

12-2015

IMPACTS OF RIVER INFLUENCE AND WAVE EXPOSURE ON THE EIPSAMMIC DIATOMS OF THE LAKE SUPERIOR WAVE ZONE

Leon R. Katona
Northern Michigan University, lekatona@nmu.edu

Follow this and additional works at: <https://commons.nmu.edu/theses>



Part of the [Biodiversity Commons](#), and the [Terrestrial and Aquatic Ecology Commons](#)

Recommended Citation

Katona, Leon R., "IMPACTS OF RIVER INFLUENCE AND WAVE EXPOSURE ON THE EIPSAMMIC DIATOMS OF THE LAKE SUPERIOR WAVE ZONE" (2015). *All NMU Master's Theses*. 70.
<https://commons.nmu.edu/theses/70>

This Open Access is brought to you for free and open access by the Student Works at NMU Commons. It has been accepted for inclusion in All NMU Master's Theses by an authorized administrator of NMU Commons. For more information, please contact kmcdonou@nmu.edu, bsarjean@nmu.edu.

IMPACTS OF RIVER INFLUENCE AND WAVE EXPOSURE ON THE
EPIPSAMMIC DIATOMS OF THE LAKE SUPERIOR WAVE ZONE

By

Leon Russell Katona

THESIS

Submitted to
Northern Michigan University
In partial fulfillment of the requirements
For the degree of

MASTER OF SCIENCE

Office of Graduate Education and Research

December 2015

SIGNATURE APPROVAL FORM

Title of Thesis: IMPACTS OF RIVER INFLUENCE AND WAVE EXPOSURE ON THE EIPSAMMIC DIATOMS OF THE LAKE SUPERIOR WAVE ZONE

This thesis by Leon Russell Katona is recommended for approval by the student's Thesis Committee and Department Head in the Department of Biology and by the Assistant Provost of Graduate Education and Research.

Committee Chair: Dr. Mac Strand Date

First Reader: Dr. Alan Rebertus Date

Second Reader: Dr. Erich Ottem Date

Department Head: Dr. John Rebers Date

Dr. Brian D. Cherry Date
Assistant Provost of Graduate Education and Research

ABSTRACT

IMPACTS OF RIVER INFLUENCE AND WAVE EXPOSURE ON THE EPIPSAMMIC DIATOMS OF THE LAKE SUPERIOR WAVE ZONE

By

Leon Russell Katona

Although little is known about primary productivity in wave zone habitats of very large lakes, it is presumably dominated by microalgae that attach to mineral substrates. Watershed energetics are linked with these wave zones through river mouth habitats, which provide nutrient and organismal input to lake systems. In this study, I assessed the abundance, productivity, and community composition of epipsammic diatoms in river mouth and beach habitats along the south-central coast of Lake Superior. Chlorophyll *a* concentrations were more than three-fold greater in river mouths (mean \pm 1SE = 1.17 ± 0.45 mg/m²), than in wave zone (0.36 ± 0.07) or beach sites (0.39 ± 0.07). Richness was lower in isolated beach sites (28.72 ± 1.07 species) than in river mouth (34.06 ± 1.53) and wave zone (31.17 ± 0.92) habitats. Habitat specificity was evident for 22% of beach species and 16% of river mouth species identified, suggesting that these habitats are biologically distinct and that river mouths are productivity hot spots in wave zone environments. Wind data were used to quantify wave exposure in sites along Lake Superior's south-central coast. Species richness was greater in low (35.06 ± 1.15 species) than in medium (28.39 ± 1.23) or high-exposure (30.50 ± 0.99) sites, indicating that wave exposure strongly influences richness of epipsammic diatom communities in locations on the south-central shore of Lake Superior.

Copyright by

LEON RUSSELL KATONA

2015

ACKNOWLEDGEMENTS

This work would not have been possible without the assistance of many individuals and organizations. I thank Bruce Leutscher and the National Parks Service team at Pictured Rocks National Lakeshore for allowing me to work in the Hurricane River and surrounding environments. Jingfang Niu was imperative for managing field and laboratory equipment and ordering chemicals necessary for my analyses. I thank Kelly Doré for thoughtfully managing funding transactions and for providing encouragement and congeniality when it was needed.

Many thanks to the Lydia M. Olson Library for its vast collection of scientific periodicals, as well as its assembly of phycology texts and diatom identification monographs. Taxonomic analyses in this study would not have been possible without items from the library. This invaluable resource deserves more credit for the services it provides.

I thank my thesis committee members, Dr. Erich Ottem and Dr. Alan Rebertus, not only for their technical support in analyzing and reporting this work, but for their encouragement and perspectives. Abundant thanks to my thesis advisor, Dr. Mac Strand, for introducing me to Great Lakes ecology and epipsammic communities. Dr. Strand's expertise and guidance on this project has made me a better scientist, for which I am eternally grateful. Each of these individuals have illuminated me to the virtues and joys of ecology and environmental science.

PREFACE

This thesis is formatted per the Instructions for Author page given by the journal *Hydrobiologia* (<http://www.springer.com/life+sciences/ecology/journal/10750>). This work was funded through a mixture of research grant opportunities available at Northern Michigan University: an Excellence in Education research grant, a Charles C. Spooner grant and a generous donation from the Merry Memorial Fund. Access to work in Pictured Rocks National Lakeshore was obtained through the National Park Service.

TABLE OF CONTENTS

List of Tables	(iv)
List of Figures	(v)
Introduction.....	1
Methods.....	6
Results.....	13
Discussion.....	17
References.....	27
Appendices.....	33

LIST OF TABLES

Table 1: Water chemistry measures for study sites.	36
Table 2: Epipsammic diatom species Richness, Diversity and Evenness between study sites.	37
Table 3: Calculated wave exposure values for June, August and November for each site.	38

LIST OF FIGURES

Figure 1: Hurricane River site map.....	39
Figure 2: Harlow Creek site map.....	40
Figure 3: Au Train River site map.	41
Figure 4: Wave exposure calculation map.	42
Figure 5: Diatom species richness across habitat types.	43
Figure 6: Chlorophyll <i>a</i> by habitat type.	44
Figure 7: Community productivity by habitat type.	45
Figure 8: Community respiration by habitat type.	46
Figure 9: Diatom species richness at areas of different calculated wave exposure.	47
Figure 10: Habitat dominance diversity curves.	48

INTRODUCTION

The littoral zones of very large lakes are heterogeneous environments that are characterized by limited macrophyte growth and nearly constant wave action (Keddy & Reznicek, 1986; Keough et al., 1999). These nearshore areas create transitional zones between terrestrial and aquatic habitats (Schindler and Scheuerell 2002; Strayer and Findlay 2010) and are often biologically diverse (Vadeboncoeur et al., 2011). Littoral zones act as an interface between the lake primary production base and higher trophic levels (Vadeboncoeur et al., 2002; Stoffels et al., 2005).

Lake systems are fueled by their watersheds. In temperate forested environments, atmospheric deposition (Carpenter et al., 1998; Kumar et al., 2007), terrestrial runoff (Peterson et al., 2001; Pace et al., 2004) and groundwater influx (Harvey et al., 2000; Kornelsen & Coulibaly, 2014) can substantially contribute to lake nutrient-loading. Allochthonous material is transported from headwaters to downstream reaches within the watershed (Vannote et al., 1980). This nutrient input stimulates productivity within rivers.

River mouths link lotic and lentic environments and form distinct physical and chemical gradients between these systems. During periods of high flow, sediment and material can form a large plume of turbid water that extends from a river mouth into a lake (Wiseman & Garvine, 1995; Slattery & Phillips, 2011) These plumes transport enormous loads of sediment, nutrients and organisms, which can either persist in littoral

areas or drift offshore (O'Donnell et al., 1998). The transfer of fluvial nutrients into lake systems increases algal biomass in littoral areas (Higgins et al., 2003) which are then transferred to higher trophic levels through consumers (Vadeboncoeur et al., 2002; Sierszen et al., 2004; Hoffman et al., 2010).

In lake ecosystems, algae are the dominant primary producers. The majority of research on lake primary productivity has focused on pelagic algae (Stevenson et al., 1996; Vadeboncoeur et al., 2002), though benthic (bottom-dwelling) algae have proven to be ecologically important in lake systems (Hecky & Hesslein, 1995; Sierszen et al., 2004). Benthic algae can be abundant in lake littoral waters (Vadeboncoeur et al., 2003), and provide significant contributions to whole lake production in deep oligotrophic lakes (Vadeboncoeur et al., 2008).

Lake Superior is the largest and deepest of the Laurentian Great Lakes, (Herdendorf et al. 1981) though its littoral zone is less than ten percent of its total area (Vadeboncoeur et al., 2011). As such, the primary productivity of Lake Superior is believed to be driven by phytoplankton (Fahnenstiel et al. 1986; Keough et al. 1996). Yoshii (1999) showed that benthic algae were major producers and trophic contributors in Lake Baikal, another deep, oligotrophic lake with an even smaller (Vadeboncoeur et al. 2011) littoral area than Lake Superior. Sierszen et al. (2004) illustrated that benthic productivity (dominated by diatoms) in some Lake Superior wetlands was more important to higher trophic levels than planktonic production. Sierszen et al. (2006) determined that benthic algae were the most important food source for *Diporeia* amphipods in coastal areas of Lake Superior, illustrating the potential importance of benthic algae in large lake energy transfer. In these lakes, energy derived from benthic

photosynthesis is transferred through *Diporeia* to larger invertebrates or fish, which may remain in the littoral zone or move to offshore waters.

The littoral zone of Lake Superior is subjected to nearly-constant wave action. This wave zone environment is the home to specialists that are adapted to withstand the impacts of the chronic wave action (Barton & Hynes, 1978). Bixby et al. (2005) described an endemic wave zone diatom (*Hannaea superiorensis*) in Lake Superior and hypothesize that it speciated from river populations of a similar species to become adapted to the wave zone environment. The constant action within the wave zone can have a profound impact on the flora and fauna that inhabit this environment. Shear stress caused by high water velocity and abrasion by suspended sediments can remove algae from substrates (Francoeur & Biggs, 2006), and sediment instability has been linked to drastically lower periphyton biomass when compared to stable-sediment communities (Biggs et al. 1999).

Much of the south-central basin of Lake Superior is underlain by Bayfield-Jacobsville sandstone, creating sandy beach shorelines (Dell, 1975; Barton & Hynes, 1978), which create large expanses of habitat for epipsammic algae. Sand grains are able to be carried by currents and have varied, heterogeneous microtopographies (Krejci & Lowe, 1986; Miller et al., 1987). Miller et al. (1987) noted that epipsammic diatoms in a Michigan stream preferentially colonized the valleys of sand grains, which may provide protection from shear stress or abrasion by suspended sediments. Harper and Harper (1967) illustrated that epipsammic species adhere to their substrates more strongly than other attached diatoms. Given the high degree of wave action on the south-central coast

of Lake Superior, it seems likely that epipsammic diatoms that tightly adhere to sand grains are the dominant producers in this environment.

This study set out to describe the epipsammic diatom communities present in the wave zone of south-central Lake Superior. By measuring the biomass and productivity and describing the community composition of epipsammic diatoms in this habitat, I aimed to assess their ecological importance in the wave zone environment. As the carbonate-poor waters (Keough et al., 1999) and coarse substrata of south-central Lake Superior are not conducive to macrophyte growth (Hecky & Hesslein, 1995), it is presumed that benthic algae must be the main producers in this portion of the Lake Superior wave zone. As wave action appears to influence the growth of both macro- and micro-autotrophs in this environment, it was predicted that the intensity of wave action within the wave zone would strongly influence epipsammic diatom assemblages and productivity.

I also assessed the relationship between river mouth and wave zone habitats. Although these river mouth to wave zone linkages have not been investigated in Lake Superior, it seems likely that river mouth inputs contribute substantially to algal and microbial productivity in the sandy wave zones of the south-central coast. I predicted that river mouth habitats would be productivity hotspots for epipsammic diatoms and that open wave zone habitats would have species assemblages distinct of those found in river mouths. To further assess the influence of river mouth habitats on Lake Superior wave zone productivity, I used stratified sampling within river mouth habitats, adjacent wave zone habitats presumed to be influenced by river mouth plumes and isolated beach environments up-current of river mouths. In comparing these three habitat types, I hoped

to assess the role of river mouth influence on epipsammic diatoms in the south-central Lake Superior wave zone.

METHODS

Sampling sites

Sampling sites included three shifting-sand “drowned” river mouths (in which the coastal waters of Lake Superior flood and mix within the tributary input) and their adjacent Lake Superior wave zone habitats, as well as three distant beach sites which were presumably isolated from river mouth influence. For the purpose of this study, “wave zone” was defined as a coastal area of Lake Superior < 2 m in depth which received chronic wave action. Sites were selected to represent the range of wave action and current exposures present in the south-central wave zone of Lake Superior.

