0/1			1/0	<b>3</b>
Ablabesmyia illinoensis	1/-	4/-	13/1	1/-	6/0	6/0	14/0	11/0	0/4	1/0	3/0	7/4	1/0	3/0	3/0	<b>83</b>
Conchapelopia fasciata									0/1							<b>1</b>
Conchapelopia cornuticaudata								0/1								<b>1</b>
Procladius abetus												2/0				<b>2</b>
Procladius nr. culiciformis												1/0				<b>1</b>
Thienemannimyia norena									0/4	0/2					0/1	<b>7</b>
Zavrelimyia cf. melanura															1/0	<b>1</b>
<b>DIAMESINAE</b>																
Pagastia orthogonia						0/5	0/4		0/1	0/3	0/1			0/7		<b>21</b>
Potthastia gaedii										0/1						<b>1</b>
Protanypus hamiltoni									0/4	0/3						<b>7</b>
Protanypus ramosus							0/3		0/2							<b>5</b>
Pseudodiamesa branickii							0/1									<b>1</b>
<b>PRODIAMESINAE</b>																
Monodiamesa tuberculata									0/1	0/1						<b>2</b>
<b>ORTHOCLADIINAE</b>																
Corynoneura arctica	9/-		4/16	1/-	0/2	0/11	5/13	4/11	30/111	41/24	13/59	11/35	2/21	10/10	6/43	<b>492</b>
Corynoneura doriceni						0/1		0/1						0/1		<b>3</b>
Cricotopus cf. albiforceps											5/0					<b>5</b>
Cricotopus bicinctus	16/-		0/5					2/5	0/1	3/5	2/0	3/1	2/1	0/2	1/0	<b>48</b>
Cricotopus curtus						0/1			0/1	0/13				0/1		<b>16</b>
Cricotopus fuscus	2/-					0/1				0/1		11/0	0/1		1/0	<b>17</b>
Cricotopus cf. magus						0/14	0/3									<b>17</b>
Cricotopus tremulus			1/0													<b>1</b>
Cricotopus triannulatus								0/1	0/5							<b>6</b>
Cricotopus tristis								0/1	0/2	0/1		0/3				<b>7</b>
Cricotopus sylvestris	2/-	15/-	0/26		0/8	18/30	1/2	3/10	0/3	3/1	1/1		0/1	0/1	1/4	<b>130</b>
Eukiefferiella claripennis			0/1								0/1					<b>3</b>
Eukiefferiella coerulescens			0/1				0/2	0/1	0/2	0/1						<b>7</b>
Heterotrissocladius changi						0/16	0/5						0/1	10	2/0	<b>34</b>
Heterotrissocladius Sp. A							0/11		0/1							<b>12</b>
Hydrosmittia ruttneri									0/3	0/13		0/1				<b>17</b>
Hydrosmittia Sp. 1					0/3		0/2				0/1	0/1				<b>7</b>
Limnophyes carolinensis					11/0						3/0				3/0	<b>17</b>

