A comparison of the vegetated nearshore to offshore regions of the Bay of Quinte using water characteristics, the composition of plankton, and *Dreissena*

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ABSTRACT

Bowen, K.L., Fitzpatrick, M.A.J., Munawar, M., Niblock, H.A., Rozon, R., Currie, W.J.S. 2023. A comparison of the vegetated nearshore to offshore regions of the Bay of Quinte using water characteristics, the composition of plankton, and *Dreissena*. Can. Manuscr. Rep. Fish. Aquat. Sci. 3264: ix + 66 p.

The Bay of Quinte has changed from historical severe eutrophication to increased clarity and macrophyte coverage improving habitat for littoral fishes. The invasion of Zebra Mussels in the mid-1990s has been suspected of contributing to this change. This study assessed if macrophyte coverage has led to improved planktonic communities within the pelagic food web. During assessments of autotrophic (phytoplankton, autotrophic picoplankton) and heterotrophic (bacteria, flagellates, ciliates, rotifers, and zooplankton) plankton comparing nearshore (macrophyte dominated) and offshore (mid-channel) sites in 2017-2018, we observed little differences in measures of physical, chemical, algal, or zooplankton. Size or taxonomic differences in zooplankton were likely indicative of predation, but overall productivity and biomass were not different. Live Dreissena mussels were found only on macrophytes in the nearshore and were effectively absent from the soft offshore sediments. This indicated that water in the bay was generally well mixed between nearshore and offshore, or that the macrophytes and associated mussels had little impact. Potential effects of macrophytes and changes to the associated fish community on the structure and function of the planktonic food web requires more detailed examination, with particular attention given to composition and diets of planktivorous and young-of-year fishes, which are not well documented.

RÉSUMÉ

Bowen, K.L., Fitzpatrick, M.A.J., Munawar, M., Niblock, H.A., Rozon, R., Currie, W.J.S. 2023. A comparison of the vegetated nearshore to offshore regions of the Bay of Quinte using water characteristics, the composition of plankton, and *Dreissena*. Can. Manuscr. Rep. Fish. Aquat. Sci. 3264: ix + 66 p.

La baie de Quinte est passée d'une eutrophisation grave historique à une clarté accrue et une couverture de macrophytes améliorant l'habitat des poissons côtiers. On soupçonne que l'invasion de moules zébrées au milieu des années 1990 a contribué à ce changement. Cette étude a évalué si la couverture de macrophytes avait conduit à une amélioration des communautés planctoniques au sein du réseau trophique pélagique. Lors des évaluations du plancton autotrophe (phytoplancton, picoplancton autotrophe) et hétérotrophe (bactéries, flagellés, ciliés, rotifères et zooplancton) comparant les sites littoraux (dominés par les macrophytes) et les sites offshore (chenal intermédiaire) en 2017-2018, nous avons observé peu de différences dans les mesures. d'origine physique, chimique, d'algues ou de zooplancton. Les différences de taille ou taxonomiques du zooplancton étaient probablement révélatrices d'une prédation, mais la productivité et la biomasse globales n'étaient pas différentes. Les moules *Dreissena* vivantes ont été trouvées uniquement sur les macrophytes du littoral et étaient effectivement absentes des sédiments meubles du large. Cela indiquait que l'eau de la baie était généralement bien mélangée entre le littoral et le large, ou que les macrophytes et les moules associées avaient peu d'impact. Les effets potentiels des macrophytes et des changements dans la communauté de poissons associée sur la structure et la fonction du réseau trophique planctonique nécessitent un examen plus détaillé, en accordant une attention particulière à la composition et au régime alimentaire des poissons planctivores et des jeunes de l'année, qui ne sont pas bien documentés.

INTRODUCTION

In the Bay of Quinte Area of Concern (AoC), Beneficial Use Impairment (BUI) 13: Degradation of phytoplankton and zooplankton populations was listed as impaired in the Stage I Remedial Action Plan (RAP) report by the Bay of Quinte RAP Coordinating Committee (1990). Currie et al. (2023b) recommended that the BUI 13 designation remain listed as impaired as little improvement in ecosystem function in the upper bay of the Bay of Quinte was seen since the 1980s. However, these findings were based on the long-term offshore / mid-channel stations at Belleville, Napanee and Hay Bay, and it was noted that undetected improvements could potentially be found in the vegetated nearshore zone of the upper bay. Submerged aquatic vegetation (SAV) was typically sparse in the AOC in the 1970s to early 1980s, but by 2000, increased clarity led to a substantial increase in the extent of SAV coverage in the upper and middle reaches (Leisti et al. 2012, Doka et al. 2016). Currently in the upper bay, the area that is <2.5 m deep, and thus suitable for macrophyte growth, represents about 32% of total surface area based on average water heights (Doka et al. 2016). Macrophytes do not become established at the mid-channel stations due to inadequate light levels at the bottom, and by resuspension of sediments by wind and currents. These stations therefore are not directly affected by the long-term changes in macrophyte cover and composition seen in shallower areas. Similarly, macrophyte beds have shown little expansion in the lower bay, largely due to limitations imposed by greater water depth and wave exposure. Increased SAV coverage has several important ecological implications in shallow eutrophic ecosystems, driving changes to water clarity, flow, sediment transport, chemistry, and benthic and fish community structure (Scheffer 1998). Submerged macrophytes in Great Lakes coastal wetlands are important habitat for over 50 fish species (Jude and Pappas 1992; Randall et al. 1996), and are especially important as spawning and nursery areas (Lane et al. 1996a; 1996b). Expansion of SAV in the upper Bay of Quinte has led to quantifiable improvements in the biomass and production of littoral fishes including Pumpkinseed (*Lepomis gibbosus*) and Yellow Perch (*Perca flavescens*) (Leisti et al. 2012; Randall et al. 2012).

However, the influence of the macrophyte-dominated nearshore zone on the Bay of Quinte lower food web is largely unknown. There is evidence in other systems that macrophyte beds can alter the structure and dynamics of the microbial-planktonic food web (van Donk and van de Bund 2002; Muylaert et al. 2003). Increased SAV has been shown to promote a shift in phytoplankton composition towards smaller flagellates but may also lead to increases in cyanobacteria (e.g. Schriver et al. 1995; Wehr et al. 1998; Cunha et al. 2012). Furthermore, macrophytes may also promote greater heterotrophic activity as the periphyton (algae, bacteria and fungi) growing on their stems and leaves are in turn grazed by ciliates, HNF and zooplankton (Sala and Güde 1999; Muylaert et al. 2002; 2003). Littoral zooplankton can also exert a strong top-down effect on heterotrophic microbes reducing the overall biomass of HNF and ciliates (Sinistro et al. 2007; Özen et al. 2018).

Macrophytes, especially those growing close to the surface, may also shade the water column and take up available phosphorus, competing with phytoplankton and lead to increases in water clarity (Mulderij et al. 2007; Scheffer 1998). These rooted plants will simultaneously reduce water flow rates and sediment resuspension, and throughout their life cycle will serve as both sources and sinks for nutrients (e.g. Best 1982; Carpenter and Lodge 1986). Macrophyte-rich habitats have been found to provide refuge, settlement substrate and food for both macroinvertebrates, especially gastropods, and herbivorous zooplankton, resulting in greater biomass and biodiversity (Cyr and Downing 1988; Jeppesen et al. 1998; Jude and Pappas 1992). Plant-inhabiting invertebrates in turn provide food for many littoral fishes (Chow-Fraser 1998; Scott and Crossman 1973). However, macrophytes may serve as important daytime refuges for large zooplankton such as *Daphnia* that are otherwise vulnerable to fish predation (Burks et al. 2001; Timms and Moss 1984).

Macrophytes in the upper Bay of Quinte also provide potentially important substrate for invasive filter-feeding dreissenid mussels (Dermott et al. 2003), which subsequently may lead to increased grazing on phytoplankton in heavily vegetated areas. Zebra mussels (*Dreissena polymorpha*) are the predominant mussel species in the upper Bay of Quinte (Dermott et al. 2003), where they are generally found on firm substrates such as rocks, macrophytes and human-made structures at water depths of 3 m or less. Quagga mussels (*D. bugensis*), which dominate the deeper lower bay and Lake Ontario, can colonize soft substrates unsuitable to zebra mussels (Karatayev et al. 2015). However, the soft mud of the shallow upper bay is too prone to resuspension by wind to allow even quagga mussels to become established as they will be buried in the loose silt (Dermott et al. 2003).

The expectation that macrophytes can have a large impact on the condition of the planktonic food web (e.g. Søndergaard and Moss 1998) prompted the addition of nearshore stations in 2017 and 2018 as part of Fisheries and Oceans Canada's (DFO) lower food web sampling program. A nearshore station in the macrophyte zone was paired with each main station in the upper bay (Belleville and Napanee) and middle bay (Hay Bay). We examined differences between these nearshore and long-term offshore stations in terms of the physical-chemical environment, plankton (microbial, phytoplankton and zooplankton) composition and biomass, and effects of macrophytes on benthos, primarily *Dreissena* mussels. Many papers on the Bay of Quinte suggest that dreissenid mussels were an important factor driving the environmental changes seen in the Bay of Quinte (Nicholls and Carney 2011; Bowen and Johannsson 2011; Shimoda et al. 2016), but recent analysis has questioned their effect on the lower food web at the main-channel stations (Currie and Koops 2022; Currie et al. 2023c). Additional sampling of macrophytes and their associated dreissenid biomass was undertaken to help to quantify these benthic effects on the planktonic food web.

METHODS

FIELD AND LABORATORY PLANKTON SAMPLING

Project Quinte has sampled stations in offshore, central channel locations at Belleville (B), Napanee (N), Hay Bay (HB) and Conway (C) since the early 1970s (Fig. 1). In 2017 new stations were selected in 1.5 to 2.5 m deep nearshore areas adjacent to the mid-bay stations in areas of known macrophyte growth (see Doka et al. 2016; Table 1). In 2017 and 2018 all stations were visited approximately monthly from early May to late October, a total of 7 times each year. A vertical YSI EXO2 sonde cast at each site measured temperature, conductivity, dissolved oxygen, pH, turbidity, fluorescent dissolved organic matter (fDOM), and in-situ fluorescence of chlorophyll *a* and phycocyanin. The EXO sonde was also towed horizontally at a 0.25 m depth from each offshore to nearshore station to try to determine the presence and extent of a zone of influence of the vegetated nearshore zone.

Clarity was measured by Secchi disk depth and light attenuation coefficient (kd) using a RBR Duo PAR-D (photosynthetically active radiation-Depth) sensor. Integrated water samples were collected using an integrator bottle sampler from surface to 2X Secchi or surface to 1 m off bottom (whichever was shallower). Water samples were kept in darkened insulated carboys on ice for transport back to the Canada Center for Inland Waters (CCIW) for next day processing.

Nutrient analyses, including total phosphorus (TP), nitrate + nitrite, and silica followed the standard protocols of the National Laboratory for Environmental Testing (NLET 1997). Chlorophyll *a* was determined by water filtration and acetone pigment extraction (Strickland and Parsons 1972).

Size-fractionated primary productivity was estimated for three size categories of phytoplankton (<2 µm, 2-20 µm and >20 µm) by the Carbon-14 technique following the standard protocol of Munawar and Munawar (1996). Whole water samples were spiked with $Na^{14}CO_3$, incubated for 4 hours at surface temperature, and exposed to a constant light level of 240 $\mu E\ s^{-1}\ m^{-2}$. Because light and temperature levels were constant, the results should be interpreted as potential rather than actual in-situ production. After incubation, size classes were determined by filtration of the sample through polycarbonate filters. All filters were rinsed with hydrochloric acid (0.5 N) in order to remove excess $^{14}C\text{-}CO_2$. Bacterial growth rates were estimated by ^{3}H-Leucine incorporation into bacterial proteins following the protocol of Jørgensen (1992). Detailed procedures are available in Heath and Munawar (2004). For both experiments, radioactivity was determined by liquid scintillation.

Phytoplankton, microbial loop, ciliate, rotifer and zooplankton samples were preserved on the day of sampling. Phytoplankton samples were fixed with acidified Lugol's iodine upon collection. Identification, enumeration and measurement were carried out by an external contactor following the HPMA (2-hydroxypropyl methacrylate) technique described by Crumpton (1987) which is broadly compatible with the Utermöhl (1958) technique. A minimum of 200 units were counted to achieve an acceptable counting efficiency (Lund et al. 1958). Within each sample, cell dimensions were measured directly and the average cell volume for each species was determined by applying the average cell dimensions to a standard geometric shape that most closely resembled the species. In the case of colonial forms, the average number of cells per colony was determined. Cell volume was converted to wet biomass assuming a specific gravity of 1.0 (Strickland 1960). Microbial loop samples, including bacteria, autotrophic picoplankton (APP) and heterotrophic nanoflagellates (HNF), were fixed with 1.6% formaldehyde and enumerated using DAPI staining (Porter and Feig 1980) under epi-fluorescence microscopy (Munawar and Weisse 1989). Wet weight biomass was estimated as 2000 fg cell^{-1} for APP, 100 fg cell^{-1} for bacteria and 140 pg cell^{-1} for HNF (Sprules et al. 1999). Ciliate samples were preserved in acidified Lugol's iodine upon collection. Within 6 months, the samples were post-fixed by adding concentrated Bouin's fluid to a final concentration of 5% and stained using the Quantitative Protargol Stain (Montagnes and Lynn 1993). Abundance and bio-volume were calculated using standard geometric shapes and the Microbiota software developed by Roff and Hopcroft (1986). Bio-volume was converted to biomass assuming a specific gravity of 1.0 and 20% shrinkage after preservation and staining (Jerome et al. 1993).

For zooplankton, at the long-term offshore stations B, N and HB (Fig. 1), samples were collected and pooled from approximately 2 m intervals through the water column using a 41 L Schindler-Patalas trap fitted with a 64 µm mesh cod-end. At each of the three nearshore stations, Schindler-Patalas trap samples were collected at depths of 0.7, 1.0 and 1.5 m and pooled. At C, zooplankton were taken using a 40 cm diameter, 64 µm mesh Wisconsin net fitted with a Rigosha flow meter to correct for net efficiency. Rotifers were collected at the seven stations by filtering 8 L of depth-integrated water (as described for nutrients) through a 20 µm mesh sieve. In 2017, three rotifer composite samples were created for each station by combining samples from May and June (spring), July, August and September (summer), and October and November (fall). In 2018, a single seasonal composite was created for each station by combining all seven samples collected through the season. Details on collection, preservation and enumeration are given in Bowen and Johannsson (2011) and Bowen (2017). Secondary production calculations are explained in Bowen (2017) and Johannsson and Bowen (2012). The egg ratio method was used to calculate production for the dominant cladoceran genera, cyclopoids (taxa pooled) and the calanoid group Diaptomids + *Eurytemora*, and the P/B method was used for the remaining taxa. Cyclopoid copepodites (juveniles) were allocated to species according to percent composition (by biomass) of adults. Mean lengths for cladocerans, cyclopoid and calanoids were weighted according to the densities of individual taxa comprising each group.

Table 1. Station locations and average depths for nearshore-offshore studies conducted in 2017-18 and the earlier studies in 2001 and 2004.