River mouth sites included: Hurricane River (high disturbance), Harlow Creek (moderate disturbance) and Au Train River (low disturbance). Isolated beach sites included: Twelve Mile Beach (high disturbance), North Country Trail Beach (moderate disturbance) and Au Train Bay (low disturbance). Sites were sampled in a river mouth influenced/non-influenced paired design, e.g., Hurricane River, adjacent wave zone habitat and Twelve Mile Beach.

Hurricane River (46°39'57.4"N 86°10'04.0"W) and Twelve Mile Beach (46°38'44.3"N 86°12'21.3"W) are located in Pictured Rocks National Lakeshore in the eastern half of the Upper Peninsula of Michigan. Hurricane River is a second-order stream that flows through mixed coniferous and deciduous forest before emptying into Lake Superior. These sites are illustrated in Figure 1. Harlow Creek (46°38'08.9"N 87°28'07.3"W) is a mid-order stream that is supplied by Harlow Lake and flows through

mixed forest. It is crossed by a commuter and industrial roadway. The last riffle of Harlow Creek is separated from the Lake Superior wave zone by a drowned river mouth-wetland complex. North Country Trail Beach (46°39'16.2"N 87°30'28.5"W) is an open stretch of sandy beach west of the Harlow Creek mouth. Land use near the Harlow sites is mixed residential, recreational and managed forest. This river mouth and wave zone complex is shown in Figure 2. Au Train River (46°26'02.9"N 86°50'05.3"W) is a sinuous, high-order stream flowing through mixed coniferous and deciduous forest. The final riffle of Au Train River is separated from Lake Superior by a shifting drowned river mouth-wetland complex. Au Train Bay (46°26'48.4"N 86°53'08.2"W) is a sheltered bay west of Au Train River. Both Au Train sites are constrained by highway infrastructure and are popular residential and recreation areas. These areas are shown in Figure 3.

Biomass and community analyses

Each site was sampled monthly during the 2014 ice-free season. Three random samples of the top 5 mm of submerged sediment in the river mouth and wave zone habitats at each site were collected using an acrylic cylinder sampler (total volume = 9.82 cm³). All samples were collected from a depth < 2 m. Collected samples were stored on ice and brought back to the lab for analysis.

During each sediment collection, I recorded water pH using an Oakton 300 waterproof probe (Vernon Hill, IL, USA), conductivity, dissolved oxygen and temperature using a YSI Model 85 probe (Yellow Springs, OH, USA) and turbidity using a Orbeco-Hellige Model 966 portable turbidimeter (Farmingdale, NY, USA). Average monthly values for these measures are provided in Table 1.

Lab analyses of sediment followed Hickman and Round (1970). Collected sediment was washed to remove suspended or lightly-attached organic matter from the sand grains by decanting any supernatant, flushing with deionized water and decanting again. A random subsample (2 cm³) of thoroughly mixed, washed sand grains were mixed with 4 ml deionized water and placed in stoppered specimen tubes. These samples were sonicated for 10 min to remove the epipsammic diatoms from sand grains. During sonication, tubes were placed in an iced (< 5°C) water bath to prevent frustule damage. After sonicating, each sample was shaken and the suspended diatoms were decanted into graduated centrifuge tubes. The sand was washed again in deionized water, and the suspension was added to the centrifuge tube.

To remove organic material from the diatom frustules, the washed sand slurry was placed in a 200 ml beaker with 20 ml 30% H₂O₂ (Sigma-Aldrich) and gently heated (to ~85°C) for 90 min. One ml of 1 N HCl was added to the remaining slurry and, once cooled, added to a 15 ml centrifuge tube. The slurry was then centrifuged at 2000 RPM for 10 min. The supernatant was decanted and the resulting pellet was washed three times in deionized water to remove any remaining H₂O₂ or acid. Subsamples of 0.05 ml were mounted on glass microscope slides using Naphrax (refractive index at least 1.65, PhycoTech, Inc). For each sample, at least 300 individual diatom valves were enumerated and identified to species using Patrick and Reimer (1966, 1975) and Wehr et al. (2002).

Chlorophyll *a* analyses followed Moss (1967) and Hickman and Round (1970). Subsamples (2 cm³) of washed sand grains were weighted on Whatman GF/C filter papers and dried to a constant weight. Epipsammic diatoms were then sonicated from

sand grains as above and filtered through a new filter paper using deionized water (total volume = 50 mL). Chlorophyll *a* was extracted by placing the filter in a sealed centrifuge tube and covering with 10 ml 90% acetone. The tube was placed in a 4°C dark chamber for at least 12 hours. Extracted samples were clarified of any filter fragments by centrifugation; the resulting supernatant was transferred to a clean glass cuvette and used in the analysis.

Spectrophotometry was used to determine chlorophyll *a* concentrations using a Genesys 20 spectrophotometer (Thermo Fisher Scientific). Initial chlorophyll *a* was determined by measuring absorbance at 750 nm (a turbidity correction) and 665 nm when compared to a 90% acetone blank. The significant fluorescence by chlorophyll degradation products (phaeopigments) was corrected for by acidifying the sample using 0.1 ml of 0.1 N HCl after the initial readings. This acidification converts all of the chlorophyll *a* to phaeopigments, allowing for determination of chlorophyll *a* concentrations in a sample by subtraction of phaeopigment concentrations. Acidified samples were placed in the dark and allowed to sit for 3 min. Absorbance was then measured at 750 and 665 nm. Final values were determined using the formula

$$\text{Chlorophyll } a \text{ } (\mu\text{g}/\text{m}^2) = \frac{A \times K (E_{665-0} - E_{665-a})(v_1)}{(V)(Z)}$$

where A is the absorption coefficient of chlorophyll *a* (11.0), K is the ratio expressing correction for acidification (2.43), E_{665-0} is the difference between absorption of the initial readings, E_{665-a} is the difference between the acidified readings, v_1 is the volume of acetone used in extraction, V is the total volume of slurry and deionized water filtered and Z is the spectrophotometer pathlength through the sample cuvette (1 cm).

Primary productivity analysis

Bottle incubation assays were used to infer primary productivity of epipsammic diatoms using the Winkler titration methods of Carignan et al. (1998) and Urban et al. (2004). During each sampling, 7 sediment samples (each 25 cm³) were collected at each sampling site in 300 mL glass biochemical oxygen demand (BOD) bottles. The bottles were then filled with lake water from the sediment-water interface and sealed. Three bottles were wrapped in aluminum foil and incubated in a cooler filled with lake water to maintain in-situ temperature. An additional three bottles were unwrapped to allow exposure to light. All bottles were transported to the lab and randomly placed in an illuminated Pervical Scientific growth chamber (~ 5 μmol/m²/s) programmed to the in-situ lake temperature in a 16/8 light/dark cycle.

The dissolved oxygen content of one bottle was fixed in the field. The sample was treated with 1 mL each manganous sulfate and potassium hydroxide iodide solution, which forms a brown precipitate of manganic hydroxide when the manganous solution combines with the dissolved oxygen in the sample. The mixture was allowed to sit for 5 min to allow the manganese and base to react with the dissolved oxygen. One mL of 95% sulfuric acid was then added to the bottle. With acidification, the manganic hydroxide forms manganic sulfate, releasing free iodine from the potassium iodide in an oxidation reaction. The iodine is stoichiometrically equivalent to the dissolved oxygen in the sample, which can then be titrated in the lab to reveal the initial concentration of dissolved oxygen in the water.

All Winkler titrations were performed in the lab. To determine the initial dissolved oxygen concentration, 201 mL of water from the initial fixed bottle was

transferred to a glass beaker and titrated using 0.0375 N sodium thiosulfate solution. Starch indicator solution was used to ease in determining the end-point of titration. Light and dark incubated bottles were fixed after 24 and 48 hr, with subsequent titration. Net primary productivity was obtained by measuring the dissolved oxygen differences after the light and dark incubations. Community respiration was obtained through measure of the dark incubations.

Wave exposure calculations

Wind data were obtained from NOAA Station STDM4 and used to quantify an index of wave exposure for each sampling site. I determined wind exposure (w) for each site through vector averaging of wind speed and wind direction throughout each month of the study. Average fetch (f) was determined by measuring the distance to the nearest emergent land masses using ArcGIS. Depth (d) was assigned for each site based on sampling protocol. The formula $E = \log(1 + fwd^{-2})$ was used to calculate index values, as adapted from Barton and Carter's (1982) index of exposure to wave action. Figure 4 shows a map generated to calculate fetch values for each site.

Statistical Analyses

Analysis of variance (ANOVA) tests were used to assess differences in chlorophyll a concentrations with sampling site, habitat type and month as fixed factors. Interactions between these factors were included in the initial ANOVA model, though were later removed when it was determined that no interactions were significant ($\alpha = 0.05$). Tukey post-hoc tests were performed to examine pairwise comparisons. ANOVA were also used to assess differences in community respiration and productivity with site,

habitat and month as factors. Differences among diatom diversity indices were assessed using ANOVA with habitat and site as factors. Data were log transformed in order to meet the assumption of normality for ANOVA tests. Data that were not normally distributed used Welch's (W) corrected F values and Games-Howell tests for post-hoc comparisons.

Stepwise multiple linear regression models were generated to determine which environmental factors (dissolved oxygen, electrical conductivity, temperature, pH, turbidity and wave exposure) most affected diatom species richness and chlorophyll *a* concentration. Data were log transformed in order to meet the assumption linearity in regression tests. Chlorophyll, productivity, respiration and diatom diversity ANOVA and environmental multiple linear regression tests were performed using SPSS 21.0 for Windows.

Differences in wave exposure between sampling site and habitat type were determined using ANOVA, with Tukey HSD post-hoc comparisons using version 3.2.2 of the R statistical software.

RESULTS

Biomass and community analyses

A total of 21,745 diatom valves were enumerated and identified as 126 different species throughout all sites during the sampling period (Appendix I). Of 102 total species counted, 16 were found to occur exclusively in river mouth environments. Wave zone and beach habitats contained 111 different species, of which 24 were unique to these environments.

Epipsammic diatom diversity, richness and evenness are shown in Table 3. Shannon-Weiner diversity was similar across sites ($F(2,51)=3.160$, $p=0.051$) and habitat types ($F(2,52)=0.784$, $p=0.462$). Diversity was greatest at river mouth sites (mean $H'=3.03$) while wave zone and beach environments had similar mean diversity indices (mean $H'=2.94$ each). Evenness of species was low (mean E_{var} evenness =0.495), and similar across sites ($F(2,51)=1.130$, $p=0.331$) and habitat type ($F(2,51)=0.115$, $p=0.891$). All sites were dominated by only a few species (*Geissleria spp.*, *Planothidium spp.*, *Psammothidium spp.*, *Achnantheidium minutissimum*, *Amphora pediculus*, *Fragilaria vaucheriae*, *Karayevia clevei*).

Diatom species richness was significantly different between habitat types ($F(2,51)=4.92$, $p=0.01$) (Figure 5). Richness was greater in river mouths than in isolated beaches (means ± 1 SE = 34.06 ± 1.53 , 28.72 ± 1.07 respectively, Tukey HSD, $p=0.008$) and similar in wave zone habitats (means ± 1 SE = 34.06 ± 1.53 , 31.17 ± 0.92 respectively, Tukey HSD, $p=0.216$). Au Train River sites had significantly higher

species richness than Harlow Creek (means \pm 1 SE = 35.06 ± 4.87 , 28.39 ± 5.21 respectively, $F=9.13$, $p<0.001$) or Hurricane River sites (means \pm 1 SE = 35.06 ± 4.87 , 33.28 ± 4.22 respectively, $F=9.13$, $p=0.017$).

The mean concentrations of chlorophyll *a* were significantly different among habitat types ($F(2,52)=4.21$, $p=0.021$) (Figure 6). Concentrations of chlorophyll *a* were over three-fold higher in river mouth sites than in river-influenced wave zone or isolated beach sites (means \pm 1 SE = 1.17 ± 0.45 , 0.36 ± 0.07 , 0.39 ± 0.07 mg/m², respectively). While there was not a significant difference in mean chlorophyll *a* from river mouth and isolated beach sites (Tukey HSD, $p=0.056$), river mouth sites had significantly greater mean chlorophyll *a* levels than river-influenced wave zone sites (Tukey HSD, $p=0.031$).

Primary productivity analysis

Measured productivity was low or negative (samples were net heterotrophic) in all productivity assays (Figure 7). Productivity values were different from respiration data, indicating that low levels of photosynthesis did occur during BOD bottle incubation. Productivity differed by site ($F(2,51)=8.00$, $p=0.001$), with Harlow Creek sites having significantly higher productivity than Au Train River (Games-Howell, $p=0.031$) and Hurricane sites (Games-Howell, $p=0.016$). Productivity was significantly different between habitat types ($F(2,51)=6.80$, $p=0.002$). Both river mouths (Games-Howell, $p=0.008$) and wave zone habitats (Games-Howell, $p=0.008$) had greater measured productivity than isolated beach sites.

