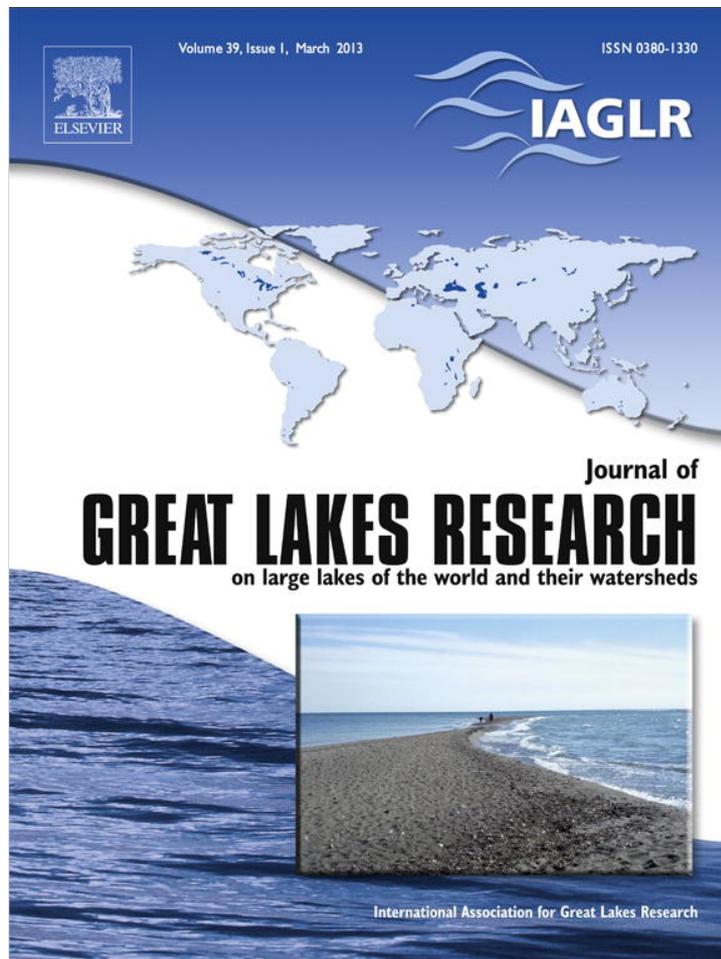


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Wave exposure and hydrologic connectivity create diversity in habitat and zooplankton assemblages at nearshore Long Point Bay, Lake Erie

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ABSTRACT

During an 11-day period in August 2008, we visited 102 sites along the nearshore (~60 km) of Long Point Bay. The purpose of our study was to evaluate the effects of wave exposure and hydrologic connectivity on zooplankton distributions. Long Point is located within the UNESCO Long Point Biosphere Reserve (26,250 ha) and encompasses the largest wetland complex in the Great Lakes system. We sampled for zooplankton, aquatic vegetation, temperature, specific conductance, pH, dissolved oxygen, dissolved organic carbon, water clarity, total nitrogen and depth. We evaluated the impacts of exposure using wind and fetch data to calculate a Relative Exposure Index (REI). Ordination techniques revealed a large variation in physical disturbance, water clarity, nutrient concentrations, water chemistry and aquatic vegetation that explained the distribution pattern of zooplankton at the 102 sites. Gradients of REI are strongly positively correlated with environmental variables, such as pH, dissolved oxygen and temperature and highly negatively correlated with conductivity and dissolved organic carbon. Visual inspection of the ordination site scores revealed the 102 sites clustering into six main groups based on spatial location and degree of surface-water connectivity to Long Point Bay. Sheltered sites (low REI) have much higher abundance of zooplankton whereas sites that have high REI scores are characterized by relatively low zooplankton abundance with a high prevalence of *Polyarthra* sp. This is the largest study on the distribution pattern of zooplankton in Long Point Bay, and it highlights the importance of wave exposure and hydrologic connectivity in structuring the zooplankton community.

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Introduction

Zooplankton live in a three-dimensional environment where they must forage for food, reproduce and escape predation, often within a very localized setting. In shallow areas along the lakeshore, these settings can be windswept, open water or quiescent with dense floating, emergent and submergent vegetation. Such habitats can be highly variable with respect to physical and chemical characteristics. Zooplankton that are distributed in these littoral habitats are largely governed by their tolerances and preferences for environmental variables such as dissolved oxygen (Stenson, 1983), temperature (Edmondson, 1965; Stenson, 1983), dissolved organic carbon (Strecker et al., 2008) and wind and wave action (Cardinale et al., 1998). Their distribution can also be influenced by the presence of aquatic vegetation. Research has shown that zooplankton biomass and diversity tend to be higher in vegetated environments (Pennak, 1966; Schriver et al., 1995), where cladocerans and copepods escape predation from fish (Duggan, 2001; Timms and Moss, 1984), where sessile rotifers and cladocerans find

substrate (Edmondson, 1944; Fairchild, 1981) and where many zooplankton (e.g. chydoridae) feed on epiphytic algae that grow on macrophytes (Duggan, 2001; Fryer, 1968).

Within the Laurentian Great Lakes basin, studies that examine factors governing the distribution of zooplankton have been conducted at two spatial scales. At the large regional scale, synoptic surveys have been conducted over hundreds of sites across the Great Lakes and have confirmed trends in zooplankton distributions that are associated with gradients in turbidity and nutrients, often related to human disturbance (e.g. Lougheed and Chow-Fraser, 2002; Patalas, 1972; Watson and Wilson, 1978). At the local scale, focused studies conducted at a single wetland have demonstrated that site-to-site variation in zooplankton abundances can be related to differences in the plant community and distance from point-source pollution (Krieger and Klarer, 1991; Lougheed and Chow-Fraser, 1998; Thomasen and Chow-Fraser, 2012). Lake-wide patterns offer important information on general trends and patterns; however at this large scale, information specific to smaller areas is lost. Studies focused on specific wetlands reveal trends and patterns on a finer scale, but fail to address what is occurring among wetlands. To address this knowledge gap we have chosen an ecosystem which provides the unique opportunity to study specific wetland complexes as well as the adjoining nearshore area. This allowed us to analyze sites with varying levels of exposure, while reducing the effects of

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confounding factors that arise across large basins, such as climate effects.

No study has demonstrated the importance of physical turbulence (wind and wave action) in structuring the rotifer community and very few have examined this effect on the cladoceran community (e.g. Cardinale et al., 1998), presumably because of the overriding influence of other factors. One reason for this may be related to the scale used in the previous studies. In this paper, we show how a strategic sampling program conducted at an appropriate scale can be used to evaluate the influence of wave exposure and hydrologic connectivity on zooplankton distributions. We hypothesize that in sites receiving low levels of human-induced disturbance, variation in physico-chemical characteristics induced by wind and wave exposure can be as important a structuring variable as nutrients and macrophytes.

Methods

Site description

We conducted our study at Long Point Bay, a large embayment located in north central Lake Erie. The Long Point area (26,250 ha) has been designated as a UNESCO Biosphere Reserve due to its many habitat types (e.g. marsh, undisturbed sand dunes, grassy ridges) supporting high biodiversity of flora and fauna. Its sports fishery is considered the best in Lake Erie (Nelson and Wilcox, 1996). Recreational use of the marsh is primarily fishing, but also includes waterfowl hunting, nature-viewing, and water-based activities such as canoeing and swimming (Kreutzweiser, 1981). The bay and surrounding marsh provide important resources for migratory waterfowl (Leach, 1981; Nelson and Wilcox, 1996; Prince et al., 1992) because of the good water quality (Leach, 1981) and abundant aquatic vegetation (Herdendorf, 1992; Knapton and Petrie, 1999). The Long Point Marsh complex experiences relatively low levels of human impact and as such is considered a reference site for Lake Erie (Chow-Fraser, 2006; Loughheed and Chow-Fraser, 2002). The biotic community of this ecosystem has been examined extensively, including studies on fish, marsh birds and waterfowl (see a list of projects at <http://www.longpointbiosphere.com>), but data on the zooplankton community do not exist for the nearshore area. In

order to understand the current health and stressors of this ecosystem to guide future management direction, the Ontario Ministry of Natural Resources (OMNR) began a large-scale comprehensive survey of the entire food web in Long Point Bay (Long Point Bay Assessment (LPBA)), funded in part by the Canada–Ontario Agreement respecting the Great Lakes Basin Ecosystem.

