

ABSTRACT

SPATIAL DISTRIBUTION OF BENTHIC INVERTEBRATES IN LAKE WINNEBAGO, WISCONSIN

By Courtney L. Heling

Numerous studies have examined the distribution of benthic invertebrates in lakes through space and time. However, most studies typically focus on single habitats or individual taxa rather than sampling comprehensively in multiple habitats in a single system. The focus of this study was to quantify the spatial distribution of the macroinvertebrate taxa present in three major lake zones (profundal, offshore reef, and littoral) in Lake Winnebago, Wisconsin, with a particular emphasis on chironomid distribution, and to determine what factors drove patterns in variation. The profundal zone was sampled for two consecutive years in August to determine if changes in spatial variation occurred from one year to the next. Using a variety of sampling methods, invertebrates were collected from all three zones in 2013 and the profundal zone in 2014. Additionally, numerous physical and biological variables were measured at each sampling site. Benthic invertebrate densities ranged from 228 to 66,761 individuals per m² and varied among lake zones and substrates. Zebra mussels (*Dreissena polymorpha*) were numerically dominant in both the offshore reef and littoral zones, while chironomids and oligochaetes comprised approximately 75% of profundal invertebrates sampled. Principal components analysis (PCA) showed that chironomid community structure differed highly among the three major lake zones. The littoral and offshore reef zones had the highest chironomid taxa richness, while the profundal zone, where *Procladius* spp. and *Chironomus* spp. were dominant, had lower richness. Chironomid density and community structure exhibited spatial variation within the profundal zone. The abundance of chironomids was correlated with several habitat variables, including organic matter content of the sediments. As aquatic systems undergo rapid modification due to the introduction of invasive species, eutrophication, and climate change it has become increasingly important to conduct comprehensive studies, such as this one, to better assess the manner in which these systems respond and adapt to change.

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by

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CHAPTER I

INTRODUCTION

Aquatic invertebrates have long been recognized as a crucial component of ecosystems. Benthic (bottom-dwelling) invertebrates, in particular, account for a considerable amount of biomass in both lentic and lotic systems (Dahl 1998; Anderson et al. 2012) and are essential in the processing of nutrients and organic matter in lakes (Efitre et al. 2001; Devine and Vanni 2002; Vadeboncoeur and VanderZanden 2002; Shang et al. 2013). Their presence (or absence) can serve as an important indicator of trophic status in lentic systems (Cain et al. 2004; Paraschiv et al. 2013) and their variation in space and time can have significant impacts on fishes and other secondary consumers (Covich et al. 1999).

Chironomids, a ubiquitous group of invertebrates in most freshwater ecosystems, have been studied frequently. They exhibit a wide range of tolerances to environmental pollution and inhabit a variety of habitats (Cranston et al. 1995). Chironomid larvae are especially useful study organisms because their chitinous head capsules remain in the sediment over time and can be used to reconstruct climatic data, providing an implicit record of past conditions through taxonomic turnover (Larocque et al. 2006; Ilyashuk et al. 2015). Additionally, chironomids experience a brief terrestrial phase (in the form of mating adult flies) and provide an influx of nutrients for terrestrial consumers, an important coupling between aquatic and terrestrial ecosystems (Gratton et al. 2008; Dreyer et al. 2015).

It is generally understood that benthic invertebrates inhabit virtually all substrate types in lentic systems and that the nearshore zones of lakes harbor a wider array of taxa relative to the offshore, profundal zones (Vadeboncoeur et al. 2011). However, there are relatively few studies that take a comprehensive approach to understanding the spatial variation of invertebrates throughout multiple zones and substrate types in lakes. Because the full extent of macroinvertebrate distribution and the factors that drive distribution are not understood in many lakes, it is not certain how invertebrates are affected by change. Aquatic systems have become increasingly affected by anthropogenic activity in recent years. For example, increased urbanization in watersheds has led to widespread changes in lake morphology (especially in nearshore zones) and trophic status, which have, collectively, altered benthic invertebrate assemblages (Bowman et al. 2006; Pilotto et al. 2012; Pilotto et al. 2015). In addition, introduced species have led to drastic modifications of macroinvertebrate communities in lakes (Rennie and Evans 2012; Bruckerhoff et al. 2015; Gallardo et al. 2016). Without baseline data, it is difficult to determine how invertebrate taxa respond and adapt over time to these continuing changes.

Lake Winnebago, located in northeastern Wisconsin, is large (55,700 ha), shallow (average depth 4.7 meters), and eutrophic. It holds many fish species, most notably, a large endemic population of benthivorous lake sturgeon (*Acipenser fulvescens*) (Bruch 1999). Benthic invertebrates have been sampled from the profundal zone of the lake discontinuously for over 50 years for various ecological studies (Hilsenhoff 1966, 1967; Koehnke 1997; Stelzer et al. 2008; Anderson et al. 2012) and assessment of the temporal

variation in the chironomid community of the profundal zone has been examined (Koehnke 1997). The dominant chironomid taxa in the profundal zone have not changed dramatically over the last five decades. Densities of profundal chironomids, however, do appear to have fluctuated between sampling periods (Koehnke 1997). Previous observations of the nearshore benthic communities of Lake Winnebago indicated that zebra mussels (*Dreissena polymorpha*) were locally abundant. However, before the study described here, little was known about the benthic communities in the lake's littoral zone and large offshore reef systems.

The primary objective of my study was to quantify the densities and assess the spatial variation of benthic invertebrates (with a special emphasis on chironomids) in the three major zones of the lake (profundal, offshore reef, and littoral zones) by expanding upon the number of sites utilized in previous studies of Lake Winnebago. A secondary objective was to assess if spatial variation in benthic invertebrate community structure varied between 2013 and 2014 sampling periods. My study is one of the most comprehensive examinations of spatial variation of benthic invertebrates in a large North American inland lake.

CHAPTER II

SPATIAL DISTRIBUTION OF BENTHIC INVERTEBRATES IN LAKE WINNEBAGO, WISCONSIN

INTRODUCTION

Knowledge of the spatial and temporal distributions of benthic macroinvertebrates in aquatic ecosystems is important for several reasons. First, benthic invertebrates are an important food source for numerous fishes and other secondary consumers (Anderson et al. 2012) and play an essential role in cycling nutrients and organic matter in aquatic systems (Efitre et al. 2001; Devine and Vanni 2002; Vadeboncoeur and VanderZanden 2002; Shang et al. 2013). Thus, the spatial distribution of benthic invertebrates has implications for the distribution of consumers and ecosystem processes such as nutrient mineralization (Hirabayashi and Wotton 1998). Second, benthic invertebrates can serve as bioindicators (Cain et al. 2004; Paraschiv et al. 2013) and have been studied to track the spatial distribution of pollution in lakes (Poma et al. 2014). The distribution of aquatic invertebrates in lentic ecosystems is influenced by several biotic and abiotic factors, including predation and competition as well as water depth, substrate complexity, organic matter content (OMC), pH, salinity, and dissolved oxygen levels (Moore 1981; Efitre et al. 2001; Fu et al. 2012).

Numerous studies have examined the spatial distribution of benthic invertebrates in some of the world's largest lakes (e.g. Lake Baikal, Lake Tahoe, and Lake Tanganyika) (Verschuren et al. 2000; Scharold et al. 2010; Namayandeh and Quinlan 2011; Findik 2013; Arva et al. 2015) and have concluded that many benthic

macroinvertebrate species are found exclusively in the littoral or profundal zones, while other species are more widely distributed (Frantz and Cordone 1996; Koshova and Izmet's'yeva 1998; Eggermont and Verschuren 2003; Vadeboncoeur et al. 2011). Littoral zones tend to exhibit relatively high invertebrate species richness, likely due to increased habitat heterogeneity (Pilotto et al. 2015) and productivity in these areas (Vadeboncoeur et al. 2011). In contrast, the profundal zone typically demonstrates higher substrate homogeneity and lower diversity (Boggero et al. 2006). Given that the littoral and profundal zones usually differ in habitat (depth, substrate, etc.) and several other physiochemical attributes (dissolved oxygen levels, light availability, etc.), the invertebrates within these zones may respond differently to habitat-specific changes induced by climate and other forcing factors (Solimini and Sandin 2012).

Most prior studies of spatial variation in lentic benthic invertebrate communities have focused on invertebrates in a single zone (e.g. littoral) (Reid et al. 1995; Suurkuukka et al. 2012; Kornijow et al. 2016) or on a single taxonomic group (Verneaux and Aleya 1998; Ali et al. 2002; Siersma et al. 2014). Relatively few studies have comprehensively examined invertebrate taxa present in multiple lake zones at fine taxonomic resolution. There are a variety of reasons for this, including the difficulty in sampling deeper benthic zones in lakes and because genus- or species-level identification of invertebrate taxa common in lakes (e.g. chironomids, oligochaetes) is laborious. Studies that have considered invertebrates in multiple depth zones with high taxonomic resolution have typically been conducted in relatively small lentic systems (< 1,000 hectares) and only included samples collected from soft sediments (Nanami et al. 2005; Kanaya and Kikuchi

2008; Findik 2013). However, one exceptionally large and taxonomically-detailed study conducted in Lake Erie by Burlakova et al. (2014), assessed spatial patterns in benthic invertebrate community structure across multiple substrates as they related to anthropogenic activity and invasive species introduction over a 50-year interval.