TAXA	WC	EC	MO	OH	DA	SH	SM	RA	BA	SG	NG	SP	ED	TH	BP	TOTAL
<b>ORTHOCLADIINAE (continued)</b>																
Limnophyes minimus			2/0										1/0			3
Limnophyes pumilio						0/1										1
Metriocnemus ursinus					10/0			1/0								11
Nanocladius speniplus															0/1	1
Nanocladius cf. branchiocolus															0/1	1
Orthocladius dubitatus	25/-	4/-	0/16		7/0	2/18	17/44	7/2	3/33	95/60	41/13	70/18	6/20	27/36	32/23	619
Orthocladius rivicola									0/5	0/1						6
Orthocladius dorenius					0/4	0/1	0/5	0/1	0/1	0/1					0/1	14
Orthocladius nigrinus						0/2	0/13	0/1	0/2	0/1				0/31		50
Orthocladius obumbratus									0/1					0/4		5
Orthocladius robacki					0/1		0/1		0/5							7
Orthocladius consobrinus										0/1						1
Orthocladius annectens										0/1						1
Paracladius alpicola									0/1							1
Parakiefferiella nr. fennica														0/150		150
Parakiefferiella nigra					0/1									0/17		18
Parakiefferiella cf. scandica										0/1	0/1					2
Parakiefferiella cf. smolandica													0/1	0/3		4
Parasmittia carinata					2/0						1/0					3
Psectrocladius pilosus												2/0				2
Psectrocladius Sp. 1												4/0				4
Psectrocladius limbatellus	16/-	3/-	7/0	1/-	6/1	3/2	14/0	4/0		23/0	19/0	22/3			2/3	129
Psectrocladius cf. sensilipes/dubius	60/-	25/-	54/9	17/-	19/0	23/8	56/3	38/2	7/1	95/1	74/2	53/24	49/0	16/2	39/16	693
Psectrocladius subsensilis		1/-					1/0	7/0			5/0	3/0	8/0		13/0	38
Pseudosmittia Sp. 1															1/0	1
Smittia Sp. 1				1/-												1
Synorthocladius semivirens			0/1		0/1		0/2		0/15					0/1		20
Thienemanniella lobapodema													0/1			1
<b>CHIRONOMINAE</b>																
Chironomus anthracinus							3/0								1/0	4
Chironomus Sp. 1	33/-	8/-	39/0	6/-	10/0	27/0	46/0	11/0	6/1	21/1	13/0	16/0	9/0	3/0	3/2	255
Chironomus Sp. 2															7/0	7
Chironomus Sp. 3										1/0					8/0	9



**Appendix C.** Seasonal emergences of Chironomidae, by zone, Isle Royale National Park, 2009. Early Spring = Apr 24-May 7, Late Spring = May 12-Jun 3, Early Summer = Jun 8-Jul 6, Late Summer = Jul 9-Aug 14, Fall = Sep 1-Oct 13.

TAXA	Lichen Zone					Splash Zone				
	Early Spring	Late Spring	Early Summer	Late Summer	Fall	Early Spring	Late Spring	Early Summer	Late Summer	Fall
<b>TANYPODINAE</b>										
Ablabesmyia (Ablabesmyia) monilis	0	1	0	0	0	0	0	0	1	1
Ablabesmyia (Karelia) illinoensis	0	11	37	17	7	0	0	2	7	2
Conchapelopia (Conchapelopia)	0	0	0	0	0	0	0	0	1	0
Conchapelopia (Helopelopia)	0	0	0	0	0	0	0	0	1	0
Procladius (Holotanypus) abetus	0	0	2	0	0	0	0	0	0	0
Procladius (Holotanypus) nr.	0	0	0	1	0	0	0	0	0	0
Thienemannimyia	0	0	0	0	0	0	0	1	0	6
Zavrelimyia cf. melanura	1	0	0	0	0	0	0	0	0	0
<b>DIAMESINAE</b>										
Pagastia orthogonia	0	0	0	0	0	0	7	11	0	3
Potthastia gaedii	0	0	0	0	0	0	0	0	0	1
Protanypus hamiltoni	0	0	0	0	0	0	0	1	0	6
Protanypus ramosus	0	0	0	0	0	0	2	3	0	0
Pseudodiamesa (Pseudodiamesa)	0	0	0	0	0	0	0	1	0	0
<b>PRODIAMESINAE</b>										
Monodiamesa tuberculata	0	0	0	0	0	0	0	0	0	2
<b>ORTHOCLADIINAE</b>										
Corynoneura arctica	41	13	30	18	35	6	3	125	174	47
Corynoneura doriceni	0	0	0	0	0	0	1	1	1	0
Cricotopus (Cricotopus) cf.	0	1	0	4	0	0	0	0	0	0
Cricotopus (Cricotopus) bicinctus	0	4	0	10	15	0	1	0	9	9
Cricotopus (Cricotopus) curtus	0	0	0	0	0	0	15	1	0	0
Cricotopus (Cricotopus) fuscus	0	11	2	1	0	0	1	2	0	0
Cricotopus (Cricotopus) cf. magus	0	0	0	0	0	0	0	17	0	0
Cricotopus (Cricotopus) tremulus	0	0	0	0	1	0	0	0	0	0
Cricotopus (Cricotopus) triannulatus	0	0	0	0	0	0	0	5	0	1
Cricotopus (Cricotopus) tristis	0	0	0	0	0	0	1	3	1	2
Cricotopus (Isocladius) sylvestris	0	16	14	7	7	0	2	4	66	14
Eukiefferiella claripennis	0	0	0	0	0	0	0	1	0	2
Eukiefferiella coeruleascens	0	0	0	0	0	0	2	2	0	3
Heterotrissocladius changi	2	0	0	0	0	0	13	19	0	0
Heterotrissocladius Sp. A	0	0	0	0	0	0	0	12	0	0
Hydrosmittia ruttneri	0	0	0	0	0	0	13	4	0	0
Hydrosmittia Sp. 1	0	0	0	0	0	0	4	3	0	0
Limnophyes carolinensis	10	0	4	2	1	0	0	0	0	0