The 102 sites in this study are part of the LPBA. Sites were selected by the OMNR to represent thorough coverage of the nearshore system, with historical sites and suitability for fish sampling with beach seines taken into consideration. The sites were located throughout Long Point Bay, extending from the southern shore (Bouck's Creek) to the northern shore (Turkey Point Marsh), and included 27 interior coastal wetland sites within Crown Marsh (Fig. 1). Fifteen of the Crown Marsh sites have no surface water connection with the bay, having been excavated and enclosed by berms several years ago (designated PDN – “ponds not connected”). The other twelve sites are still hydrologically connected to Long Point Bay via boat channels that are maintained by dredging (designated PD – “ponds connected”). All sites were sampled for water characteristics, zooplankton and aquatic macrophyte species richness and composition between August 11 and 21, 2008.

Sampling design

We used a hand-held Global Positioning System unit (GPS; Garmin GPSmap76; accuracy of 10 m) to georeference all sites. We sampled for nine physico-chemical variables and analyzed all water samples in triplicate. Water temperature (TEMP), dissolved oxygen (DO), specific conductance (COND), and pH were measured with a hand-held YSI™ 600 QS multi-parameter monitoring unit (YSI, Yellow Springs, Ohio). We collected water samples (1-L capacity) in polyethylene bottles at 20-cm depth for analysis of total nitrite–nitrate nitrogen (TNN), total suspended solids (TSS), dissolved organic carbon (DOC) and chlorophyll *a* (CHL). Subsamples were poured into 100-ml polypropylene bottles and preserved with 50% sulfuric acid for later analysis of total Kjeldahl nitrogen (TKN). Total nitrogen (TN) was determined as the sum of TKN and TNN. TNN, TSS, DOC and TKN samples were immediately placed in coolers with ice and then transported on the same day to a walk-in cooler (4 °C). Within one week of collection, samples were

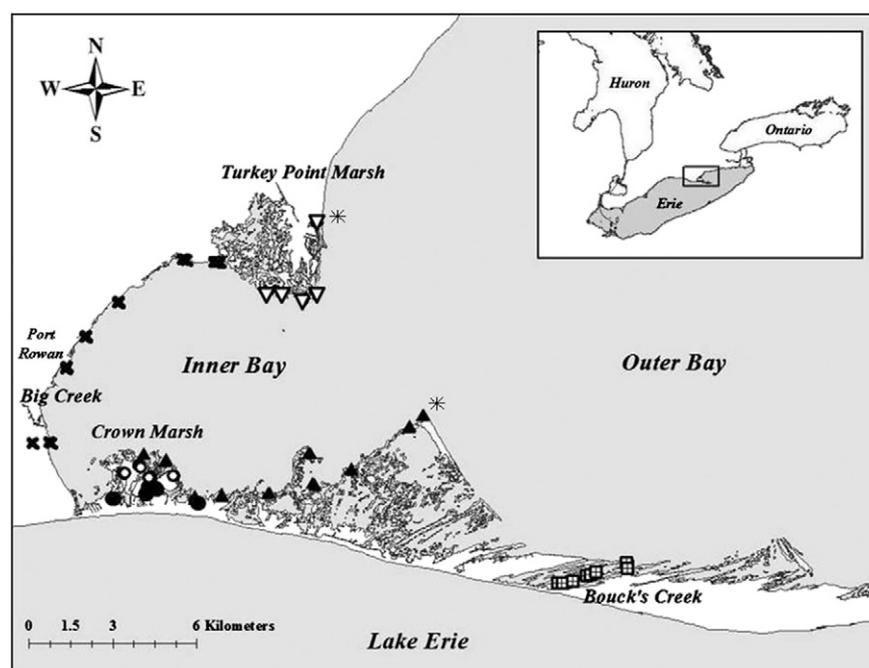


Fig. 1. Location of study sites sampled in August 2008 at Long Point Bay, Lake Erie. Symbols correspond to habitat groupings TP – Turkey Point (▽), WS – West Shore (X), PDN – Ponds Not Connected (●), PD – Ponds Connected (○), SS – South Shore (▲) and CC – Bouck's Creek (■). Asterisk (*) indicates sites without any vegetation.

transported on ice to E3 Laboratories Inc. (Niagara-on-the-Lake, ON) and analyzed following standard procedures. CHL water samples were stored in a dark cooler with ice. All CHL samples were processed within 8 h of collection with a vacuum pump and a glass filter unit. Each replicate water sample per sampling point was filtered using a Whatman GF/C glass fiber filter, labeled and combined into a sealed plastic bag with silica gel. Between samples, the filter unit was rinsed three times with distilled water. All filters were stored at -20°C until analysis at the OMNR's Lake Erie Management Unit laboratory located in Wheatley, ON. Since the DO and TEMP data were collected at different times over the 11-day sampling period, we screened the data to ensure that different measurements at each site were not confounded by differences in air temperature and the hour at which they had been sampled. We did not detect any confoundments.

We assessed the aquatic macrophyte community within 15 1-m^2 randomly distributed quadrats extending from the shoreline out and enclosing the water and zooplankton sampling station. All macrophytes within this grid were identified and ranked for abundance according to a coarse scale: dense ($\sim 70\text{--}100\%$ coverage); common ($\sim 20\text{--}60\%$ coverage) and sparse ($\sim 1\text{--}15\%$ coverage). Voucher samples were collected when samples could not be identified in the field. In plots with both emergent and submergent taxa, percent coverage was estimated separately above and below the water surface. Scientific nomenclature followed Crow and Hellquist (2000) and Gleason and Cronquist (1991).

We sampled for zooplankton at the same time and place of water sample collection. All samples were collected from mid-depth with a 5-L Schindler–Patalas trap, filtered through $63\text{-}\mu\text{m}$ Nitex mesh, backwashed into 60-mL bottles and immediately preserved in 4% sugar formalin. We collected one sample at each site. Organisms were identified, enumerated and measured with a dissection microscope at $40\times$ magnification. A light microscope at $200\text{--}400\times$ magnification aided initial identification. When samples were dense, a stratified sampling approach was applied, where at least 100 individuals of the dominant species were counted, and the entire sample was scanned for rare and large organisms. Copepods were categorized as adult, copepodid or nauplii. Adult copepods were identified to order (cyclopoid, harpacticoid, calanoid). Cladocera and Rotifera were identified to genus or species. Rotifer identification was based on Stemberger (1979) and crustacean identification was based on Pennak (1989).

Quantifying wind and wave action

We refer to the potential effects of wind and wave action as exposure and have modified the Relative Exposure Index (REI), developed by Keddy (1982) in order to quantify these potential effects at each site. The REI is calculated using the following equation:

$$\text{REI} = \sum_{i=1}^{12} (V_i \times P_i \times F_i) \quad (1)$$

where i is the i th compass heading (1 to 12), V is the average monthly wind speed (m s^{-1}), P is the percent frequency with which wind occurred from the i th direction, and F is fetch (m). Wind speed and direction were obtained from the Environment Canada weather station located at Long Point. Keddy (1982) found that although the magnitude of the index changed according to the months from which wind data were used, the relative difference did not change. Thus, we calculated the index based on the growing season (May–September) since this is the period of time that we are most interested in. We calculated effective fetch (F) using high-resolution (30-cm) imagery from the Southwestern Ontario Orthophotography Project (SWOOP) collected during the leaf-off season of 2006 using ArcView 9.2, measuring the straight-line distance from each site to the nearest shoreline.