Community respiration was not significantly different between sites ($F(2,51)=1.01$, $p=0.372$; Figure 8). Calculated respiration was significantly greater

($F(2,51)=9.40$, $p<0.001$) in river mouth (Games-Howell, $p=0.004$) and beach habitats (Games-Howell, $p<0.001$) than in wave zones. The average respiration rate in river mouth habitats was $0.66 \pm 0.10 \text{ mgC m}^{-2}\text{hr}^{-1}$, $0.25 \pm 0.06 \text{ mgC m}^{-2}\text{hr}^{-1}$ in wave zones and $0.64 \pm 0.06 \text{ mgC m}^{-2}\text{hr}^{-1}$ in beach habitats (mean \pm S.E., $n=18$ for each habitat).

Wave exposure calculations

Wave exposure was significantly different among sites ($F(2,51)=116.7$, $p<0.001$), with Au Train River sites having the lowest calculated wave exposure, Harlow Creek sites having intermediate exposure and Hurricane River sites having the highest (Table 4). There was no difference in mean exposure between habitat types ($F(2,51)=0.01$, $p=0.92$). Diatom species richness was greater in low (35.06 ± 4.87 species) compared to medium wave exposure sites (28.39 ± 5.21 species, $W=256.5$, $p<0.01$) and in low compared to high wave exposure sites (30.50 ± 4.22 species, $W=228$, $p=0.03$) (Figure 9). Species diversity was similar across sites in relation to wave exposure ($F(2,51)=3.160$, $p=0.051$). Sites with the highest calculated exposure also had the greatest mean diversity and evenness values ($H'=3.04$, $E_{\text{var}}=0.52$), though low-disturbance sites ($H'=3.00$, $E_{\text{var}}=0.47$) and intermediate-disturbance sites ($H'=2.86$, $E_{\text{var}}=0.50$) had similar indices. Mean chlorophyll *a* did not differ significantly among the sampling sites in relation to wave exposure ($F(2,50)=2.99$, $p=0.059$).

A stepwise multiple linear regression revealed that exposure was the environmental factor that most affected both diatom species richness and chlorophyll *a* concentration. When richness was predicted it was found that exposure ($\beta=-0.404$, $p=0.002$) was the only significant environmental predictor. The overall model fit was $R^2=0.178$. Likewise, when chlorophyll *a* was predicted it was found that exposure ($\beta=-$

0.329, $p=0.002$) was the only significant environmental predictor. The overall model fit was $R^2=0.108$.

DISCUSSION

This study revealed that (1) river mouths are productivity and biomass hotspots in sandy wave zone environments, (2) sandy river mouth and beach wave zone habitats are biologically distinct and (3) wave energy exerts an over-arching influence on habitat quality for wave zone diatoms and strongly effects richness of epipsammic diatom communities in locations on the south-central shore of Lake Superior.

The Lake Superior epipsammic diatom community

While studies have investigated benthic diatom communities in a variety of freshwater habitats (Kingston et al., 1983; Potapova & Charles, 2002; Soininen et al., 2004; Kopalová & van de Vijver, 2013), few have specifically investigated epipsammic diatoms (Round & Bukhtiyarova, 1996; Bere & Tundisi, 2010) In this study, 126 diatom species from 46 genera were identified. These results are similar to the number of taxa described in other studies of epipsammic communities in lotic habitats (Round & Bukhtiyarova, 1996; Bere & Tundisi, 2010). Only a few studies have investigated the physiology of epipsammic diatoms in lakes (Kingston et al., 1983; Üveges et al., 2011) and I am unaware of any that have specifically identified the taxa comprising the epipsammic flora in lakes. Thus, as the first study to document the epipsammic diatoms of a nearshore lake environment, the data presented here can serve as a baseline for future investigations.

As is also true with surf diatom communities (Odebrecht et al., 2009; Harris et al., 2014), the epipsammic flora of the Lake Superior wave zone appears to be dominated by

a few common species (Figure 10). At most sites, over 50% of all species identified occurred in only a few instances and accumulated less than 1% each to the sampled population. Although epipsammic existence appears to require a high-degree of specialization, the epipsammic community of Lake Superior included the substrate generalists *Fragilaria vaucheriae* and *Reimeria sinuata*. Round and Bukhityarova (1996) also noted these species in river sand samples which suggests the potential for sand grain colonization from diatoms that inhabit other substrates.

It appears that the taxa identified within river mouths and wave zone or isolated beach environments comprise distinct assemblages within the greater Lake Superior epipsammic diatom community. Of 102 total species counted, 16 species (15.68%) were found to occur exclusively in river mouth environments. Wave zone and beach habitats contained 111 different species, of which 24 species (21.62%), were unique to these environments. These findings illustrate that habitat-specific conditions within the wave zone strongly influence community composition and thus, in this environment that seems homogenous at the microscopic scale, major features of the limnological landscape can be seen in the shifting sands of Lake Superior's south-central coast.

Samples obtained from river mouths were greater in biomass, productivity and richness, and had the advantages of added nutrients and materials from river discharge. Though wave exposure was the driving environmental factor in determining both richness and chlorophyll *a* concentrations in my regression models, exposure was not significantly different between habitat types. As such, it is hypothesized that the nutrient input and flow regime of local hydrology play an important role in determining epipsammic community composition in river mouth habitats. Humphrey and Stevenson

(1992) identified relatively minor increases in discharge as potential simulants for benthic algal biomass in streams. The pulses of nutrients provided by these spates, in addition to the greater nutrient content of river water during normal flow, may create an environment that is accommodating to a wider range of epipsammic diatom species than the environment in wave zone habitats.

Nutrient inputs from groundwater at drowned river mouth habitats may have contributed to the greater biomass and productivity recorded in these habitats. Hagerthey and Kerfoot (1998) found that littoral areas of low or moderate discharge had higher epibenthic diatom diversity than areas of high discharge in a Wisconsin lake. Further, they determined that these low and moderate discharge sites lacked clear dominant species (Hagerthey & Kerfoot, 1998). In the present study, a small group (*Achnantheidium minutissimum*, *Amphora pediculus*, *Geissleria acceptata*, *Planothidium frequentissimum*, *Psammothidium spp.*) each comprised over 5% of the populations enumerated in each river mouth site. All of these species with known environmental tolerances are listed as generally cosmopolitan, meso- or oligosaprobic and either indifferent to pH or alkaliphilous (Lowe, 1974). It follows that, even at low levels, the nutrients from watershed and groundwater input are influential in determining the community structure in river mouths and may provide a broader nutrient range than in wave zone or beach habitats.

Biomass assessment

Chlorophyll *a* concentrations for epipsammic diatoms were over three-fold greater in river mouth environments compared to both river-influenced wave zones and isolated beach sites. Overall biomass was low, with mean river mouth chlorophyll *a* only

reaching a peak of $3.37 \pm 2.49 \text{ mg/m}^2$ in mid-summer. These results are much lower than the mean epipsammic biomass recorded in the shallow portions of a Hungarian lake ($35.24 \pm 12.19 \text{ mg/m}^2$), though are comparable to epipsammic biomass recorded in the deeper portions ($5.77 \pm 2.58 \text{ mg/m}^2$) (Úveges et al., 2011).

The heightened biomass of river mouth diatoms is likely due to the increased allochthonous input from the connected river systems. Though river-influenced wave zone sites had similar species richness as river mouth sites, biomass was significantly lower in wave zones than in river mouths. This marked difference may be the result of the flushing effects of wave action on dissolved nutrients essential for diatom metabolism. Chlorophyll *a* concentrations in isolated beach sites were not significantly different from river mouth sites, however. There were no significant differences between log-transformed values of turbidity, electrical conductivity, pH, water temperature or dissolved oxygen content between habitat types.

The differences in river-influenced wave zone and isolated beach flora may arise within the taxa that are found in these sites. Isolated beach sites had the lowest mean species richness of the different habitats investigated. Though individual biovolume measures were not calculated for each taxa present in the various diatom samples, beach sites could have been dominated by larger species that contain more chlorophyll *a*, inflating the measured concentrations at these sites. Several large, mobile (*Fragilaria*, *Navicula*, *Nitzschia*) and immobile (*Brachysira*, *Eunotia*, *Stephanodiscus*) species were found exclusively in isolated beach environments. Pringle (1990) showed that similar surface-adhering taxa (*Navicula* and *Nitzschia* spp.) can have dominant biovolumes on artificial sand-agar substrates in lotic environments and may limit the growth of smaller

taxa that would colonize “valley” portions of sand grains. In beach environments, these larger taxa could comprise greater biovolume and impede growth of taxa of smaller biovolume, thus concentrating more chlorophyll pigments to beach sites.

Algal biomass is controlled by a variety of biotic and abiotic factors, but chief among them are light and nutrient availability (Lowe, 1996). Samples were taken from depths < 2 m in the Lake Superior wave zone in open areas that received full access to sunlight. Though we were unable to measure attenuated light at the sediment-water interface, each sampling date had ambient light levels of > 350 $\mu\text{mol}/\text{m}^2/\text{s}$, and lake water turbidity measures were low during each sampling. As benthic algal metabolism can reach high rates in light levels < 50 $\mu\text{mol}/\text{m}^2/\text{s}$ (Carlton & Wetzel, 1987), it is assumed that light is not the limiting factor for wave zone epipsammic diatoms.

Lake Superior is a cold, oligotrophic lake with low nutrient concentrations. Phosphorus is thought to be an important limiting factor for algal growth in Lake Superior due to low annual phosphorus loading and quick assimilation by organisms (Weiler, 1978; Nalewajko et al., 1981). Further, Sterner et. al. (2004) illustrated the likelihood of both macronutrient (P) and micronutrient (trace metals, Fe, Mn, Zn) limitations in Lake Superior using nutrient-enrichment bioassays. Nutrient analyses (Nitrate-Nitrite [N] and TP) of water samples from half of our study sites (including both wave zone and river mouth habitats) had undetectable (< 0.01 mg/L P) levels of phosphorus, with mean values only reaching 0.02 mg/L P with all sites combined.

Phosphorus adheres to a variety of sediment types and becomes trapped in lake benthic zones (Kalff, 2001). It has been demonstrated that this phosphorus can be accessed by benthic algae by way of enzymatic activity (Pringle, 1990) and the formation

of an oxidized microhabitat over the sediment-water interface as a result of photosynthesis (Carlton & Wetzel, 1988). This action by benthic algae can reduce productivity and biomass of phytoplankton in phosphorus-limited systems by conserving phosphorus in the sediments. In the wave zone of Lake Superior, however, this confined resource is easily dispersed by wave action. The displacement of sandy sediments due to wave action releases this phosphorus into the water column (Kalff, 2001), where it is more available to phytoplankton than benthic algae. As such, the scouring effects of river pulses or wave action in our sampling sites may hinder any additional nutrients that could be utilized by epipsammic diatoms in this already limited system.

Primary productivity analysis

Measured productivity was low or negative in all productivity assays, indicating net heterotrophy in the epipsammic community. Though light levels were quite low in the incubation chamber, productivity values differed from measured respiration, indicating that low levels of photosynthesis occurred. Thus, the epipsammic diatoms present in biomass samples were likely low-light adapted and metabolizing. As such, the obtained values were used as a proxy for community productivity and indicate that river mouth habitats had the greatest levels of productivity. In addition, these data suggest the river mouths and river-influenced wave zone sites had significantly greater productivity levels than beach sites isolated from river influence.

These results are consistent with data establishing Lake Superior as net heterotrophic (Urban et al., 2004), like many oligotrophic systems (del Giorgio & Peters, 1994). As productivity was not correlated with calculated biomass via chlorophyll *a* concentrations in our sites (Spearman's $R = 0.194$, $n=6-9$, $p=0.164$) it can be assumed

that factors other than epipsammic diatom abundance, such as increased nutrient input, are driving the greater productivity in river mouth sites.

Also illustrated in these results is the impact of river influence to the wave zone of Lake Superior. River-influenced wave zone sites had productivity rates similar to river mouth environments and were significantly greater than rates in isolated beach sites. Rivers can create habitat heterogeneity in lake littoral zones through allochthonous input that form plumes at river discharge sites (Grimes & Kingsford, 1996; Reichert et al., 2010). Though biomass in river-influenced wave zones was significantly lower than in river mouth sites, the allochthonous input provided by river mouths likely provides a nutrient increase, leading to metabolic increases in these wave zone autotrophs.