TAXA	Lichen Zone					Splash Zone				
	Early Spring	Late Spring	Early Summer	Late Summer	Fall	Early Spring	Late Spring	Early Summer	Late Summer	Fall
<b>ORTHOCLADIINAE (continued)</b>										
Limnophyes minimus	1	0	2	0	0	0	0	0	0	0
Limnophyes pumilio	0	0	0	0	0	0	1	0	0	0
Metriocnemus ursinus	9	1	0	0	1	0	0	0	0	0
Nanocladius (Nanocladius)	0	0	0	0	0	0	0	1	0	0
Nanocladius (Plecopteracoluthus) cf. branchiocolus	0	0	0	0	0	0	0	1	0	0
Orthocladius (Eudactylocladius)	258	59	10	1	7	93	72	71	7	41
Orthocladius (Euorthocladius)	0	0	0	0	0	0	0	4	0	2
Orthocladius (Orthocladius) dorenius	0	0	0	0	0	0	1	12	1	0
Orthocladius (Orthocladius) nigritus	0	0	0	0	0	0	32	18	0	0
Orthocladius (Orthocladius)	0	0	0	0	0	0	5	0	0	0
Orthocladius (Orthocladius) robacki	0	0	0	0	0	0	0	2	0	5
Orthocladius (Pogonocladius)	0	0	0	0	0	0	0	0	0	1
Orthocladius (Symposiocladius)	0	0	0	0	0	0	0	0	1	0
Paracladius alpicola	0	0	0	0	0	0	0	0	0	1
Parakiefferiella nr. fennica	0	0	0	0	0	0	150	0	0	0
Parakiefferiella nigra	0	0	0	0	0	0	17	1	0	0
Parakiefferiella cf. scandica	0	0	0	0	0	0	0	1	1	0
Parakiefferiella cf. smolandica	0	0	0	0	0	0	0	1	3	0
Parasmittia carinata	0	3	0	0	0	0	0	0	0	0
Psectrocladius (Allopsectrocladius)	0	1	0	1	0	0	0	0	0	0
Psectrocladius (Allopsectrocladius)	2	0	0	0	2	0	0	0	0	0
Psectrocladius (Psectrocladius)	21	57	13	13	16	4	4	0	1	0
Psectrocladius (Psectrocladius) cf. sensilipes/dubius	164	195	56	123	87	16	23	11	14	4
Psectrocladius (Psectrocladius)	6	1	15	16	0	0	0	0	0	0
Pseudosmittia Sp. 1	1	0	0	0	0	0	0	0	0	0
Smittia Sp. 1	0	1	0	0	0	0	0	0	0	0
Synorthocladius semivirens	0	0	0	0	0	0	1	6	1	12
Thienemanniella lobapodema	0	0	0	0	0	0	0	1	0	0
<b>CHIRONOMINAE</b>										
Chironomus (Chironomus)	0	0	4	0	0	0	0	0	0	0
Chironomus (Chironomus) Sp. 1	1	80	54	75	41	0	0	1	3	0
Chironomus (Chironomus) Sp. 2	7	0	0	0	0	0	0	0	0	0
Chironomus (Chironomus) Sp. 3	0	8	0	1	0	0	0	0	0	0