Community structure and the spatial distributions of benthic invertebrates frequently changes through time (Suurkuukka et al. 2012; Burlakova et al. 2014). In addition to natural variation (e.g. seasonal changes), many lakes have undergone rapid changes in recent decades due to anthropogenically-induced factors such as increased urban development, intensive agriculture, and invasive species (Bowman et al. 2006; Karatayev et al. 2013; Gallardo et al. 2016). These factors are capable of producing ecosystem-wide effects that influence all trophic levels, including benthic fauna. For example, a comparison of benthic surveys conducted over a 35-year period in Lake Simcoe (Ontario, Canada) reported that total abundances of benthic invertebrates declined significantly over time while the biomass of some taxa, including chironomid larvae, increased. These changes were largely attributed to increased nutrient loading and the introduction of non-native species (Jimenez et al. 2011; Rennie and Evans 2012). As many lakes throughout the world are subjected to similar stressors it is imperative to have baseline data on the densities and distribution of organisms to assess how anthropogenic disturbance will impact aquatic ecosystems through time.

Chironomids are widely distributed and found at nearly all depths and substrates in both lentic and lotic ecosystems (Cranston et al. 1995). They frequently dominate the

biomass of benthic communities in lakes (Specziar and Biro 1998; Ayuushsuren and Shcherbina 2015) and are an important component of many aquatic food webs (Balci et al. 2005; Reuss et al. 2013) and regulators of ecosystem dynamics (Holker and Stief 2005; Soster et al. 2015). Chironomid species distributions have been used to reconstruct past climatic data because their chitinous head capsules persist in lake sediments (Larocque et al. 2006; Fortin et al. 2015). In addition, because chironomids are not exclusively aquatic, they establish an important ecological link between aquatic and terrestrial ecosystems by contributing to a significant water-to-land influx of nutrients for terrestrial consumers (e.g. arthropods, birds, detritivores, etc.) in regions where adult swarms are large (Gratton et al. 2008; Dreyer et al. 2015). Swarming events have been observed in many lakes including Lake Myvatn (Iceland), many of the African and Laurentian Great Lakes (Vadeboncoeur et al. 2011, Dreyer et al. 2015), and Wisconsin's largest inland lake, Lake Winnebago (Hilsenhoff 1966).

Data spanning over six decades indicates that chironomid larvae are an important component of the Lake Winnebago food web (Schneberger and Woodbury 1944; Probst and Cooper 1955; Choudhury et al. 1996; Stelzer et al. 2008). Chironomid larvae comprise approximately half of the carbon assimilated by lake sturgeon (*Acipenser fulvescens*) in Lake Winnebago (Stelzer et al. 2008) and their secondary production rates in the lake are higher than that of many other North American lakes (Anderson et al. 2012). As Lake Winnebago holds one of the largest endemic populations of lake sturgeon in North America (Bruch 1999), gaining further insight into the spatial and

temporal distribution of chironomids as well as other invertebrates may have important long-term implications for lake sturgeon and other fish species in Lake Winnebago.

Several studies have described the spatial variation of chironomids in lakes but, as with most other spatial assessments of benthic macroinvertebrate communities, were typically focused on a single habitat type or lake zone (Boggero et al. 2006) or on an individual species (Hirabayashi et al. 2003; Balci et al. 2005; DeHaas et al. 2006). There have been a limited number of comprehensive analyses of chironomid spatial distribution in multiple zones of large lakes at fine taxonomic resolution (Heinis 1994; Burlakova et al. 2014; Arva et al. 2015). Studies of temporal variation in lentic chironomids are also uncommon as there are relatively few lakes with the necessary continuous data. Chironomid abundance data have been collected intermittently from Lake Winnebago over the last several decades. However, the density, biomass, and production estimates of Hilsenhoff (1966, 1967), Koehnke (1997), Stelzer et al. (2008), and Anderson et al. (2012) were based on samples collected from only four profundal locations in the 55,000 hectare lake. Beyond these four sites, the benthic invertebrate community in Lake Winnebago has not been broadly quantified, including the littoral and offshore reef communities. Because the littoral zone often has the highest diversity of benthic invertebrates in lakes (Vadeboncoeur et al. 2011), it is important that these habitats are included in lake-wide assessments. I conducted a study which expanded upon the spatial coverage from previous examinations of benthic invertebrates in Lake Winnebago to include 33 profundal, 17 offshore reef, and 15 littoral sampling locations representing

multiple depths and substrates. This study is one of the most comprehensive evaluations of benthic invertebrate spatial variation in a large North American lake.

I addressed the following objectives:

1. Describe the spatial variation of benthic invertebrates, with an emphasis on the chironomid community, throughout Lake Winnebago.
2. Describe the temporal variation of profundal chironomid communities between two consecutive years.
3. Evaluate potential causes of the spatial variation of benthic invertebrates throughout the lake and temporal variation of profundal chironomid communities.

METHODS

Lake Winnebago

Lake Winnebago is Wisconsin's largest inland lake, with an area of approximately 55,728 hectares. The lake is approximately 48 kilometers long by 16 kilometers wide with an average depth of 4.7 meters and a maximum depth of 6.4 meters (Stelzer et al. 2008). The lake ranges from eutrophic to hypereutrophic and large algal blooms routinely occur in summer. Because the lake is shallow and well-mixed, dissolved oxygen (DO) concentrations and water temperatures tend to be uniform throughout the water column during the ice-free months, but DO may decline at depth following algal blooms (WDNR, 2004). The vast majority of the sediment in the

profundal zone is comprised of fine-grained, highly organic silt. The littoral zone primarily consists of rocks (particle size ranges from gravel to boulders), where natural and artificial inshore reefs are present, and sand. A rocky offshore reef system, 0.5 to 5.0 kilometers from and approximately parallel to the western shoreline, occurs along the entire length of the lake. Rocky reefs are present to a lesser extent along the eastern shoreline (WDNR, 2004).

Chironomids are one of the most abundant types of macroinvertebrates in the lake and comprise the majority of the insects in the profundal zone (Hilsenhoff 1967). Chironomid taxa known to occur in Lake Winnebago include *Chironomus plumosus*, *Tanytarsus* spp., *Dicrotendipes* spp., *Procladius* spp., *Coelotanypus* spp., and *Cryptochironomus* spp. (Hilsenhoff 1966, 1967; Koehnke 1997). Other invertebrate taxa present in the profundal zone include leeches, molluscs (gastropods and clams), oligochaetes, nematodes, and crustaceans (cladocerans, copepods, ostracods) (Hilsenhoff 1967). Lake Winnebago contains a diverse fish community, which includes a large population of lake sturgeon (*Acipenser fulvescens*) (Bruch 1999), walleye (*Sander vitreus*) (Koenigs et al. 2015), yellow perch (*Perca flavescens*), and freshwater drum (*Aplodinotus grunniens*) (Davis-Foust et al. 2009).

Site Selection

Sixty-five benthic sampling locations were selected representing all major lake zones including profundal (33 locations), offshore reefs (17), and littoral (15) (Fig. 1). Average depths for profundal, offshore reef, and littoral locations were 4.8, 2.4, and 0.5

m, respectively (Table 1). To ensure adequate spatial coverage of the entire lake, sites were chosen systematically by selecting the middle point of quadrats (1.4 km x 1.8 km) on a map of the lake. Four long-term benthic invertebrate sampling sites used by

Hilsenhoff (1966, 1967), Koehnke (1997), Stelzer et al. (2008), and Anderson et al. (2012) were also included in the profundal sampling locations. Water depth tended to vary within individual reefs and most of the offshore reef locations were sampled at three different depths to reflect this variation. Littoral sampling sites were selected based on their proximity to relatively undisturbed public access points (Fig. 1).

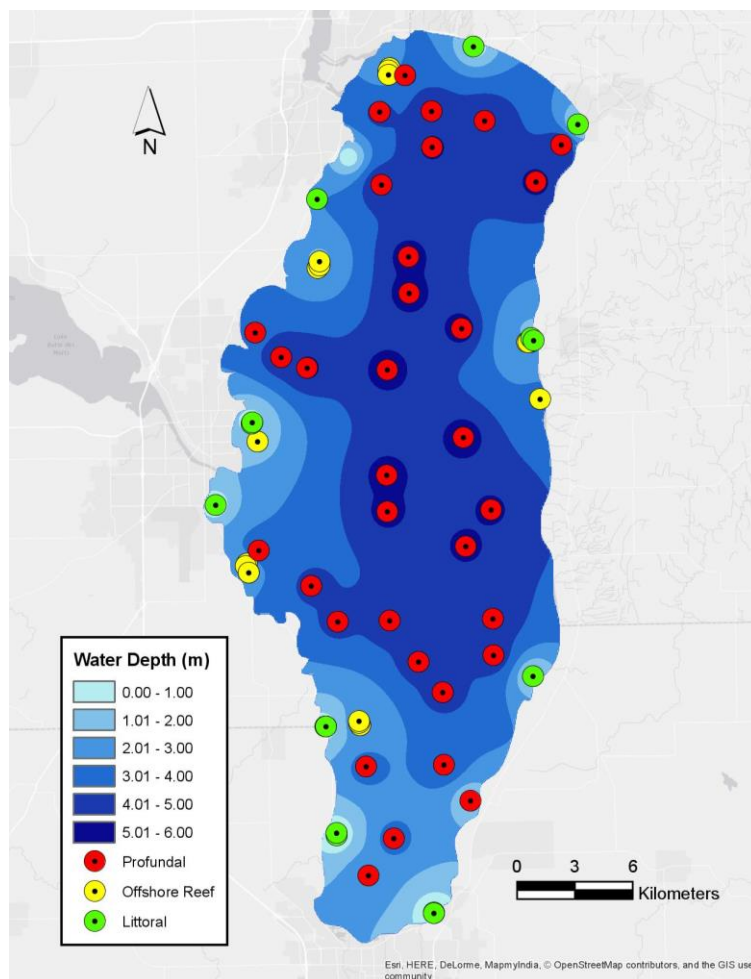


Figure 1. Depth contour map of Lake Winnebago, Wisconsin – indicating the locations of benthic invertebrate sampling sites in the profundal, offshore reef, and littoral zones. Overlapping circles for the offshore reef and littoral locations indicate that samples were collected at multiple depths (for offshore reefs) or from multiple substrates (for littoral sites).