Wave exposure

Exposure to wave action was the most important environmental predictor in determining both biomass and species richness in the Lake Superior epipsammic diatom community. Regression analyses indicated that wave exposure was the only significant variable in determining these measures, however the overall model fit for predicting each was low ($R^2 < 0.20$). Sites with low calculated wave exposure had greater species richness than both medium and high exposure sites. Conversely, sites with high calculated wave exposure had greater species diversity and evenness indices, though these were similar to indices for both low and medium exposure sites. Mean chlorophyll *a* did not differ significantly among the sites in relation to wave exposure.

Abiotic stressors, such as wave exposure, directly affect the ability of benthic algae to use resources either because of physical removal of cells or due to disruption of

metabolic processes (Stevenson, 1997). Further, adequate light only penetrates to 2-4 mm into sediments, limiting photosynthesis of benthic algae to the surficial layer of sediment (Kiih & Jorgensen, 1994), which is most affected by wave action (Cyr, 1998; Francoeur & Biggs, 2006). As such, level of wave exposure is an intuitive driver of benthic algal communities.

Increased river flow from flooding causes a decrease in benthic algal biomass (Tett et al. 1978). In river systems, there is often a mix of substrata available for benthic algal colonization and pocketed refugia that are less-affected by current velocity or flood regimes (Tett et al., 1978; Francoeur et al., 1998). For epipsammic diatom communities on the exposed coast of south-central Lake Superior, the only shelter from wave disturbance may be the microtopography of sand grains. Sand provides a heterogeneous environment for epipsammic diatoms to colonize. Miller et. al. (1987) noted that epipsammic diatoms preferentially colonize the crevices of sand grains, which are more sheltered from shear stress and scouring. The ability to be sheltered from suspended sediment or other physical disturbance may be the key factor in determining epipsammic diatom survival in the Lake Superior wave zone. Few chain-forming diatoms were found in our assessment, likely because their persistence in this system is more limited by wave action than it is for tightly-adhering, singular taxa.

High current velocity limits species membership in communities and causes stress when it increases in habitats (Stevenson, 1983, 1984, 1997). Likewise, wave exposure seems to be constraining the epipsammic diatom community to taxa which can tolerate shear stress by colonizing crevices or by their ability to relocate after experiencing burial in sediments. Given that epipsammic diatom communities are known to perpetually exist

in a “pioneer” state (Miller et al., 1987), it appears that only taxa that are able to withstand constant abrasion, movement of sediment and variable environmental measures can survive as a part of these populations.

Conclusions

This study highlights the impact that river mouth habitats have on the Lake Superior wave zone epipsammic flora. River mouth sites proved to be not only hotspots for productivity but for respiration and epipsammic diatom species richness. Wave zone sites which were assumed to be influenced by river mouth discharge were also highly productive and had similar species richness to river mouth habitats. These taxonomic investigations indicate a diverse Lake Superior epipsammic diatom community that is dominated by a few generalist, cosmopolitan species that are able to withstand constant wave action. The common species, such as *Planothidium frequentissimum*, *Amphora pediculus* and *Geissleria acceptata*, grow prostrate on sediment surfaces and likely colonize crevices of sand grains.

These findings support my hypothesis that wave exposure has a strong influence on the Lake Superior epipsammic diatom community. Wave action was the most important factor in determining chlorophyll *a* and epipsammic diatom species richness in the south-central Lake Superior wave zone. These results are consistent with the literature from streams and rivers which highlight current velocity as the most significant factor in determining benthic algal biomass in those systems (Horner & Welch, 1981; Stevenson, 1983; Ghosh & Gaur, 1998). These results also mirror the benthic macroinvertebrate populations in Lake Huron, which tended to decrease in abundance with increasing wave exposure (Barton & Carter, 1982).

The wave-swept and sandy shores of south-central Lake Superior provide an expansive habitat for epipsammic algae that can endure constant wave action. Though some assume that littoral benthic algae in Lake Superior play a minor role in trophic coupling or overall lake-wide energetics (Keough et al. 1996), others show that benthic primary productivity is a greater contributor than planktonic productivity to higher trophic levels in Lake Superior wetlands (Sierszen et al., 2004) and in portions of the littoral zone (Sierszen et al., 2006). Due to the prevalence of sandy substrate, it can be assumed that epipsammic diatoms are the greatest components to the benthic energy base throughout the south-central wave zone of Lake Superior. In areas near river mouth habitats epipsammic diatoms are abundant and exhibit the highest productivity rates. These river mouth-wave zone habitats are thus energetically important links that connect the lotic and lentic systems in the Lake Superior watershed.

REFERENCES

- Barton, D. R., & J. C. H. Carter, 1982. Shallow-water epilithic invertebrate communities of eastern Georgian Bay, Ontario, in relation to exposure to wave action. *Canadian Journal of Zoology* 60: 984–993.
- Barton, D. R., & H. B. N. Hynes, 1978. Wave-zone macrobenthos of the exposed Canadian shores of the St. Lawrence Great Lakes. *Journal of Great Lakes Research* 4: 27–45.
- Bere, T., & J. G. Tundisi, 2010. Epipsammic diatoms in streams influenced by urban pollution, São Carlos, SP, Brazil. *Brazilian Journal of Biology* 70: 920–930.
- Carignan, R., A.-M. Blais, & C. Vis, 1998. Measurement of primary production and community respiration in oligotrophic lakes using the Winkler method. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 1078–1084.
- Carlton, R. G., & R. G. Wetzel, 1987. Distributions and fates of oxygen in periphyton communities. *Canadian Journal of Botany* 65: 1031–1037.
- Carlton, R. G., & R. G. Wetzel, 1988. Phosphorus flux from lake sediments: Effect of epipelagic algal oxygen production. *Limnology and Oceanography* 33: 562–570.
- Carpenter, S. R., N. F. Caraco, D. L. Correll, R. W. Howarth, A. N. Sharpley, & V. H. Smith, 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecological Applications* 8: 559–568.
- Cyr, H., 1998. Effects of wave disturbance and substrate slope on sediment characteristics in the littoral zone of small lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 967–976.
- del Giorgio, P. A., & R. H. Peters, 1994. Patterns in planktonic P:R ratios in lakes: Influence of lake trophic and dissolved organic carbon. *Limnology and Oceanography* 39: 772–787.
- Dell, C. I., 1975. Relationships of till to bed rock in the Lake Superior region. *Geology* 3: 563–564.
- Fahnenstiel, G. L., L. Sicko-Goad, D. Scavia, & E. F. Stoermer, 1986. Importance of picoplankton in Lake Superior. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 235–240.
- Francoeur, S. N., & B. J. F. Biggs, 2006. Short-term effects of elevated velocity and sediment abrasion on benthic algal communities In Stevenson, R. J., Y. Pan, J. P.

Kociolek, & J. C. Kingston (eds), *Advances in Algal Biology: A Commemoration of the Work of Rex Lowe*. Springer Netherlands: 59–69,
http://link.springer.com/chapter/10.1007/1-4020-5070-4_4.

Francoeur, S. N., B. J. F. Biggs, & R. L. Lowe, 1998. Microform bed clusters as refugia for periphyton in a flood-prone headwater stream. *New Zealand Journal of Marine and Freshwater Research* 32: 363–374.

Ghosh, M., & J. P. Gaur, 1998. Current velocity and the establishment of stream algal periphyton communities. *Aquatic Botany* 60: 1–10.

Grimes, C., & M. Kingsford, 1996. How do riverine plumes of different sizes influence fish larvae: do they enhance recruitment? *Marine and Freshwater Research* 47: 191–208.

Hagerthey, S. E., & W. C. Kerfoot, 1998. Groundwater flow influences the biomass and nutrient ratios of epibenthic algae in a north temperate seepage lake. *Limnology and Oceanography* 43: 1227–1242.

Harper, M. A., & J. F. Harper, 1967. Measurements of diatom adhesion and their relationship with movement. *British Phycological Bulletin* 3: 195–207.

Harris, L., E. E. Campbell, R. Nel, & D. Schoeman, 2014. Rich diversity, strong endemism, but poor protection: addressing the neglect of sandy beach ecosystems in coastal conservation planning. *Diversity and Distributions* 20: 1120–1135.

Harvey, F. E., D. L. Rudolph, & S. K. Frape, 2000. Estimating ground water flux into large lakes: Application in the Hamilton Harbor, Western Lake Ontario. *Ground Water* 38: 550–565.

Hecky, R. E., & R. H. Hesslein, 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. *Journal of the North American Benthological Society* 14: 631–653.

Herdendorf, C. E., S. M. Hartley, & M. D. Barnes, 1981. Fish and wildlife resources of the Great Lakes coastal wetlands within the United States. U.S. Fish and Wildlife Service, http://pubs.er.usgs.gov/publication/fwsobs81_02.

Hickman, M., & F. E. Round, 1970. Primary production and standing crops of epipsammic and epipelagic algae. *British Phycological Journal* 5: 247–255.

Higgins, S. N., H. J. Kling, R. E. Hecky, W. D. Taylor, & H. A. Bootsma, 2003. The community composition, distribution, and nutrient status of epilithic periphyton at five rocky littoral zone sites in Lake Malawi, Africa. *Journal of Great Lakes Research* 29, Supplement 2: 181–189.

Hoffman, J. C., G. S. Peterson, A. M. Cotter, & J. R. Kelly, 2010. Using stable isotope mixing in a Great Lakes coastal tributary to determine food web linkages in young fishes. *Estuaries and Coasts* 33: 1391–1405.

- Horner, R. R., & E. B. Welch, 1981. Stream periphyton development in relation to current velocity and nutrients. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 449–457.
- Humphrey, K. P., & R. J. Stevenson, 1992. Responses of benthic algae to pulses in current and nutrients during simulations of subscouring spates. *Journal of the North American Benthological Society* 11: 37–48.
- Kalff, J., 2001. Phosphorus concentrations and cycling. In *Limnology: inland water ecosystems*. Prentice-Hall, New Jersey, USA: 247–269.
- Keddy, P. A., & A. A. Reznicek, 1986. Great lakes vegetation dynamics: The role of fluctuating water levels and buried seeds. *Journal of Great Lakes Research* 12: 25–36.
- Keough, J.R., Sierszen, M.E., & Hagley, C.A., 1996. Analysis of a Lake Superior coastal food web with stable isotope techniques. *Limnology and Oceanography* 41: 136–146.
- Keough, J. R., T. A. Thompson, G. R. Guntenspergen, & D. A. Wilcox, 1999. Hydrogeomorphic factors and ecosystem responses in coastal wetlands of the Great Lakes. *Wetlands* 19: 821–834.
- Kiih, M., & B. B. Jorgensen, 1994. The light field of microbenthic communities: Radiance distribution and microscale optics of sandy coastal sediments. *Limnology and Oceanography* 39: 1368–1398.
- Kingston, J. C., R. L. Lowe, E. F. Stoermer, & T. B. Ladewski, 1983. Spatial and temporal distribution of benthic diatoms in northern Lake Michigan. *Ecology* 64: 1566–1580.
- Kopalová, K., & B. van de Vijver, 2013. Structure and ecology of freshwater benthic diatom communities from Byers Peninsula, Livingston Island, South Shetland Islands. *Antarctic Science* 25: 239–253.
- Kornelsen, K. C., & P. Coulibaly, 2014. Synthesis review on groundwater discharge to surface water in the Great Lakes Basin. *Journal of Great Lakes Research* 40: 247–256.
- Krejci, M. E., & R. L. Lowe, 1986. Importance of sand grain mineralogy and topography in determining micro-spatial distribution of epipsammic diatoms. *Journal of the North American Benthological Society* 5: 211–220.
- Kumar, S., R. W. Sterner, J. C. Finlay, & S. Brovold, 2007. Spatial and temporal variation of ammonium in Lake Superior. *Journal of Great Lakes Research* 33: 581–591.
- Lowe, R. L., 1974. Environmental requirements and pollution tolerance of freshwater diatoms. National Environmental Research Center, Cincinnati, OH: 334, <http://library.wur.nl/WebQuery/clc/177327>.