TAXA	Lichen Zone					Splash Zone				
	Early Spring	Late Spring	Early Summer	Late Summer	Fall	Early Spring	Late Spring	Early Summer	Late Summer	Fall
<b>CHIRONOMINAE (continued)</b>										
Chironomus (Chironomus) Sp. 5	0	2	0	0	0	0	0	0	0	0
Chironomus (Lobochironomus)	0	0	0	0	0	0	0	0	1	0
Dicrotendipes fumidus	0	2	0	0	0	0	0	0	0	1
Dicrotendipes modestus	0	0	27	0	0	0	0	0	0	0
Dicrotendipes nervosus	0	0	1	0	0	0	0	1	0	0
Glyptotendipes (Phytotendipes) nr.	0	6	54	16	0	0	0	0	0	0
Micropsectra geminata	2	0	0	0	1	0	0	0	0	0
Micropsectra logani	0	0	0	0	0	0	0	1	0	0
Micropsectra cf. nana	1	0	0	0	0	0	0	0	0	0
Micropsectra nr. sedna	0	0	0	0	0	0	0	1	0	0
Micropsectra subletteorum	0	0	0	0	0	0	43	5	0	0
Micropsectra xantha	0	0	0	0	0	0	6	0	0	0
Neozavrelia cf. luteola	0	0	0	0	0	0	0	54	1	0
Parachironomus Pe. 3	0	0	0	0	0	0	0	1	0	0
Paratanytarsus laccophilus	0	2	66	58	25	0	0	1	0	5
Sergentia coracina	0	0	0	0	0	0	0	1	0	0
Tanytarsus mendax group Sp. 1	0	0	2	0	0	0	0	0	0	0
Tanytarsus wirthi	0	0	0	0	1	0	0	0	0	0

**Appendix D.** Chironomidae species abundance per site and zone, Isle Royale National Park, 2010.

	Passage Lichen	Passage Splash	Raspberry Lichen	Raspberry Splash	Blueberry Lichen	Blueberry Splash	Datolite Lichen	Datolite Splash	TOTAL
<b>PRODIAMESINAE</b>									
<i>Prodiamesa cf. olivacea</i>	0	0	0	0	0	1	0	0	1
<b>PODONOMINAE</b>									
<i>Parochlus kiefferi</i>	0	0	0	0	0	0	1	0	1
<b>TANYPODINAE</b>									
<i>Ablabesmyia illinoensis</i>	7	3	4	1	7	5	9	2	38
<i>Ablabesmyia aspera</i>	0	0	0	0	11	0	0	0	11
<i>Conchapelopia fasciata</i>	0	0	0	2	0	0	0	0	2
<i>Conchapelopia cornuticaudata</i>	0	1	0	0	0	2	0	1	4
<i>Procladius abetus</i>	3	0	0	0	0	0	0	0	3
<i>Thienemannimyia norena</i>	0	0	0	2	0	0	0	0	2
<i>Zavrelimyia melanura</i>	0	0	0	0	1	0	0	0	1
<b>DIAMESINAE</b>									
<i>Diamesa insignipes</i>	0	0	0	2	0	0	0	0	2
<i>Potthastia gaedii</i>	0	0	0	1	0	1	0	0	2
<i>Protanyus hamiltoni</i>	0	0	0	1	0	1	0	0	2
<i>Pseudodiamesa branickii</i>	0	0	0	0	0	5	0	0	5
<b>ORTHOCLADIINAE</b>									
<i>Corynoneura doriceni</i>	0	0	0	9	12	3	0	0	24
<i>Corynoneura arctica</i>	3	15	3	11	2	19	2	9	64
<i>Cricotopus bicinctus</i>	5	7	9	14	19	52	4	1	111
<i>Cricotopus curtus</i>	0	0	0	3	0	6	0	0	9
<i>Cricotopus fuscus</i>	1	7	0	0	2	14	0	0	24
<i>Cricotopus tristis</i>	0	0	0	1	0	1	0	0	2
<i>Cricotopus magus</i>	0	0	0	0	0	2	0	0	2
<i>Cricotopus Sp. 1 (cylindraceus group)</i>	0	0	0	6	0	2	0	0	8
<i>Cricotopus annulator</i>	0	0	0	0	0	2	0	0	2
<i>Cricotopus sylvestris</i>	0	0	6	62	0	1	0	2	71
<i>Cricotopus intersectus</i>	0	0	0	2	0	0	0	0	2
<i>Eukiefferiella claripennis</i>	0	3	0	6	0	1	0	0	10
<i>Eukiefferiella coeruleascens</i>	0	0	0	11	0	12	0	0	23