Statistical methods

Before carrying out parametric analyses to explore relationships in the dataset, we used SAS JMP software (Version 7.0.1, SAS Institute Inc., Cary, North Carolina, USA) to transform the data using either a least-squares method ($\text{Log}_{10} [(X + X_{\text{mean}})/X_{\text{Std dev}} + 1]$) or log-transformation ($\text{Log}_{10}(X + 1)$) in order to reduce the effects of outliers (Lougheed and Chow-Fraser, 2002). For our first ordination technique, we conducted a Principal Components Analysis (PCA; JMP 7.0.1 software). This technique finds the strongest linear correlation structure among the physico-chemical variables (Table 1) and extracts synthetic axes that best explain variation in the dataset (McCune and Grace, 2002). Only axes with an eigenvalue greater than one were retained for further analysis. We interpreted the principal component (PC) axes by using Spearman correlation (JMP 7.0.1 software) to examine the strength of the relationships between the physico-chemical variables and each retained PC axis.

During preliminary analyses of the environmental (physico-chemical and macrophyte) and zooplankton data we determined that the more common method of canonical correspondence analysis (CCA) was inappropriate because the dataset does not have the required unimodal distribution (McCune and Grace, 2002) and analysis required the application of canonical correlation (CANCOR; PASW Statistics 18, IBM software, Chicago, Illinois, USA) instead. This method maximizes the linear relationship between environmental data and zooplankton abundances by finding linear combinations of these variables that have the highest possible between-set correlations (Tabachnick and Fidell, 2007). During initial screening various physico-chemical descriptors (Table 1) and terms describing the macrophyte community (Table 2) were evaluated for their effectiveness. The final form of environmental variables used in these analyses was determined to be the best descriptor based on their loadings in the final and preliminary ordination analyses. The environmental variables were transformed using least-squares to reduce the effects of outliers when necessary. The zooplankton dataset consists of 45 taxa abundances (listed in Table 3) log-transformed to reduce the effects of outliers. In order to interpret the canonical variates, we examined the cross loadings of the environmental variables and the zooplankton species. Redundancy analysis (PASW 18) quantified the amount of variance that the canonical variates of the environmental variables extracted from the zooplankton species, and vice versa.

In order to further assess trends in zooplankton distribution we classified the cladoceran and rotifer taxa based on their habitat preference and functional feeding group (Table 3). Habitat preferences were grouped according to those that favored 1) vegetation, 2) open-water, 3) no strong preference for either, and 4) benthos, based on the following studies: Duggan (2001), Duggan et al. (2001), Fairchild (1981), Fryer (1974), Paterson (1993), Pejler (1962), Pejler and Bērziņš (1994) and Pennak (1966). Feeding groups were classified as being raptorial, planktonic, scraper, or mechanical according to information from Fairchild (1981), Fryer (1968, 1974), Obertegger et al. (2011), Paterson (1993), and Smith (2001). Macrothricidae were the only zooplankton in this study classified as benthic and mechanical feeders; however, due to

Table 1

Description of the physico-chemical variables at 102 sites along the shoreline of Long Point Bay, based on sampling conducted during August 2008.

Environmental variable	Abbreviation	Mean \pm SE	Range
Temperature ($^{\circ}\text{C}$)	TEMP	22.72 ± 0.24	17.42–26.92
Conductivity ($\mu\text{S}/\text{cm}$)	COND	318.38 ± 7.03	240–567
pH	pH	8.22 ± 0.06	7.09–9.65
Dissolved oxygen (mg/L)	DO	8.61 ± 0.34	0.22–16.20
Dissolved organic carbon (mg/L)	DOC	7.17 ± 0.30	2.9–15.5
Total suspended solids (mg/L)	TSS	7.65 ± 1.23	0–101
Total nitrogen ($\mu\text{g}/\text{L}$)	TN	783.17 ± 49.81	300–3190
Chlorophyll a ($\mu\text{g}/\text{L}$)	CHL	2.93 ± 0.40	0.77–24.09
Depth (m)	DEPTH	0.72 ± 0.02	0.3–1.9
Relative Exposure Index	REI	$5.9 \times 10^6 \pm 6.5 \times 10^5$	$0\text{--}2.4 \times 10^7$

Table 2

Macrophyte species detected at 102 sites along the shoreline of Long Point Bay, based on sampling conducted during August 2008. Asterisk indicates non-native species.

Scientific name	Common name	% occurrence
Floating		
<i>Hydrocharis morsus-ranae</i> *	Frogbit	9
<i>Nelumbo lutea</i>	Yellow water lotus	2
<i>Nuphar variegatum</i>	Yellow pond lily	9
<i>Nymphaea odorata</i>	Fragrant white water lily	25
<i>Potamogeton natans</i>	Floating pondweed	27
Emergent		
<i>Eleocharis smallii</i>	Marsh spikerush	2
<i>Juncus</i> sp.	Rush	1
<i>Phragmites australis</i> subsp. <i>americanus</i> *	Common reed	1
<i>Pontederia cordata</i>	Pickerelweed	1
<i>Schoenoplectus acutus</i>	Hardstem bulrush	17
<i>Schoenoplectus cyperinus</i>	Woolgrass	2
<i>Schoenoplectus pungens</i>	Common three-square	5
<i>Schoenoplectus tabernaemontani</i>	Soft-stem bulrush	2
<i>Sagittaria latifolia</i>	Broad-leaved arrowhead	2
<i>Sagittaria rigida</i>	Stiff arrowhead	10
<i>Sparganium eurycarpum</i>	Large-fruited burreed	6
<i>Typha angustifolia</i> *	Narrow-leaved cattail	7
<i>Typha latifolia</i>	Common cattail	1
<i>Zizania aquatica</i>	Southern wild rice	31
Submergent		
<i>Callitriche verna</i>	Common water-starwort	8
<i>Ceratophyllum demersum</i>	Coontail	10
<i>Chara</i> spp.	Stonewort	74
<i>Elodea canadensis</i>	Common waterweed	24
<i>Megalodonta beckii</i>	Water marigold	5
<i>Myriophyllum exalbescens</i>	Northern water milfoil	3
<i>Myriophyllum spicatum</i> *	Eurasian water milfoil	23
<i>Myriophyllum</i> sp.	Milfoil	5
<i>Myriophyllum verticillatum</i>	Bracted water milfoil	14
<i>Najas flexilis</i>	Slender naiad	6
<i>Nitella</i> spp.	Nitella	34
<i>Potamogeton amplifolius</i>	Bigleaf pondweed	3
<i>Potamogeton ephedrous</i>	Leafy pondweed	1
<i>Potamogeton gramineus</i>	Variable pondweed	3
<i>Potamogeton pectinatus</i>	Sago pondweed	24
<i>Potamogeton zosteriformis</i>	Flat-stemmed pondweed	2
<i>Utricularia pusilla</i>	Tiny bladderwort	1
<i>Utricularia vulgaris</i>	Common bladderwort	23
<i>Vallisneria americana</i>	Wild celery	33

their low occurrence they were excluded from further analyses. Sites were grouped into six habitat groups based on geographic location and degree of surface water connection: TP (Turkey Point), WS (west shore), PDN (ponds not connected), PD (ponds connected), SS (south shore) and CC (Bouck's Creek) (sites are shown in Fig. 1). Differences among the six habitat groupings between mean zooplankton biomass for each of the three types of habitat preference (vegetation, open-water, generalist) and three feeding types (raptorial, planktonic, scrapers) were determined with one-way ANOVA and a post-hoc Tukey–Kramer test using JMP 7.0.1 software. We estimated dry-weights (biomass) by applying appropriate length–weight regression equations compiled by Loughheed and Chow-Fraser (1998). The biomass was log-transformed in order to reduce the effects of outliers.