- Lowe, R. L., 1996. Periphyton patterns in lakes Algal ecology: freshwater benthic ecosystems. Academic Press, San Diego, CA: 57–76.
- Miller, A. R., R. L. Lowe, & J. T. Rotenberry, 1987. Succession of diatom communities on sand grains. *Journal of Ecology* 75: 693–709.
- Moss, B., 1967. A spectrophotometric method for the estimation of percentage degradation of chlorophylls to pheo-pigments in extracts of algae. *Limnology and Oceanography* 12: 335–340.
- Nalewajko, C., K. Lee, & H. Shear, 1981. Phosphorus kinetics in Lake Superior: Light intensity and phosphate uptake in algae. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 224–232.
- Odebrecht, C., M. Bergesch, L. R. Rörig, & P. C. Abreu, 2009. Phytoplankton interannual variability at Cassino Beach, Southern Brazil (1992–2007), with emphasis on the surf zone diatom *Asterionellopsis glacialis*. *Estuaries and Coasts* 33: 570–583.
- O'Donnell, J., G. O. Marmorino, & C. L. Trump, 1998. Convergence and downwelling at a river plume front. *Journal of Physical Oceanography* 28: 1481–1495.
- Pace, M. L., J. J. Cole, S. R. Carpenter, J. F. Kitchell et al., 2004. Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. *Nature* 427: 240–243.
- Patrick, R., & C. W. Reimer, 1966. The diatoms of the United States: exclusive of Alaska and Hawaii Vol. 1: Fragilariaceae, Eunotiaceae, Achnantheaceae, Naviculaceae. The Academy of Natural Sciences of Philadelphia, Philadelphia.
- Patrick, R., & C. W. Reimer, 1975. The diatoms of the United States: exclusive of Alaska and Hawaii Vol. 2, pt. 1: Entomoneidaceae, Cymbellaceae, Gomphonemaceae, Epithemiaceae. The Academy of Natural Sciences of Philadelphia, Philadelphia.
- Peterson, B. J., W. M. Wollheim, P. J. Mulholland, J. R. Webster, J. L. Meyer, J. L. Tank, E. Martí, W. B. Bowden, H. M. Valett, A. E. Hershey, W. H. McDowell, W. K. Dodds, S. K. Hamilton, S. Gregory, & D. D. Morrall, 2001. Control of nitrogen export from watersheds by headwater streams. *Science* 292: 86–90.
- Potapova, M. G., & D. F. Charles, 2002. Benthic diatoms in USA rivers: Distributions along spatial and environmental gradients. *Journal of Biogeography* 29: 167–187.
- Pringle, C. M., 1990. Nutrient spatial heterogeneity: Effects on community structure, physiognomy, and diversity of stream algae. *Ecology* 71: 905–920.
- Reichert, J. M., B. J. Fryer, K. L. Pangle, T. B. Johnson, J. T. Tyson, A. B. Drelich, & S. A. Ludsin, 2010. River-plume use during the pelagic larval stage benefits recruitment of a lentic fish. *Canadian Journal of Fisheries and Aquatic Sciences* 67: 987–1004.

- Round, F. E., & L. Bukhtiyarova, 1996. Epipsammic diatoms—Communities of British Rivers. *Diatom Research* 11: 363–372.
- Sierszen, M. E., J. A. Morrice, M. F. Moffett, & C. W. West, 2004. Benthic versus planktonic foundations of three Lake Superior coastal wetland food webs. *Journal of Great Lakes Research* 30: 31–43.
- Sierszen, M. E., G. S. Peterson, & J. V. Scharold, 2006. Depth-specific patterns in benthic–planktonic food web relationships in Lake Superior. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 1496–1503.
- Slattery, M. C., & J. D. Phillips, 2011. Controls on sediment delivery in coastal plain rivers. *Journal of Environmental Management* 92: 284–289.
- Soininen, J., R. Paavola, & T. Muotka, 2004. Benthic diatom communities in boreal streams: community structure in relation to environmental and spatial gradients. *Ecography* 27: 330–342.
- Sterner, R. W., T. M. Smutka, R. M. L. McKay, Q. Xiaoming, E. T. Brown, & R. M. Sherrell, 2004. Phosphorus and trace metal limitation of algae and bacteria in Lake Superior. *Limnology and Oceanography* 49: 495–507.
- Stevenson, R. J., 1983. Effects of current and conditions simulating autogenically changing microhabitats on benthic diatom immigration. *Ecology* 64: 1514–1524.
- Stevenson, R. J., 1984. How currents on different sides of substrates in streams affect mechanisms of benthic algal accumulation. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 69: 241–262.
- Stevenson, R. J., 1997. Scale-dependent determinants and consequences of benthic algal heterogeneity. *Journal of the North American Benthological Society* 16: 248–262.
- Stevenson, R. J., M. L. Bothwell, R. L. Lowe, & J. H. Thorp, 1996. *Algal Ecology: Freshwater Benthic Ecosystem*. Academic Press.
- Tett, P., C. Gallegos, M. G. Kelly, G. M. Hornberger, & B. J. Cosby, 1978. Relationships among substrate, flow, and benthic microalgal pigment density in the Mechums River, Virginia 1. *Limnology and Oceanography* 23: 785–797.
- Urban, N. R., D. S. Apul, & M. T. Auer, 2004. Community respiration rates in Lake Superior. *Journal of Great Lakes Research* 30, Supplement 1: 230–244.
- Üveges, V., L. Vörös, J. Padisák, & A. W. Kovács, 2011. Primary production of epipsammic algal communities in Lake Balaton (Hungary). *Hydrobiologia* 660: 17–27.
- Vadeboncoeur, Y., E. Jeppesen, M. J. V. Zanden, H.-H. Schierup, K. Christoffersen, & D. M. Lodge, 2003. From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. *Limnology and Oceanography* 48: 1408–1418.

- Vadeboncoeur, Y., P. B. McIntyre, & M. J. V. Zanden, 2011. Borders of biodiversity: Life at the edge of the world's large lakes. *BioScience* 61: 526–537.
- Vadeboncoeur, Y., G. Peterson, M. J. V. Zanden, & J. Kalff, 2008. Benthic algal production across lake size gradients: Interactions among morphometry, nutrients, and light. *Ecology* 89: 2542–2552.
- Vadeboncoeur, Y., M. J. V. Zanden, & D. M. Lodge, 2002. Putting the lake back together: Reintegrating benthic pathways into lake food web models. *BioScience* 52: 44–54.
- Wehr, J.D., Sheath, R.G, Kociolek, P., & Thorp, J.H., 2002. *Freshwater Algae of North America: Ecology and Classification*. Academic Press, San Diego, CA.
- Weiler, R. R., 1978. Chemistry of Lake Superior. *Journal of Great Lakes Research* 4: 370–385.
- Wiseman, W.J., & R. W. Garvine, 1995. Plumes and coastal currents near large river mouths. *Estuaries* 18: 509–517.
- Yoshii, K., 1999. Stable isotope analyses of benthic organisms in Lake Baikal. *Hydrobiologia* 411: 145–159.

APPENDIX A

The composition of epipsammic diatoms across habitats.

This survey represents species that accounted for at least 1% of the population at each site when abundances were averaged throughout the study. Taxa are listed by average abundance, from greatest to least, throughout all sites. Cell counts in the columns represent rounded percentages of community abundance at each site. + = present.

	<u>Au Train River</u>			<u>Harlow Creek</u>			<u>Hurricane River</u>		
	mouth	wave zone	beach	mouth	wave zone	beach	mouth	wave zone	beach
<i>Geissleria acceptata</i>	11	14	9	17	16	18	9	12	13
<i>Planothidium frequentissimum</i>	13	15	6	16	16	13	8	9	9
<i>Amphora pediculus</i>	10	9	5	6	7	6	7	9	9
<i>Psammothidium levanderi</i>	5	7	2	6	7	7	8	6	9
<i>Achnantheidium minutissimum</i>	3	2	9	5	4	4	4	3	6
<i>Psammothidium bioreti</i>	2	2	15	2	4	2	2	1	4
<i>Karayevia clevei</i>	5	3	1	3	2	3	5	4	3
<i>Karayevia laterostrata</i>	2	3	+	4	4	5	3	3	2
<i>Diatoma sp.</i>	+	-	3	-	-	-	+	-	+
<i>Fragilaria vaucheriae</i>	-	+	1	+	-	+	+	6	2

<i>Cocconeis placentula</i>	4	5	1	1	2	2	4	3	3
<i>Geissleria decussis</i>	6	1	+	3	2	2	1	2	3
<i>Platessa conspicua</i>	2	2	1	4	3	3	2	2	3
<i>Cymbella delicatula</i>	+	-	2	-	+	-	+	-	+
<i>Amphora minutissima</i>	2	2	+	2	2	3	2	2	3
<i>Planothidium oestrupii</i>	1	2	+	1	2	2	4	3	3
<i>Navicula schmassmannii</i>	2	3	1	2	3	3	+	1	1
<i>Planothidium rostratum</i>	2	1	2	2	1	1	5	3	+
<i>Achnantheidium exiguum</i>	3	1	+	+	+	+	3	1	+
<i>Planothidium abbreviatum</i>	1	1	-	1	1	2	4	3	+
<i>Sellaphora subfasciata</i>	1	1	5	3	-	1	1	+	+
<i>Planothidium lanceolatum</i>	2	2	+	2	3	2	1	1	+
<i>Reimeria sinuata</i>	1	2	1	1	1	2	4	3	1
<i>Encyonema norvegicum</i>	-	+	2	+	+	+	+	2	1
<i>Aneumastus minor</i>	2	2	1	1	1	2	1	2	2
<i>Cymbellonitzschia diluviana</i>	+	-	-	-	-	-	2	-	-
<i>Cavinula cocconeiformis</i>	1	2	+	1	2	2	1	1	1
<i>Navicula cari</i>	+	+	1	-	-	-	-	-	-
<i>Navicula goersii</i>	2	2	+	1	1	1	2	1	2
<i>Cyclotella sp.</i>	+	1	4	1	1	2	1	1	1
<i>Navicula vilaplani</i>	-	1	-	-	-	-	-	-	-
<i>Achnantheidium atomus</i>	1	2	2	1	2	1	2	1	1
<i>Cymbella affinis</i>	+	-	2	+	+	-	-	1	1
<i>Nitzschia palea</i>	+	-	1	+	1	1	+	1	3
<i>Eucoconeis sp.</i>	+	+	3	+	+	-	1	1	1
<i>Nitzschia spp.</i>	-	-	-	+	-	-	-	2	1
<i>Navicula subminiscula</i>	1	1	-	-	-	-	+	+	+

<i>Sellaphora pupula</i>	1	1	1	2	1	1	1	1	2
<i>Cavinula jaernefelti</i>	+	-	-	1	-	-	+	-	-
<i>Cocconeis fluviatilis</i>	2	1	-	+	1	+	2	1	1
<i>Placoneis elginensis</i>	1	+	-	+	1	+	-	-	+
<i>Diatoma tenuis</i>	+	+	+	+	+	-	-	-	-
<i>Achnantheidium bioreti</i>	-	-	-	-	-	-	1	1	-
<i>Planothidium jouracense</i>	1	2	-	+	1	1	1	1	+
<i>Navicula reichardtiana</i>	1	1	1	1	+	1	+	1	1
<i>Gomphoneis geitleri</i>	1	1	1	1	1	1	1	1	2
<i>Planothidium calcar</i>	1	1	+	1	1	1	1	1	+
<i>Cocconeis sp.</i>	-	-	-	-	-	1	1	1	-
<i>Nitzschia perminuta</i>	1	+	1	-	+	+	-	+	1
<i>Cavinula pseudoscutiformis</i>	1	1	+	1	1	+	1	+	1

Table 1. Water chemistry measures for study sites. All data were collected monthly at each sampling site. Numbers represent mean \pm standard error for each variable during the study period.

	<u>Au Train</u>		
	mouth	wave zone	beach
Conductivity (μ S)	183.28 \pm 28.14	115.57 \pm 14.08	93.65 \pm 5.70
Turbidity (NTU)	13.22 \pm 4.17	36.83 \pm 18.16	27.38 \pm 10.04
pH	7.14 \pm 0.10	7.23 \pm 0.13	7.60 \pm 0.19
Temperature ($^{\circ}$ C)	15.22 \pm 3.75	13.02 \pm 2.80	14.92 \pm 2.29
D.O. (mg/L)	5.45 \pm 0.54	7.18 \pm 0.48	6.98 \pm 0.50
	<u>Harlow Creek</u>		
	mouth	wave zone	beach
Conductivity (μ S)	86.27 \pm 15.37	82.65 \pm 9.40	91.45 \pm 4.17
Turbidity (NTU)	21.75 \pm 8.78	18.93 \pm 7.33	18.2 \pm 7.14
pH	6.78 \pm 0.21	7.16 \pm 0.19	7.05 \pm 0.20
Temperature ($^{\circ}$ C)	14.75 \pm 3.73	13.32 \pm 3.03	13.52 \pm 2.94
D.O. (mg/L)	7.64 \pm 0.99	7.84 \pm 0.90	7.64 \pm 0.76
	<u>Hurricane River</u>		
	mouth	wave zone	beach
Conductivity (μ S)	100.17 \pm 7.30	96.35 \pm 2.26	98.05 \pm 1.07
Turbidity (NTU)	16.08 \pm 6.53	21.77 \pm 11.97	23.78 \pm 16.63
pH	7.32 \pm 0.13	7.33 \pm 0.17	7.35 \pm 0.16
Temperature ($^{\circ}$ C)	11.82 \pm 2.03	13.23 \pm 1.78	13.25 \pm 1.94
D.O. (mg/L)	9.01 \pm 0.48	8.13 \pm 0.57	8.35 \pm 0.47

Table 2. Epipsammic diatom species Richness, Diversity and Evenness between study sites. Values represent mean \pm standard deviation.