	Passage Lichen	Passage Splash	Raspberry Lichen	Raspberry Splash	Blueberry Lichen	Blueberry Splash	Datolite Lichen	Datolite Splash	TOTAL
<b>ORTHOCLADIINAE (continued)</b>									
<i>Heterotrissocladius changi</i>	0	0	0	1	0	0	0	0	1
<i>Heterotrissocladius oliveri</i>	0	1	0	0	0	0	0	0	1
<i>Heterotrissocladius</i> Sp. A	0	0	0	2	0	4	0	0	6
<i>Limnophyes carolinensis</i>	1	1	4	0	6	1	62	1	76
<i>Limnophyes natalensis</i>	0	0	0	0	0	0	0	1	1
<i>Limnophyes</i> Sp. 1	0	0	0	0	0	0	2	0	2
<i>Metriocnemus ursinus</i>	0	0	4	0	0	0	0	0	4
<i>Nanocladius</i> nr. <i>branchiocolus</i>	0	1	0	2	0	0	0	0	3
<i>Orthocladius dubitatus</i>	3	65	50	167	32	111	49	100	577
<i>Orthocladius dorenius</i>	0	0	0	5	0	7	0	0	12
<i>Orthocladius nigritus</i>	0	0	0	4	0	1	0	0	5
<i>Orthocladius obumbratus</i>	0	0	0	4	0	8	0	0	12
<i>Orthocladius</i> nr. <i>lapponicus</i>	1	0	0	0	0	0	0	0	1
<i>Orthocladius annectens</i>	0	0	0	0	0	3	0	0	3
<i>Paracladius quadrinodosus</i>	0	0	0	7	0	0	0	0	7
<i>Parakiefferiella</i> cf. <i>smolandica</i>	0	0	0	0	0	1	0	0	1
<i>Parakiefferiella</i> nr. <i>fennica</i>	0	0	0	1	0	0	0	0	1
<i>Parakiefferiella</i> Sp. 1	0	0	0	1	0	0	0	0	1
<i>Psectrocladius pilosus</i>	2	0	0	0	20	0	8	0	30
<i>Psectrocladius</i> cf. <i>sensilipes/dubius</i>	63	2	31	2	29	2	26	0	155
<i>Psectrocladius limbatellus</i>	2	0	6	1	4	1	6	0	20
<i>Psectrocladius subsensilis</i>	24	0	16	0	32	0	9	0	81
<i>Pseudorthocladius</i> nr. <i>virgatus</i>	0	0	0	0	1	0	0	0	1
<i>Hydrosmittia ruttneri</i>	0	0	0	2	0	1	0	0	3
<i>Hydrosmittia</i> Sp. 1	0	0	0	1	0	0	0	0	1
<i>Synorthocladius semivirens</i>	0	0	0	11	0	1	0	1	13
<i>Thienemanniella lobapodema</i>	0	0	0	1	0	0	0	0	1
<i>Smittia</i> Sp. 1	0	0	0	1	0	0	0	0	1
<b>CHIRONOMINAE</b>									
<i>Chironomus</i> Sp. 1	2	0	11	0	16	0	2	0	31