Years	Station	Location	Habitat Type	Reach	Latitude (°)	Longitude (°)	Depth (m)
2017-2018							
	B	Belleville	offshore	upper	44.1537	-77.3456	4.9
	N	Napanee	offshore	upper	44.1803	-77.0397	5.2
	HB	Hay Bay	offshore	middle	44.0933	-77.0717	11.8
	Bns	Belleville	nearshore	upper	44.1416	-77.3510	2.8
	Nns	Napanee	nearshore	upper	44.1661	-77.0649	2.5
	HBns	Hay Bay	nearshore	middle	44.1009	-77.0809	2.6
	C	Conway	offshore	lower	44.1089	-76.9089	29.6
2001, 2004							
	1	Big Bay	offshore	upper	44.1567	-77.2474	6.0
	2	Big Bay	offshore	upper	44.1545	-77.2505	5.0
	3	Big Bay	offshore	upper	44.1526	-77.2499	6.0
	22	Big Bay	high macro.	upper	44.1404	-77.1935	1.5
	23	Big Bay	high macro.	upper	44.1360	-77.1918	1.5
	25	Big Bay	high macro.	upper	44.1417	-77.1943	1.5
	26	Big Bay	high macro.	upper	44.1357	-77.1897	1.5
	29	Big Bay	low macro.	upper	44.1361	-77.2208	1.5
	31	Big Bay	low macro.	upper	44.1349	-77.2383	1.5
	32	Big Bay	low macro.	upper	44.1320	-77.2480	1.5

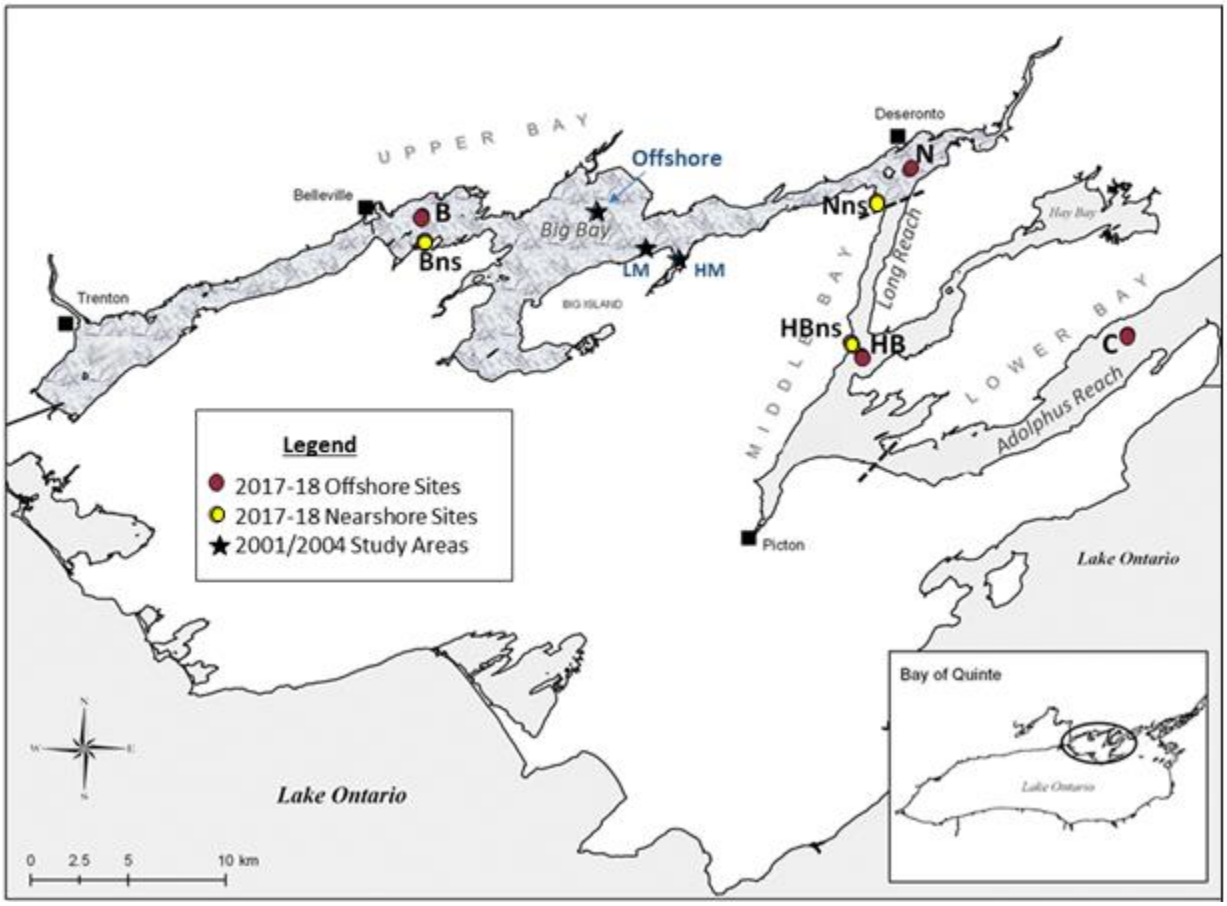

Figure 1. Map of the Bay of Quinte showing the 2017 and 2018 lower food web sampling stations, as well as the earlier study sites in Big Bay. The darker patterned area denotes the extent of the upper bay.

STATISTICAL ANALYSES

All data was examined for outliers and possible unit misreporting. For instance, an outlier SRP value of 72.4 µg L^{-1} at N, which was not possible given simultaneous TP values on cruise 2 of 2018 was removed prior to further analysis. All statistical analysis was run in JMP v14 and Systat v11. A 3-way ANOVA using Year, Station and Cruise was used to check for the effect of an individual station on water chemistry and physical parameters. If no effect of station was seen, stations were grouped into nearshore and offshore habitats and a 3 way ANOVA of year, cruise and habitat was run using JMP 14.2 by SAS institute Inc. with the intent of determining if there is a difference between the nearshore and the offshore regions. Differences between years and cruises (~time of year) are expected and were included to separate those from any habitat effect. For parameters where an effect was seen for station, a 4 way ANOVA was run with the addition of a ‘distance downstream’ factor which grouped B and Bns as upstream, N and Nns next and HB and HBns as the furthest downstream (Fig. 1).

Most of the biomass measures exhibited significant deviations from normality. As such all zooplankton, microbial loop and phytoplankton biomass data were log transformed

(BM+1) prior to statistical analyses. For the microbial loop and phytoplankton, to test for differences between nearshore and offshore parameters, 3-way ANOVAs were first run with ‘Station’, ‘Season’ and ‘Year’ as factors. If both the overall ANOVA and station effect were significant then a following 3-way ANOVA was run using ‘Habitat’ (Nearshore vs Offshore), ‘Season’ and ‘Year’ as factors.

Biomass of dominant zooplankton taxa and mean lengths of zooplankton groups were tested using ANOVA, with Habitat (nearshore vs offshore) and Reach [upper bay (N, NNS, B and BNS) vs. middle bay (HB and HBNS)] as factors. Data from both 2017 and 2018 were used, and data from each of the summer sampling dates (June to September) were treated as replicates. Conway and the first and last cruises were excluded to minimize seasonal and spatial influences. Reach (upper vs. middle bays) and Reach * Habitat were found to be not significant for all parameters, so Reach was excluded as a factor in subsequent tests.

MACROPHYTE AND *DREISSENA* COLLECTION

To determine where ZM are predominantly located in the sediment or on the macrophytes, in August 2018, two paired sites in Bay of Quinte (B, Bns and N, Nns) were each sampled in triplicate with a 3.5 L Ekman sampler (15 cm x 15 cm) to collect benthos, and once with a macrophyte rake (bottom area of 56 cm x 40 cm) to collect aquatic vegetation (Leisti et al. 2006).

Collected sediment samples were preserved in entirety using 70% isopropyl alcohol until they could be processed. Sediment samples were sectioned using stacked screens (0.30 mm, 0.71 mm, 1.7 mm and 3.3 mm) and each mussel was counted, photographed and measured for size using digital imaging software *Northern Eclipse*™. At Bns, one Ekman sample was mislabeled so subsequently removed from the analysis. Macrophytes were stored wet in plastic bags and refrigerated. As soon as possible after collection, plants were identified to species, weighed wet, and each strand was photographed and examined for attached ZM. Only mussels visible to the naked eye were included in the counts. Attached mussels were removed, preserved and sized. When macrophytes were abundant or strands were long, portions of the strands were photographed, weighed and counted for ZM, and estimates based on subsampled partial strands (by % of biomass) were extrapolated to provide 100% coverage of the macrophytes collected.

To estimate *Dreissena* biomass, a length-weight regression was applied based on data from Lake Michigan collected in 2018 by Ashley K. Elgin (NOAA-GLERL, pers. comm.), where:

$$\text{Mussel dry tissue shell-free weight} = 0.8155 * e^{(0.2011 * \text{shell length mm})} \qquad (1)$$

2001 NEARSHORE-OFFSHORE SURVEYS

We are including here, for purposes of comparing nearshore to offshore, results from monthly lower trophic level sampling carried out by DFO from late April to mid-October 2001 in Big Bay, in the Upper Bay of Quinte east of Belleville (Bowen et al. 2003). Three stations were located in the 5-6 m deep offshore area, three at a depth of 1.5 m in the rocky, sparsely vegetated nearshore area along the NE shore of Big Island (Low Macrophytes, LM area), and four at about 1.5 m deep in the shallow, densely vegetated wetland area to the east of the island (High Macrophytes, HM area) (Fig. 1; Table 1). The high macrophyte stations 22 and 25 were more exposed to wave action and mixing with the open water of Big Bay relative to 23 and 26, which were located deeper in the embayment. The 1.5 m deep sites were in shallower water compared to the 2017 – 2018 nearshore sites, and the 2001 HM area was in a more protected embayment with denser macrophyte growth.

Sampling was carried out as described for the 2017 – 2018 surveys, except that each station consisted of a 100 m long transect following a consistent depth contour, Sampling gear was typically lowered into openings among the plants, as physical disturbance potentially contaminated samples with periphyton, attached animals and detritus. Secchi depth and surface temperature were taken at the mid-point of each transect. Light attenuation was measured from the surface to bottom using a LI-COR™ submersible quantum sensor with an on-deck cell for reference to correct for cloudy conditions. Depth-integrated water samples were collected with a bottle integrator from the ends and the middle of each transect and pooled. The only water chemistry parameters measured were chlorophyll *a*, total suspended solids (TSS) and TP.

Phytoplankton, microbial loop and ciliate samples were drawn from the integrated water. All laboratory analyses were carried out as described for the recent survey except for phytoplankton enumerations, which followed the Utermöhl inverted microscope technique as described by Nicholls and Carney (1979). Phytoplankton samples were not counted in August due to budgetary constraints. For zooplankton, water was collected at equal intervals through the water column using a hand operated diaphragm pump, with 60 L taken at each nearshore station, and 135 L at each offshore station. Zooplankton were filtered from the pumped water using a 64 µm mesh net, preserved and enumerated as in the 2017 – 2018 study. Rotifers were not collected in 2001. Aquatic macro-invertebrates were sampled in June, August and October using a mini Ponar grab sampler (area 0.0225 m^2). One grab was collected at each of three points along each transect, sieved through 580 µm mesh, and pooled together. Samples were preserved and processed as described in Dermott et al. (2003).

For water quality, phytoplankton and zooplankton parameters, statistical comparisons were made using ANOVA with month and area as factors. Only the July to October 2001 sampling dates were used as this represents the period when macrophytes were well established. When this reduced season was used there were generally no significant interactions between month and area. Phytoplankton, microbial loop and zooplankton biomass data were log transformed prior to analyses.

RESULTS AND DISCUSSION

PHYSICAL AND CHEMICAL PARAMETERS

2017 – 2018 Survey

Overall, conditions in 2017 and 2018 continued to reflect a phosphorus enriched, nitrogen limited eutrophic environment typical of the Bay of Quinte (e.g. Munawar et al. 2018; Currie et al. 2023b). During the May to October period of 2017, surface temperatures in the upper and middle bays ranged from 9.3 – 24.4 °C (highest and lowest values both at N), total phosphorus ranged from 14.0 µg L^{-1} at Bns to 61.3 µg L^{-1} at Nns, Nitrate + Nitrite varied from a low of <5 µg L^{-1} (i.e. below detection) at Bns to a high of 282 µg L^{-1} (at HB), silica ranged from 1.9 – 6.0 mg L^{-1} (both at Nns) and chlorophyll *a* ranged from 2.4 – 21.7 µg L^{-1} at N and B, respectively (Appendix 1). During the sampling season of 2018, surface temperatures ranged from 6.3 – 26.4 °C, total phosphorus from 9.6 – 117 µg L^{-1}, nitrate + nitrite from 5.0 – 250 µg L^{-1}, silica from 1.06 – 5.91 mg L^{-1}, and chlorophyll a from 1.5 – 58.22 µg L^{-1}.

Nearshore station depth averaged 2.6 m and showed no significant difference between years or through the season (Fig. 2A). Although water depth in the Bay varies temporally, differences were minimized at the nearshore stations by stopping the vessel in a patch of macrophytes at the correct depth, but within ~20 m of the desired coordinates. Offshore stations were accessed at fixed location moorings and so a slight but significant difference was seen in depth between years with the upper bay averaging 5.2 m in 2017 and 4.9 m in 2018 (Fig. 2A; F=6.4, p=0.020). Surface temperature showed a wider range of values in 2018 (Fig. 2B) averaging 18.9 °C offshore and 19.0 °C nearshore in 2018, compared to 18.0 °C offshore and 18.3 °C nearshore in 2017. Light attenuation in the water column showed no difference between years or habitat and averaged 1.1 m^{-1} overall (Fig. 2C; Appendix 1). Light attenuation rates in Bay of Quinte are similar to Hamilton Harbour (avg. 0.91 m^{-1} in 2017) and much higher than Toronto Harbour (avg. 0.42 m^{-1} in 2016) or offshore Lake Ontario (0.33 m^{-1} in 2017). The range of attenuation values is highest in mid-summer to early fall when we were more likely to encounter an algal bloom at a station.

A 3-way ANOVA considering Station, Year and Cruise, showed Station to be a significant effect for only 4 of 19 physical and chemical parameters measured. These were fluorescent dissolved organic matter (fDOM), dissolved organic and inorganic carbon (DOC and DIC) and soluble reactive phosphorus (SRP). The remaining 15 parameters measured showed no effect of station and so stations were grouped to test for habitat differences and a 3-way ANOVA (using Year, Cruise and Habitat) was run. Cruise, a time of year equivalent, was significant for all the variables tested and year was significant for most variables (Appendices 2, 3, 4), but habitat was not shown to be significant for dissolved oxygen, total dissolved solids, pH, in vivo and extracted chlorophyll, phycocyanin, fluorescent dissolved organic material, turbidity, chloride, surface temperature, total phosphorus, total Kjeldahl nitrogen (TKN), silica, particulate organic carbon or nitrogen (Appendices 2, 3, 4). This indicates that the water body is well mixed nearshore to offshore in these open-coast, non-embayment areas and there is less of an influence of the macrophytes and their associated fauna than expected except for organic carbon measurements.

fDOM, a fluorometric measure of CDOM (coloured dissolved organic matter) is a complex mix of organic molecules that influence the optical properties of the water column. These molecules are sourced from organic leaching of plant matter and detritus (especially from peatland watersheds), and excretion from animals, and is a source of energy for the microbial loop (Jones 1992; Wetzel 1995) and macrophytes (Lapierre and Frenette 2009). With runoff being a major source of fDOM, higher values in the high water year (2017; avg. 12.2 RFU) compared to the lower water year (2018; avg. 8.2 RFU) and a declining trend through the season (Fig. 3), as terrestrial runoff decreases was expected and seen in both years. There was no difference in fDOM between nearshore and offshore habitats (Table 2; Fig. 3) indicating a well-mixed water body between the nearshore and offshore.

SRP showed a slight increasing trend through the season, with increased variability in the mid-summer to fall and higher values downstream (Table 2; Fig. 3). This suggests that SRP is being sourced from internal loading, and this matches analysis of seasonal phosphorus at the offshore stations (Currie and Frank 2015; Doan et al. 2018). Like fDOM, average SRP was higher in 2017 (5.1 µg L^{-1}) than in 2018 (2.4 µg L^{-1}; Table 2; Appendix 1), but there was no difference between nearshore and offshore habitats. There was an expectation of higher SRP values in the vegetated, littoral region of the Bay of Quinte given findings of previous studies (Cyr et al. 2009), but the similarity among habitats also matches the other chemistry values indicating strong mixing of nearshore and offshore waters.

DOC and DIC were the only parameters shown to have a significant effect of nearshore vs offshore habitat as well as year, distance downstream and cruise (Table 2; Fig. 3). Overall, DIC was higher in the offshore (avg. 24.7 mg L^{-1}) compared to the nearshore (23.8 mg L^{-1}). DIC concentrations (consisting of free CO_2 gas, carbonic acid, and the carbonate and bicarbonate ions) are generally based on the alkalinity of the bedrock. DIC is also influenced by the biological processes of autotrophic productivity and respiration and organic matter mineralization. Given the very high rate of decay of aquatic macrophytes late in the season (Bridgham and Ye 2013), increased decay in the nearshore should contribute higher DIC values as was seen in 2017, but in 2018 peak DIC was seen in August during the peak in macrophyte growth. Higher rates of DIC uptake by the macrophytes themselves explain lower DIC nearshore. At other Lake Ontario sites, seasonal average DIC is highest in Hamilton Harbour (26.2 mg L^{-1}) followed by Bay of Quinte offshore (24.7 mg L^{-1}), Bay of Quinte nearshore (23.8 mg L^{-1}), Toronto Harbour (22.4 mg L^{-1}) and offshore Lake Ontario (21.2 mg L^{-1}; DFO unpublished data).

The organic portion of dissolved carbon (DOC) showed the opposite pattern to DIC, being higher nearshore (6.6 mg L^{-1}) than offshore (5.3 mg L^{-1}). DOC is composed of a variety of organic molecules and DOC can comprise large portion of the fDOM. A similar pattern between fDOM and DOC is seen in the nearshore and is far less evident in the offshore (Fig. 3). While a majority of DOC comes from the terrestrial landscape, sources of DOM include excretion by planktonic or benthic fauna, but the vast majority is sourced from macrophytes (Lapierre and Frenette 2009) and associated organisms. The presence of higher macrophyte biomass in the nearshore (See: macrophytes and zebra mussels section) is likely to account for the increased DOC in this area.