	<u>Au Train River</u>		
	mouth	wave zone	beach
Richness	39.33 \pm 2.25	34 \pm 2.68	31.83 \pm 5.71
Shannon Diversity (H')	3.12 \pm 0.21	2.88 \pm 0.32	3.01 \pm 0.32
Evenness (E_{var})	0.50 \pm 0.09	0.42 \pm 0.08	0.50 \pm 0.12
	<u>Harlow Creek</u>		
	mouth	wave zone	beach
Richness	30.33 \pm 7.12	28.33 \pm 4.32	26.5 \pm 3.78
Shannon Diversity (H')	2.87 \pm 0.36	2.88 \pm 0.20	2.83 \pm 0.17
Evenness (E_{var})	0.49 \pm 0.08	0.51 \pm 0.15	0.50 \pm 0.10
	<u>Hurricane River</u>		
	mouth	wave zone	beach
Richness	32.5 \pm 5.92	31.17 \pm 2.64	27.83 \pm 2.14
Shannon Diversity (H')	3.09 \pm 0.15	3.06 \pm 0.08	3.00 \pm 0.13
Evenness (E_{var})	0.50 \pm 0.05	0.54 \pm 0.04	0.52 \pm 0.10

Table 3. Calculated wave exposure values for June, August and November for each site. Fetch, wind and wave exposure index for each river mouth (m), river-influenced wave zone (w) and isolated beach (b) sampling site at Au Train River (AT), Harlow Creek (HAR) and Hurricane River (HUR) in June, August and November 2014. Wave exposure was significantly different across sites, with Hurricane River sites having the highest wind exposure, Harlow Creek sites having intermediate exposure, and Au Train River sites having the lowest exposure throughout the sampling period.

month	site	Fetch (km)	wind exposure	Exposure Index		
		(f)	(w)	0.5 m	1 m	2 m
June	AT m	54.94	6.86	3.18	2.58	1.98
	AT w	55.98	6.86	3.19	2.59	1.99
	AT b	42.65	6.86	3.07	2.47	1.87
	HAR m	74.31	7.88	3.37	2.77	2.17
	HAR w	117.60	7.88	3.57	2.97	2.37
	HAR b	114.67	7.88	3.56	2.96	2.36
	HUR m	137.33	7.11	3.59	2.99	2.39
	HUR w	140.00	7.11	3.60	3.00	2.40
	HUR b	120.30	7.11	3.53	2.93	2.33
August	AT m	54.94	6.46	3.15	2.55	1.95
	AT w	55.98	6.46	3.16	2.56	1.96
	AT b	42.65	6.46	3.04	2.44	1.84
	HAR m	74.31	6.74	3.30	2.70	2.10
	HAR w	117.60	6.74	3.50	2.90	2.30
	HAR b	114.67	6.74	3.49	2.89	2.29
	HUR m	137.33	6.3	3.54	2.94	2.34
	HUR w	140.00	6.3	3.55	2.95	2.35
	HUR b	120.30	6.3	3.48	2.88	2.28
November	AT m	54.94	12.04	3.42	2.82	2.22
	AT w	55.98	12.04	3.43	2.83	2.23
	AT b	42.65	12.04	3.31	2.71	2.11
	HAR m	74.31	11.41	3.53	2.93	2.33
	HAR w	117.60	11.41	3.73	3.13	2.53
	HAR b	114.67	11.41	3.72	3.12	2.52
	HUR m	137.33	11.3	3.79	3.19	2.59
	HUR w	140.00	11.3	3.80	3.20	2.60
	HUR b	120.30	11.3	3.74	3.13	2.53

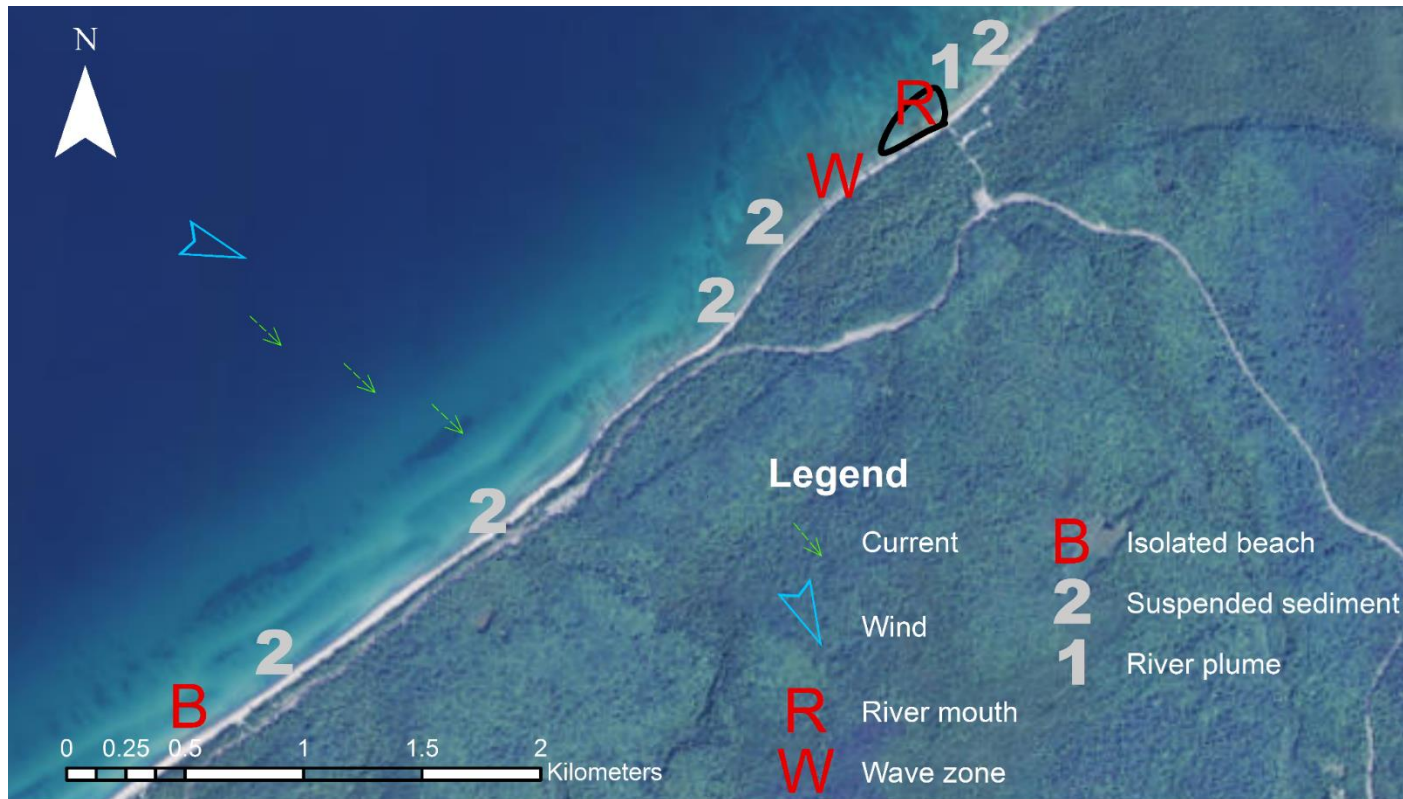


Figure 1. Hurricane River site map. Characteristic features, prevailing annual wind direction and sampling sites are shown. Three samples were collecting in each area (river mouth, ‘R’, river-influenced wave zone, ‘W’, and isolated beach, ‘B’) monthly during the ice-free field season. The immediate river plume is outlined and river and lake sediments suspended by wave action are noted.

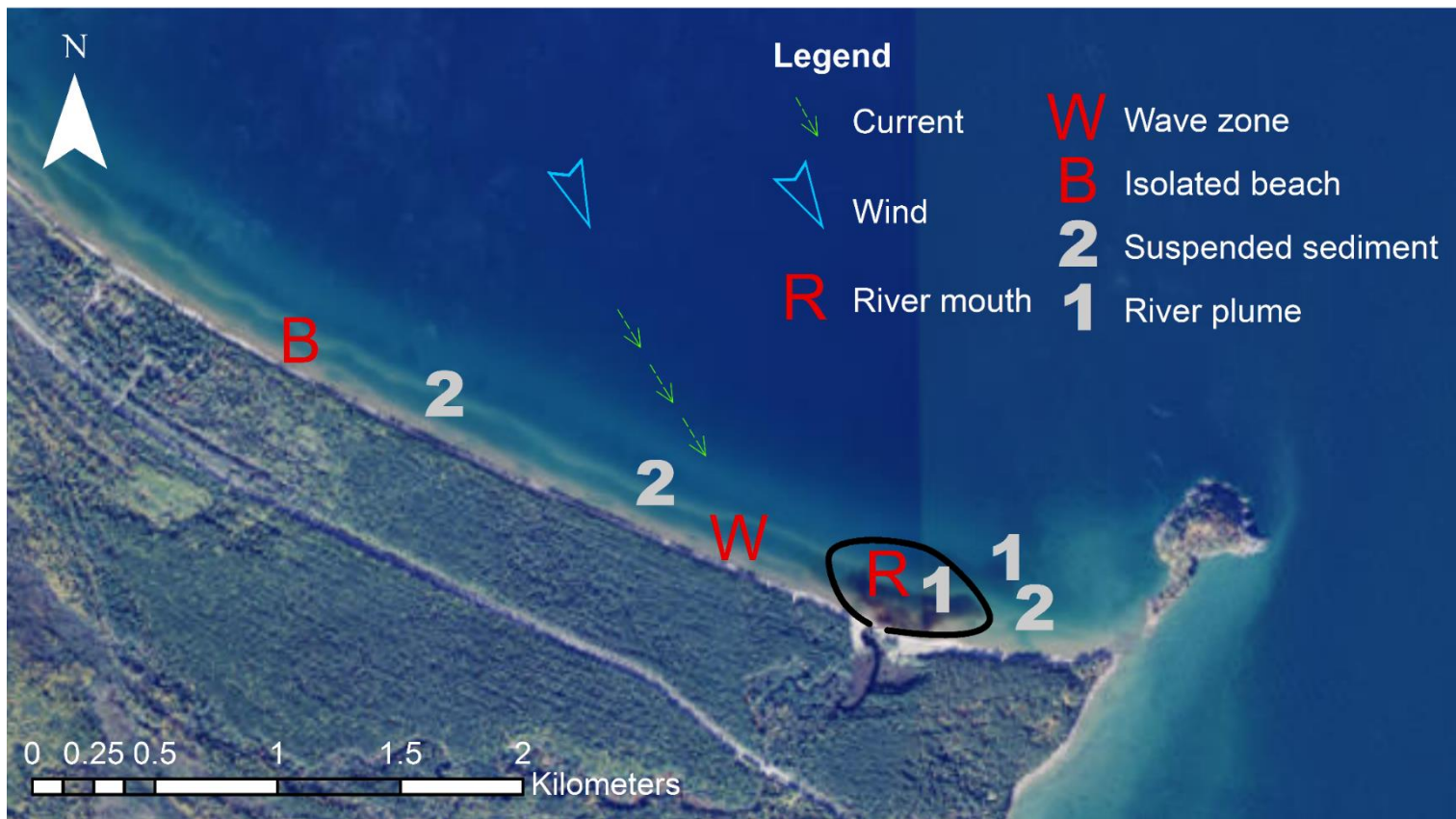


Figure 2. Harlow Creek site map. Characteristic features, prevailing annual wind direction and sampling sites are shown. Three samples were collecting in each area (river mouth, ‘R’, river-influenced wave zone, ‘W’, and isolated beach, ‘B’) monthly during the ice-free field season. The immediate river plume is outlined and river and lake sediments suspended by wave action are no