Results

Environmental variables

All of the physico-chemical variables we measured showed large variation among the 102 sites (Table 1). Currently, Long Point is predominantly an alkaline system, with only a few interior sites that are circumneutral (see Fig. 2A). Oxygen levels ranged from anoxic to supersaturated, but most sites were well-oxygenated (mean for 102 sites was 8.6 mg L⁻¹; Fig. 2B). Despite the order-of-magnitude variation in both TN and CHL values, Long Point is primarily oligotrophic with mean

Table 3

Common zooplankton species detected at 102 sites along the shoreline of Long Point Bay, based on sampling conducted during August 2008. Species that occurred at less than 5% of sites are not listed. Dash (–) indicates the zooplankton could not be classified.

Code	Species	Habitat preference ^a	Feeding classification ^b	% occurrence	Mean density (#/L)
Cladoceran					
ACHA	<i>Acroporus harpae</i>	Vegetation	Scraper	59	5.9
AL	<i>Alona</i> sp.	Vegetation	Scraper	27	2.6
AO	<i>Alonella</i> sp.	Vegetation	Scraper	5	0.9
BOLO	<i>Bosmina</i> sp. <i>longirostris</i>	Generalist	Planktonic	85	19.6
BUSE	<i>Bunops serricaudata</i>	Benthic	Mechanical	13	10.9
CE	<i>Ceriodaphnia</i> sp.	Generalist	Planktonic	78	10.9
CH	<i>Chydorus</i> sp.	Vegetation	Scraper	51	4.5
CM	<i>Camptocercus</i> sp.	Vegetation	Scraper	6	0.5
DIBI	<i>Diaphanosoma</i> sp. <i>birgei</i>	Generalist	Planktonic	4	2.6
DIBR	<i>Diaphanosoma</i> sp. <i>brachyurum</i>	Open-water	Planktonic	47	2.2
EHRO	<i>Echinisca rosea</i>	Benthic	Mechanical	10	4.3
ER	<i>Eurycercus</i> sp.	Vegetation	Scraper	7	0.5
EU	<i>Eubosmina</i> sp.	Generalist	Planktonic	6	0.7
GR	<i>Graptoleberis</i> sp.	Vegetation	Scraper	6	0.7
OPGR	<i>Ophryoxus gracilis</i>	Vegetation	Scraper	5	0.5
PE	<i>Pleuroxus</i> sp.	Vegetation	Scraper	19	8.3
SA	<i>Saphroleberis</i> sp.	Generalist	Planktonic	6	5.7
SICR	<i>Sida crystallina</i>	Vegetation	Planktonic	7	1.5
SM	<i>Simocephalus</i> sp.	Vegetation	Planktonic	13	8.7
Rotifer					
AP	<i>Asplanchna</i> sp.	Generalist	Raptorial	19	1.4
AS	<i>Ascomorpha</i> sp.	Vegetation	Raptorial	32	1.9
CO	<i>Collotheca</i> sp.	Vegetation	Raptorial	22	7.9
EC	<i>Euchlanis</i> sp.	Vegetation	Planktonic	75	8.3
FIBR	<i>Filinia brachiata</i>	Open-water	Planktonic	75	77.3
KELO	<i>Kellicotia longispina</i>	Open-water	Planktonic	12	0.2
KR	<i>Keratella</i> sp.	Generalist	Planktonic	69	13.9
LE	<i>Lecane</i> sp.	Vegetation	Planktonic	100	2.6
MA	<i>Macrochaetus</i> sp.	Generalist	Planktonic	26	1.6
MO	<i>Monostyla</i>	Vegetation	Planktonic	65	2.2
MY	<i>Mytilina</i> sp.	Vegetation	Planktonic	11	1.2
NO	<i>Notommata</i> sp.	Vegetation	Raptorial	8	0.5
PLPA	<i>Platylas patulus</i>	Vegetation	Planktonic	30	5.5
PO	<i>Ploesoma</i> sp.	Generalist	Raptorial	12	1.0
PY	<i>Polyarthra</i> sp.	Generalist	Raptorial	82	16.2
SC	<i>Scardium</i> sp.	Vegetation	Raptorial	5	1.4
TR	<i>Trichoerca</i> sp.	Vegetation	Raptorial	58	1.1
TT	<i>Trichotria</i> sp.	Vegetation	Planktonic	17	0.5
Copepod					
CA	Calanoid	–	–	42	6.3
CP	Copepodid	–	–	83	12.9
CY	Cyclopoid	–	–	78	20.9
HA	Harpacticoid	–	–	32	3.4
NA	Nauplius	–	–	100	63.8

^a Duggan (2001), Duggan et al. (2001), Fairchild (1981), Fryer (1974), Paterson (1993), Pejler (1962), Pejler and Bērziņš (1994), Pennak (1966).

^b Fairchild (1981), Fryer (1968, 1974), Obertegger et al. (2011), Paterson (1993), Smith (2001).

values of 0.78 mg L⁻¹ and 2.9 µg L⁻¹, respectively (Table 1). Conductivity ranged widely from 240 to 567 µS cm⁻¹, with sites further inland having highest values (Fig. 2C). All sites were less than 2-m deep (Table 1) and the degree of exposure varied from completely protected to relatively exposed (REI of 0–2.4 × 10⁷; Fig. 2D).

A PCA of physico-chemical variables (listed in Table 1) yielded three axes with eigenvalues greater than one, together explaining 76.3% of the variation in the dataset (Table 4). PC1 explained 45.7% of the variation in the dataset, and showed strong positive correlations with REI, pH, DO and TEMP, and strong negative correlations with COND, TN and DOC (Table 4). PC2 explained an additional 19.8% of the variation and was highly positively correlated with TSS, CHL, pH, DEPTH and REI, and was negatively correlated with DOC and COND. PC3 explained