	Passage Lichen	Passage Splash	Raspberry Lichen	Raspberry Splash	Blueberry Lichen	Blueberry Splash	Datolite Lichen	Datolite Splash	TOTAL
<b>CHIRONOMINAE (continued)</b>									
Chironomus Sp. 3	0	0	0	0	13	0	0	0	13
Chironomus Sp. 4	0	0	1	0	0	0	0	0	1
Chironomus anthracinus	3	0	0	0	0	0	0	0	3
Chironomus cf. aberratus	0	0	0	0	1	0	0	0	1
Chironomus montuosus	1	0	0	0	1	0	0	0	2
Neozavrelia cf. luteola	0	1	0	51	0	3	0	0	55
Dicrotendipes modestus	7	0	89	0	17	0	131	0	244
Endochironomus nigricans	1	0	0	0	0	0	0	0	1
Glyptotendipes nr. paripes	18	0	10	0	11	0	5	0	44
Polypedilum Sp. 1	41	0	0	0	0	0	0	0	41
Micropsectra nana	0	0	0	0	0	0	2	0	2
Micropsectra logani	0	0	0	1	0	0	0	0	1
Paratanytarsus laccophilus	94	0	63	0	24	15	0	0	196
Paratanytarsus dimorphus	0	0	0	2	0	1	0	0	3
Paratanytarsus natvigi	0	0	0	2	0	1	0	0	3

**Appendix E.** Chironomidae species abundance per date, Isle Royale National Park, 2010.

	April 22nd-28th	May 9th-17th	June 3rd-8th	July 3rd-9th	August 3rd-6th	October 2nd-4th
<b>PRODIAMESINAE</b>						
<i>Prodiamesa cf. olivacea</i>	0	0	0	1	0	0
<b>PODONOMINAE</b>						
<i>Parochlus kiefferi</i>	1	0	0	0	0	0
<b>TANYPODINAE</b>						
<i>Ablabesmyia illinoensis</i>	0	2	12	8	16	0
<i>Ablabesmyia aspera</i>	0	0	1	3	7	0
<i>Conchapelopia fasciata</i>	0	0	2	0	0	0
<i>Conchapelopia cornuticaudata</i>	0	0	0	3	1	0
<i>Procladius abetus</i>	0	0	1	2	0	0
<i>Thienemannimyia norena</i>	0	0	0	0	2	0
<i>Zavrelimyia melanura</i>	0	0	0	1	0	0
<b>DIAMESINAE</b>						
<i>Diamesa insignipes</i>	2	0	0	0	0	0
<i>Potthastia gaedii</i>	0	0	2	0	0	0
<i>Protanypus hamiltoni</i>	0	0	1	1	0	0
<i>Pseudodiamesa branickii</i>	0	0	0	5	0	0
<b>ORTHOCLADIINAE</b>						
<i>Corynoneura doriceni</i>	0	8	1	4	10	1
<i>Corynoneura arctica</i>	5	0	2	8	19	30
<i>Cricotopus bicinctus</i>	0	1	69	19	21	1
<i>Cricotopus curtus</i>	0	6	2	0	1	0
<i>Cricotopus fuscus</i>	0	3	14	2	5	0
<i>Cricotopus tristis</i>	0	0	1	1	0	0
<i>Cricotopus magus</i>	0	0	0	2	0	0
<i>Cricotopus Sp. 1 (cylindraceus group)</i>	0	0	8	0	0	0
<i>Cricotopus annulator</i>	0	0	0	2	0	0
<i>Cricotopus sylvestris</i>	0	0	2	8	60	1
<i>Cricotopus intersectus</i>	0	0	2	0	0	0
<i>Eukiefferiella claripennis</i>	5	2	0	1	1	1