Benthic Invertebrate Sampling

Benthic invertebrates from profundal, offshore reef, and littoral locations were sampled in August 2013 while only profundal sites were sampled in August 2014. Profundal locations were visited by boat and samples were collected with a 523-cm² Ekman grab. The sediment collected was washed in the field through a 541- μ m sieve bucket to remove fine sediment. The remaining material was immediately preserved in 95% ethanol. At each location, two Ekman grab drops were performed and invertebrate samples were pooled. A third (unsieved) sediment sample was collected with the Ekman grab, placed on ice in the field, and stored at -20 °C in the laboratory for determination of ash-free dry mass (AFDM).

Benthic invertebrates from the offshore reef locations were sampled by SCUBA. At each location, the diver collected all coarse sediment and associated invertebrates within two of four quadrants (each quadrant had an area of 0.055m²) of a randomly positioned PVC quadrat (total quadrat area was 0.22 m²) and placed the material in a mesh (2 mm²) diving bag before returning to the boat. Invertebrates from large rocks were removed in the field and preserved in 95% ethanol. Smaller substrates (pebbles and gravel) and their associated invertebrates were placed together in 95% ethanol.

The collection method for benthic invertebrates from littoral locations depended on the substrate type present. Locations with cobble and boulders were sampled by collecting substrate enclosed within two quadrants of the 0.22 m² quadrat. All visible invertebrates were removed from the substrates in the field and preserved in 95% ethanol.

Locations with fine sediment (mostly sand) were sampled by removing sediment to a depth of 10 cm with a cylindrical polycarbonate corer (44 cm² cross-sectional area) and washing it through a 541- μ m sieve. Invertebrates from three replicate cores per sampling location were pooled and preserved in 95% ethanol. A separate (unsieved) core was collected for AFDM determination.

Physical Data Collection

Water depth, Secchi disc depth, and temperatures (sediment and surface water) were measured at each sampling location. At profundal and offshore reef sites water depth and surface water temperature were measured with a Lowrance Model LMS-334C iGPS and sediment temperature was measured using a digital thermometer inserted into the sediment (profundal only) immediately after collection. At littoral sites, water depth was measured using a meter stick and surface water and sediment temperature (for soft substrates) were collected using a handheld thermometer.

Invertebrate Sample Processing

Invertebrate samples from all profundal and offshore reef sites were stained with Rose Bengal (Williams & Williams 1974). All invertebrates were sorted, identified, and enumerated under a dissection microscope (magnification: 6.3 to 40x; Stereozoom, S4E, Leica Microsystems, Wetzlar, Germany) with the exception of large specimens (i.e. adult zebra mussels), which were sorted and enumerated without magnification. All insect larvae were identified to genus and other macroinvertebrates were identified to family, order, or class using dichotomous keys (Hilsenhoff 1992; Wiggins 1996; Merritt et al.

2012). Large-bodied (e.g. *Chironomus* spp.) and late instar chironomid larvae (e.g. *Procladius* spp., *Coelotanypus* spp., *Cryptochironomus* spp., etc.) were identified to genus with a dissection microscope using mentum and ventromental plate characteristics as well as ventral tubules (present in *Chironomus* spp.). Head capsules of smaller-bodied chironomids and early instars, especially those from littoral locations, were viewed under higher power (magnification: 100 to 450x magnification; American Optical Series 150) with a compound microscope to establish or confirm identity. Head capsules were mounted on glass slides using polyvinyl alcohol (PVA) mounting medium. Benthic invertebrate densities were expressed per m² of the lake bottom.

Sediment Sample Processing

Organic matter content of the sediments was determined by measuring ash-free dry mass. Sediments were dried at 80°C and a subsample (approximately 5-10 grams) was combusted in a muffle furnace at 500 °C for three hours. Samples were weighed prior to and after combustion and percent organic matter was determined by dividing the mass loss after combustion by the original dry mass.

Data Analysis

Principal components analysis (PCA) was performed on chironomid relative abundance data (only taxa with a relative abundance greater than one percent were included) to characterize the chironomid community and determine whether there were distinctions among profundal, offshore reef, and littoral communities. Analysis of variance (ANOVA) was used to determine if significant differences existed among

average densities of invertebrates among zones. Pearson correlations were used to determine whether relationships existed between invertebrate densities and physical variables. Paired t-tests were used to compare average densities of total invertebrates and total chironomids between years at profundal sites. Unpaired t-tests were used to compare mean densities of chironomids in the northern sampling sites to densities in the southern sites. PCA, ANOVA, and correlation analyses were performed in Systat (v. 13). The t-tests were conducted in R (v. 3.2.2).

I used ArcGIS to visualize variation in invertebrate community structure and physical data among sampling locations throughout Lake Winnebago. Biological and physical data were used from each location to build a geographic information system (GIS) database. Maps of densities for profundal chironomids were constructed in ArcMap (v. 10.3) using inverse distance weighted (IDW) interpolation methods carried out inside of a polygon created from the lake's shoreline boundaries. Differences in chironomid community structure within the profundal zone between years were explored by constructing pie chart maps in ArcMap (v. 10.3).

RESULTS

Physical Data

Mean water depth and water depth range for the profundal, offshore reef, and littoral zones were 4.8 meters (1.0 to 5.9 meters), 2.4 meters (1.7 to 3.4 meters), and 0.5 meters (0.3 to 0.8 meters), respectively. The profundal zone consisted of mostly silt with a mean OMC of 19.4% (SD = 4.2) and 19.3% (SD = 4.0) in 2013 and 2014 respectively.

The average OMC for the four sandy littoral sites sampled in 2013 was 2.9% (SD = 1.1). The average Secchi disc reading was 2.4 m (SD = 0.5) in 2013 and 0.7 m (SD = 0.2) in 2014. Mean sediment and surface water temperatures in 2013 were 21.3°C (SD = 0.9) and 22.7°C (1.5). Mean sediment and surface water temperatures in 2014 were 21.6°C (SD = 0.7) and 23.2°C (SD = 1.4) (Table 1).

Macroinvertebrate Density and Community Structure Among Zones

Invertebrate densities differed among the three zones of the lake [$F_{(2, 62)} = 6.65$, $p = 0.002$]. Of the three major zones sampled, offshore reef sites had the highest average invertebrate densities in 2013 while profundal densities were the lowest (Table 2). However, when only rocky littoral sites were considered, this subzone had the highest average density in comparison to other individual habitats (Table 2).

There were broad differences in the community structure of the three major zones of Lake Winnebago (Fig. 2). Chironomids comprised approximately half of all macroinvertebrates collected (44% and 53% in 2013 and 2014, respectively) from the profundal zone while oligochaetes and sphaeriid clams were also common (31% and 17% average relative abundance for both sample years, respectively) (Fig. 2). One shallow profundal site (near the southeastern shoreline, consisting of sandy substrate) had a benthic community much different from the deeper, siltier profundal locations. Invertebrates collected from this site included zebra mussels (*Dreissena polymorpha*), trichopteran larvae (primarily *Hydroptila* spp.), amphipods (Gammaridae), and

Table 1. Physical data (mean and SD) collected from each of the three major zones of Lake Winnebago in 2013 and for profundal sites in 2014.

	Sample Year	Water Depth (m)	OMC (% OMC)	Secchi Disc Depth (m)	Surface Water Temp. (°C)	Sediment Temp. (°C)
Littoral	2013	0.5	2.9 (1.1)	-	24.0 (2.1)	22.8 (2.4)
Offshore Reef	2013	2.4	-	2.4 (0.6)	22.4 (1.3)	-
Profundal	2013	4.8	19.4 (4.2)	2.5 (0.5)	22.2 (0.7)	21.1 (0.3)
Profundal	2014	4.9	19.3 (4.0)	0.7 (0.2)	23.2 (1.4)	21.6 (0.7)

gastropods along with several chironomid genera (e.g. *Cryptochironomus* spp., *Polypedilum* spp., *Dicrotendipes* spp.) not found at other profundal sites. Zebra mussels were numerically dominant at nearly all offshore reef locations, comprising over 75% of the total macroinvertebrates sampled. Chironomids comprised approximately 7% of invertebrates sampled at offshore reef locations with turbellarian flatworms, leeches, amphipods, and isopods occurring as well (Fig. 2). Zebra mussels were also abundant in the littoral zone, particularly in sample locations with rocky substrate while sandy littoral locations held much lower abundances of invertebrates overall. Chironomids comprised

Table 2: Mean (SD) benthic invertebrate densities (individuals/m²) for major habitat types sampled in Lake Winnebago.

Habitat	Number of Sites Sampled	Year	Total Invertebrates	Total Chironomids
Profundal	33	2013	2027 (1001)	896 (393)
Profundal	33	2014	2064 (763)	1084 (406)
Offshore Reef	17	2013	13987 (18755)	899 (624)
Littoral (All sites)	15	2013	10638 (14471)	1404 (1733)
Littoral (Cobble/Boulder)	10	2013	14511 (6212)	1865 (2049)
Littoral (Sand)	4	2013	808 (941)	152 (76)
Littoral (Clay/Gravel)	1	2013	1894	152

9% of invertebrates collected from the littoral zone. Trichopteran larvae (mostly

Cheumatopsyche spp. and *Hydroptila* spp.), turbellarian flatworms, amphipods

(Gammaridae), gastropods, leeches, and isopods were also encountered frequently in littoral samples (Fig. 2). Many invertebrate taxa were found exclusively in the littoral zone, including water penny beetles (*Ectopria* spp. and *Psephenus* spp.), mayfly larvae (*Caenis* spp.), and several chironomid genera (Table 3).