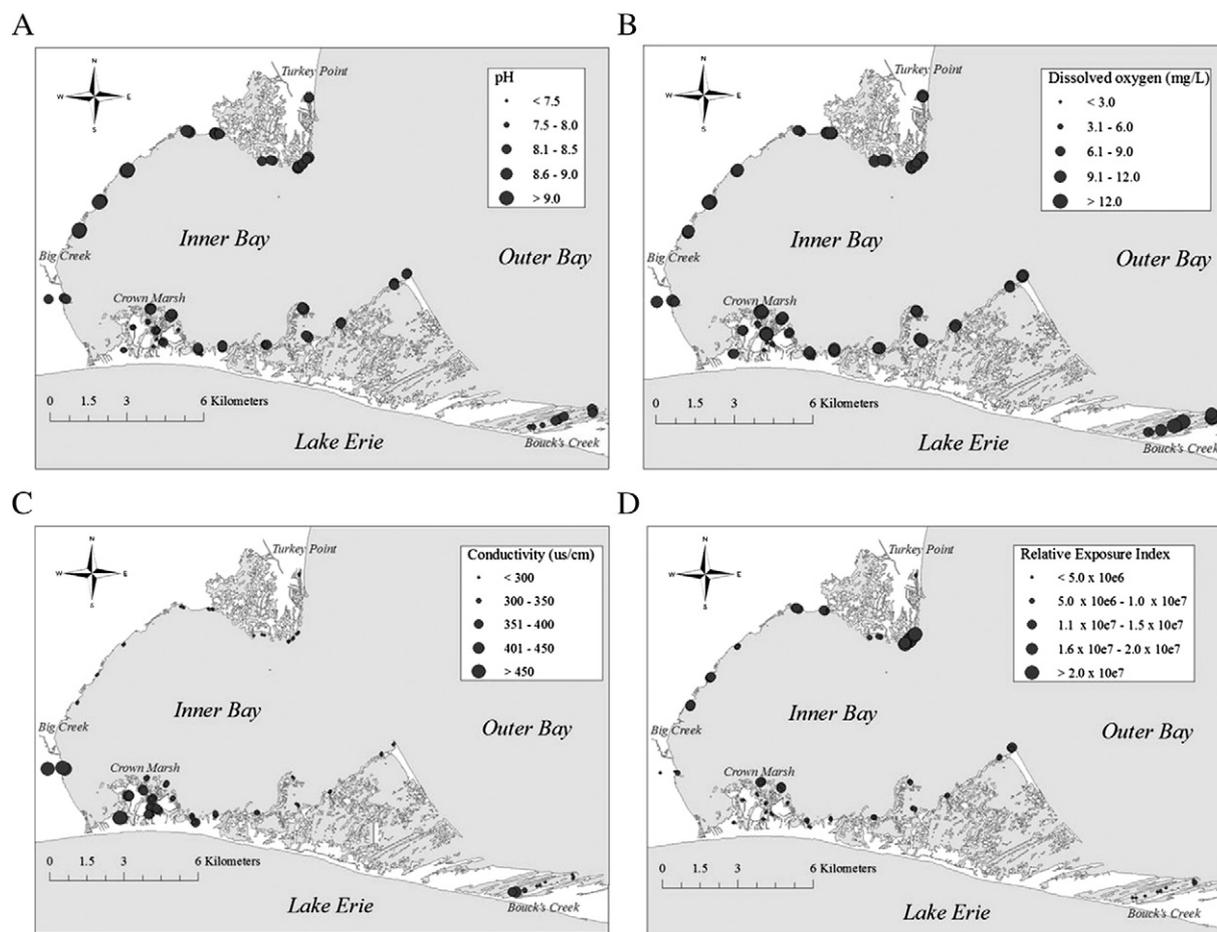


Fig. 2. Map showing A) pH, B) dissolved oxygen, C) conductivity, and D) Relative Exposure Index scores recorded during this study along the nearshore of Long Point Bay.

an additional 10.8% of variation and was strongly positively correlated with DEPTH and negatively correlated with COND. PC1 represents a gradient from highly exposed, alkaline, well-oxygenated, warm water to high COND and high concentrations of TN and DOC. PC2 represents a gradient from deep sites with low water clarity to shallower sites with higher water clarity.

Of the 102 sites, only five did not have any vegetation; in the remaining 97 sites, we identified 39 taxa of aquatic macrophytes (see Fig. 1; Table 2). Submergent taxa were the dominant growth form,

occurring in 91% of all 102 sites. *Chara* spp. (stonewort) was the most common submergent taxa and was detected at 74% of our sites, providing > 20% cover in 51 sites. Other common submergent taxa present in our surveys included *Elodea canadensis* (common waterweed), *Nitella* spp., *Potamogeton pectinatus* (sago pondweed), *Utricularia vulgaris* (common bladderwort), *Vallisneria americana* (wild celery) and the non-native species *Myriophyllum spicatum* (Eurasian water milfoil). These taxa were detected at 23–34% of the sites and primarily provided sparse (1–15%) coverage. *Zizania aquatica* (southern wild rice) was the dominant emergent species, providing more than 20% coverage at 12 sites and sparse coverage at additional 20 sites. *Schoenoplectus acutus* (hardstem bulrush) and *Sagittaria rigida* (stiff arrowhead) were less common (17% and 10% occurrence, Table 2), providing only sparse coverage. The most common floating taxa were *Nymphaea odorata* (fragrant white water lily) and *Potamogeton natans* (floating pondweed) which occurred in 25% and 27% of sites, respectively (Table 2). Both species provided sparse coverage, except for 12 sites where white water lily covered at least 20% of the sample quadrats.

Zooplankton and environmental variables

In total we identified 89 zooplankton taxa: 55 rotifers, 29 cladocerans and 3 copepods. Table 3 summarizes characteristics of the zooplankton detected in our surveys. The most common zooplankton were nauplii (mean density 64 L⁻¹) and *Lecane* sp. (rotifer, mean density 3 L⁻¹), which were found at every site (Table 3). The cladoceran *Bosmina longirostris* was also very common, occurring at all but 15 sites with a mean density of 20 L⁻¹. Common rotifers included *Polyarthra* sp., *Euchlanis* sp. and *Filinia brachiata*, which were detected at 75–82% of all sites (Table 3). *Filina brachiata* had the highest

Table 4
Summary of Spearman's rank correlations between environmental variables and the first three principal components (PC) axes (n=102). Only results with p<0.05 are shown. Environmental variables associated with the abbreviations are given in Table 1.

Axis	Variance explained (%)	Abbreviated variable	Spearman's rho (ρ)	p-Value		
PC1	45.7	REI	0.85	<0.001		
		pH	0.84	<0.001		
		COND	-0.76	<0.001		
		TN	-0.74	<0.001		
		DOC	-0.68	<0.001		
		DO	0.67	<0.001		
		TEMP	0.67	<0.001		
		PC2	19.8	TSS	0.82	<0.001
				CHL	0.73	<0.001
				DOC	-0.62	<0.001
pH	0.45			<0.001		
DEPTH	0.37			<0.001		
REI	0.36			<0.001		
PC3	10.8	COND	-0.34	<0.001		
		DEPTH	0.88	<0.001		
		COND	-0.19	0.040		

density of any rotifer or cladoceran in this study (mean 77 L^{-1} , density 1495 L^{-1}). Common cladocerans included *Ceriodaphnia* sp., *Diaphanosoma brachyurum*, and members of the chydoridae family (*Acroperus harpae* and *Chydorus* sp.). Cyclopoid copepods (78% occurrence) were more prevalent than either calanoid (42%) or harpacticoid (32%) copepods (Table 3).

The Canonical Correlation Analysis (CANCOR) determined the best linear combinations of the ten physico-chemical variables (listed in Table 1) and four macrophyte variables (total macrophyte richness – Tot#PL, submergent species richness – #SUB, floating species richness – #FL, and emergent species richness – #EM) that described variation in zooplankton abundances across the 102 sites (listed in Table 3). The CANCOR yielded five axes that were significantly different from zero. The correlations among the first five synthetic variates ranged from 0.85 to 0.98, with 71–95% of over-lapping variance between the variates (Table 5). The first five canonical variates extracted 58% of the variance from the environmental variables and 28% from the species. Along the first five variates, 24% variance in the species dataset is predicted by the variance in the environmental dataset. The environmental dataset extracted two to three times more variance than the species dataset along the first two variates. The first two variates explained the largest proportion of redundancy for both the environmental variables (0.503, 0.160, Table 5) and the species (0.331, 0.161, Table 5). Despite the large value of the third canonical correlation (0.905), the third canonical variates extracted only a small amount of variance (4% environmental and species, Table 5). The remaining axes explained very little of the remaining variation in the datasets.

To interpret the canonical variates, we examined the canonical loadings of the environmental variables and the species abundances (Fig. 3A). In the figure, we only display species abundances greater than 0.25 to decrease the background noise. The macrophyte community variables were associated with lower loadings than the physico-chemical variables. The loadings contributing to water clarity (TSS and CHL) and number of floating species (#FL) were closely correlated with each other and were only weakly correlated with the other environmental variables. REI, pH, TEMP and DO were strongly positively correlated with each other and negatively correlated with TN, DOC and COND. Axis 1 represents a gradient from exposed well-oxygenated alkaline water (high REI, DO and pH) to sheltered oxygen-poor acidic water (low REI, DO and pH). Axis 2 represents a gradient from high COND and water clarity (low TSS) to low COND and water clarity (high TSS).