	April 22nd-28th	May 9th-17th	June 3rd-8th	July 3rd-9th	August 3rd-6th	October 2nd-4th
<b>ORTHOCLADIINAE (continued)</b>						
<i>Eukiefferiella coerulescens</i>	0	11	2	0	9	1
<i>Heterotrissocladius changi</i>	0	0	1	0	0	0
<i>Heterotrissocladius oliveri</i>	0	0	0	1	0	0
<i>Heterotrissocladius</i> Sp. A	0	0	0	6	0	0
<i>Limnophyes carolinensis</i>	69	6	1	0	0	0
<i>Limnophyes natalensis</i>	1	0	0	0	0	0
<i>Limnophyes</i> Sp. 1	2	0	0	0	0	0
<i>Metriocnemus ursinus</i>	1	0	0	1	2	0
<i>Nanocladius</i> nr. <i>branchiocolus</i>	0	0	0	0	3	0
<i>Orthocladius dubitatus</i>	322	62	119	38	3	33
<i>Orthocladius dorenius</i>	0	0	5	7	0	0
<i>Orthocladius nigrinus</i>	0	0	4	1	0	0
<i>Orthocladius obumbratus</i>	0	0	4	8	0	0
<i>Orthocladius</i> nr. <i>lapponicus</i>	0	0	0	0	1	0
<i>Orthocladius annectens</i>	0	0	0	3	0	0
<i>Paracladius quadrinodosus</i>	0	0	7	0	0	0
<i>Parakiefferiella</i> cf. <i>smolandica</i>	0	0	0	1	0	0
<i>Parakiefferiella</i> nr. <i>fennica</i>	0	0	0	1	0	0
<i>Parakiefferiella</i> Sp. 1	0	0	0	1	0	0
<i>Psectrocladius pilosus</i>	1	2	0	19	3	5
<i>Psectrocladius</i> cf. <i>sensilipes/dubius</i>	64	33	14	29	13	2
<i>Psectrocladius limbatellus</i>	6	4	1	6	2	1
<i>Psectrocladius subsensilis</i>	1	0	8	43	29	0
<i>Pseudorthocladius</i> nr. <i>virgatus</i>	1	0	0	0	0	0
<i>Hydrosmittia ruttneri</i>	0	0	2	1	0	0
<i>Hydrosmittia</i> Sp. 1	0	0	1	0	0	0
<i>Synorthocladius semivirens</i>	0	0	2	1	10	0
<i>Thienemanniella lobapodema</i>	0	0	1	0	0	0
<i>Smittia</i> Sp. 1	0	1	0	0	0	0

	April 22nd-28th	May 9th-17th	June 3rd-8th	July 3rd-9th	August 3rd-6th	October 2nd-4th
<b>CHIRONOMINAE</b>						
Chironomus Sp. 1	0	17	6	4	2	2
Chironomus Sp. 3	3	0	0	10	0	0
Chironomus Sp. 4	0	0	0	1	0	0
Chironomus anthracinus	0	0	3	0	0	0
Chironomus cf. aberratus	0	0	0	1	0	0
Chironomus montuosus	0	0	2	0	0	0
Neozavrelia cf. luteola	0	0	39	0	16	0
Dicrotendipes modestus	0	1	241	0	2	0
Endochironomus nigricans	0	0	0	1	0	0
Glyptotendipes nr. paripes	0	12	27	2	3	0
Polypedilum Sp. 1	0	0	0	40	1	0
Micropsectra nana	2	0	0	0	0	0
Micropsectra logani	0	0	1	0	0	0
Paratanytarsus laccophilus	0	0	120	24	51	1
Paratanytarsus dimorphus	0	0	3	0	0	0
Paratanytarsus natvigi	1	0	2	0	0	0
Sum per month	487	171	736	321	293	79
Count per month	17	16	40	42	27	12