Table 2. Results of the 4 Way ANOVA for chemical parameters with Year (2017 and 2018), Cruise (1 – 7), distance downstream (1 – 3) and Habitat (nearshore vs. offshore) as factors. P values > 0.05 are listed as not significant, "n.s.".

	Overall		**Effect: Year**		**Effect: Cruise**		**Effect: Distance Downstream**		**Effect: Habitat**	
Parameter	**F(71,10)**	**P**	**F(1,80)**	**P**	**F(6,74)**	**P**	**F(2,79)**	**P**	**F(1,80)**	**P**
fDOM	28.0	<.0001	91.7	<.0001	30.0	<.0001	5.2	0.0077	1.8	n.s
DIC	7.2	<.0001	4.3	0.0428	7.2	<.0001	4.1	0.0211	16.3	<.0001
DOC	13.7	<.0001	48.2	<.0001	5.2	0.0002	10.3	0.0001	37.2	<.0001
SRP**	4.9	<.0001	18.1	<.0001	2.9	0.0132	9.7	0.0002	0.9	n.s.

** single outlier at N (Jun 2018) removed

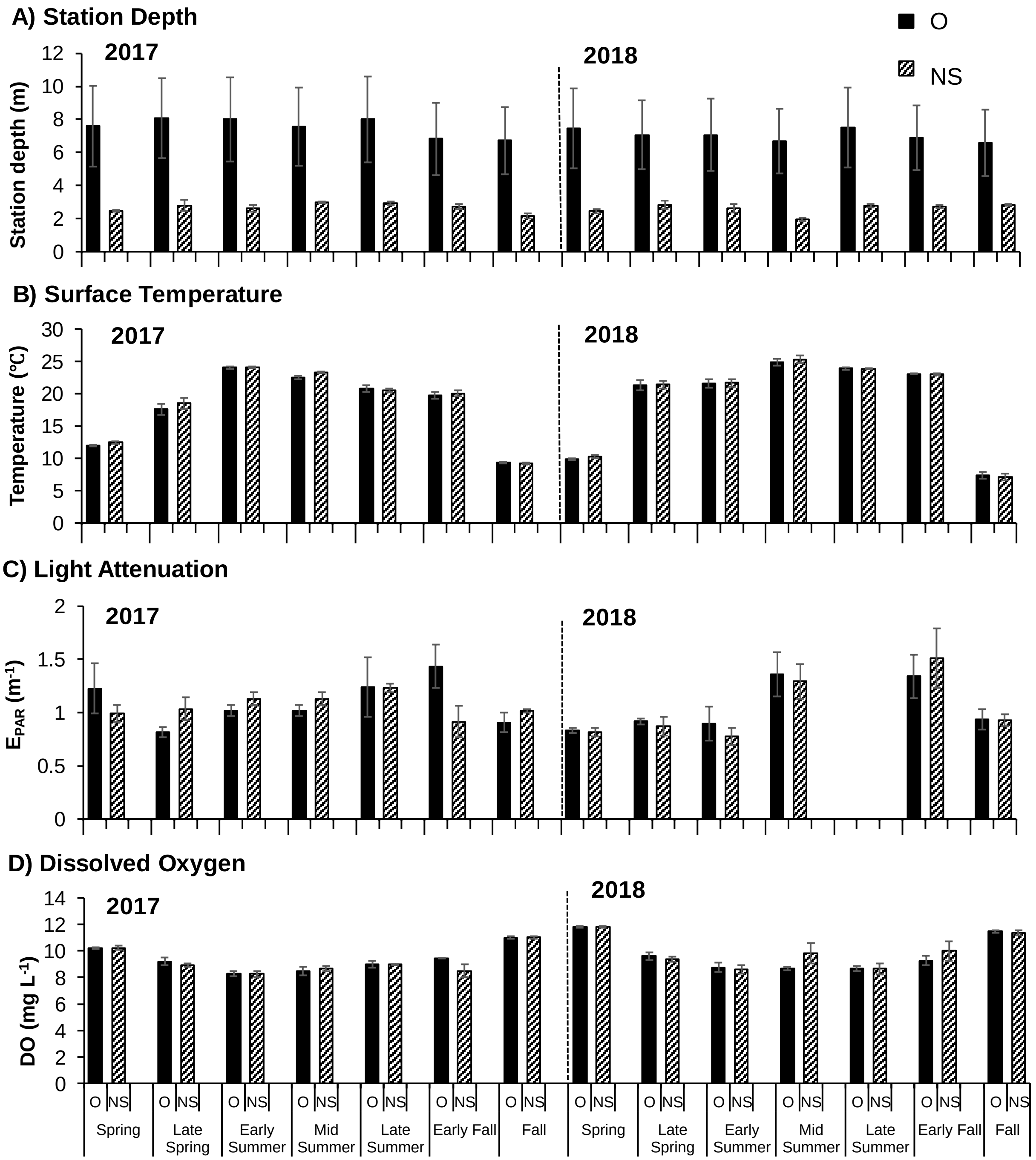

Figure 2. Physical and chemical properties of the Bay of Quinte including A) station depth (m), B) surface temperature (°C), C) light attenuation (m-1) and D) dissolved oxygen (mg L-1) shown by cruise season in 2017 and 2018 for offshore (O) and nearshore (NS) stations. All values are the arithmetic mean ±1 standard error.

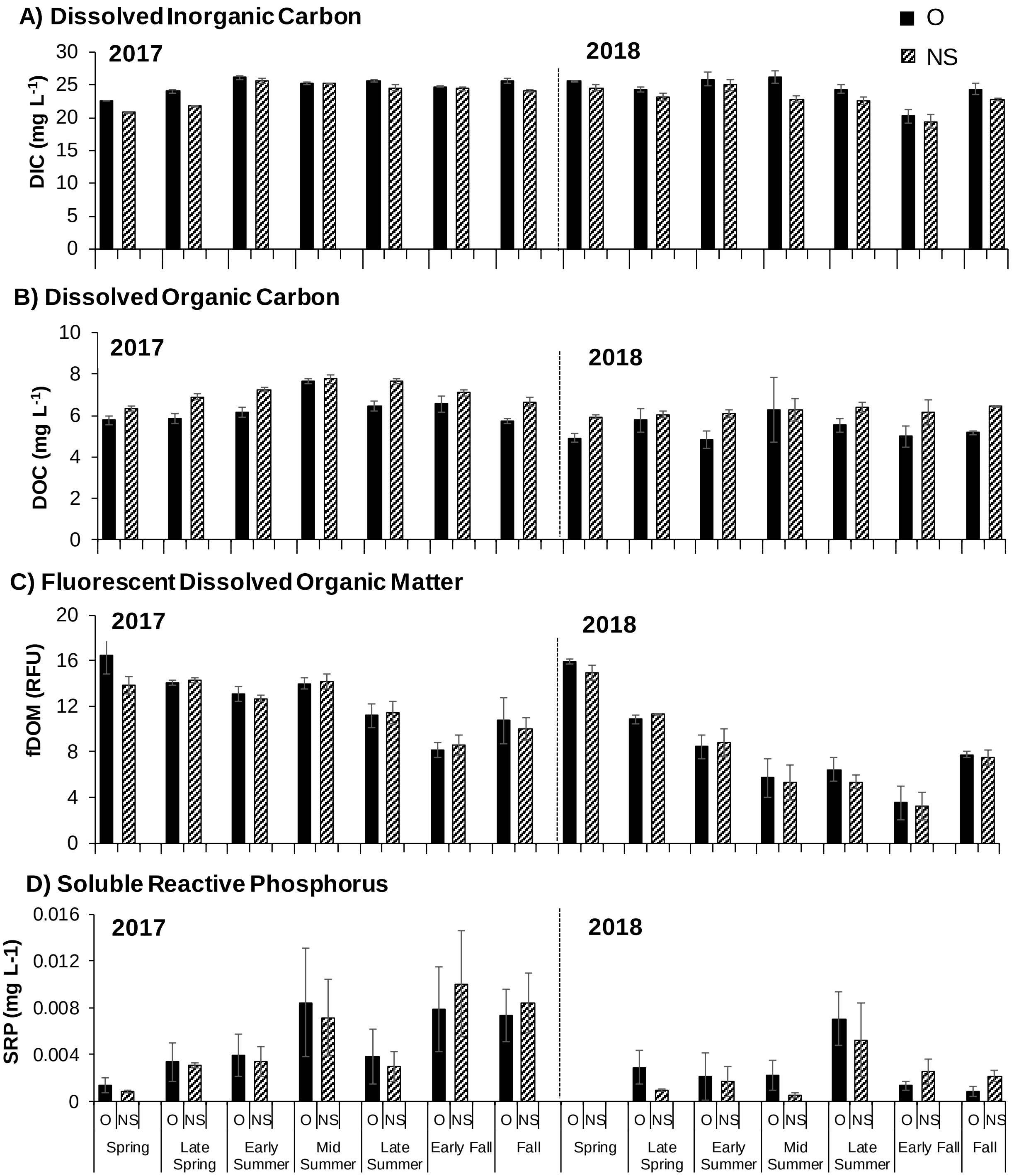

Figure 3. Chemical properties of the Bay of Quinte shown by cruise season in 2017 and 2018 for offshore (O) and nearshore (NS) stations including: A) dissolved inorganic carbon (mg L^{-1}), B) dissolved organic carbon (mg L^{-1}), C) fluorescent dissolved organic matter (RFU), and D) soluble reactive phosphorus (mg L^{-1}). All values are the arithmetic mean ±1 standard error.

2001 Nearshore – Offshore Survey

In contrast to the recent survey when water characteristics were similar at the nearshore and offshore sites, water quality in 2001 was generally poorer at the offshore Big Bay stations compared to the adjacent shallow areas during the summer and fall (Table 3; Fig. 4). July – Oct 2001 chlorophyll *a* and total suspended solids (TSS) were significantly higher in the offshore relative to the two nearshore areas, and TP was greater in the offshore than in the HM area. Surface temperature and particulate organic material were similar in the three areas. Many parameters such as TP and chlorophyll were more variable in the HM, as plant disturbance sometimes dislodged fragments of leaves and periphyton that contaminated the samples. Light attenuation was higher in the HM compared to the LM area, but it is likely that the light sensor was intermittently shaded by macrophytes. It is unlikely that the water was genuinely more turbid, given lower levels of chlorophyll and TSS relative to the offshore. As the Secchi disk was usually clearly visible on the bottom at the nearshore sites, Secchi depth was not a useful measure at these 1.5 m deep sites.

Changes were also evident across the season in 2001, with TP levels in the July to October period significantly higher (overall mean = 41.9 µg L^{-1}, excluding 3 outliers), compared to April and June (mean = 17.1 µg L^{-1}). Similarly, both TSS and chlorophyll *a* reached their highest levels in August and September, which in the offshore corresponded to the period of highest light attenuation. In all areas, water clarity tended to be highest in spring and early summer. Overall, July – October water quality was generally similar in the 2001 and recent surveys, based on the limited suite of parameters measured in both studies. Offshore TP was an exception, with the 2001 mean of 49.7 ± 2.9 µg L^{-1} significantly greater than the 2017 – 2018 mean of 36.0 ± 2.7 µg L^{-1} (two-tailed t-test; p=0.005).

Table 3. Untransformed means, standard errors (SE) and sample size (N) of physical/chemical parameters, phytoplankton and microbial loop in offshore (Off), nearshore high macrophyte (HM) and nearshore low macrophyte (LM) areas in Big Bay, Bay of Quinte in 2001. SS represents suspended solids, and euphotic depth is the depth to which 1% of surface light reaches. The April and June cruises were excluded to represent the months when macrophytes were well established. F and p values were determined using ANOVA. P values > 0.05 are listed as not significant, "n.s.". The area differences based on Bonferroni multiple comparisons tests are also shown. Log-transformed phytoplankton and microbial loop data were used for statistical analyses.

	Offshore		**High Macro.**		**Low Macro**					
Parameter	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**N**	**F**	**P**	**Bonferonni**
Temperature (ºC)	20.6	1.2	21.1	1.2	21.3	1.2	38	0.1	n.s.	--
Chlorophyll *a* (µg L^{-1})	17.5	2.1	10.7	1.7	9.0	1.7	40	5.7	0.007	Off>HM, LM
Organic SS (mg L^{-1})	3.8	0.4	2.7	0.4	2.4	0.4	39	2.5	n.s.	--
Total SS (mg L^{-1})	7.0	0.8	4.2	0.7	4.0	0.6	39	5.0	0.012	Off>HM, LM
Total Phos. (µg L^{-1})	49.7	2.9	37.0	3.9	40.4	2.7	37	3.8	0.033	Off>HM
Light Attenuation (m^{-1})	1.1	0.1	1.5	0.1	1.1	0.1	39	4.1	0.024	HM>LM
Euphotic depth (m)	4.6	0.5	3.4	0.3	4.9	0.6	39	2.9	n.s.	--
Biomass (mg m^{-3})										
Total phytoplankton	7327	1710	5940	2389	2536	843	36	5.8	0.007	Off>LM
Diatomeae	6462	1716	3704	1598	1973	803	36	6.6	0.005	Off>LM
Cyanophyta	604	114	838	243	358	141	36	1.9	n.s.	--
Chlorophyta	66	10	1280	885	49	13	36	13.1	0.001	HM>Off, LM
Bacteria	593	49	613	33	541	37	40	1.3	n.s.	--
APP	114	42	98	39	123	43	40	0.2	n.s.	--
HNF	202	25	163	19	125	17	40	3.0	n.s.	--
Ciliates	7.6	1.4	26	8.6	9.0	3.5	40	3.0	n.s.	--

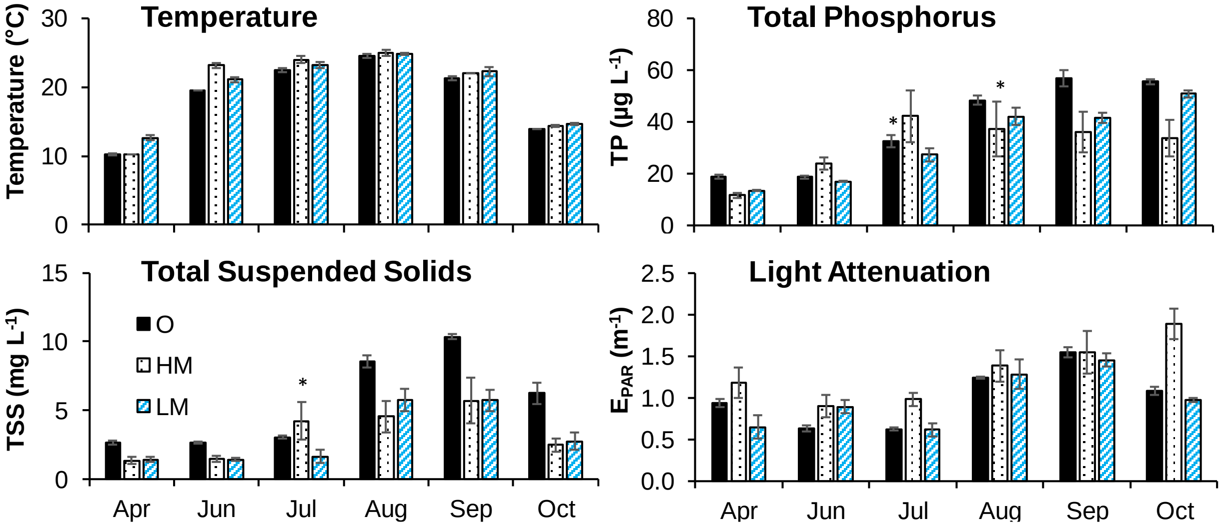

*Figure 4. Mean monthly trends in physical and chemical parameters at the offshore (O), high macrophyte (HM) and low macrophyte (LM) stations in the 2001 inshore-offshore study. Shown are temperature (°C), total phosphorus (µg L^{-1}), total suspended solids (mg L^{-1}), and light attenuation rate (m^{-1}). Higher light attenuation values indicate more turbid water. * indicates an outlier was removed.*

PHYTOPLANKTON AND MICROBIAL LOOP

Overview

Phytoplankton biomass and taxonomic composition for 2017 and 2018 is summarized in Fig. 5. Total phytoplankton biomass ranged from 357 mg m^{-3} to 9 742 mg m^{-3} during the 2017 sampling season. Diatoms and cyanobacteria typically accounted for the largest portion of the phytoplankton biomass with Diatomeae on average contributing 15.4 – 63.2% of the total biomass and Cyanophyta accounting for 11.6 – 59.8%. It should not be surprising that the targets for nuisance algae in BUI 13 are built around these groups (filamentous diatoms, filamentous cyanobacteria and colonial cyanobacteria) and these results show that nuisance algae persist throughout the upper and middle bays. Other major taxonomic groups of phytoplankton included Chlorophyta (2.0 – 11.8%), Chrysophyceae (0.6 – 5.5%), Cryptophyceae (5.8 – 21.6%) and Dinophyceae (1.7 – 13.0%). Total phytoplankton during 2018 ranged from 316 mg m^{-3} to 11 152 mg m^{-3} during the 2018 survey of the upper and middle bays. Diatoms on average accounted for 25.0 – 57.3% of the total biomass and cyanobacteria accounted for 11.3 – 32.1% of the total biomass. As observed previously, the nuisance algal forms (filamentous and colonial) dominate the assemblage. The other major phytoplankton observed during 2018 included Chlorophyta (2.7 – 14.0%), Chrysophyceae (1.0 – 8.1%) Cryptophyceae (7.9 – 24.3%) and Dinophyceae (7.9 – 24.3%).