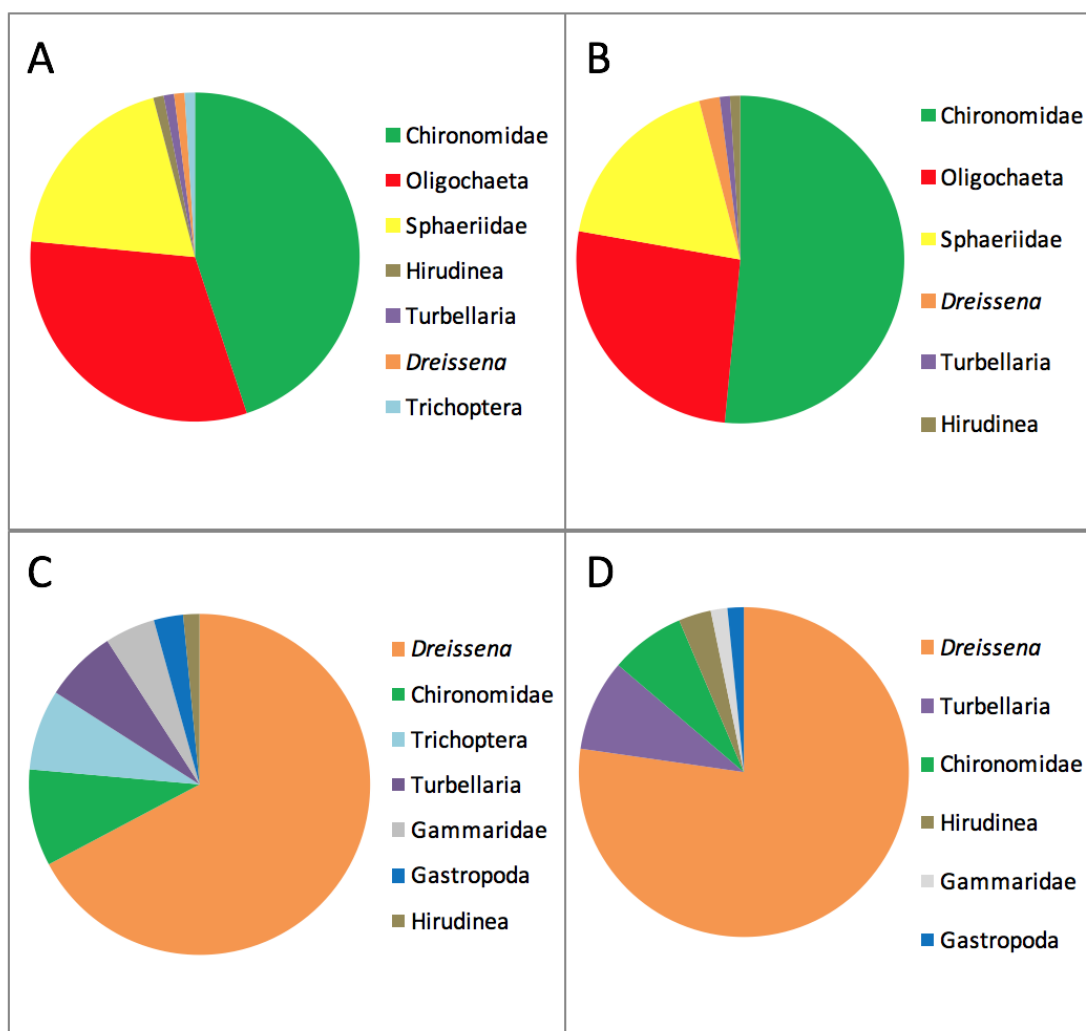


Figure 2. Relative abundances of common invertebrate taxa (greater than 1% relative abundance) in profundal (A = 2013, B = 2014), littoral (C), and offshore reef (D) sample locations.

Table 3. Presence/absence data of chironomid genera by zone.				
	Littoral	Offshore Reef	Profundal (2013)	Profundal (2014)
<i>Procladius</i> spp.	×	×	×	×
<i>Tanytarsus</i> spp.	×	×	×	×
<i>Chironomus</i> spp.		×	×	×
<i>Coelotanypus</i> spp.		×	×	×
<i>Cryptochironomus</i> spp.	×		×	×
<i>Dicrotendipes</i> spp.	×	×		×
<i>Glyptotendipes</i> spp.	×	×		
<i>Pseudochironomus</i> spp.	×	×		
<i>Microtendipes</i> spp.	×	×		
<i>Polypedilum</i> spp.	×			×
<i>Parachironomus</i> spp.	×	×		
<i>Eukieferiella</i> spp.	×			
<i>Asheum</i> spp.	×			
<i>Endotribelos</i> spp.	×			
<i>Acricotopus</i> spp.	×			
<i>Endochironomus</i> spp.	×			
<i>Orthocladius</i> spp.	×			
<i>Stictochironomus</i> spp.	×			
<i>Nanocladius</i> spp.	×			

Chironomid Community Structure: Variation among Lake Zones

The chironomid community in the profundal zone was dramatically different from that in the offshore reef and littoral zones (Fig. 3, 4). There were more similarities between the offshore reef and littoral zones although these two zones also differed substantially in chironomid community structure. The profundal zone consisted predominantly of *Procladius* spp. and *Chironomus* spp. (Fig. 4). *Dicrotendipes* spp. was the most common chironomid taxon collected at the offshore reef sites and *Tanytarsus* spp. was most prominent in the samples collected from the littoral zone.

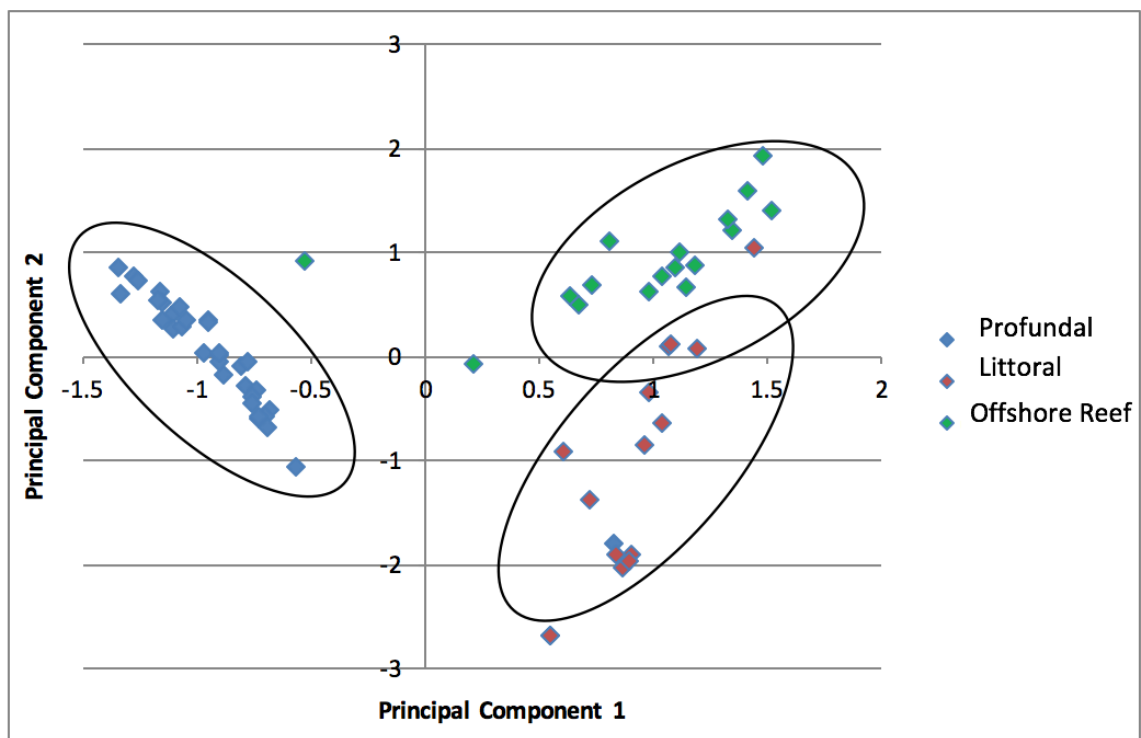


Figure 3. Principal component scores for chironomid relative abundance data for profundal, littoral, and offshore reef locations in Lake Winnebago in 2013.

Nineteen different chironomid genera were identified. Taxa richness was highest in the littoral zone (17 genera) followed by the offshore reefs (9 genera) and profundal zone (7 genera). The littoral zone contained multiple chironomid genera (e.g. *Asheum* spp., *Endochironomus* spp., *Stictochironomus* spp., *Endotribelos* spp., *Pseudochironomus* spp.) that were either observed at a single sampling site or were in very low abundance at multiple sites. In contrast, the profundal zone contained relatively few chironomid taxa in relatively high abundance. Only two chironomid taxa (*Procladius* spp. and *Tanytarsus* spp.) were present in all three zones. Nearly half of the chironomid genera identified were exclusively found in the littoral zone (Table 3). The offshore reefs contained two taxa (*Chironomus* spp. and *Coelotanypus* spp.) that were also found in the profundal, but not in the littoral zone. In contrast, several taxa (*Dicrotendipes* spp., *Glyptotendipes* spp., *Pseudochironomus* spp., *Microtendipes* spp., *Parachironomus* spp.) that occurred in the offshore reefs were also found in the littoral, but not the profundal zone (Table 3).

Chironomid Variation within the Profundal Zone

Chironomid density varied within the profundal zone (Fig. 5). Density hotspots primarily occurred in the northern half of the lake in 2013 and were located throughout the lake in 2014. In 2013 chironomid density was higher in the northern half of the lake (above the Fox River inlet) than the southern half of the lake (unpaired t-test, $t = 2.0822$, $df = 29.739$, $p = 0.0463$) (Fig. 5A). Chironomid density did not differ between the north and south regions of the lake in 2014 (unpaired t-test, $t = -0.59786$, $df = 29.603$, $p =$

0.5545) (Fig. 5B). Although the distribution of chironomids changed between years, mean chironomid densities were not significantly different between 2013 and 2014 at the whole-lake scale (paired t-test, $t = 1.879$, $df = 32$, $p = 0.069$).