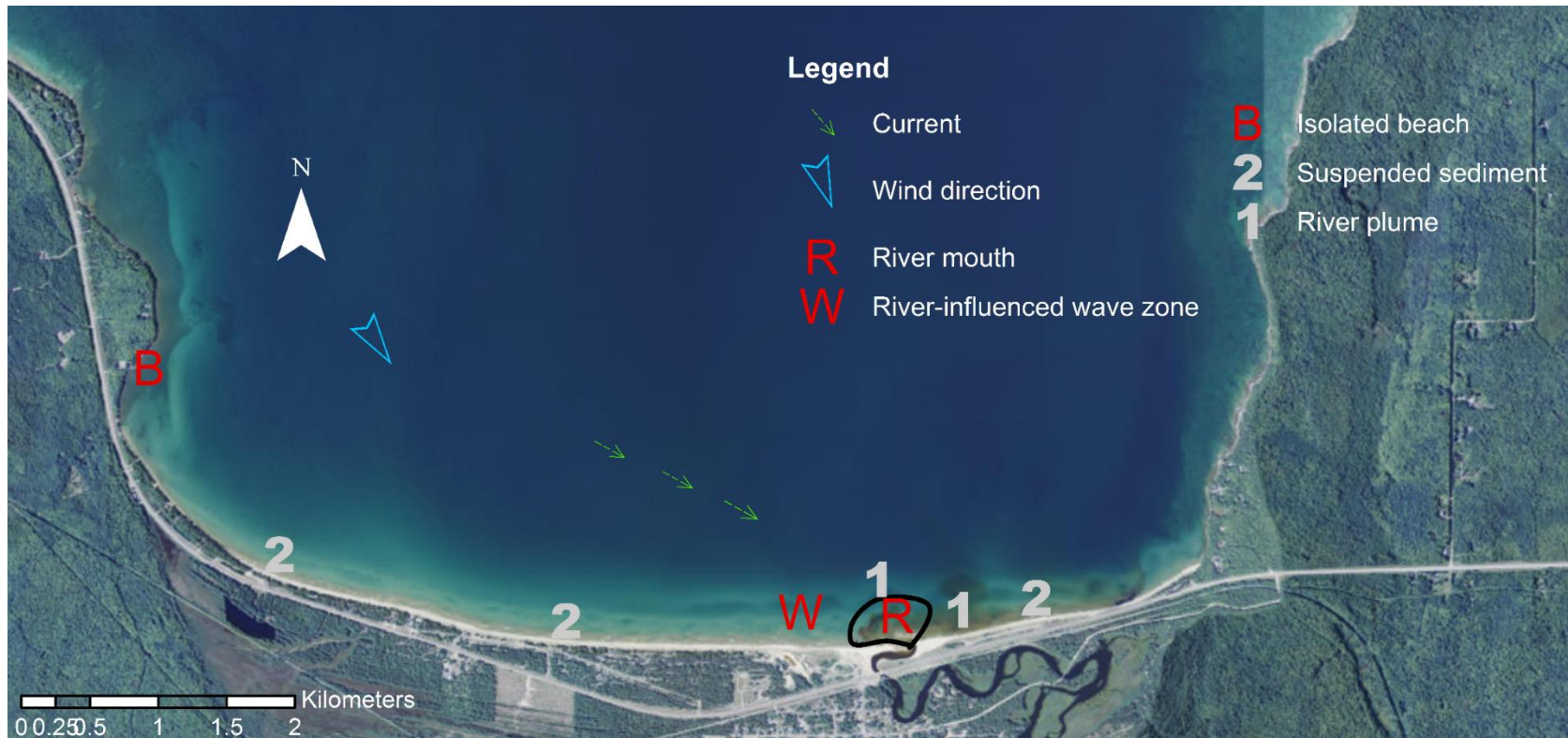


Figure 3. Au Train River site map. Characteristic features, prevailing annual wind direction and sampling sites are shown. Three samples were collecting in each area (river mouth, 'R', river-influenced wave zone, 'W', and isolated beach, 'B') monthly during the ice-free field season. The immediate river plume is outlined and river and lake sediments suspended by wave action are noted.

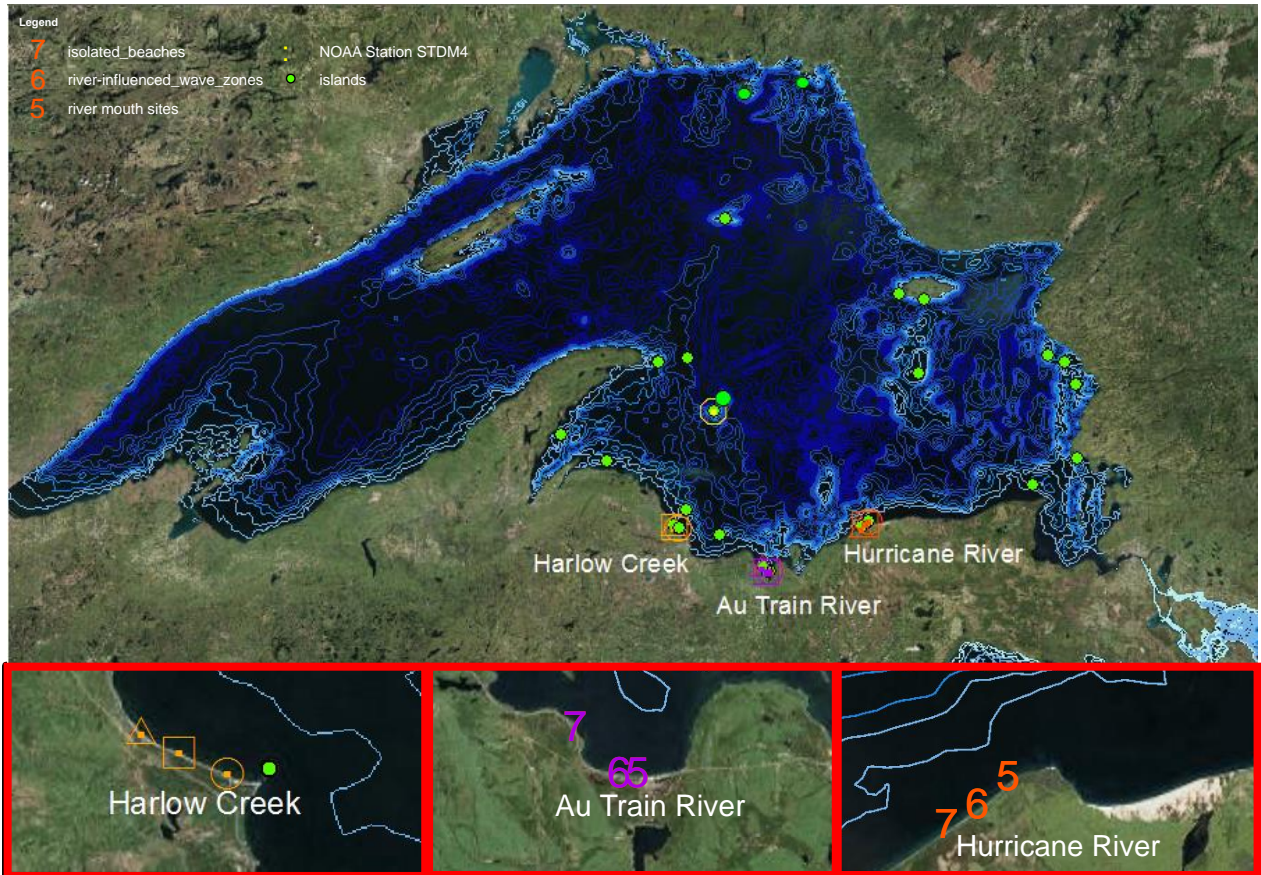


Figure 4. Wave exposure calculation map. Wave energy was calculated for each site based on calculated fetch, depth and proportion of time wind blew toward each site during the sampling period.

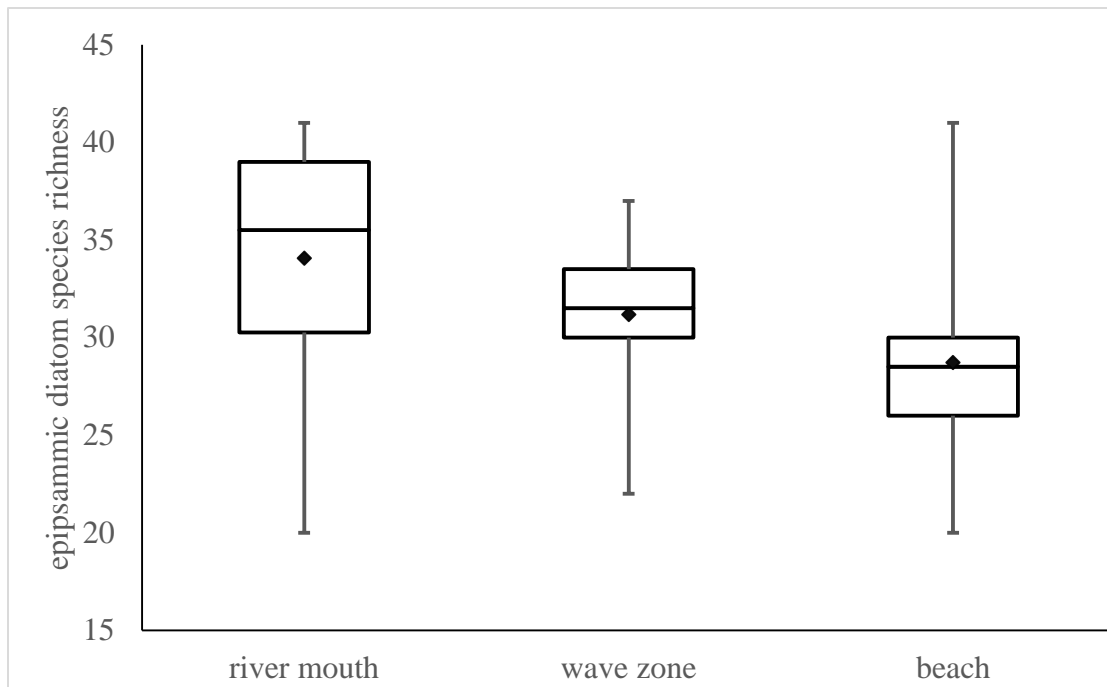


Figure 5. Diatom species richness across habitat types. Richness was greater in river mouths than in isolated beach habitats (means \pm 1 SD = 34.06 \pm 6.50, 28.72 \pm 4.53, respectively), and similar in river-influenced wave zone habitats (means \pm 1 SD = 34.06 \pm 6.50, 31.17 \pm 3.91, respectively) throughout the study period. Diamond markers represent mean richness values for each habitat type.

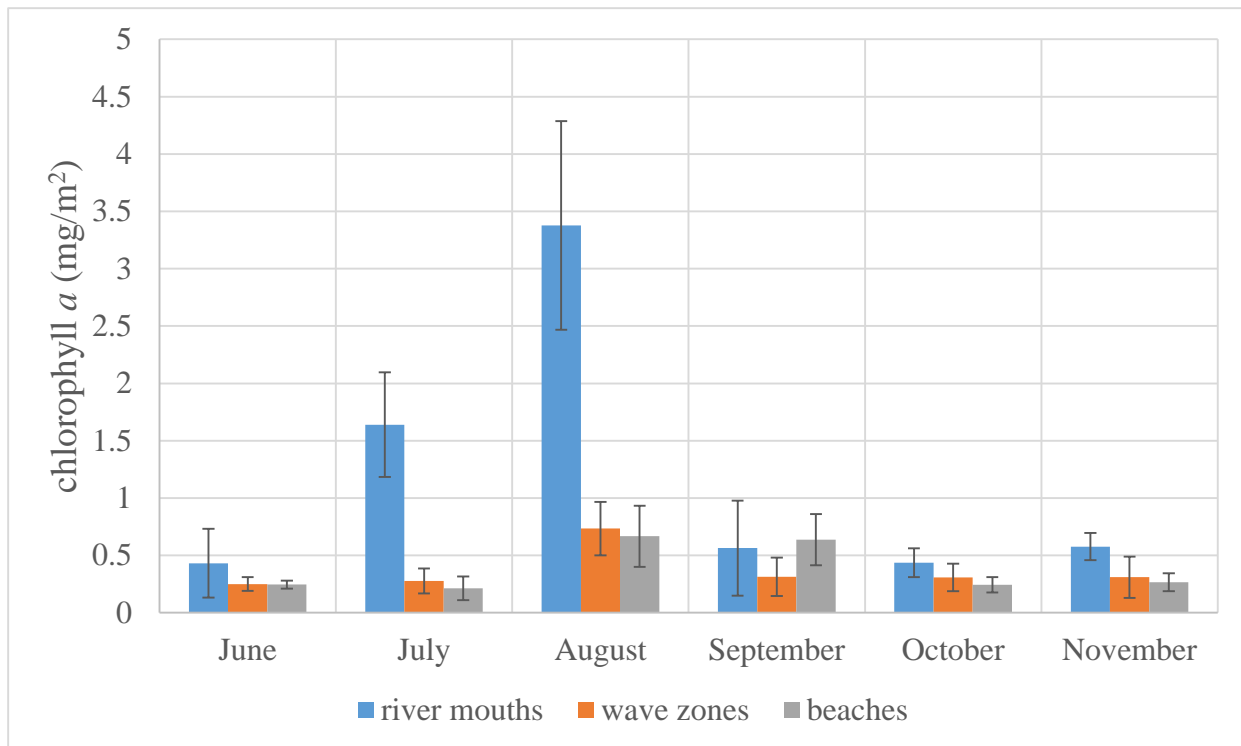


Figure 6. Chlorophyll *a* by habitat type. Mean concentrations of chlorophyll *a* were pooled for river mouth, river-influenced wave zone and isolated beach habitats monthly during the study period. River mouth chlorophyll *a* concentrations were greater than wave zone and beach concentrations for the majority of the season and were significantly greater than river-influenced wave zone sites (Tukey HSD, $p=0.031$). Error bars denote standard error about the mean.