An algal bloom has been defined as when phytoplankton biomass exceeds 3000 mg m^{-3} (Munawar et al. 2018) and in that regard, blooms were observed at all sites except HBns at some point during 2017 (Table 4a). However, as sampling frequency was 1/month, it's entirely possible that blooms occurred at HBns between visits. Blooms of the filamentous diatom *Aulacoseira* were observed at B and Bns on August 9 and September 6. Blooms containing a combination of filamentous and colonial blue greens (*Lyngbya birgei* and *Microcystis aeruginosa,* respectively) were also observed at HB and Nns on September 6. On October 2 at N, a bloom containing a mixture of Dinophyceae (*Peridinium cunningtonii*), diatoms (*Actinocyclus normanii*) and cryptophytes (*Cryptomonas erosa*) was observed. While blooms of diatoms and cyanobacteria and often mixtures of the two are common in the bay (Munawar et al. 2018; Nicholls and Carney 2011), this latter bloom was unique in that it had no dominant taxon and contained both flagellated (Dinophyceae, Cryptophyceae) and centric (diatom) forms. Algal blooms were also observed on May 29, July 26, August 23 and September 19 of 2018 (Table 4b). On May 29, filamentous diatom blooms were observed at HBns (*Aulacoseira* spp.) and Nns (*Fragilaria capucina*). Blooms were observed at all sites on July 26 including a cyanobacteria bloom at B (*Microcystis aeruginosa*, *Dolichospermum crassa*), and diatom blooms at Bns (*Aulacoseira granulata*, *A. ambigua*), N and Nns (*Aulacoseira* sp., *Fragilaria crotonensis*), as well as HB and HBns (*Aulacoseira* sp., *F. crotonensis)*. On the following cruise (Aug 23), blooms were observed at B, Bns and N. The bloom at station B included Diatomeae (*Aulacoseira granulata*), Cryptopyceae (*Cryptomonas erosa*), and Chrysophyceae (*Mallomonas* sp). Likewise, Bns contained a mixture of diatoms (*A. granulata*) and cyanobacteria (*Dolichospermum planctonica*; *D. macrospora*). Phytoplankton at N on Aug 23 was predominantly filamentous and colonial cyanobacteria (*Oscillatoria* sp., *Microcystis* sp.). The final observations of algal blooms occurred on September 19 at B and N. The late summer bloom at B contained a mixture of Chlorophyta (*Chlamydomonas* sp), Diatomeae (*A. granulata*), Cyanobacteria (*Pseudanabaena limnetica*) and Chrysophyceae (*Chrysochromulina parva*); at N, the bloom was dominated by Dinophyceae (*Gymnodinium* sp).

The microbial food web includes autotrophic picoplankton (APP), bacteria, heterotrophic nanoflagellates (HNF) and ciliates. Over the course of sampling during 2017, APP biomass ranged from 46.4 – 1890 mg m^{-3}, bacteria from 554 – 1969 mg m^{-3}, HNF from 216 – 1403 mg m^{-3}, and ciliates from 3.0 – 533 mg m^{-3} (Fig. 6). Overall, a substantial amount of the planktonic biomass was contained within the micro-heterotrophs (bacteria, HNF, ciliates). In 2018, APP biomass ranged from 3.1 – 1902 mg m^{3}, bacteria from 231 – 3447 mg m^{-3}, HNF from 108 – 4963 mg m^{-3} and ciliates from 17.3 – 762 mg m^{-3} (Fig. 6). Note that ciliates were not assessed at N or Nns during 2018. As with the other chemical and biological parameters measured, the range of values observed in 2018 appears to be more extreme than those observed in 2017. During the growing season of 2017, primary productivity ranged from: 0.7 – 44.3 mg C m^{-3} h^{-1} for larger net plankton (> 20 µm), 2.5 – 31.0 mg C m^{-3} h^{-1} for nanoplankton (2-20 µm) and 0.6 – 10.7 mg C m^{-3} h^{-1} for smaller picoplankton (Fig. 7). The values were more extreme in 2018, when net plankton (>20 µm) productivity ranged from 0.4 – 176.5 mg C m^{-3} h^{-1}, nanoplankton (2-20 µm) from 1.2 – 63.3 mg C m^{-3} h^{-1} and picoplankton (<2 µm) from 1.0 – 8.9 mg C m^{-3} h^{-1} (Fig. 7). In 2017, bacterial productivity ranged from 0.4 – 2.4 mg C m^{--3} h^{-1} throughout the upper and middle bay and in 2018 bacterial productivity ranged from 0.06 – 4.1 mg C m^{-3} h^{-1} (Fig. 8) showing more variable conditions.

Table 4a. Dominant phytoplankton species observed contributing to algal blooms in the Bay of Quinte during 2017. Algal blooms (phytoplankton biomass > 3 g m^{-3}) were sorted first by taxa (contributing >50% to total biomass) and then by species within those taxa.

Date	**Station**	**Total Biomass (g m^{-3})**	**Taxa**	**Morphology**	**Species**
Aug 9	*B*	*4.1*	*Diatomeae*	*Filamentous*	*Aulacoseira ambigua*
Aug 9	Bns	4.1	Diatomeae	Filamentous	*A. granulata*
Sep 6	B	4.2	Diatomeae	Filamentous	*A. ambigua*
Sep 6	Bns	3.6	Diatomeae Cyanophyta	Filamentous	*A. ambigua* *Dolichospermum circinalis*
Sep 6	HB	5.0	Cyanophyta	Filamentous	*Lyngbya birgei*
Sep 6	Nns	9.7	Cyanophyta	Filamentous	*Lyngbya birgei*
Oct 2	N	3.2	Dinophyceae Diatomeae Cryptophyceae	Flagellate (Lg) Centric Flagellate (Sm)	*Peridinium cunningtonii* *Actinocyclus normanii* *Cryptomonas erosa*

Table 4b. Dominant phytoplankton species observed contributing to algal blooms in the Bay of Quinte during 2018. Algal blooms (phytoplankton biomass > 3 g m^{-3}) were sorted first by taxa (contributing >50% to total biomass) and then by species within those taxa.

Date	**Stn**	**Total Biomass (g m^{-3})**	**Taxa**	**Morphology**	**Species**
May 29	HBns	4.1	Diatomeae	Filamentous	*Aulacoseira* sp.
May 29	Nns	3.0	Diatomeae	Pennate	*Fragilaria capucina*
Jul 26	B	5.7	Cyanophyta	Colonial Filamentous	*Microcystis aeruginosa* *Dolichospermum crassa*
Jul 26	Bns	4.5	Diatomeae	Filamentous Filamentous	*Aulacoseira granulata* *A. ambigua*
Jul 26	HB	4.0	Diatomeae	Pennate Filamentous	*Fragilaria crotonensis* *Aulacoseira* sp.
Jul 26	HBns	6.3	Diatomeae	Pennate Filamentous	*F. crotonensis* *Aulacoseira* sp.
Jul 26	N	11.1	Diatomeae	Filamentous Pennate	*Aulacoseira* sp. *F. crotonensis*
Jul 26	Nns	8.1	Diatomeae	Filamentous Pennate	*Aulacoseira* sp. *F. crotonensis*
Aug 23	B	3.7	Cryptophyceae Chrysophyceae Diatomeae	Flagellate Filamentous Filamentous	*Cryptomonas erosa* *Mallomonas* sp. *A. granulata*
Aug 23	Bns	3.8	Diatomeae, Cyanophyta	Filamentous Filamentous	*A. granulata* *Dolichospermum planctonica*
Aug 23	N	3.8	Cyanophyta	Filamentous	*Oscillatoria* sp.
Sep 19	B	4.5	Diatomeae Chlorophyta Cyanophyta	Filamentous Flagellate Filamentous	*A. granulata* *Chlamydomonas* sp. *Pseudanabaena limnetica*
Sep 19	N	4.2	Dinophyceae	Flagellate	*Gymnodinium* sp.

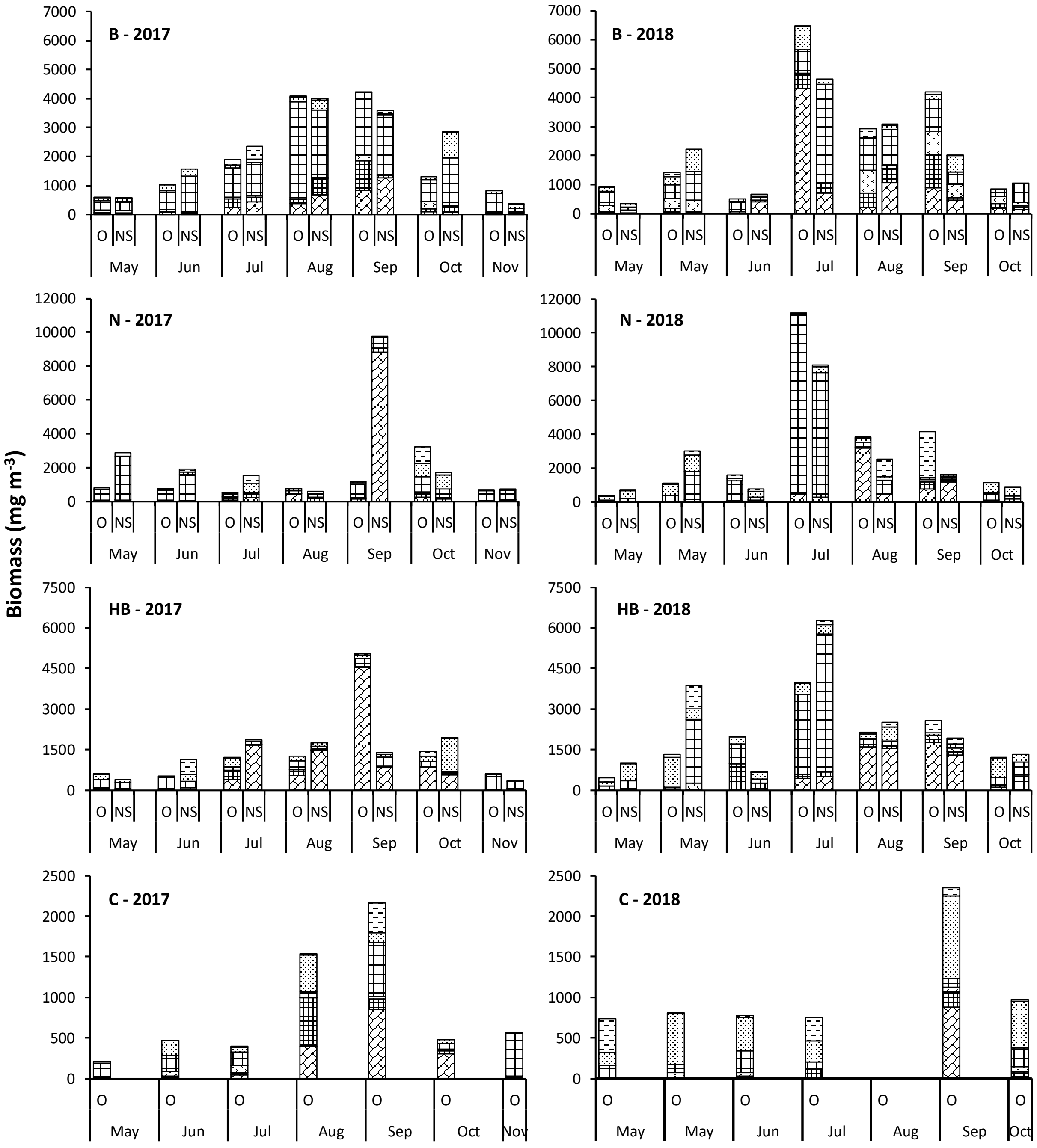

Figure 5. Monthly biomass (mg m^{-3}) of dominant phytoplankton groups during 2017 and 2018 at Belleville (B), Napanee (N), Hay Bay (HB) and Conway (C). Both offshore (O) and nearshore (NS) sites are shown, except at C where the nearshore was not sampled.

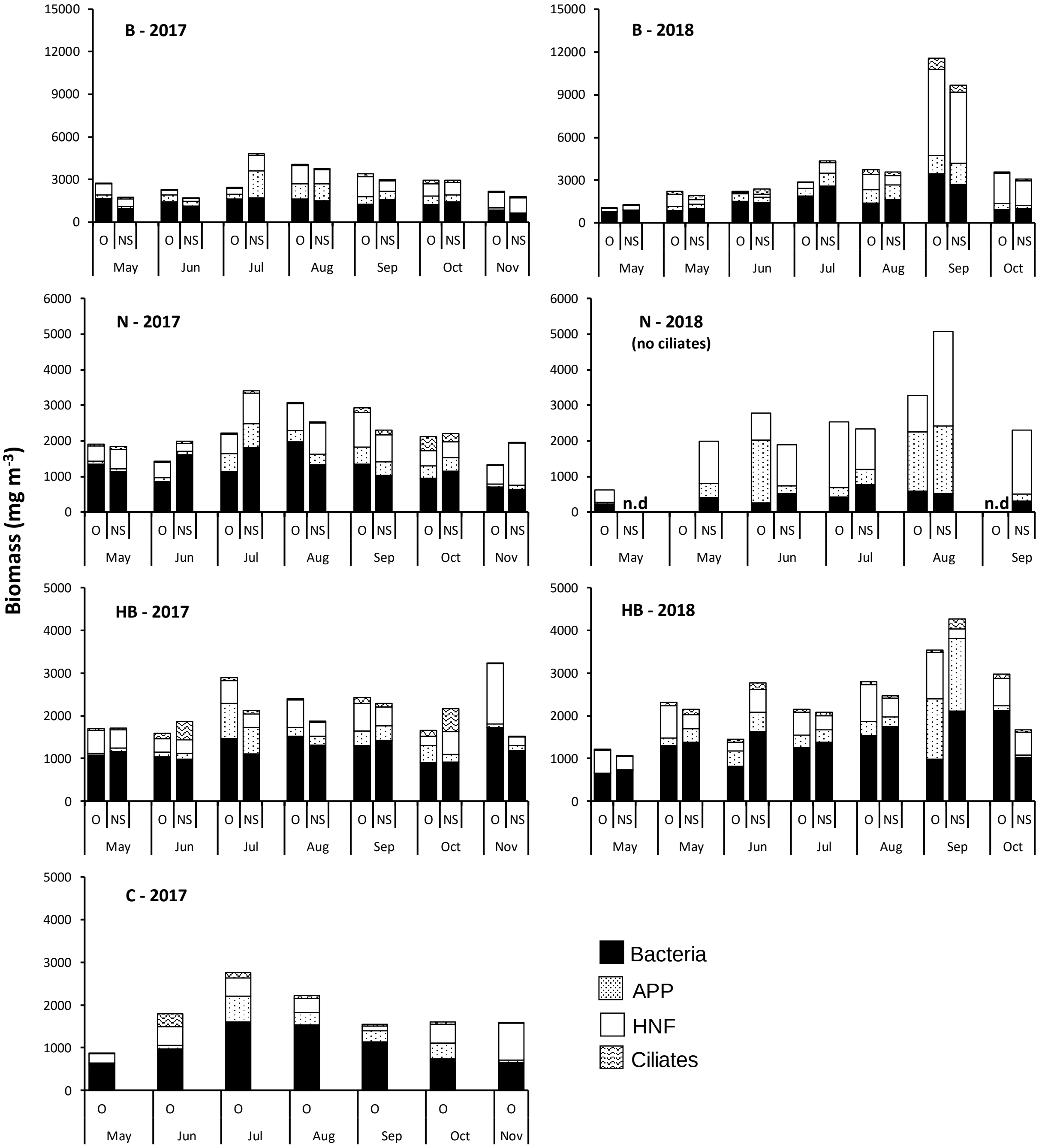

Figure 6. Microbial loop biomass (mg m^{-3}) including bacteria, autotrophic picoplankton (APP), heterotrophic nanoflagellates (HNF) and ciliates observed during 2017 and 2018 at offshore (O) and nearshore (NS) sites. Note that ciliate data was not available for station N (Napanee) during 2018. Missing data points are indicated as "n.d." (no data) where applicable.