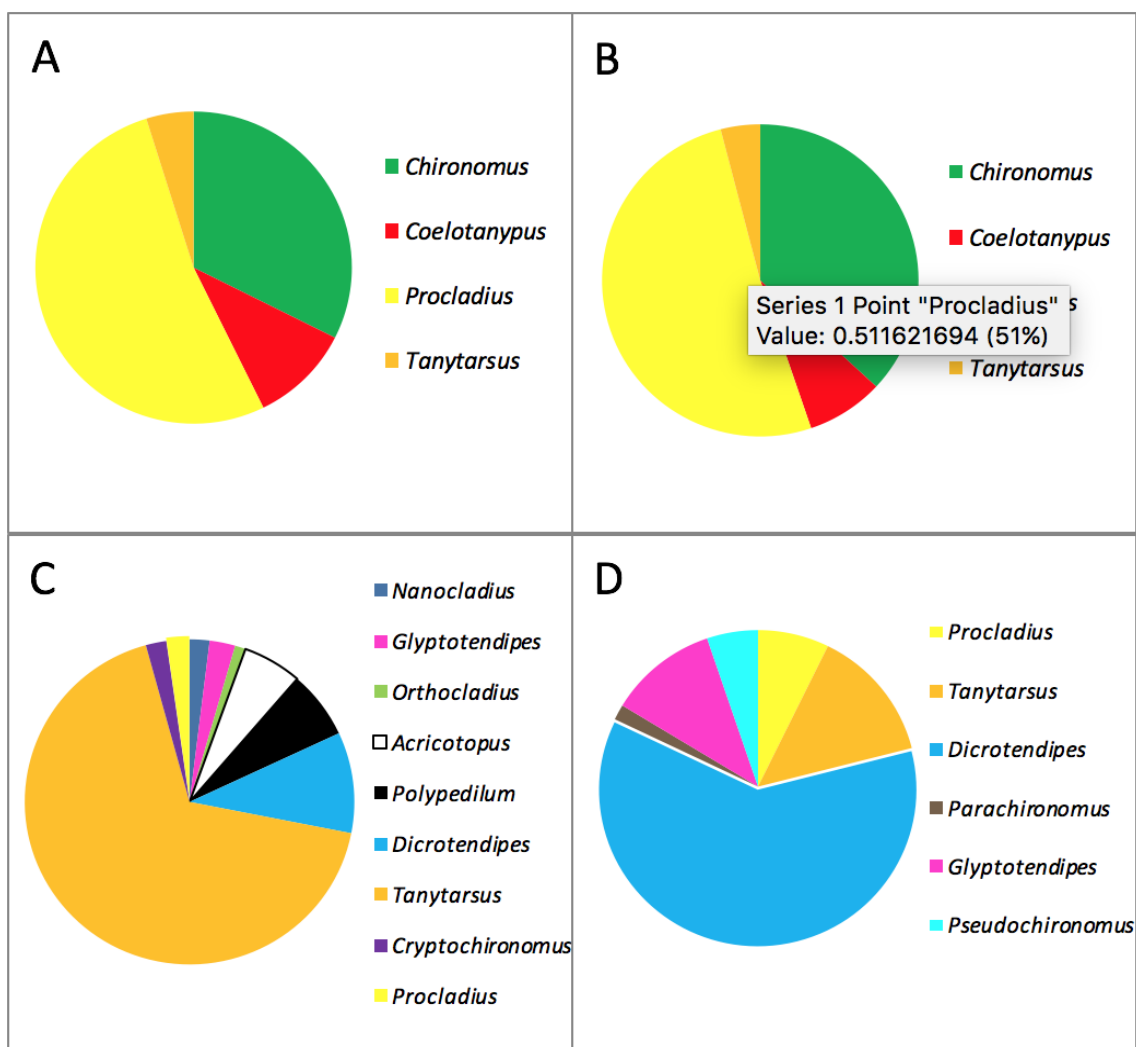


Figure 4. Relative abundances of common (greater than 1%) chironomid genera in profundal (A = 2013, B = 2014), littoral (C), and offshore reef (D) sample locations.

Variation in chironomid community structure also occurred in the profundal zone. In both years, *Procladius* spp. was numerically dominant (comprising 52% and 51% of profundal chironomids in 2013 and 2014, respectively). In 2013, *Procladius* spp. was overrepresented (i.e. its percent relative abundance at an individual site was higher than the lake-wide average relative abundance for the profundal zone) at 12 of 15 sites in the southern half of the lake, but only at 7 of the 17 sites in the north. *Chironomus* spp. was overrepresented at 11 of 17 northern sites but only 3 of 15 sites in the south in 2013 (Fig. 6A). In 2014, there was less evidence of spatial variation in chironomid community structure within the profundal zone, but *Procladius* spp. was once again overrepresented in the southern region of the lake (Fig. 6B).

Relationships between Invertebrate Densities and Habitat Variables

Few habitat variables were significantly correlated with total invertebrate and total chironomid densities in Lake Winnebago when all zones were considered. Latitude ($r = 0.431$, $df = 64$, $p = 0.012$), Secchi disc depth ($r = -0.346$, $df = 64$, $p = 0.049$), and sediment temperature ($r = 0.509$, $df = 64$, $p = 0.003$) were correlated with total invertebrate density in 2013 while sediment temperature was the only variable linked to chironomid density that year ($r = 0.442$, $df = 64$, $p = 0.010$). There were no significant correlations between habitat variables and total invertebrate or total chironomid density in 2014.

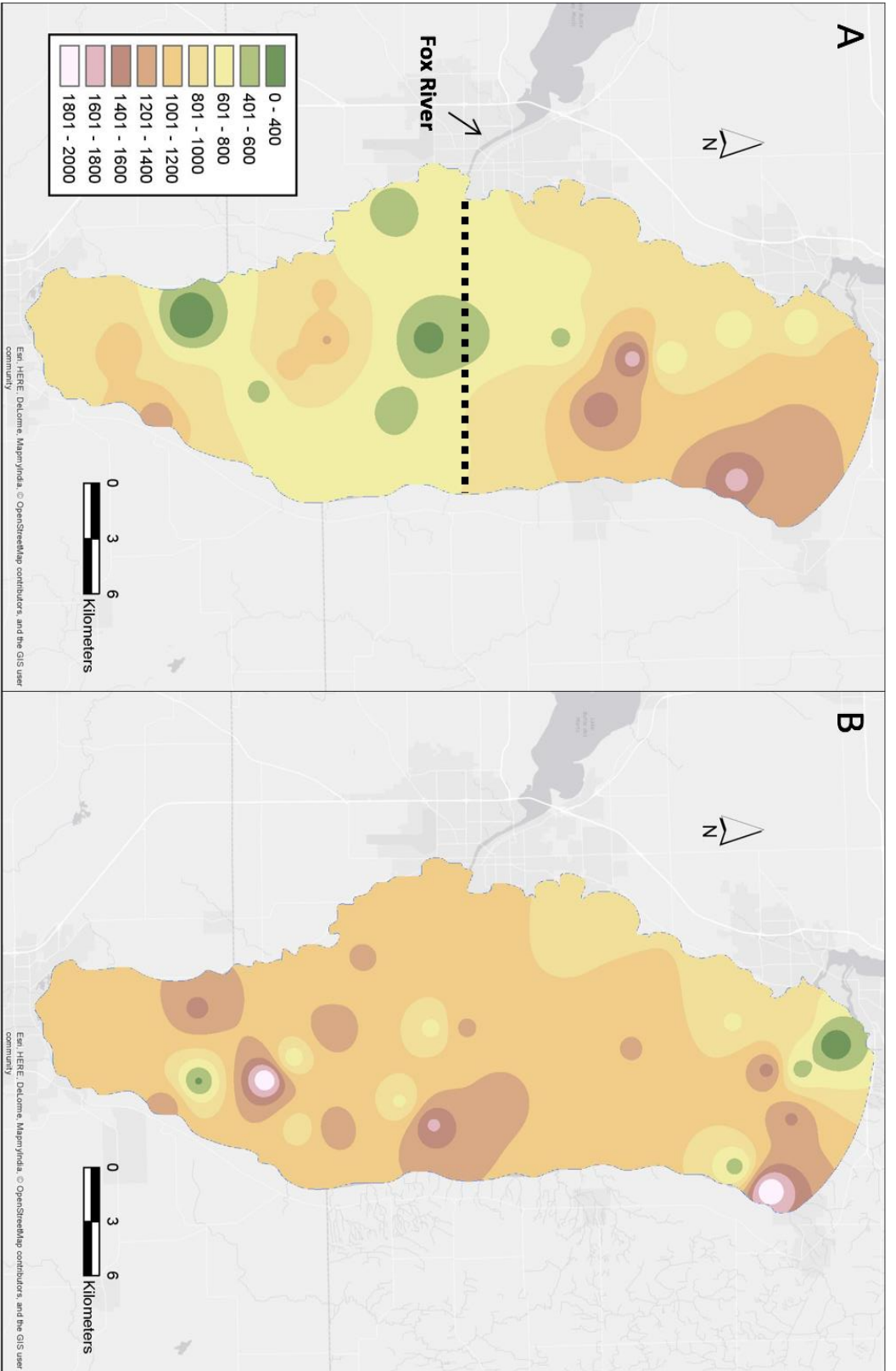


Figure 5. Maps of chironomid densities (m⁻²) for the profundal zone of Lake Winnebago, WI in 2013 (A) and 2014 (B). Dashed line drawn across lake on 5A indicates dividing line between northern and southern halves of the lake.