Overall, most zooplankton loadings were found in the third quadrant of the biplot and were thus correlated with CHL (Fig. 3A). The rotifers *Asplanchna* sp. (AP), *Lecane* sp. (LE), *Euchlanis* sp. (EC), cladocerans *Bosmina longirostris* (BOLO) and *Chydorus* sp. (CH), and copepods (calanoid – CA, cyclopoid – CY, copepodid – CP, nauplii – NA) had higher abundances in locations characterized by higher productivity (high TSS and CHL) and more floating vegetation species. The rotifers *Monostyla* sp. (MO), *Platyias* sp. (PL) and *Collotheca* sp. (CO), and the cladoceran *Ceriodaphnia* sp. (CE) were found in abundance at sites with high concentrations of DOC and TN, many floating species, and low exposure (REI). *Polyarthra* sp. (PY) is the only species whose abundance was highest in the warm exposed alkaline sites. The rotifers

Ploesoma sp. (PO) and *Trichotria* sp. (TT), and chydoridae *Alonella* sp. (AO) were correlated with higher COND and water clarity (low TSS).

Characteristics of habitat groupings

We were able to discern the characteristics of the habitat groupings using the gradients explained by the ordination techniques (Table 4, Fig. 3A) and the location of the site scores in the ordination diagrams (Figs. 3B and 4). The interior sites in Crown Marsh (PDN and PD) tended to be very sheltered from wind and wave exposure, with more stagnant water that was circumneutral pH and higher in COND and DOC. These conditions promoted growth of dense vegetation that tended to shade out sunlight, keeping the water cooler and creating fewer opportunities for re-oxygenation. This explains why DO levels were also lower in these ponds, with some of the PDN sites approaching anoxic levels. Sites to the west (WS) and north (TP) were more exposed and open to the influence of Long Point Bay. With less vegetation cover, they tended to be warmer and better oxygenated; the greater mixing with bay water meant that these sites had lower COND and DOC, and higher pH. Turkey Point (TP) was one of the most exposed sites and had the lowest nutrients (DOC and TN).

Zooplankton biomass in the Crown Marsh sites without surface water connection (PDN) was up to several orders of magnitude higher than those in other sites ($217.2 \mu\text{g L}^{-1}$, Fig. 5) and was comprised mostly of habitat generalists (Fig. 5A). Typical species included *Bosmina longirostris* and *Ceriodaphnia* sp., which also comprised a large component of the cladoceran community in the rest of Long Point. Biomass of planktonic feeders was also highest at PDN (Fig. 5B), and was largely driven by high occurrence of the rotifer, *Filinia brachiata*. Scraper biomass was lowest at sites along the southern shore (SS) and in Bouck's Creek (CC) and highest at the Crown Marsh sites hydrologically connected to Long Point Bay (PD) (Fig. 5B).

The outliers of the ordination biplots identify sites with extreme values of the environmental variables and zooplankton communities. The sites circled on the PCA biplot (Fig. 4) labeled as PiP (pig pond) have the highest CHL of any sites sampled (mean $\text{CHL} = 24 \mu\text{g L}^{-1}$). The other set of sites circled and labeled as BC (Big Creek) are located at the outfall of Big Creek, one of the major tributaries emptying into Long Point Bay. They have the highest COND (mean $\text{COND} = 565 \mu\text{S cm}^{-1}$) and TN (mean $\text{TN} = 3.1 \text{ mg L}^{-1}$) of any sites sampled. On the CANCOR biplot, PDN are clearly distinct from the other sites (Fig. 3B), due to the extremely high abundance of zooplankton. ZYP (zany zooplankton pond) was distinguished from the PD grouping due to the comparatively higher abundance of *Ploesoma* sp. and *Alonella* sp. (Fig. 3B). The sites near Port Rowan on the western shore (labeled PR) have high TSS (mean 28 mg L^{-1}) and a high prevalence of *Asplanchna* sp. and *Macrochaetus* sp.

Discussion

We hypothesized that variation in physico-chemical characteristics induced by wind and wave exposure can be as important a structuring variable for the zooplankton community as are nutrient and macrophyte density. The canonical loadings of the macrophyte variables in the

Table 5
Description of canonical variates 1–5 from the canonical correlation between environmental variables (14) and zooplankton species (45 taxa).

Root	Canonical correlation (R)	R ²	Environmental variable dataset			Species dataset		
			Variance extracted	Redundancy (Env. by Sp.)	Proportion of total redundancy	Variance extracted	Redundancy (Sp. by Env.)	Proportion of total redundancy
1	0.976	0.953	0.285	0.271	0.503	0.097	0.092	0.331
2	0.950	0.903	0.096	0.087	0.160	0.050	0.045	0.161
3	0.905	0.819	0.044	0.036	0.067	0.043	0.035	0.126
4	0.879	0.773	0.046	0.036	0.066	0.053	0.041	0.147
5	0.845	0.714	0.104	0.074	0.137	0.035	0.025	0.089

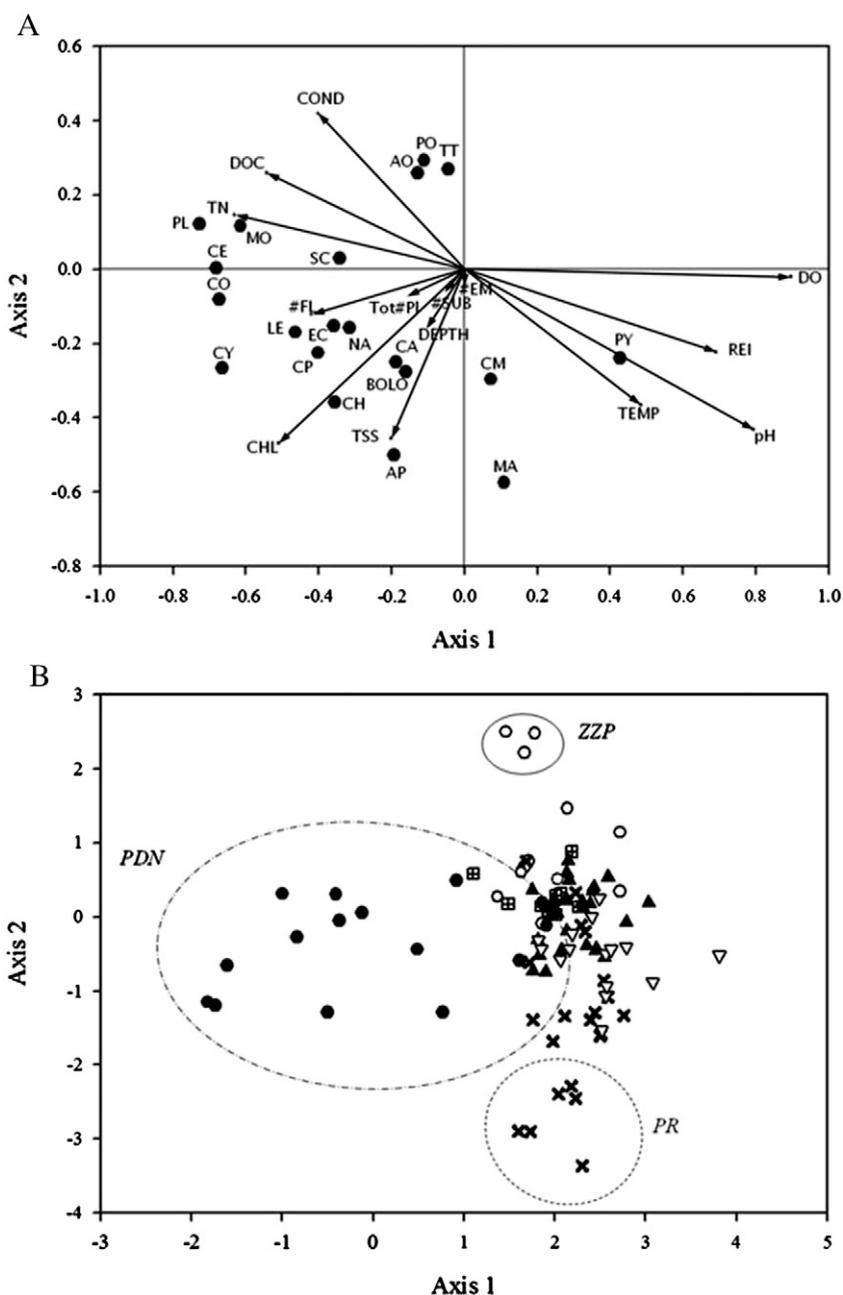


Fig. 3. Results from the CANCOR ordination of zooplankton and environmental variables showing A) canonical loadings of zooplankton > 0.25 and all environmental loadings. Environmental codes are listed in Table 1 and zooplankton codes are listed in Table 3. Filled circles indicate zooplankton and arrowheads indicate environmental loadings. #EM – emergent species richness, #FL – floating species richness, #SUB – submergent species richness, Tot#PL – total macrophyte species richness, and B) site scores corresponding to the first two axes. Symbols correspond to habitat groupings shown in Fig. 1. TP (▽), WS (X), PDN (●), PD (○), SS (▲), CC (■). ZZP, PDN and PR are discussed in text.