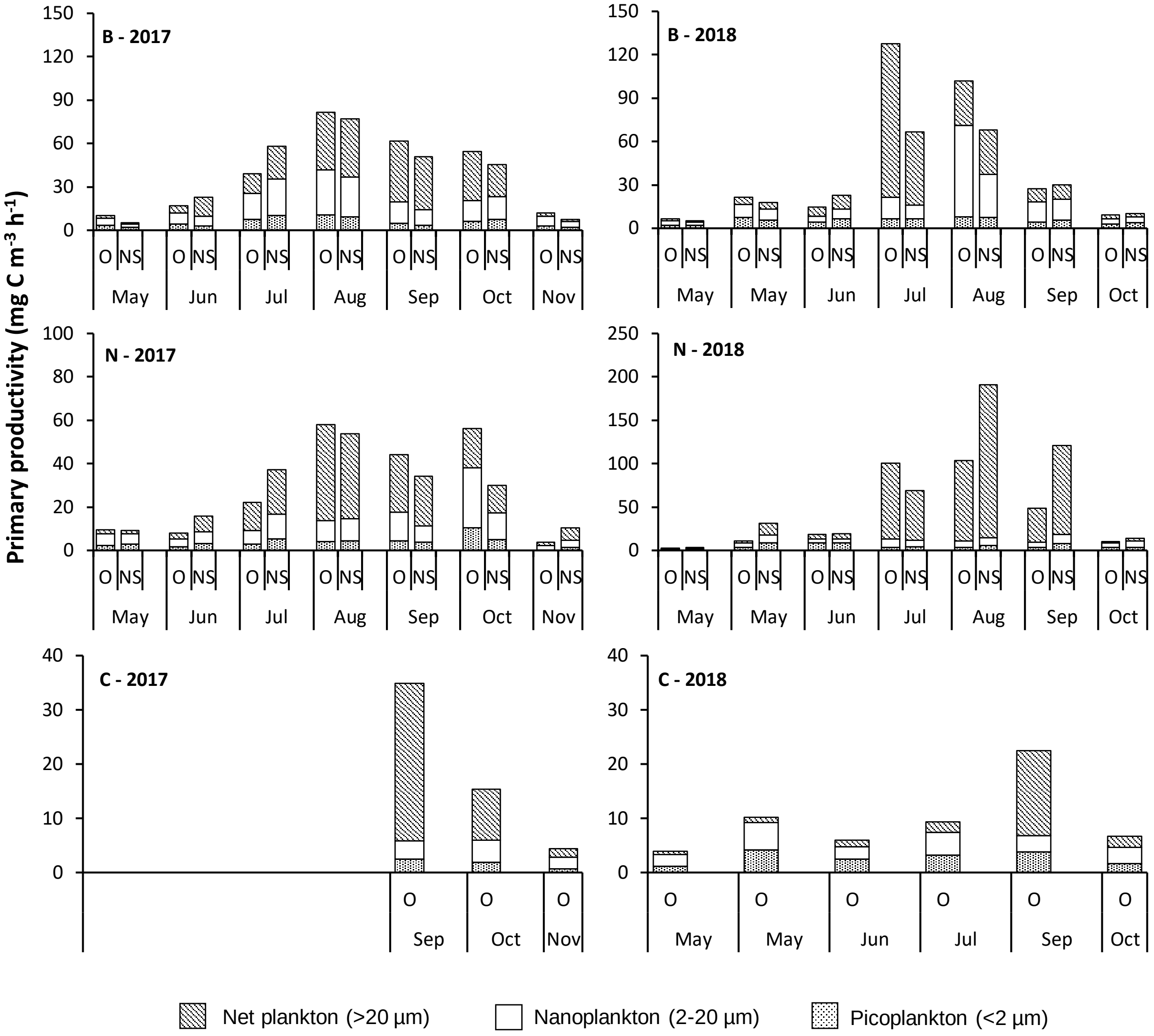

Figure 7. Size fractionated primary productivity (mg C m^{-3} h^{-1}) in the Bay of Quinte for net plankton (>20 µm), nanoplankton (2-20 µm) and picoplankton (<2 µm) observed during 2017 and 2018 at offshore (O) and nearshore (NS) sites.

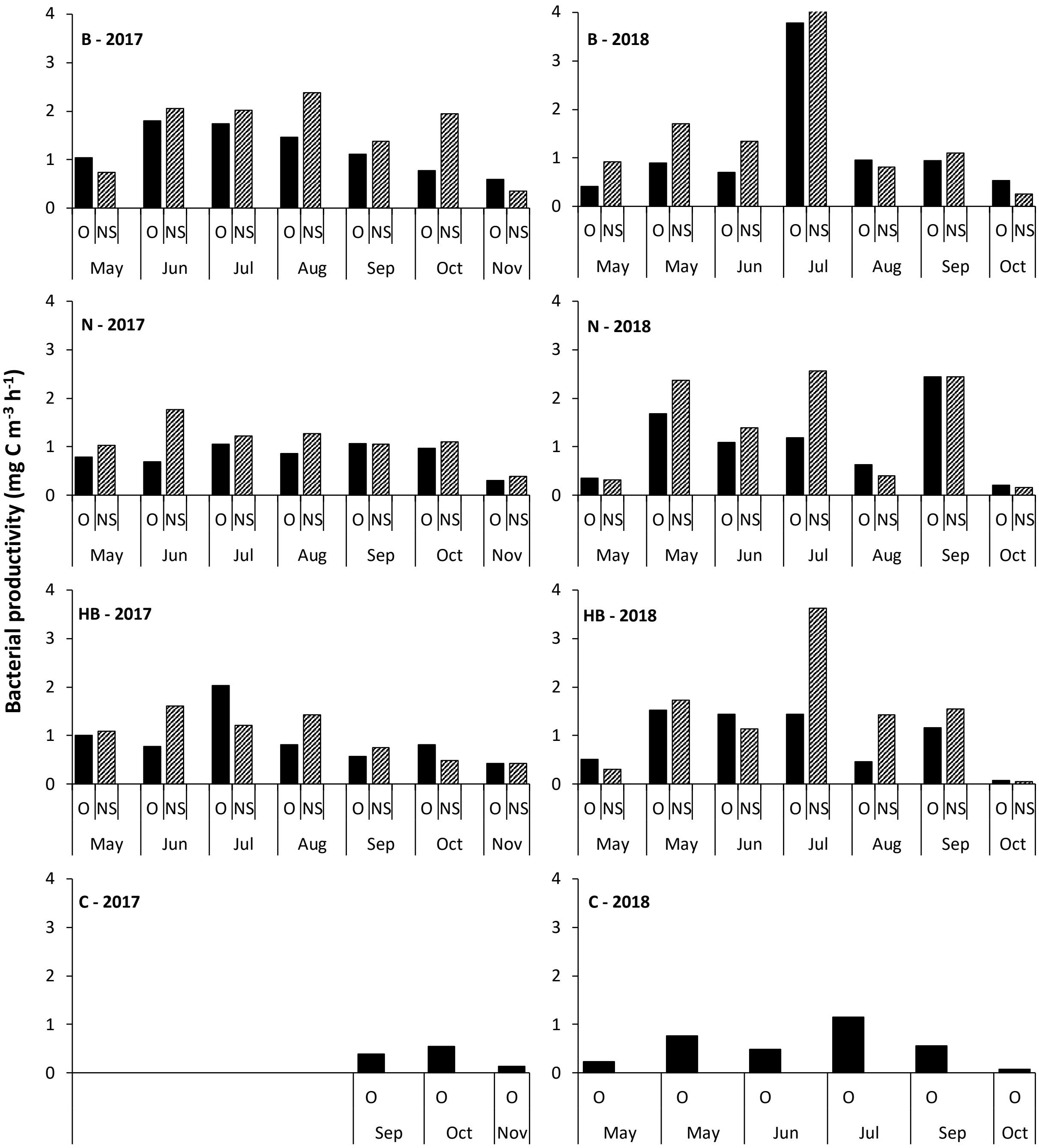

Figure 8. Bacterial productivity (mg C m^{-3} h^{-1}) in the Bay of Quinte observed during 2017 and 2018 at offshore (O) and nearshore (NS) sites.

2001 Phytoplankton and Microbial Loop

In 2001, Jul-Oct total phytoplankton biomass was significantly higher in the offshore (7.33 ± 1.71 g m^{-3}) relative to the LM area (2.54 ± 0.84 g m^{-3}; Table 3), which matches the chlorophyll and TP results. Biomass was intermediate in the HM area (5.94 ± 2.39 g m^{-3}), and not significantly different from the other two areas. The July – October offshore value was considerably greater than the 2017 – 2018 average of 2.77 ± 0.45 g m^{-3}, although the 2001 LM value was similar to the recent nearshore mean of 2.72 ± 0.44 g m^{-3}. Most 2001 samples were dominated by diatoms, with this group comprising 75% of biomass over the July to October period (Fig. 9a). Blue-green algae (Cyanophyta) were most common in August, when they comprised 24% of total biomass in the offshore, 33% in the LM area, and 54% in the HM area. Green algae (Chlorophyta) were also important in the HM in July (23%), and this area had the greatest biomass of this group overall. However, there were no differences among areas for Cyanophyta and components of the microbial loop, including bacteria, APP, HNF or ciliates. There were also less dramatic seasonal trends in the microbial loop (Fig. 9b). Bacteria generally comprised the highest proportion of biomass, followed by HNF and APP. Across all stations, July – October bacteria biomass averaged 0.58 ± 0.02 g m^{-3} in 2001, compared to 1.33 ± 0.08 g m^{-3} in 2017 – 2018.

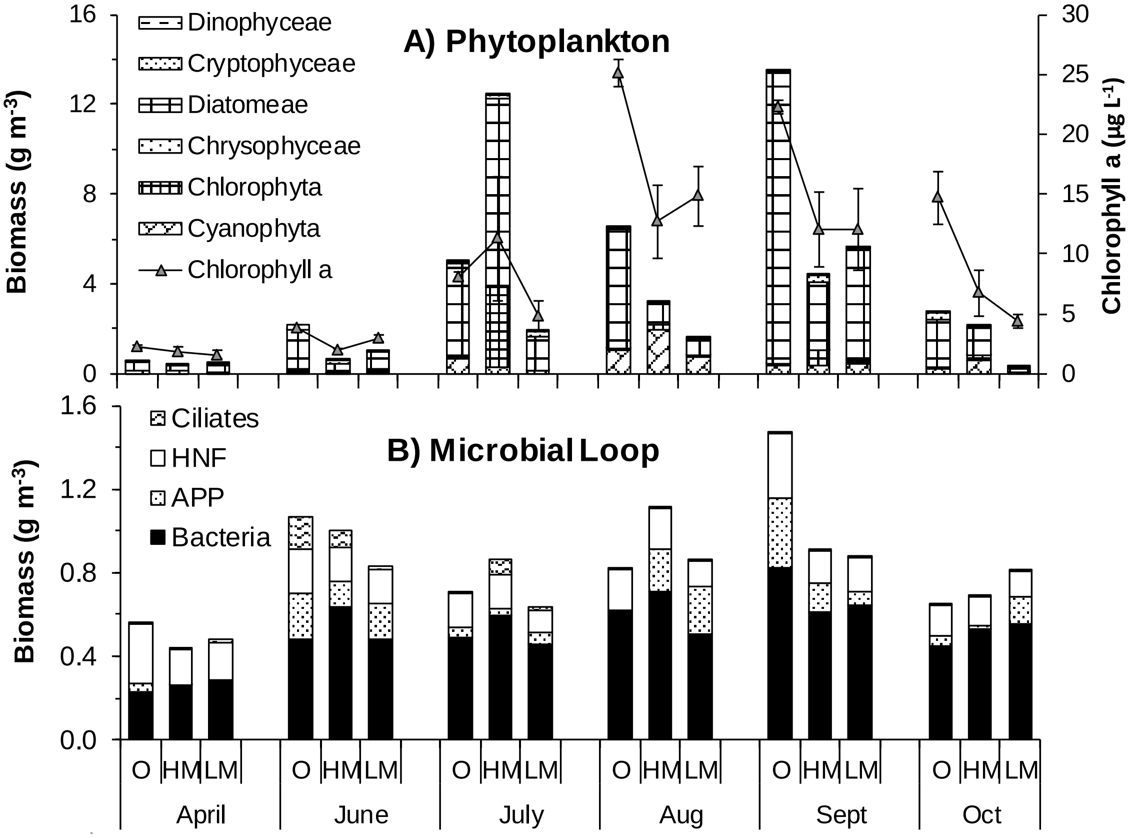

Figure 9. Mean monthly biomass of A) phytoplankton groups and chlorophyll a and B) microbial loop at the offshore (O), high macrophyte (HM) and low macrophyte (LM) stations in the 2001 inshore-offshore study.

Nearshore – offshore comparisons

The results so far suggest considerable spatial and temporal variability in the structure and dynamics of the microbial-planktonic food web, much of which is expected. One of the main objectives of this study was to test whether nearshore macrophyte dominated sites were having an impact on the composition of microbial-planktonic food web. With respect to the phytoplankton community, significant differences both overall and among stations were observed for Chlorophyta ($F_{30,53}$=3.84, p<0.0001) and Chrysophyceae ($F_{30,53}$=8.51, p<0.0001) along with significant seasonal differences; Chrysophyceae also showed a significant inter-annual effect (see Table 5a for summary stats). In addition to standard taxonomic groupings, we also tested phytoplankton groupings based on morphology (i.e. total filamentous phytoplankton, filamentous diatoms, filamentous cyanobacteria and colonial cyanobacteria). Of these, total filamentous phytoplankton ($F_{30,53}$=2.03, p=0.02) and filamentous diatoms ($F_{30,53}$=1.94, p=0.03) showed significant differences overall as well as for station and season. The microbial loop and ciliate communities also showed some significant differences among stations. Both APP ($F_{18,37}$=9.62, p<0.0001) and HNF ($F_{18,37}$=2.09, p=0.0478) showed significant differences overall as well as for station and season (Table 4a). With respect to ciliates, only Tintinnina ($F_{18,37}$=3.29, p=0.004) showed a significant difference overall along with a station effect; Tintinnina also showed a seasonal and inter annual effect. Both nanoplankton productivity ($F_{30,53}$=3.66, p<0.0001) and picoplankton productivity ($F_{29,53}$=3.31, p=0.0004) showed significant differences overall as well as among stations, seasons and years.

No significant differences in phytoplankton or microbial plankton were observed during comparisons of nearshore and offshore Habitat (Table 5b). The 3-way ANOVA (Habitat, Season, Year) for Chlorophyta ($F_{21,62}$=3.62, p<0.0001), Chrysophyceae ($F_{21,62}$=2.67, p=0.0015), total filamentous phytoplankton ($F_{21,62}$=3.37, p<0.0001), filamentous diatoms ($F_{21,62}$=2.17, p=0.01), and APP ($F_{21,34}$=7.71, p<0.0001) showed significant results overall, but Season was the only significant factor, and no Habitat (nearshore vs offshore) differences were found. Likewise, nanoplankton productivity ($F_{21,62}$=4.82, p<0.0001) and picoplankton productivity ($F_{21,61}$=4.66, p<0.0001) were significant overall and showed significant effects for Season and Year but not for Habitat. HNF and the ciliate Tintinnina did not show any significant differences. Importantly, no significant differences were observed with respect to nearshore vs offshore habitats.

Table 5a. Results of 3-way ANOVAs using “Station”, “Season” and “Year” as factors comparing the microbial-planktonic food web. Only results that are significant ($p<0.05$) overall are reported. For individual factors, P values > 0.05 are listed as not significant, “n.s.” All values were log transformed prior to analysis.