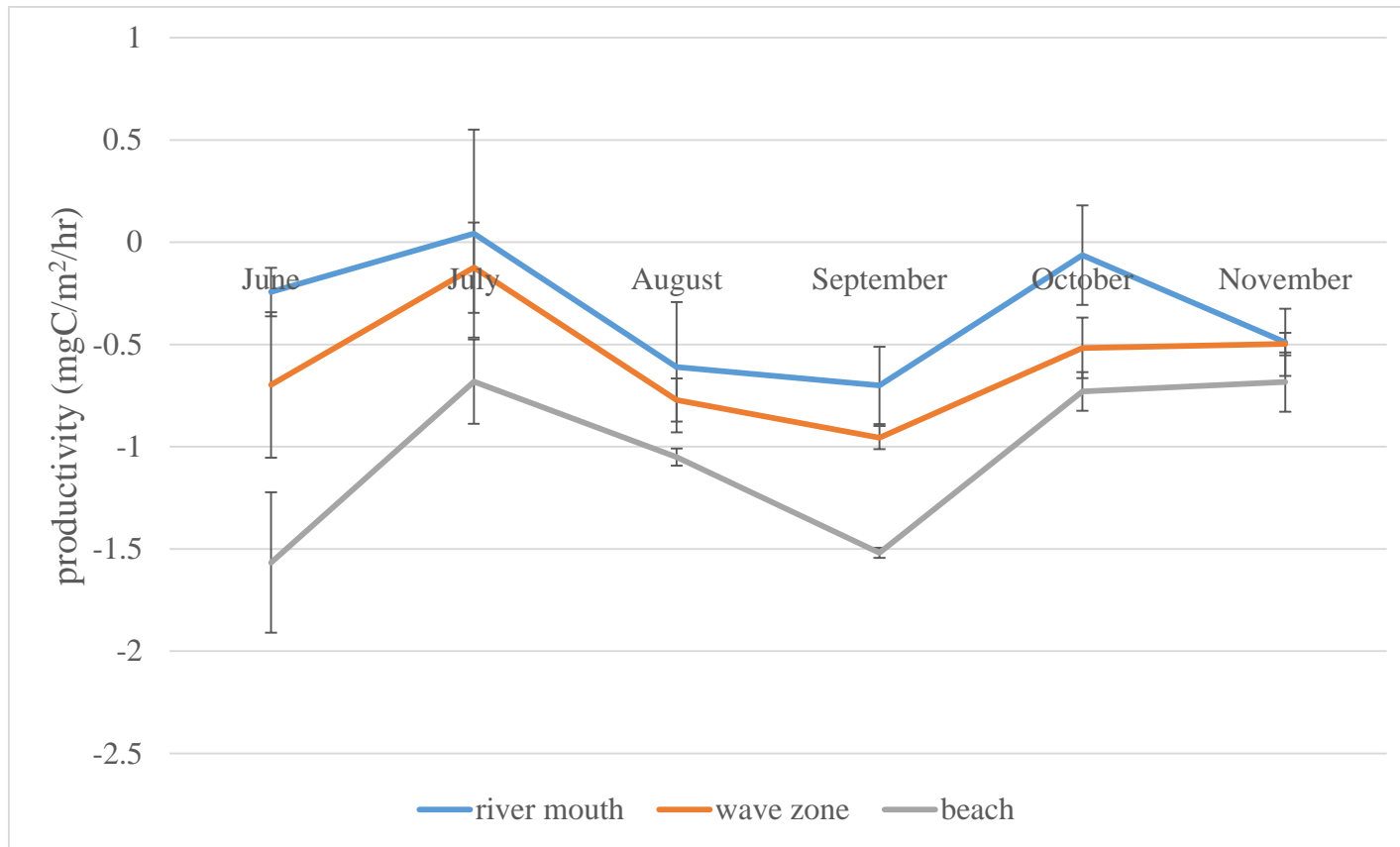


Figure 7. Productivity by habitat type. Productivity was significantly different across habitat types ($F(2,51)=6.80$, $p=0.002$). Both river mouth (Games-Howell, $p=0.008$) and wave zone (Games-Howell, $p=0.008$) environments had significantly greater productivity than isolated beach sites.

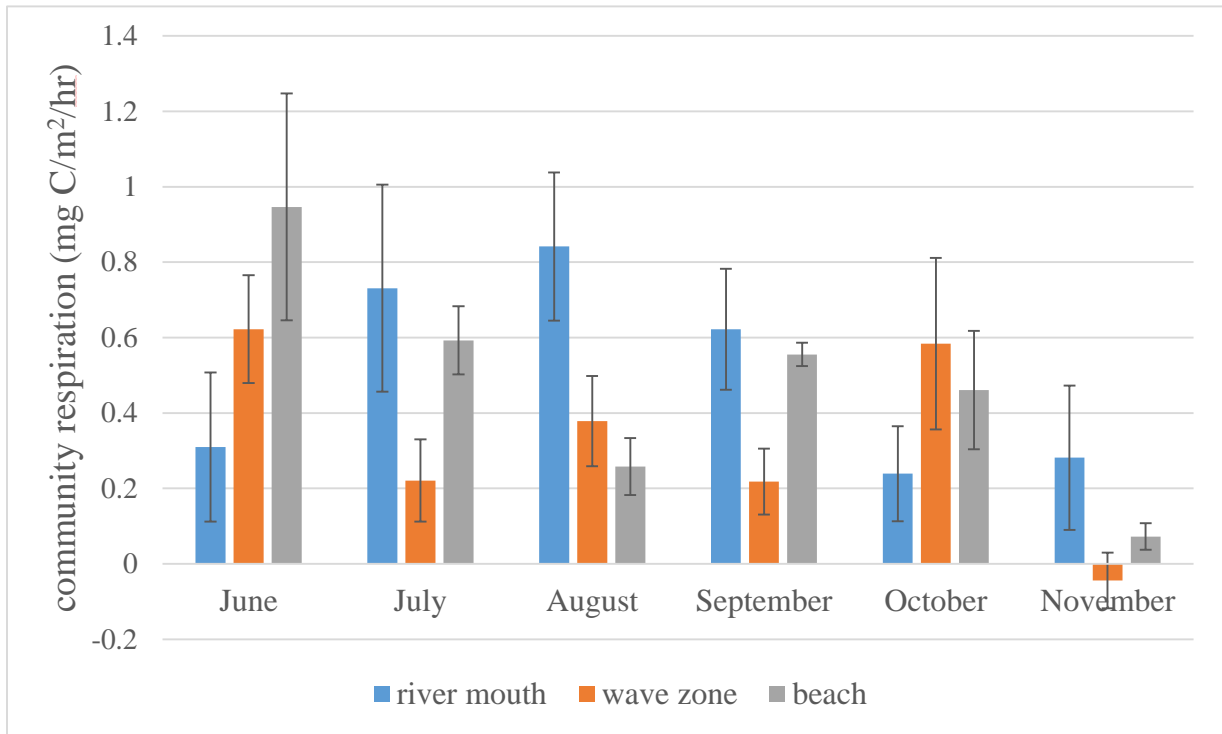


Figure 8. Community respiration by habitat type. Calculated respiration was significantly greater ($F(2,51)= 9.40, p<0.001$) in river mouth (Games-Howell, $p=0.004$) and beach habitats (Games-Howell, $p<0.001$) than in wave zones.

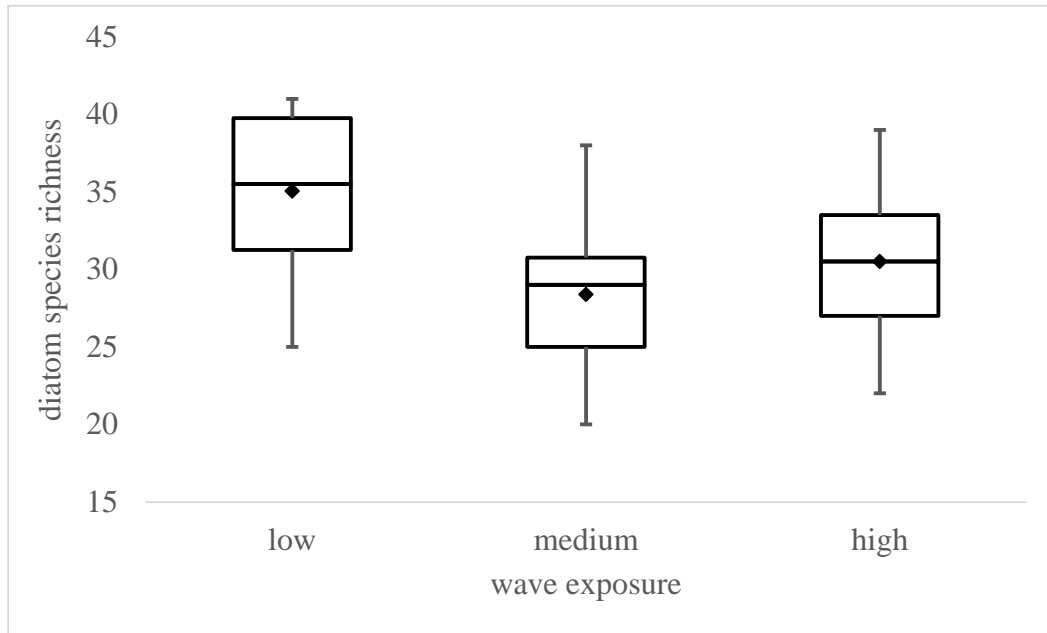


Figure 9. Diatom species richness at areas of different calculated wave exposure. Sites with low calculated wave exposures had greater (mean \pm 1 S.E. = 35.05 ± 1.15) species richness than medium (28.39 ± 1.23) or high (30.50 ± 0.99) calculated wave exposure sites. Boxes show the 25th and 75th percentiles, the solid line within the boxes show the median values, and the diamonds denote the means. Whiskers represent the 10th and 90th percentiles. Data points that do not share lowercase letters are significantly different ($p < 0.05$).

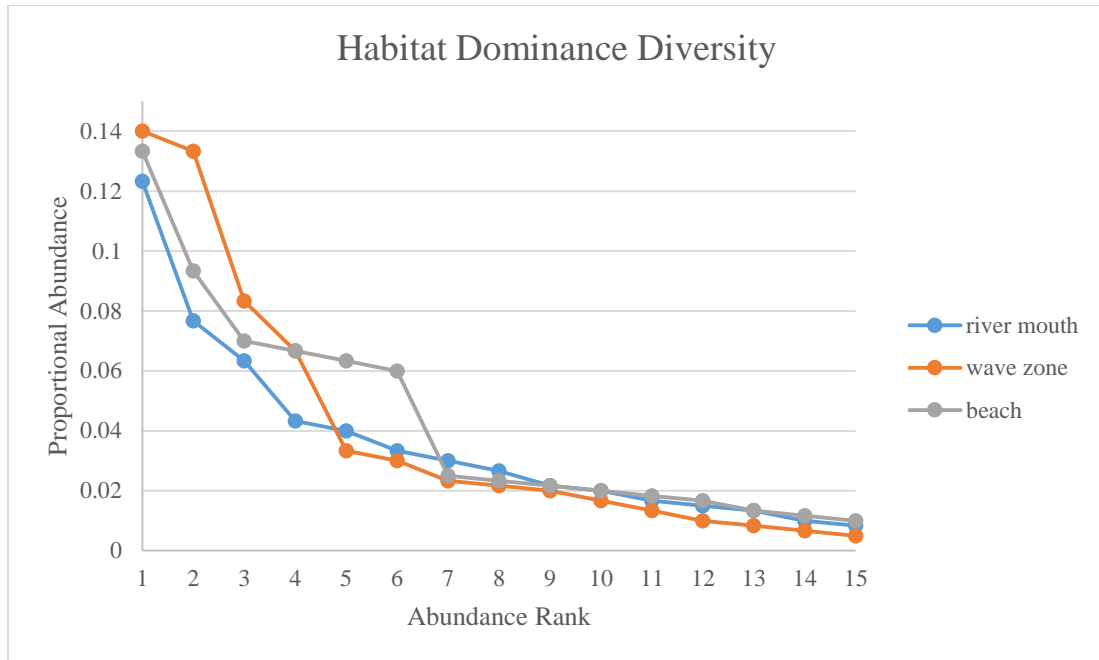


Figure 10. Habitat dominance diversity curves. The number of individual taxa and their proportional abundance in each habitat type were averaged over the sampling period. The most abundant taxa in each habitat type comprised 12 – 14% of the diatoms sampled. Only the seven most abundant taxa in each habitat comprised over 1% of the diatoms sampled in those areas. All habitats had a large number of taxa which were only found a few times at each site, indicating low evenness in species composition of the epipsammic diatom community.