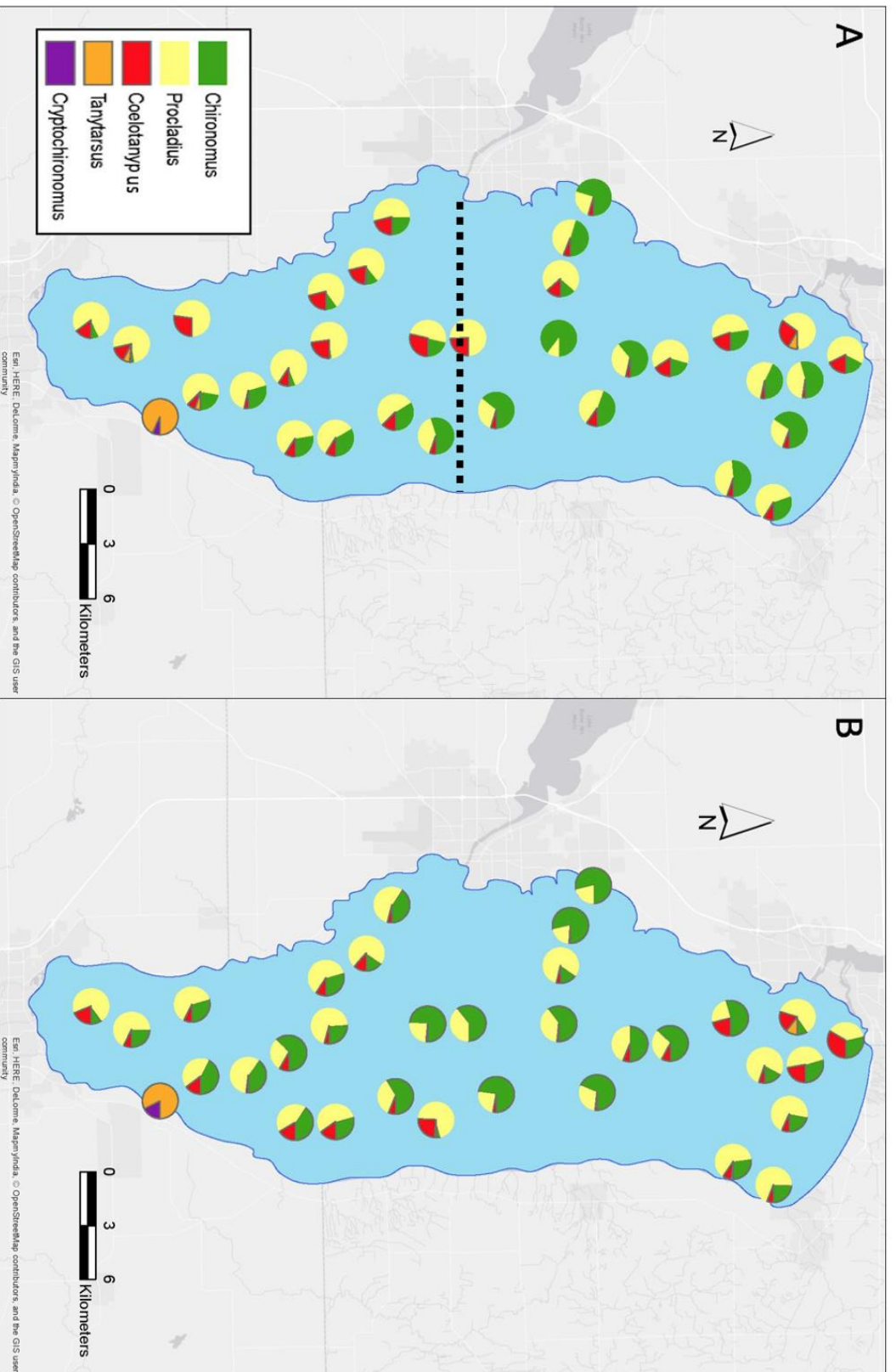


Figure 6. Relative abundances of profundal chironomid genera by site (relative abundance greater than 1%) in 2013 (A) and 2014 (B) in Lake Winnepago, WI. Dashed line drawn across lake on 6A indicates dividing line between northern and southern halves of the lake.

When considering individual lake zones and specific taxa, there were also significant correlations. In the offshore reef zone, total invertebrate density was negatively correlated with water depth ($r = -0.597$, $df = 16$, $p = 0.011$). Zebra mussel density was negatively correlated with water depth ($r = -0.588$, $df = 16$, $p = 0.013$) at the offshore reefs. In the profundal zone in 2013, *Chironomus* spp. density was positively correlated with water depth ($r = 0.458$, $df = 32$, $p = 0.008$) and latitude ($r = 0.541$, $df = 32$, $p = 0.001$) and negatively correlated with Secchi disc depth ($r = -0.405$, $df = 32$, $p = 0.022$). *Chironomus* spp. density was positively correlated with OMC ($r = 0.468$, $df = 32$, $p = 0.006$) in the profundal zone in 2014.

There were also several associations between various invertebrate taxa in the profundal zone in 2013 and 2014. In both years, densities of *Chironomus* spp. were negatively correlated with *Coelotanypus* spp. densities (2013: $r = -0.380$, $df = 32$, $p = 0.032$; 2014: $r = -0.539$, $df = 32$, $p = 0.001$). Additionally, *Procladius* spp. density showed a consistent positive correlation with both *Coelotanypus* spp. density (2013: $r = 0.630$, $df = 32$, $p = 0.001$; 2014: $r = 0.413$, $df = 32$, $p = 0.019$) and oligochaete density (2013: $r = 0.502$, $df = 32$, $p = 0.003$; 2014: $r = 0.394$, $df = 32$, $p = 0.026$).

DISCUSSION

Macroinvertebrate Variation among Zones

Among the three zones of Lake Winnebago, the littoral and offshore reef zones showed the most similarity in macroinvertebrate densities and community structure. These parallels can likely be explained by the similar substrates (gravel, cobble, and

boulders) in these two zones in contrast to the soft sediments that dominate the profundal zone. Zebra mussels, the most common littoral and offshore reef invertebrate, became established in Lake Winnebago in 1998 (Bruch 2008) and likely affected other benthic species in both zones as other studies have documented. Ozersky (2011) reported that abundance of several non-dreissenid invertebrates (e.g. amphipods, isopods, chironomids, oligochaetes) increased dramatically following zebra mussel invasion in Lake Simcoe (Ontario, Canada) probably because of the increased surface area for colonization and increased amounts of periphyton and benthic organic matter provided by the mussels, which likely benefited some benthic taxa (Ozersky et al. 2013) while being detrimental to others (e.g. native unionids) (Karatayev et al. 2014). The only major taxonomic group not shared between the littoral and offshore reef zones were trichopteran larvae, especially hydropsychids. The most numerous hydropsychid encountered, *Cheumatopsyche* spp, was observed primarily on algae-covered cobble/boulders in the littoral zone. Qualitative observations suggest there was less epilithic biomass on the offshore reefs than in the rocky littoral, which may have affected abundance of *Cheumatopsyche* spp. The dominant taxa in the profundal zone of Lake Winnebago, including several chironomid genera, oligochaetes, and sphaeriid clams require soft sediment. Some of these taxa, such as *Chironomus*, are known to be able to tolerate the hypoxic conditions that often prevail in organic-rich sediments (McGarrigle 1980). Although silt and sand are preferred habitat for some taxa, the low substrate diversity and physicochemical limitations probably contributed to the low taxa richness and relatively

low invertebrate densities in the profundal zone of Lake Winnebago relative to the other zones.

Chironomid Variation among Zones

Large differences in chironomid community structure were observed among the three major zones of Lake Winnebago. Several variables including water depth, substrate type, organic matter abundance, and dissolved oxygen concentration could have contributed to the spatial pattern observed (Heinis et al. 1994; Nakazato et al. 1998; Vos et al. 2002; Fu et al. 2012). Differing habitat requirements and preferences by chironomid taxa likely determined where taxa were most abundant in the lake.

Chironomus spp., for example, prefers a thick layer of organic-rich sediment (McGarrigle 1980; Prat and Rieradevall 1992; Nakazato et al. 1998; Hirabayashi 2003) and is highly tolerant of hypoxic (even anoxic) conditions which likely allows it to exploit areas other taxa cannot (Heinis et al. 1994). *Chironomus* spp. larvae require a minimum depth of soft sediment in order to burrow which may not be met in the littoral zones of lakes (McLachlan and Cantrell 1976; Ali et al. 2002), including Lake Winnebago. *Procladius* spp. thrives in many microhabitats (Wolfram 1996; Specziar and Biro 1998), which is consistent with the wider distribution of *Procladius* spp. observed across the three major lake zones (Table 3). *Procladius* spp., which is typically predaceous, was more abundant in the profundal zone than chironomids occupying lower trophic levels in both 2013 and 2014. This can be explained, in part by body size differences. *Chironomus* spp., the second most abundant profundal chironomid taxon, is much larger than *Procladius* spp.

and likely has more total biomass than *Procladius* spp. in Lake Winnebago (Anderson et al. 2012). The distribution of *Tanytarsus* spp. (a tube builder), the most prevalent littoral species, may have resulted from competition with *Chironomus* spp. Cantrell and McLachlan (1977) reported that, upon initial colonization of a newly flooded lake, the activities of *Chironomus* spp. caused *Tanytarsus* spp. to settle around the lake margins. Additionally, *Tanytarsus* spp. exhibits a positive phototaxis (unlike *Chironomus* spp.) indicating *Tanytarsus* spp. may have a higher proclivity toward the littoral zone (Cantrell and McLachlan 1977). *Dicrotendipes* spp., the most common offshore reef chironomid, is known to inhabit a wide variety of microhabitats in shallower lentic systems (Johnson and Krieger 2005; Merritt et al. 2012). Because it belongs to the same functional feeding group (collector-gatherer) as *Chironomus* spp. and *Tanytarsus* spp., it is possible that *Dicrotendipes* spp. is most numerous in the offshore reef zone because it fills a niche that neither *Chironomus* spp. nor *Tanytarsus* spp. can exploit.