Parameter	**Overall**		**Effect: Station**		**Effect: Season**		**Effect: Year**	
Phytoplankton	***F(30,53)***	***P***	***F(5,78)***	***P***	***F(6,77)***	***P***	***F(1,82)***	***P***
Cyanophyta	7.847	<0.0001	0.993	n.s.	51.598	<0.0001	1.605	n.s.
Chlorophyta	3.840	<0.0001	4.731	0.0026	16.583	<0.0001	4.893	0.0347
Chrysophyceae	8.516	<0.0001	32.37	<0.0001	21.737	<0.0001	4.636	0.0395
Dinophyceae	1.865	0.0343	0.435	n.s.	6.059	0.0003	6.329	0.0175
Total Phytoplankon	3.054	0.0008	0.495	n.s.	15.624	<0.0001	8.835	0.0058
Total Filamentous	2.034	0.0193	2.783	0.0351	7.199	<0.0001	0.360	n.s.
Filamentous Diatoms	1.94	0.0261	4.499	0.0035	4.719	0.0017	0.052	n.s.
Fil Cyanophyta	3.439	0.0002	1.147	n.s.	20.615	0.0001	7.095	0.0123
Colonial Cyanophyta	7.578	<0.0001	1.763	n.s.	43.327	<0.0001	12.514	0.0013
Microbial Loop	***F(18,37)***	***P***	***F(3,52)***	***P***	***F(6,49)***	***P***	***F(1,54)***	***P***
Bacteria	2.487	0.0208	0.734	n.s.	4.823	0.0042	1.641	n.s.
APP	9.692	<0.0001	11.363	0.0002	34.339	<0.0001	0.636	n.s.
HNF	2.094	0.0478	4.681	0.0138	3.697	0.0143	0.010	n.s.
Ciliates (total)	2.199	0.0381	2.531	n.s.	5.998	0.0014	1.158	n.s.
Halteria	10.452	<0.0001	0.793	n.s.	49.639	<0.0001	12.208	0.0026
Haptoria	2.410	0.0244	0.380	n.s.	10.013	<0.0001	1.627	n.s.
Tintinnina	3.292	0.0044	11.791	0.0002	5.365	0.0025	6.161	0.0231
Vorticella	2.86	0.0098	1.133	n.s.	9.031	<0.0001	1.338	n.s.
Primary Productivity	***F(30,53)***	***P***	***F(5,78)***	***P***	***F(6,77)***	***P***	***F(1,82)***	***P***
> 20 µm	12.863	<0.0001	1.100	n.s.	98.575	<0.0001	0.048	n.s.
2-20 µm	3.662	<0.0001	5.656	0.0009	16.095	<0.0001	5.959	0.0208
<2 µm	3.314	0.0004	5.228	0.0015	13.367	<0.0001	5.895	0.0216
	F(29,53)		**F(5,77)**		**F(6,76)**		**F(1,81)**	
Bacteria	1.977	0.0234	0.976	n.s.	8.293	<0.0001	0.054	n.s.

Table 5b. Results of 3-way ANOVAs using "Habitat (nearshore vs. offshore)", "Season" and "Year" as factors comparing the microbial-planktonic food web. Only results that are significant (p<0.05) overall are reported. For individual factors, P values > 0.05 are listed as not significant, "n.s.". All values were log transformed prior to analysis.

Parameter	**Overall**		**Effect: Habitat**		**Effect: Season**		**Effect: Year**	
Phytoplankton	***F(21,62)***	***P***	***F(1,82)***	***P***	***F(6,77)***	***P***	***F(1,82)***	***P***
Chlorophyta	3.621	<0.0001	0.249	n.s.	9.161	<0.0001	2.131	n.s.
Chrysophyceae	2.667	0.0015	0.790	n.s.	5.427	<0.0001	0.988	n.s.
Total Filamentous	3.367	<0.0001	0.153	n.s.	7.133	<.0001	0.381	n.s.
Filamentous Diatoms	2.173	0.0096	0.134	n.s.	3.833	0.0026	0.040	n.s.
Microbial Loop	***F(21,34)***	***P***	***F(1,54)***	***P***	***F(6,49)***	***P***	***F(1,54)***	***P***
APP	7.717	<0.0001	0.071	n.s.	17.582	<0.0001	0.667	n.s.
HNF	1.598	n.s.	1.781	n.s.	2.643	0.0326	0.046	n.s.
Tintinnina (Ciliate)	1.417	n.s.	0.906	n.s.	2.408	0.0477	2.250	n.s.
Primary Productivity	***F(21,62)***	***P***	***F(1,82)***	***P***	***F(6,77)***	***P***	***F(1,82)***	***P***
2- 20 µm	4.820	<0.0001	0.005	n.s.	12.000	0.0001	4.621	0.035
<2 µm	4.662 F(21,61)	<0.0001	2.534 F(1,81)	n.s.	10.637 F(6,76)	0.0001	4.451 F(1,81)	0.039

ORGANIC CARBON RESOURCES

The organic carbon pool represents the amount of energy available in the system to support higher trophic levels and includes both phytoplankton derived (autotrophic) and bacterial derived (heterotrophic) sources. In general, a higher proportion of phytoplankton derived carbon is viewed as being critical for sustaining higher trophic levels (e.g. Brett et al. 2009), but there is also evidence that when autotrophic carbon is in short supply, then heterotrophic sources can be much more important (e.g. McCauley et al. 2018; Pace et al. 2004). In previous work on the Bay of Quinte, we observed that as much as 50 – 60% of the organic carbon was bound up in heterotrophs (overwhelmingly HNF) in some years and dramatically switched to autotrophic sources (up to 75%) in successive years (Munawar et al. 2011). It is also important to point out that much of the observed switch in food web structure could be attributed to algal blooms and much of that energy may not be available to higher trophic levels (ibid). Furthermore, excess autotrophic production from eutrophication can mask significant heterotrophic activity in the food web (Dodds and Cole 2007; Munawar and Fitzpatrick 2017).

In constructing carbon budgets, we separated the phytoplankton into the functional categories of ‘filamentous diatoms’, ‘filamentous cyanobacteria’, ‘colonial cyanobacteria’ and ‘edible + other phyto’ in order to account for the potential effects of excess phytoplankton production (algal blooms). Mean values (± 1 S.E.) for the sampling seasons of 2017 and 2018 for nearshore and offshore habitats are shown in Fig. 10. The size of the organic carbon pool ranged from ≈700 – 1000 mg C m^{-3}. Approximately 60 – 70% of the organic carbon pool was composed of autotrophs, compared to 15 – 20% heterotrophs and 15 – 20% bacteria, and there are few observable differences among years and among habitats (Fig. 11). Of the autotrophic organisms most likely to be grazed by zooplankton, the combined categories of ‘APP’ and ‘Edible + other phyto’ accounted for 200 – 400 mg C m^{-3} (30 – 40%). Likewise, bacteria which may also be an important (though less preferred) food resource for zooplankton on average accounted for 134.6 – 167.5 mg C m^{-3} (15 – 20%) of the organic carbon pool. Overall, there is no evidence from the structure of the organic carbon pool that the microbial – planktonic food web is operating fundamentally differently in nearshore macrophyte dominated habitats than in offshore open-water habitats.

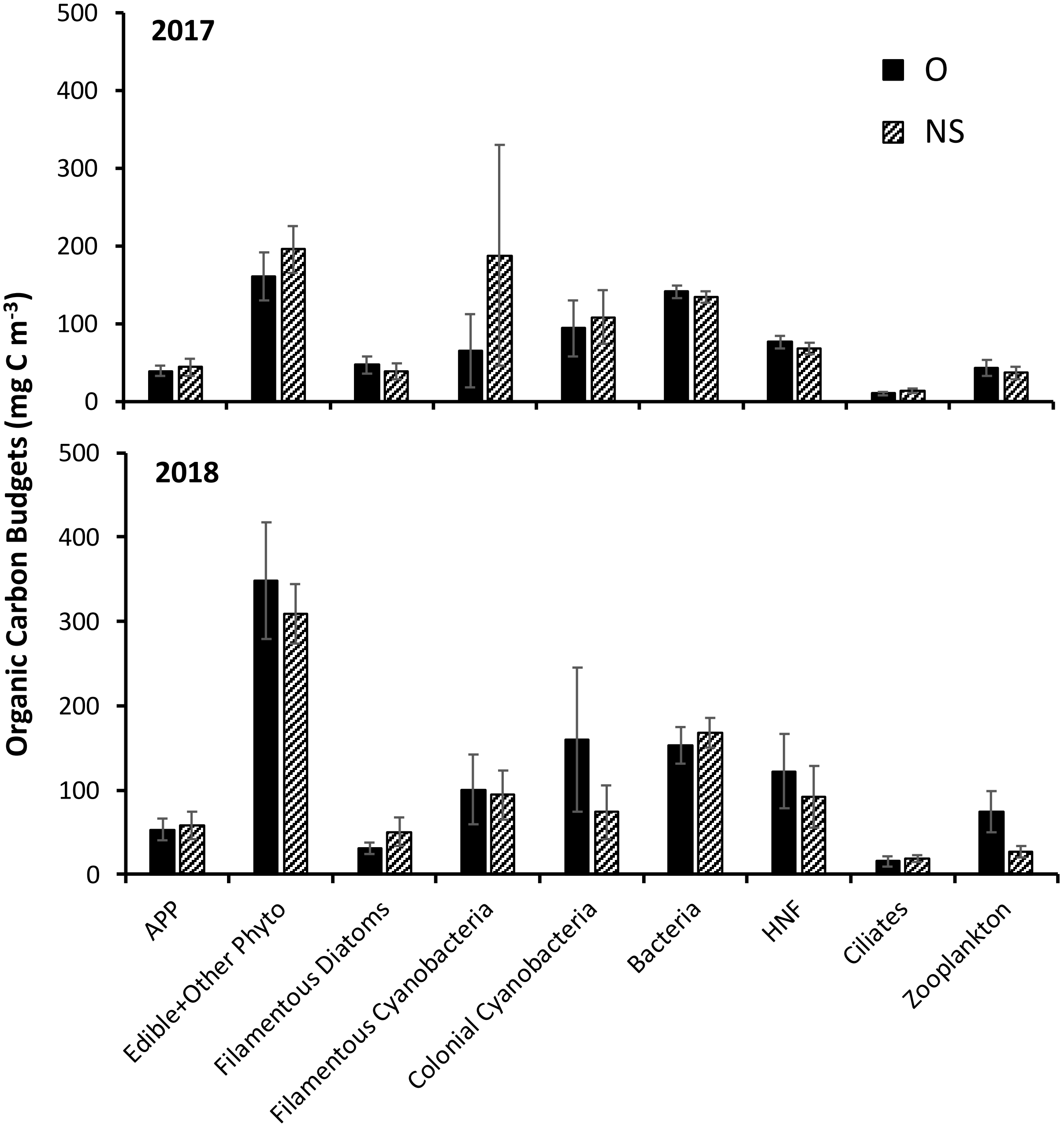

Figure 10. A comparison of May – Oct/Nov organic carbon budgets (mg C m^{-3}) for the microbial-planktonic food web observed during 2017 and 2018 at offshore (O) and nearshore (NS) habitats.

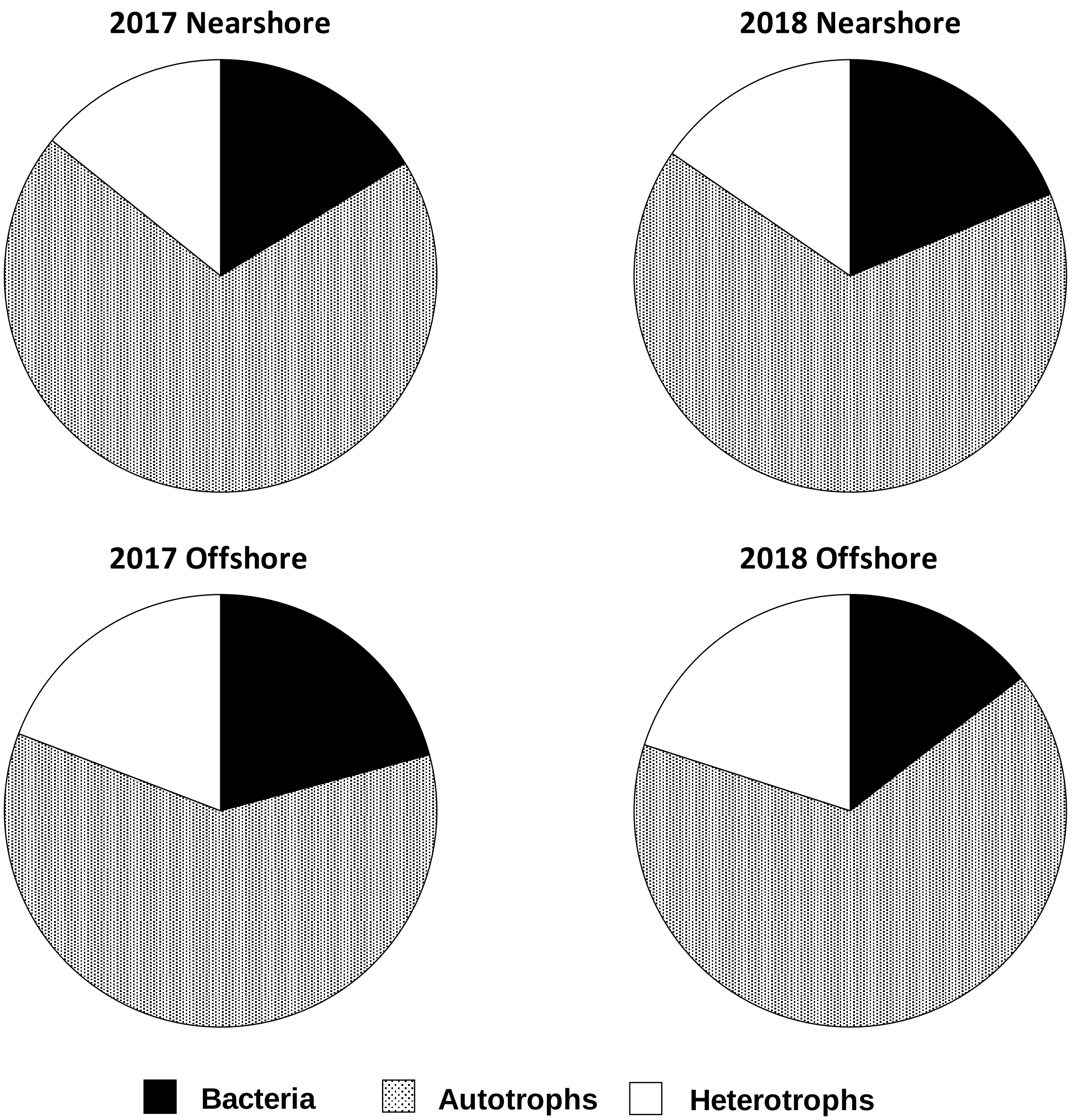

Figure 11. The relative composition (% organic carbon) of bacteria, autotrophs (phytoplankton, APP) and heterotrophs (HNF, ciliates, zooplankton) to the organic carbon budget of the Bay of Quinte during 2017 and 2018 at nearshore and offshore habitats.

ZOOPLANKTON

Biomass

Zooplankton at the nearshore and offshore sites within the Bay of Quinte showed typical seasonal trends, with low biomass in early May when few cladocerans such as bosminids and *Daphnia* were present, but these taxa were well established by early June (Fig. 12). Both biomass and taxa richness were typically highest during the warmer months and generally dropped off again by late October. When statistically comparing areas, the first and last sampling trips were omitted due to these seasonal patterns. Although the remaining (summer) sampling events were treated as replicates, there was considerable variation among samples, and no consistent nearshore to offshore differences were observed. When tested using ANOVA, total zooplankton summer biomass and biomass of dominant groups (herbivorous cladocerans, predatory cladocerans, cyclopoids, calanoids and veligers) were not significantly different between the nearshore and offshore habitats (Table 6). However, there were a few compositional differences, especially in the larger taxa. The biomass of *Daphnia*, particularly the larger species *D. galeata mendotae*, the large cyclopoid *Mesocyclops edax* and adult diaptomid calanoids were higher at the offshore sites relative to the nearshore. As a percent of crustacean biomass, *D. galeata mendotae* was also higher in the offshore. As a percent of total cyclopoid biomass, *Mesocyclops edax* and *Diacyclops thomasi* were higher in the offshore, and the eutrophic species *Acanthocyclops vernalis* was higher in the nearshore. Finally, mean length of herbivorous cladocerans was higher in the offshore than the nearshore, but lengths of both cyclopoids and calanoid (excluding nauplii larvae) were not different (Table 6).

Typical for the Bay of Quinte, cladocerans were the most important group in terms of biomass at all nearshore and offshore stations in 2017 and 2018, comprising between 64 and 84% of total zooplankton in the upper and middle bays, and 44% in the lower bay (Fig. 13). Veliger larvae and cyclopoids were also important, especially in the lower bay. As in previous years, biomass was dominated by herbivorous bosminids (*Bosmina* and/or *Eubosmina*) from late May to early October, as well as *Daphnia retrocurva* and *D. galeata mendotae* during the summer (Fig. 12). The eutrophic indicator species *Chydorus sphaericus* reached its highest biomass (83.9 mg m^{-3}) over the two year period at Nns in June 2017. It was also elevated at HB in Sept. 2017 and at both HB and HBns in August 2018, ranging between 20 and 40 mg m^{-3}. Of these, HB in Sept. 2017 was the only sample that corresponded with an algal bloom. Summer *Chydorus* biomass values were similar in the two depth zones, averaging 5.0 ± 1.2 mg m^{-3} at the offshore sites (excluding Conway) and 7.6 ± 3.0 mg m^{-3} at the nearshore sites (Table 6). These values are similar to the 2001 to 2014 mean of 6.4 ± 0.6 mg m^{-3} at these stations. Biomass values for the littoral cladoceran *Ceriodaphnia* sp. were also similar at the nearshore and offshore sites. Other littoral cladocerans such as *Alona* sp. and *Sida* sp. tended to be more common at the nearshore sites (3.5 ± 2.7 mg m^{-3}) than the offshore (0.2 ± 0.1 mg m^{-3}), but overall they comprised only a small part of the zooplankton community.