CANCOR were much lower than all of the physico-chemical variables except for depth (Fig. 3A), indicating that the environmental variables described the variation in the data set better than the macrophyte variables. We interpret the high correlation between exposure (REI) and many of the environmental variables as evidence that site-to-site variation in water chemistry is largely driven by wind and wave action. The spatial scale of this study has allowed us to measure different levels of wind and wave exposure and evaluate their effect on the biotic and abiotic factors within the wetland complex, while reducing the effects of confounding factors that arise across large basins. A smaller spatial scale would not have yielded as many differences in wind and wave exposure, making it more difficult to detect any influence of wind and wave exposure. The intermediate scale used in this study contains enough site

variation to create differences in exposure levels, but not so much that confounding factors, such as climate effects, are introduced.

In general, the highly exposed sites (large REI) were well-oxygenated, had lower COND and DOC, and higher pH. By contrast, sheltered sites within Crown Marsh (small REI) that had limited mixing with bay water had poorly-oxygenated water, higher COND, DOC and circumneutral pH. The sheltered sites also had dense vegetative growth, shading the water column, keeping the water temperatures lower than the more exposed sites which did not support vegetation. This created the counter-intuitive pattern of higher temperatures in more exposed sites. The 15 sites in Crown Marsh that had no surface connectivity to Inner Bay (PDN in Fig. 1) were associated with the most extreme conditions relative to the other sites and were the most

unique. Factors other than wind and wave exposure can influence the variables studied, such as the influence of land processes, groundwater intrusion, drainage and direct anthropogenic effects. Additional investigation is required to ascertain that exposure is indeed the true cause of the patterns we have observed at the Long Point Complex.

In this system highly exposed sites have characteristics similar to the surrounding bay water whereas less exposed sites are more heavily influenced by the land. Brant and Herdendorf (1972) made similar observations when studying the intrusion of Lake Erie water into drowned river mouths, noticing that highly conductive river water was diluted by the lake water. Wind action also tended to keep the water well oxygenated, consistent with the findings of Brodersen (1995). Wave exposure causes a more turbulent environment that prevents the development of dense vegetation. By contrast, the plant community can become very dense in sheltered sites and the shade results in much cooler conditions as seen in the sites of Crown Marsh. We suspect that higher concentrations of CHL and TN at these sites are related to the lack of dilution from bay water but further investigations are required to verify this. Stations along the Big Creek outfall had higher COND (mean of $565 \mu\text{S cm}^{-1}$) and higher concentrations of TN (mean of 3.1 mg L^{-1}), likely due to watershed influence since Big Creek drains primarily agricultural land with a relatively dense road network.

The CANCOR indicated several species whose abundances were highly correlated with exposure. *Polyarthra* sp. was the only taxon whose abundance was positively correlated with REI (Fig. 3A), with higher abundances at exposed sites such as those in Turkey Point and the western shore (Fig. 6A). Smith (2001) observed that this rotifer is mostly found in deep open-water areas, although Pennak (1966) observed no strong preference for open-water when compared with vegetation. Duggan et al. (2001) explain this disparity in the literature with their findings that *Polyarthra* sp. tolerate plant species with small narrow leaves that allow them to swim among the foliage and maintain their planktonic habits. Species that were highly negatively correlated with REI included *Ceriodaphnia* sp. and the rotifers *Monostyla* sp. and *Platyias* sp. (Fig. 3A). These species are more commonly associated with macrophytes in the littoral zone (Fairchild, 1981; Pennak, 1966), and this is consistent with our finding that they were most abundant in the sheltered sites of Crown Marsh with high vegetation coverage (Figs. 6B, C and D). It is interesting to note that the most exposed site, Bouck's Creek, (Fig. 2D) was dominated by *Polyarthra*, and as exposure decreased the abundance of *Ceriodaphnia* sp., *Monostyla* sp. and *Platyias* sp. increased (Fig. 6).

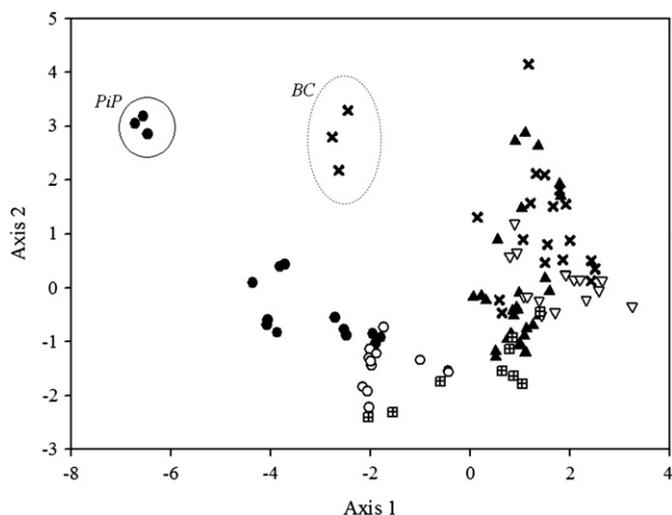


Fig. 4. Biplot showing the site scores from PCA of the physico-chemical variables. Symbols correspond to the habitat groupings shown in Fig. 1. TP (∇), WS (X), PDN (\bullet), PD (\circ), SS (\blacktriangle), CC (\blacksquare). Circled scores are discussed in text.

The zooplankton community in the nearshore of Long Point Bay is driven chiefly by physical conditions at the site level. In addition to exposure, hydrological connectivity to the bay is important in structuring the zooplankton community. The most striking feature is the high biomass of zooplankton at the sites that no longer had surface water connection to Inner Long Point Bay (i.e., PDN – Fig. 5). One explanation is that higher food availability (highest CHL at these sites) may be supporting a higher zooplankton biomass. Another explanation could be the absence of predatory fish, since fish predation has profound impacts on the distribution of zooplankton (Dodson, 1974; Luecke and Litt, 1987; Lynch, 1979). These sites are likely uninhabitable by fish because of the low oxygen concentrations and the hydrologic isolation. They also have high DOC and plant cover which suggests that if predators are present, zooplankton have many opportunities to evade capture (Strecker et al., 2008; Timms and Moss, 1984). Further investigation is required to determine the correct explanation for the extremely high zooplankton biomass.