In addition to differences in the dominant chironomid genera among the three major zones of the lake, there were also differences in chironomid taxa richness among the zones. There are several possible reasons why the littoral zone was highest in chironomid taxa richness. First, physical heterogeneity and substrate complexity are relatively high in the littoral zone which suggests increased niches for chironomid taxa (Abdallah and Barton 2003; Vadeboncoeur et al. 2011; Pilotto et al. 2015). Zebra mussels further increase substrate complexity and may provide a food source in the form of nutrient-rich feces and pseudofeces (Beekey et al. 2004; Ozersky et al. 2011; Rennie and Evans 2012). Second, light availability declines with depth, which can negatively

impact the abundance of photoautotrophs (likely food sources for many chironomid taxa) and dissolved oxygen availability (Ruess et al. 2014; Vadeboncoeur et al. 2014). The littoral zone probably has higher light availability, on average, than at offshore reefs, and much higher light availability than the profundal zone which likely affects the food supply for chironomids who are primary consumers.

Chironomid Spatial and Temporal Variation within the Profundal Zone

Chironomid densities were not uniform throughout the profundal zone of Lake Winnebago. Because *Chironomus* spp. density was positively correlated with OMC it is possible that variation in OMC drove spatial variation in chironomid community structure within the profundal zone. However OMC did not differ between the northern and southern halves of the lake in 2013 (unpaired t-test, $t = -0.6512$, $df = 26.491$, $p = 0.5199$) or 2014 ($t = 0.9026$, $df = 29.928$, $p = 0.374$) even though total chironomid density was higher in the northern half in 2013. However, the far southern portion of the lake tends to have sandier sediment than most profundal locations to the north and the five southernmost sites consistently measured below 20% OMC. These observations are consistent with the relatively low abundance of *Chironomus* (which prefers silty, organic-rich sediments) in the far southern portion of the lake in 2013 but not 2014 (Fig. 5). Although sediment characteristics may influence the structure of chironomid communities in the profundal zone there are likely other factors that are responsible for year-to-year variation at local and regional scales (Fig. 5, 6).

Stochastic factors, including wind speed and direction during emergence events, could affect chironomid distribution patterns in the lake by impacting the position of mating swarms (and thus oviposition location) and the settling locations of eggs and first instars (Hilsenhoff 1967, Davies 1976). Early instar chironomid larvae are limnetic and will drift throughout the water column until a suitable substrate is reached (Hilsenhoff 1966; Davies 1976; Franquet 1999). Disconnect between emergence and oviposition locations could impart randomness to distribution patterns through time (Hilsenhoff 1967). Conversely, if adult flies oviposit close to where they emerged, this could lend stability to spatial distributions at a local scale (Fig. 6). Factors that tend to be more fixed, such as sediment characteristics, could interact with stochastic factors, such as lake currents, to shape chironomid community structure in the profundal zone. Lake currents likely shape propagule (e.g. eggs) delivery to locations whereas sediment characteristics (e.g. grain size, DO, food supply) probably impact survivorship and growth of larvae at local scales (Vos et al. 2002, DeHaas et al. 2006). Silt-dominated habitats may bury some newly settled larvae causing fine particles to clog filtering mechanisms, thus, making these habitats unsuitable for some filter-feeding taxa.

Previous studies of chironomids in the profundal zone of Lake Winnebago, spanning several decades, have revealed broad similarities in community structure but order of magnitude differences in the density of *Chironomus*, the most intensively studied invertebrate taxon in the lake (Hilsenhoff 1967; Koehnke 1997; Anderson et al. 2012) (Fig. 7). In all previous studies of chironomid community structure in the lake,

Chironomus spp., *Procladius* spp., and *Coelotanypus* spp. were the most common genera observed (Hilsenhoff 1961, 1962; Koehnke 1997).

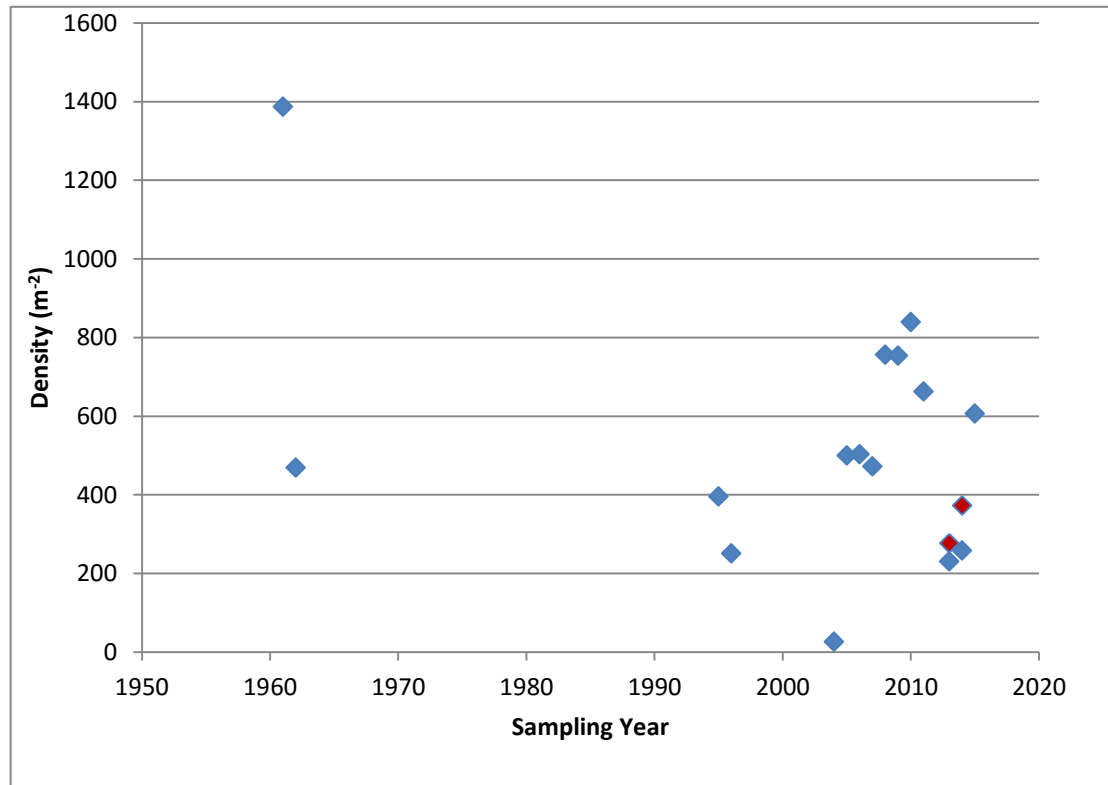


Figure 7. Average densities of 4th instar *Chironomus* spp. in early August sampled from four long-term profundal sites (shown in blue) by Hilsenhoff (1961 and 1962), Koehnke (1995 and 1996), Wisconsin Department of Natural Resources (2004 - 2011), and Heling (2013 and 2014). Red markers in 2013 and 2014 indicate densities of 4th instar *Chironomus* spp. averaged from 33 profundal sites.

Conclusions

The results of this study indicate that there are differences in the spatial distribution of invertebrates, including chironomids, among the three major zones (profundal, offshore reef, and littoral) of Lake Winnebago. The highest degree of

variation occurred between the littoral and profundal zones although the three zones were highly distinct overall. The littoral and offshore reef zones exhibited the highest densities of invertebrates while densities in the profundal zone were substantially lower in comparison. Zebra mussels were the dominant taxon in both the littoral and offshore reef zones and likely influenced the non-dreissenid assemblages present in those zones. Chironomids were the most abundant invertebrates in the profundal zone, likely due to the requirement for soft sediments needed for burrowing/tube-building taxa. Chironomids exhibited variation among lake zones as well with a higher number of taxa present in the littoral and offshore reef zones in comparison to the profundal zone with several taxa found exclusively in the littoral zone. The profundal zone held the lowest number of chironomid taxa but in much higher abundance in comparison to the littoral and offshore reef zones. Within the profundal zone, chironomids exhibited spatial variation in both 2013 and 2014. Although the average larval density did not change significantly throughout the lake from year to year, spatial patterns fluctuated and relative abundances of the common profundal taxa (*Chironomus* spp., *Procladius* spp., and *Coelotanypus* spp.) at individual sampling locations varied. It is uncertain which factors play a more decisive role in the determination of larval distribution but it is likely that several fixed (e.g. sediment type) and stochastic variables (e.g. oviposition) have an effect.

Because lakes, like Lake Winnebago, exhibit a high degree of variation among and within lake zones it is crucial that spatial and temporal studies of benthic invertebrates be comprehensive (i.e. take multiple substrates and depths into account,

sample over consecutive years, etc.) in order to determine which factors drive patterns in distribution and to observe how densities and distributions change over time. Because most lakes are currently undergoing rapid changes as a result of increasingly present anthropogenic activity, it has become imperative to better understand spatial and temporal patterns in order to predict how systems will respond to change in the future.

CHAPTER III

CONCLUSIONS

The results of this study indicate that there are differences in the spatial distribution of invertebrates, including chironomids, among the three major zones (profundal, offshore reef, and littoral) of Lake Winnebago. Principal component analysis (PCA) showed clear distinctions among zones and indicated that the profundal zone was highly dissimilar to the offshore reef and littoral zones. Additionally, while the offshore reef and littoral zones were similar to one another in terms of invertebrate community composition and invertebrate densities, they still exhibited clear differences, likely due to numerous depth-related variables that distinguish the two habitats. However, because the two zones are more similar in terms of habitat (dominated by rocky substrates) and shared commonalities in their most abundant taxa (zebra mussels), the higher degree of resemblance between the offshore reef and littoral zones (in comparison to the profundal zone) was expected.