Tropocyclops extensus and *Mesocyclops edax* were the most important cyclopoid copepods in the offshore upper and middle reaches, comprising 47 ± 8% and 34 ± 7% of cyclopoid biomass, respectively, whereas *Diacyclops thomasi* dominated the lower bay (Table 6). The eutrophic species *Acanthocyclops vernalis* averaged 8 ± 3% of cyclopoid biomass at B, N and HB, and 23 ± 6% at the corresponding nearshore sites. Herbivorous cladocerans were unusually scarce at B in 2017, resulting in the third lowest May to October mean zooplankton biomass since 1975 (58 mg m^{-3}; Fig. 13). Values were similarly depressed at the adjacent nearshore station Bns in both 2017 and 2018. In the upper bay, there have been a few years in the last decade where zooplankton biomass have reached abnormally low levels given the amount of phosphorus in the system, and if this trend continues, may result in food shortages and lower survival for YOY and larval fishes. However, as sampling was conducted monthly in 2017 – 2018 compared to biweekly collection in the previous years, the recent estimates are likely less robust given the rapidly changing nature of planktonic communities. Zooplankton biomass recovered at B in 2018, slightly exceeding the 2001 – 2016 average of 134 mg m^{-3}. The same pattern was seen at HB, with average offshore biomass values of 124 mg m^{-3} in 2017 and 166 mg m^{-3} in 2018, which were in the same range as the 2000s average of 144 mg m^{-3}. In comparison, biomass at nearshore station HBns only averaged around 70 mg m^{-3}. Total biomass at N and the nearshore station Nns were less variable, ranging from 71 to 114 mg m^{-3}, but still below the 2001 – 2016 mean of 133 mg m^{-3}. The lowest biomass was found at C, where values averaged 36 mg m^{-3} in 2017 and 2018. This represented an increase compared to the two previous years and was close to the 2000s average of 43 mg m^{-3}.

Biomass and percent composition values for individual zooplankton taxa from 2017 – 2018 were usually similar to those from the earlier 2001 to 2014 period, based on June to September biomass averages in the offshore (B, N and HB) (Table 6). Biomass of *Daphnia* and cyclopoids, % *Mesocyclops* and herbivorous cladoceran mean size were generally a bit lower in the recent period.

Table 6: Comparison of Nearshore (Bns, Nns, HBns) vs. Offshore (B, N, HB) zooplankton parameters in 2017 and 2018. The first and last cruises have been excluded to minimize seasonal variation. F and P values were determined using ANOVA on log-transformed biomass data, with bolded taxa indicating significant differences (<0.05). June to September offshore means and SE from the 2001 to 2014 period at B, N and HB are included for comparison.

	2001-2014		**Offshore**		**Nearshore**			
Parameter	**Means**	**SE**	**Means**	**SE**	**Means**	**SE**	**F**	**P**
Biomass (mg m^{-3})								
Herbivorous Cladocera	138.11	8.89	114.10	22.23	71.79	12.44	2.69	n.s.
D. galeata mendotae	46.15	6.70	36.40	12.37	5.29	3.15	5.90	0.02
D. retrocurva	18.91	1.69	12.11	3.51	4.79	1.94	5.93	0.02
Bosmina	30.86	2.75	28.82	6.20	34.91	7.89	0.16	n.s.
Eubosmina	28.29	3.09	23.20	8.28	10.33	2.87	1.35	n.s.
Diaphanosoma	1.72	0.31	0.78	0.35	0.71	0.35	0.31	n.s.
Ceriodaphnia	4.92	0.57	6.48	2.22	4.26	0.77	1.03	n.s.
Chydorus	6.35	0.62	4.95	1.20	7.62	2.97	0.00	n.s.
Holopedium	0.29	0.05	1.18	0.98	0.37	0.17	0.26	n.s.
Other littoral Cladocera	0.10	0.02	0.16	0.13	3.52	2.68	1.25	n.s.
Predatory Cladocera	0.39	0.06	0.20	0.07	0.08	0.04	1.24	n.s.
Cyclopoids	21.93	1.23	14.26	3.47	11.11	2.43	1.90	n.s.
Cyclopoid nauplii	1.02	0.06	0.44	0.08	0.44	0.09	0.00	n.s.
Mesocyclops	14.93	1.20	8.63	3.44	1.75	1.19	8.76	0.00
A. vernalis	0.73	0.12	0.68	0.23	4.34	1.96	3.40	n.s.
Tropocyclops	5.04	0.44	3.88	0.83	3.84	0.86	0.00	n.s.
Diacyclops	1.02	0.16	0.63	0.33	0.34	0.17	0.33	n.s.
Calanoids	3.67	0.31	3.39	0.63	2.96	0.59	0.26	n.s.
Diaptomids	0.90	0.14	0.71	0.24	0.17	0.11	6.26	0.02
Eurytemora	0.24	0.04	0.19	0.07	0.19	0.08	0.02	n.s.
Veligers	11.19	1.08	10.92	3.38	5.13	1.59	1.10	n.s.
Total biomass	175.28	9.76	142.88	25.80	91.08	14.12	3.20	n.s.
Percent by BM								
D. galeata mendotae	15.4	1.2	14.7	4.1	5.5	2.2	4.33	0.04
Mesocyclops	49.0	2.4	34.3	7.0	11.6	3.8	8.91	0.00
A. vernalis	3.2	0.5	7.9	3.5	22.8	6.2	7.62	0.01
Diacyclops	7.4	1.0	11.0	5.2	3.6	2.3	4.30	0.04
Herb Clad Length (µm)	429	7.1	381	17.8	333	10.8	4.30	0.04
% Daphnia >750 µm	0.54	0.01	0.43	0.04	0.33	0.04	2.69	n.s.

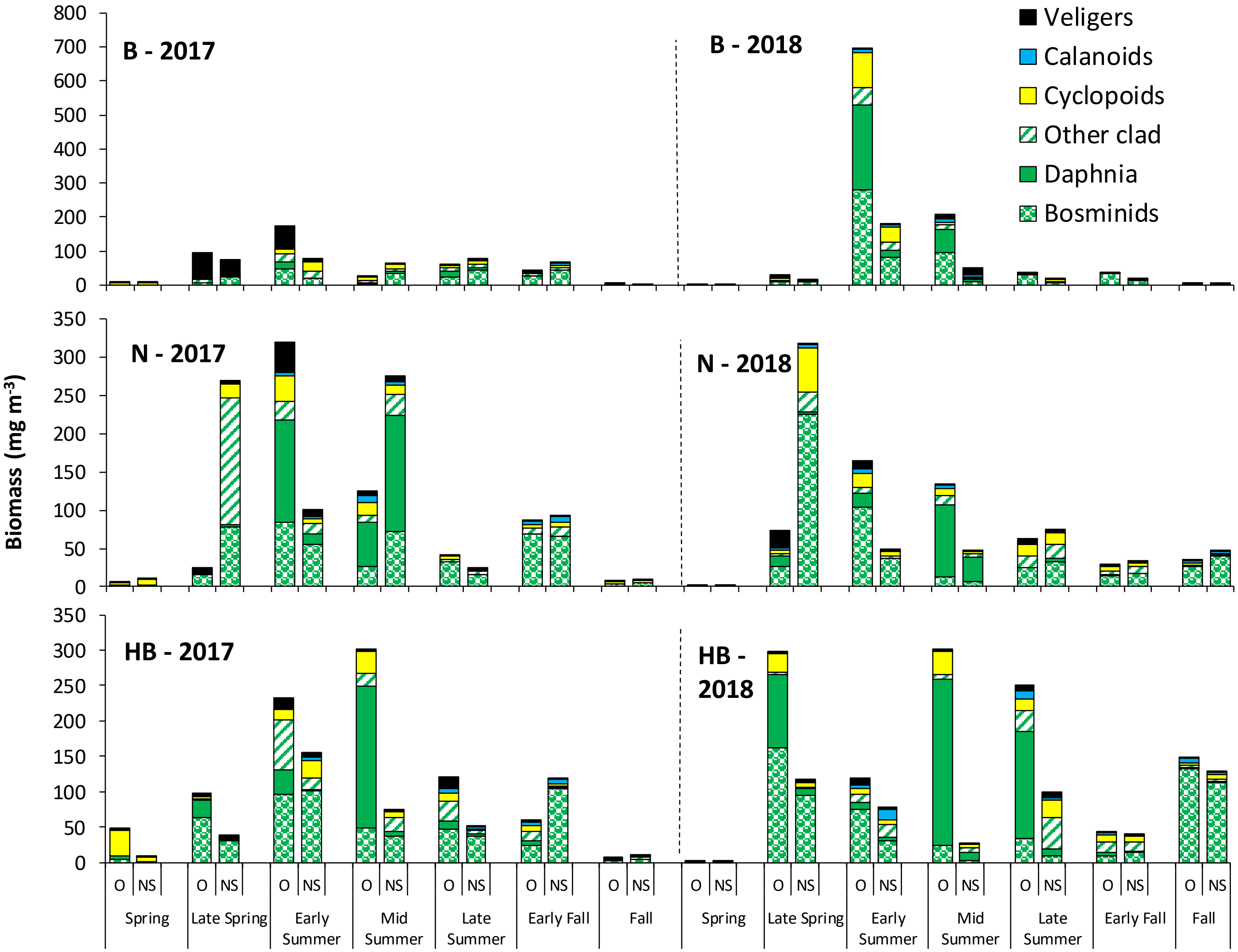

Figure 12. Seasonal patterns in biomass (mg m^{-3}) of dominant zooplankton groups at Belleville (B), Napanee (N) and Hay Bay (HB) in 2017 and 2018. O represents the long-term offshore stations, and NS represents the nearshore stations. Note the different scale for B.

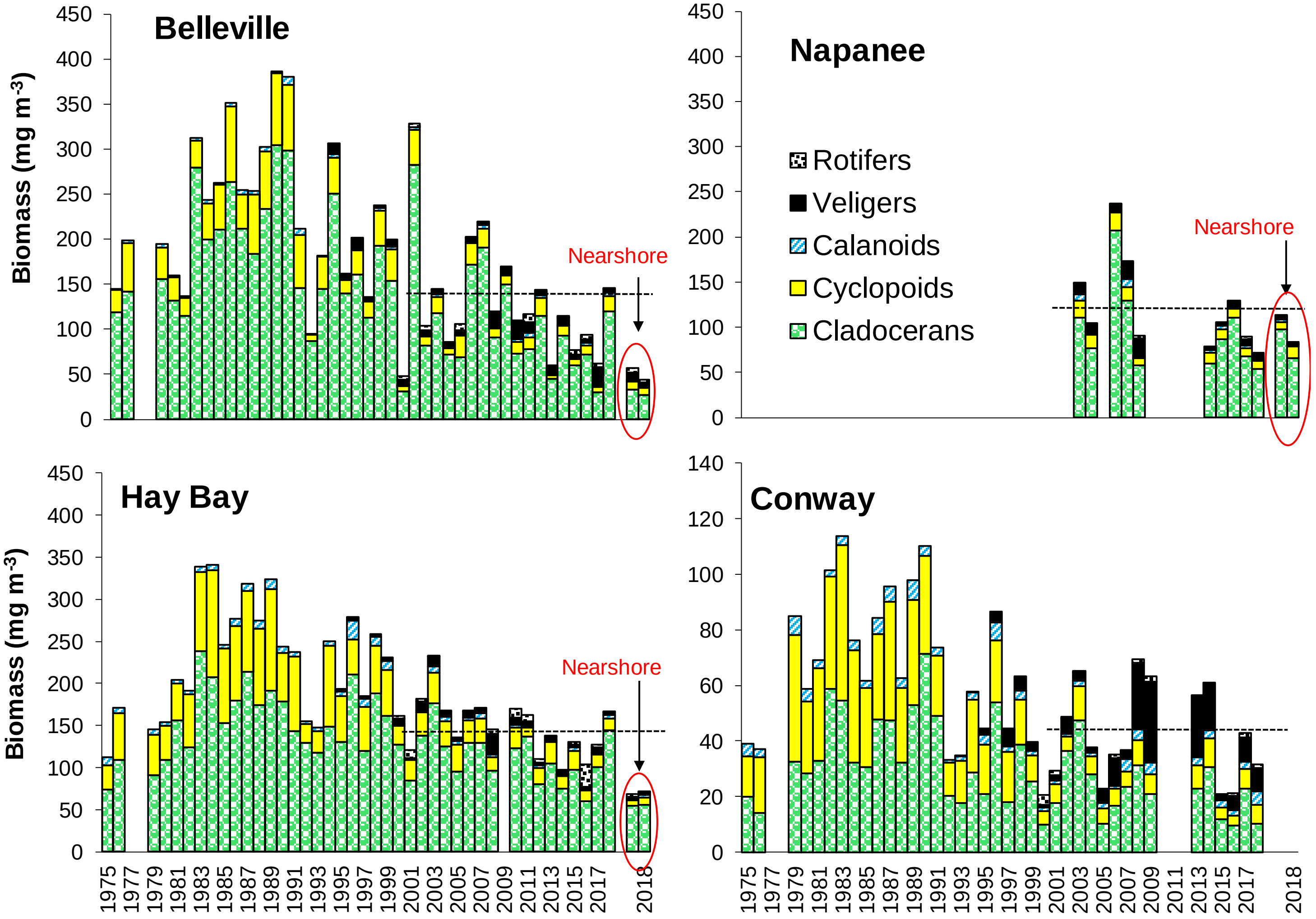

Figure 13. Mean May to October biomass (mg m^{-3}) of dominant zooplankton groups at the four long-term offshore Bay of Quinte stations over the 1975 to 2018 period. The nearshore stations at B, HB and N are given on the right side of each graph. A nearshore station was not sampled at C. The 2001 – 2016 total biomass average at each stations is shown by the dashed line. Note the different scale at C. Rotifers were not measured at any station prior to 2000 or 2013 – 2015 at C and 2014 – 2016 at N.

Zooplankton Production

Secondary production of zooplankton estimates the potential biomass produced by a population across time (Lehman 1988). Production estimates for each taxon take into account water temperature, biomass, and where appropriate, the mean number of eggs carried per individual, known as egg ratio method (Bowen 2017). Total zooplankton production for the May to October sampling period was dominated by cladocerans at all stations (Fig. 14), with the genera *Bosmina*, *Eubosmina*, *Daphnia*, *Chydorus* and *Ceriodaphnia* contributing most. Production by veligers and cyclopoids was also noteworthy. Year-to-year differences in total production were variable among stations and generally mimic the patterns in biomass discussed above. During the 2017 – 2018 study, the highest level (6.81g m^{-3} including rotifers) was found at B in 2018, largely due to high populations of *Eubosmina* during June and July. When the two years were averaged, the nearshore station Bns tended to be less productive (2.28 g m^{-3}) than the offshore station B (4.61 g m^{-3}) or compared to the 2001 to 2016 average (3.13 ± 0.35 g m^{-3}; Fig. 14). Since secondary productivity calculations use changes in biomass over the sampling season, only annual values are produced, resulting in only 2 values for nearshore-offshore comparisons per site. When the upper and middle bay stations were pooled, total annual production in the offshore was not significantly different from the nearshore using a two-tailed t-test (offshore = 3.69 ± 0.68 g m^{-3}, nearshore = 2.81 ± 0.28 g m^{-3}; n=6; p=0.25; Fig. 15). Summer mean egg ratios were significantly higher for *Daphnia* sp. in the offshore than the nearshore (0.32 ± 0.06 eggs ind^{-1} vs 0.13 ± 0.06 eggs ind^{-1}; p=0.030; Fig 16). There were no egg ratio differences for other dominant groups (*Bosmina*, *Eubosmina*, *Ceriodaphnia*, *Chydorus*, cyclopoids and diaptomid copepods). The 2017 – 2018 mean production value at HBns (3.05 g m^{-3}) was also lower than at the corresponding offshore station HB (3.90 g m^{-3}), but both were higher than the 2000s average of 2.21 ± 0.16 g m^{-3}. Conversely, Nns tended to be slightly more productive (3.35 g m^{-3}) than offshore N (2.75 g m^{-3}) over the last two years or relative to the previous 16 years (2.77 ± 0.55 g m^{-3}). C is less productive than the other Bay of Quinte stations, with a 2017 – 2018 mean of 0.78 g m^{-3}, although this is higher than the 2001 to 2016 mean of 0.57 ± 0.08 g m^{-3} at this station.