The observation that exposure and connectivity have a large influence on the zooplankton community is an important consideration when predicting the effects of changing water levels and climate on this system. We can predict that if areas become hydrologically disconnected, they will have lower oxygen levels and higher concentrations of DOC, TN, CHL and COND, as well as higher zooplankton biomass. If water levels rise so that connectivity is regained, then such differences may be ameliorated. A second consideration is the impact of predicted increase in severity and frequency of storm

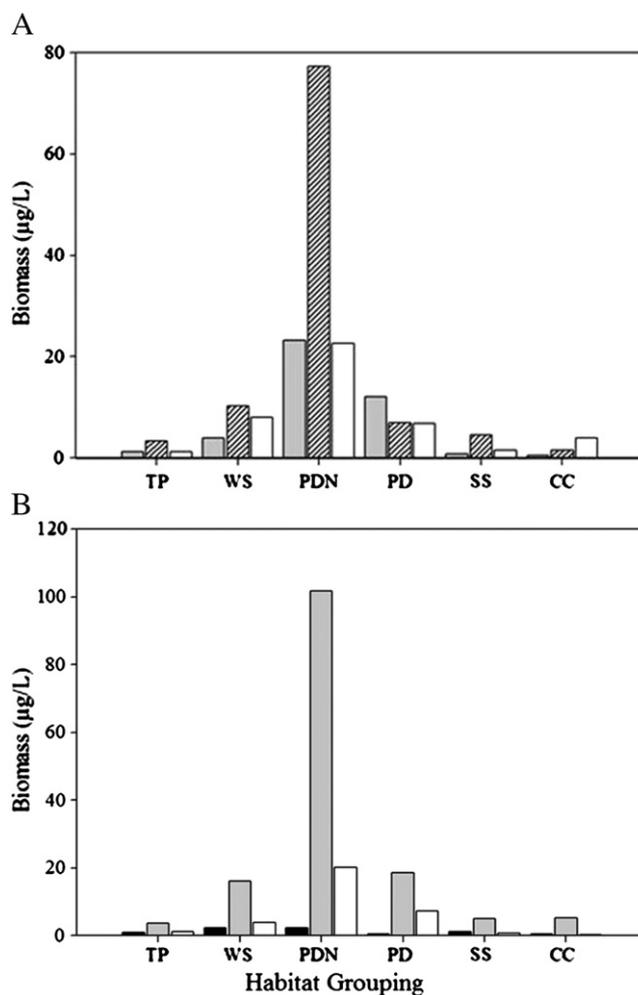


Fig. 5. Mean zooplankton biomass ($\mu\text{g/L}$) across site groups coded by A) habitat preference (gray = aquatic plant association, hatched = generalist, open = open-water association) and B) feeding mode (black = raptorial, gray = planktonic, open = scraper).

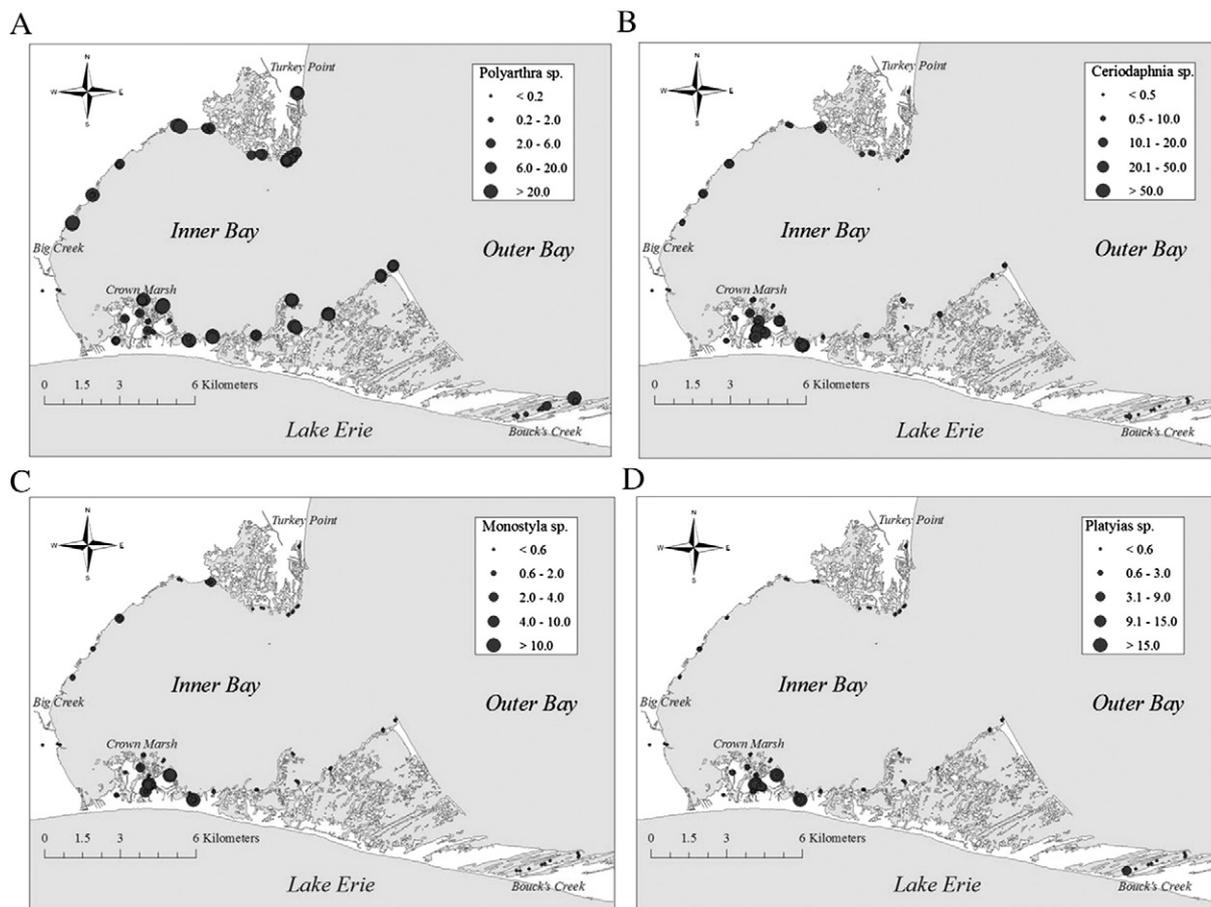


Fig. 6. Abundance (#/L) of A) *Polyarthra* sp., B) *Ceriodaphnia* sp., C) *Monostyla* sp., and D) *Platyias* sp. at study sites in Long Point Bay.

events due to climate change (Bates et al., 2008), which has the potential to amplify the impacts of wave exposure as well.

Abundance of zooplankton has been directly linked to the foraging success of larval fish (Bremigan and Stein, 1994) and the bay provides important spawning and nursery habitat for both local and lake-wide fish populations (MacGregor and Witzel, 1987 as cited in Nelson and Wilcox, 1996). The highest zooplankton biomass in nearshore Long Point was found in the ponds of Crown Marsh (PDN, Fig. 5). However, these sites also have oxygen levels that approach anoxic conditions and they have no surface water connection to the bay. Therefore, sites in Crown Marsh that have adequate oxygen, hydrologic connectivity, and high zooplankton biomass are predicted to offer the best nursery habitat for larval fish (i.e., PD, Fig. 1). By determining which factors influence the zooplankton community we will be able to predict the prime nursery habitat for larval fish. This information will help managers understand the influence of environmental variation on lower trophic levels, and thus make informed management decisions when considering spawning and nursery habitat protection and management.

The lower trophic levels of nearshore Long Point Bay have never been examined before and this study provides a starting point for future research. The data collected for this study cover a brief window of time (11 days in late August) and establish a basic description of the zooplankton community, physico-chemical environment, and aquatic vegetation. The scale of this study allowed us to examine the effects of physical disturbance and understand how it shapes the water chemistry and zooplankton assemblage in the system. Further investigations into temporal trends of the zooplankton community are necessary to fully understand the dynamics of the system. It will also be beneficial to incorporate studies on the habitat and other food web components of nearshore Long Point, such as fish distribution. Long Point is one of

the largest remaining coastal habitats in Lake Erie and there is an urgent need to conduct research at the appropriate scale to ensure its protection and conservation for future generations.

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