The littoral zone exhibited the highest taxa richness (for both invertebrates, collectively, and chironomids) among the three zones and held the highest densities of invertebrates when only hard substrate sites were considered. It is typical that littoral zones hold the most diversity and highest densities of benthic invertebrates in lakes as the habitat is more complex than in the profundal zone (Vadeboncoeur et al. 2011).

Because the littoral and offshore reef sites were only sampled in 2013 it cannot be determined to what extent these communities fluctuate over time. The profundal zone,

however, does appear to experience a degree of variation in the distribution of total chironomid densities between years although major representative groups and average densities throughout the lake did not change from year to year. It is likely that several stochastic factors, such as oviposition, play a role in the spatial distribution of chironomids within zones between years (Hilsenhoff 1967; Davies 1976; Vos et al. 2002). Fixed variables, such as substrate type, likely contribute to and impart stability on the long-term chironomid community dynamics among zones (Moore 1981; Efitre et al. 2001; Fu et al. 2012).

For many reasons, it is important to study spatial and temporal variation of invertebrates comprehensively, especially when considering large lakes such as Lake Winnebago. By taking into account a variety of substrates and collecting a representative number of samples from each zone, patterns of distribution can be better elucidated and lake-wide densities more accurately estimated. At present, many lakes are currently undergoing a variety of anthropogenically-induced modifications; therefore, it is crucial that the extent of the ecological role and dynamics of benthic invertebrates be better understood. As aquatic systems rapidly undergo these changes, variations in invertebrate density and community structure will both directly and indirectly impact other organisms (e.g. fishes).

APPENDIX A

Summary of physical data collected from all sample locations in Lake Winnebago in
2013 and 2014

Table 4. Environmental data collected from profundal (P) sites. LOI = loss on ignition.

Site	Substrate Description	Depth (m)		Sediment Temperature (°C)		Surface Water Temperature (°C)		Secchi Disc Depth (m)		Organic Matter (% LOI)	
		Aug. 2013	Aug. 2014	Aug. 2013	Aug. 2014	Aug. 2013	Aug. 2014	Aug. 2013	Aug. 2014		
P1	Silt	4.9	5.1	20.7	21.1	21.3	21.3	3.4	0.6	21.57	20.82
P2	Silt	5.3	5.3	21.6	21.6	22.6	23.4	1.2	0.3	17.9	17.96
P3	Silt	4.9	4.9	21	22	21.4	24.3	2.7	0.9	21.51	22.01
P4	Silt	5.9	5.9	21.2	23.1	21.4	23.9	2.1	0.9	22.17	22.23
P5	Silt	4.8	4.8	21.2	22.5	22.9	23.9	2.1	0.6	18.06	18.19
P6	Silt	4.5	4.5	20.8	21.7	22.4	23.8	2.4	0.9	19.31	18.95
P7	Silt	5.2	5.1	21.6	21.5	22.5	23.3	2.1	0.6	19.94	19.36
P8	Silt	5.4	5.4	21.3	21.6	22.3	23.1	2.1	0.6	20.43	21.07
P9	Silt	4.9	4.9	22	22	22.5	24.7	1.8	0.9	12.4	12.58
P10	Silt	5.3	5.3	20.8	21.4	22.7	23.3	1.8	0.9	21.58	21.92
P11	Silt	5.4	5.5	21.9	21.8	22.5	24.8	2.1	0.6	17.16	17.24
P12	Silt	5.7	5.6	21	21.5	22.4	24.3	2.4	0.9	22.03	21.3
P13	Silt	5.8	5.9	20.7	21.6	22.3	23.6	2.7	0.9	22.3	21.84
P14	Silt/Pebbles	3.8	3.7	21.4	22.1	22.1	24.1	2.7	0.6	7.83	20.34
P15	Silt	5.8	5.8	21.2	22.3	23	23.7	2.4	0.9	21.25	21.56
P16	Silt	5.5	5.5	20.9	21	22.2	23.2	2.4	0.6	23.35	22.91
P19	Silt	5.8	5.8	20.9	22.1	23.7	23.8	2.4	0.6	21.84	22.25
P20	Silt	5.7	5.7	20.8	21.8	22.7	24.6	3.0	0.9	22.9	22.39
P21	Silt	5.5	5.7	20.8	22.4	22.8	24.9	3.7	0.3	23.49	22.27
P22	Silt	5.3	5.4	21.2	21.9	23.3	24	2.7	0.6	21.2	20.59
P23	Silt	3.9	3.8	20.8	22.6	22.7	25.2	2.7	1.2	20.61	20.4
P24	Silt	5.4	5.4	21.2	21.9	23.2	24.5	3.0	0.6	22.73	20.52
P25	Silt	4.5	4.6	20.9	21.9	21.4	24.8	2.7	1.2	22.3	21.1
P26	Silt	4.5	4.5	21.2	21	21.6	21.8	2.4	0.6	20.74	20.29
P27	Silt	5	5	20.9	20.8	21.6	21.4	2.4	0.6	22.54	21.25
P28	Silt	5	5	21	20.9	21.2	21.2	1.8	0.6	21.35	20.66
P29	Silt	4.8	4.9	21.2	20.6	21.5	20.9	2.1	0.6	19.77	19.55
P30	Silt	4.8	4.9	21.1	20.7	21.4	21.4	2.4	0.6	20.97	20.31
P31	Silt	4.1	4.3	20.8	20.6	21.3	21.6	2.1	0.6	16.58	16.09
P32	Silt	3.9	3.9	21	21.9	21.8	22.6	2.4	0.6	16.22	15.91
P33	Sand/ Vegetation	1	1	21.7	19.9	21.3	20.4	2.4	0.6	5.25	1.33
P34	Silt	3.6	3.7	21	20.6	21.6	21.4	2.7	0.6	17.42	16.46
P35	Silt	3.2	3.3	21.1	20.8	21.6	21.8	2.7	0.9	16.78	15.8

Table 5. Environmental data collected for littoral (L) sites.

Site	Substrate Description	Depth (m)		Sediment Temperature (°C)		Surface Water Temperature (°C)		Secchi Disc Depth (m)		Organic Matter (% LOI)	
		Aug. 2013	Aug. 2014	Aug. 2013	Aug. 2014	Aug. 2013	Aug. 2014	Aug. 2013	Aug. 2014	Aug. 2013	Aug. 2014
L1A	Cobble/ Boulders	0.4	-	-	-	21.5	-	-	-	-	-
L1B	Sand	0.8	-	21	-	21.5	-	-	-	3.29	-
L2	Cobble/ Boulders	0.4	-	-	-	22.5	-	-	-	-	-
L3	Cobble/ Boulders	0.4	-	23	-	25	-	-	-	1.77	-
L4	Cobble/ Boulders	0.4	-	-	-	25.5	-	-	-	-	-
L5A	Cobble/ Boulders	0.7	-	-	-	25.5	-	-	-	-	-
L5B	Cobble/ Boulders	0.8	-	-	-	25.5	-	-	-	-	-
L6	Cobble/ Boulders	0.7	-	-	-	21	-	-	-	-	-
L7A	Cobble/ Boulders	0.6	-	-	-	22	-	-	-	-	-
L7B	Sand	0.5	-	21	-	22	-	-	-	2.21	-
L8A	Cobble/ Boulders	0.3	-	-	-	25	-	-	-	-	-
L8B	Sand	0.4	-	26	-	27.5	-	-	-	4.12	-
L9A	Cobble/ Boulders	0.4	-	-	-	26	-	-	-	-	-
L9B	Sand/ Vegetation	0.4	-	-	-	26	-	-	-	-	-
L10	Cobble/ Boulders	0.3	-	-	-	24	-	-	-	-	-

Table 6. Environmental data collected from offshore reef (R) sites.

Site	Site Description	Depth (m)		Sediment Temperature (°C)		Surface Water Temperature (°C)		Secchi Disc Depth (m)		Organic Matter (% LOI)	
		Aug. 2013	Aug. 2014	Aug. 2013	Aug. 2014	Aug. 2013	Aug. 2014	Aug. 2013	Aug. 2014	Aug. 2013	Aug. 2014
R17	Gravel	3.4	-	-	-	21.8	-	0.7	-	-	-
R18	Cobble/ Gravel	1.7	-	-	-	22.8	-	0.9	-	-	-
R1A	Cobble/ Gravel	2.3	-	-	-	22.5	-	1.1	-	-	-
R1B	Cobble/ Gravel	2.7	-	-	-	22.5	-	1.1	-	-	-
R1C	Cobble/ Gravel	3	-	-	-	23.3	-	1.1	-	-	-
R2A	Cobble/ Gravel	2.4	-	-	-	24.3	-	0.8	-	-	-
R2B	Gravel/Sand	2.1	-	-	-	24.6	-	0.8	-	-	-
R2C	Gravel/Sand	2.3	-	-	-	25.2	-	0.8	-	-	-
R3A	Cobble/ Gravel	2.6	-	-	-	21.8	-	0.8	-	-	-
R3B	Cobble/ Gravel	2.7	-	-	-	22.1	-	0.8	-	-	-
R3C	Cobble/ Gravel	2.9	-	-	-	21.6	-	0.8	-	-	-
R4A	Gravel/Cobble	1.4	-	-	-	21.8	-	0.6	-	-	-
R4B	Gravel/Cobble	2.1	-	-	-	21.9	-	0.6	-	-	-
R4C	Gravel/Cobble	3.3	-	-	-	21.8	-	0.6	-	-	-
R5A	Gravel/Cobble	1.3	-	-	-	21.1	-	0.8	-	-	-
R5B	Gravel/Cobble	1.7	-	-	-	21	-	0.8	-	-	-
R5C	Gravel/Cobble	2.9	-	-	-	21	-	0.8	-	-	-

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