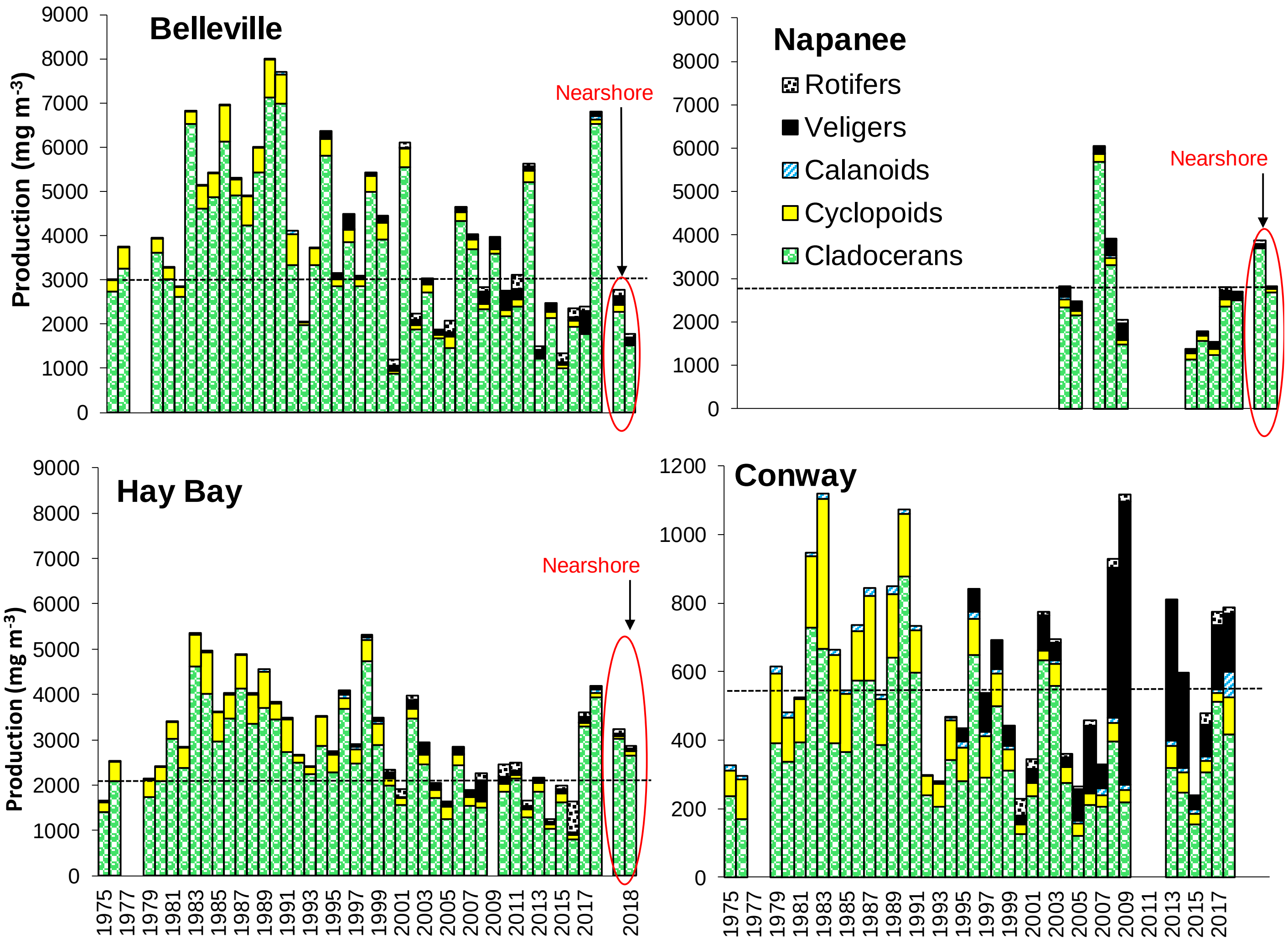

Figure 14. Total May to October production (mg m^{-3}) of dominant zooplankton groups at the four long-term offshore Bay of Quinte stations over the 1975 to 2018 period. The nearshore stations at B, HB and N are given on the right side of each graph. A nearshore station was not sampled at C. The 2001 to 2016 total production average at each stations is shown by the dashed line. Note the different scale at C. Rotifers were not measured at any station prior to 2000 or 2013 – 2015 at C and 2014 – 2016 at N.

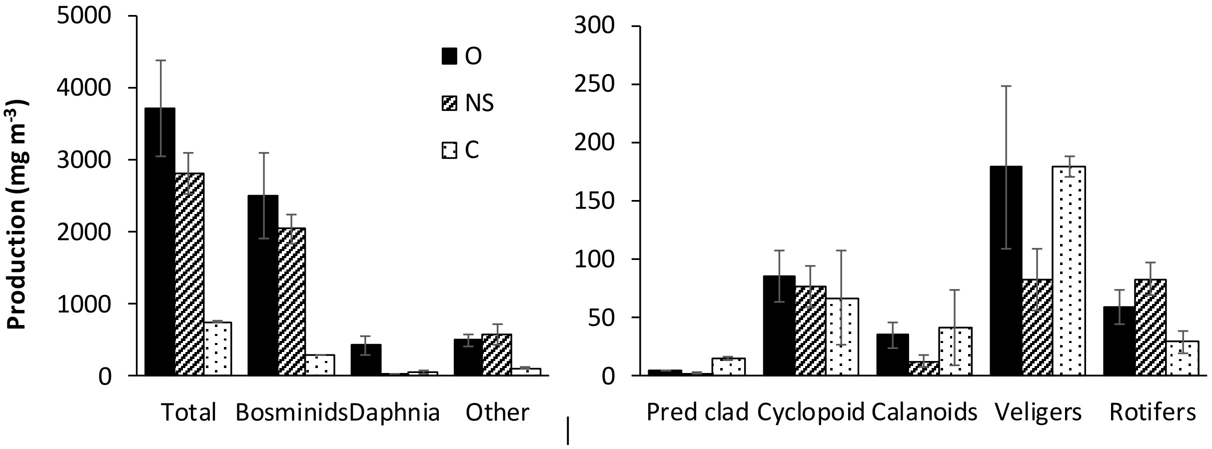

Figure 15. Mean May to October total production (mg m^{-3}) and standard errors for dominant zooplankton taxa in the Bay of Quinte offshore (O), nearshore (NS) and Conway (C) in 2017 and 2018.

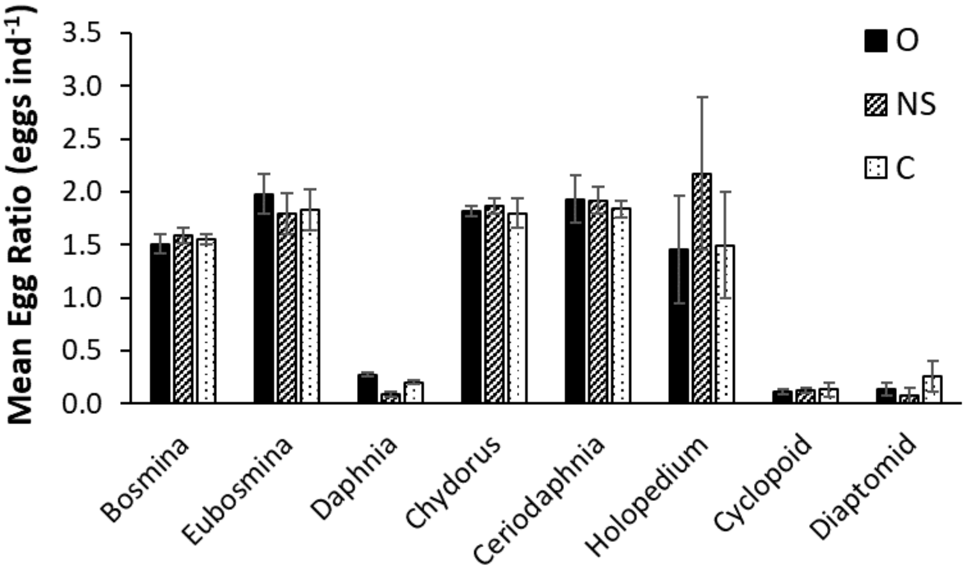

Figure 16. Mean egg ratio (eggs per individual) and standard errors for dominant zooplankton taxa in the Bay of Quinte offshore (O), nearshore (NS) and Conway (C) in 2017 and 2018.

Rotifers

May to October mean rotifer biomass in the Bay of Quinte in 2017 and 2018 was relatively inconsequential (Fig. 13), averaging only 3.2 ± 0.6 % of total zooplankton + rotifer biomass. Rotifer biomass averaged 3.1 ± 0.4 mg m^{-3} in 2017 and only 1.2 ± 0.3 mg m^{-3} in 2018. Values in the offshore (B, N and HB) were not significantly different from the nearshore using a two-tailed t-test (offshore = 2.0 ± 0.5 mg m^{-3}, nearshore = 2.6 ± 0.5 g m^{-3}; N=6; p=0.47). In 2017, when seasons were enumerated separately, rotifer biomass was typically highest in the spring and/or fall, with means of 4.9 and 4.0 mg m^{-3}, respectively, and lowest during the summer (1.2 mg m^{-3}; Fig. 17). In terms of biomass, spring samples were mostly comprised of the genera *Keratella*, *Polyarthra* and *Synchaeta*, whereas in summer and fall, biomass was dominated by the large predatory rotifer *Asplanchna*. The rotifer communities at the offshore and nearshore sites were similar in terms of community composition. The two areas were also similar in terms of % eutrophic species by density (sum of *Anuraeopsis fissa, Brachionus angularis, Filinia* sp., *Keratella cochlearis tecta, Pompholyx sulcata* and *Trichocerca* sp.), with values of 3.6 ± 0.9% in the offshore and 5.1 ± 1.3% in the nearshore. Percent oligotrophic species (*Kellicottia longispina* and *Synchaeta kitina*) were also similar in the offshore (4.2 ± 1.3%) and nearshore (3.6 ± 1.0%). These rotifer indicators are discussed in Currie et al. (2023a).

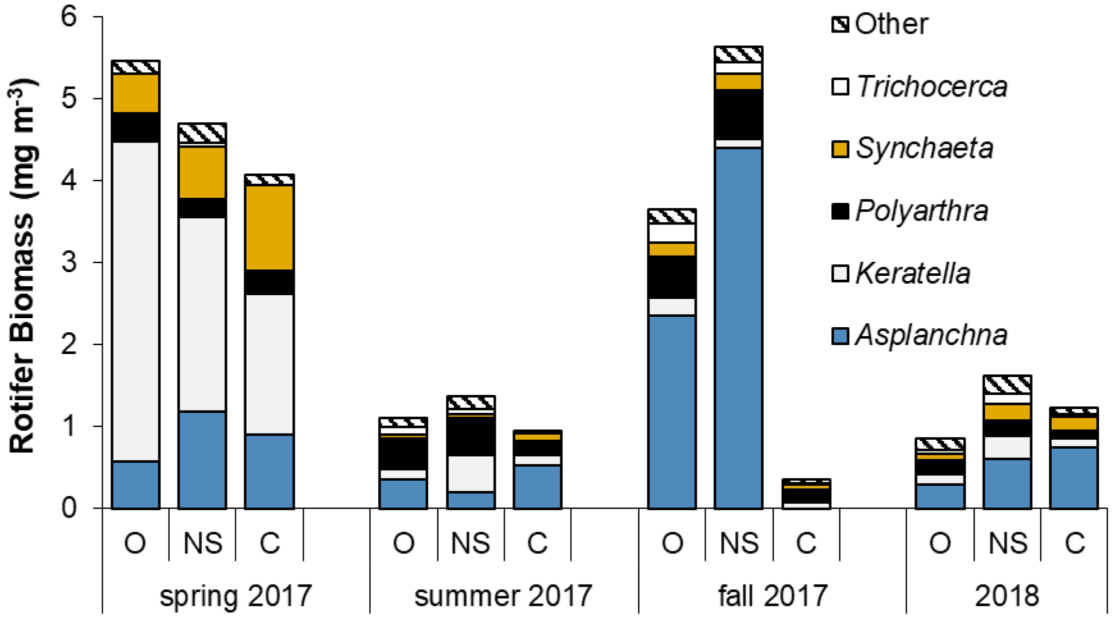

Figure 17. Biomass (mg m^{-3}) of dominant rotifer genera in spring, summer and fall composite samples in 2017, and May to October composite samples in 2018. Given are the means for offshore (O) and nearshore (NS) stations and Conway (C).

2001 AND 2004 NEARSHORE – OFFSHORE SURVEYS

For the 2001 nearshore – offshore survey in Big Bay, statistical comparisons were made using log-transformed data for the July to October period when macrophytes were well established. Zooplankton biomass, and cladocerans in particular, were very low in April and June as a result of normal seasonal succession (Fig. 18) and these dates were excluded from the analyses. Total phytoplankton biomass was greater in the offshore than in the LM area. Biomass of Cyanophyta, bacteria, APP, HNF and ciliates were not different among areas.

In terms of zooplankton biomass, *Daphnia, Eubosmina*, and *Dreissena* veliger larvae were highest in the offshore (Table 7; Fig. 18), and both the offshore and HM area had greater biomass of total zooplankton, cladocerans and cyclopoids than the LM area. *Bosmina*, calanoids and predatory cladocerans were not different among areas. Although total zooplankton biomass in the offshore and HM areas were similar, taxonomic composition differed and a greater number of taxa were present among the macrophytes. Littoral cladocerans such as the chydorid genera *Alona*, *Acroperus* and *Pleuroxus* and littoral cyclopoids including *Eucyclops agilis* had higher biomass in the wetland than the other two areas. These taxa were often absent in the offshore and were sparse in the low macrophyte area. *Chydorus sphaericus* biomass was also higher in the HM than in the LM area. Conversely, large taxa such as *D. galeata mendotae*, *Holopedium gibberum*, *Mesocyclops edax* and diaptomid copepods were more abundant offshore than at the nearshore sites.

Cyclopoid mean length was highest in the offshore, and cladocerans were larger in the offshore compared to the HM sites. The percentage of large *Daphnia* (> 750 µm) was lowest in the HM area, and there were typically very few *Daphnia* of any size at these stations throughout the year. Mean cladoceran size varied month to month and was largely driven by taxonomic changes. Cladocerans were relatively small (mean length < 400 µm) at all stations in April, June and September, and at the wetland sites until October. Size increased dramatically to about 725 µm at offshore sites in July and August when *Daphnia* (typically the largest herbivorous cladocerans) were abundant.

In July 2004, DFO completed another survey of zooplankton in Big Bay at an offshore station, three low macrophyte (LM) stations and two high macrophyte (HM) stations. Locations and methodologies generally matched the 2001 survey. Zooplankton biomass was highest at the offshore site, moderate but variable at the LM sites, and lowest in the wetland (Fig. 19). The offshore community was comprised mostly of *Eubosmina*, *D. galeata mendotae*, the cyclopoid *Mesocyclops* and veligers. The community composition varied from station to station in the LM area, and was mostly comprised of *Daphnia*, veligers and cyclopoids. The HM zooplankton were mostly *Eubosmina*, littoral cladocerans and cyclopoids. As in the other surveys, there were very few *Daphnia* in the wetland, and few littoral cladocerans in the offshore or in the LM area.

Table 7. Comparison of zooplankton parameters in offshore (Off), nearshore high macrophyte (HM) and nearshore low macrophyte (LM) areas in Big Bay, Bay of Quinte in 2001. The April and June cruises have been excluded to minimize seasonal variation. F and P values were determined by ANOVA. P values > 0.05 are listed as not significant, "n.s.". The area differences based on Bonferroni multiple comparisons tests are also shown.

Zooplankton	**Offshore**		**High Macro.**		**Low Macro**				
Parameter	**Means**	**SE**	**Means**	**SE**	**Means**	**SE**	**F**	**P**	**Bonferonni**
Biomass (mg m^{-3})									
Cladocerans	309.8	76.6	177.6	41.7	33.4	6.0	18.3	<0.001	Off, HM>LM
D. galeata mendotae	178.3	55.0	1.4	0.6	7.6	3.6	39.0	<0.001	Off>HM, LM
D. retrocurva	39.1	24.0	0.4	0.2	2.4	1.9	4.7	0.015	Off>HM
Bosmina	7.1	3.1	11.4	2.9	9.8	2.8	1.6	n.s.	
Eubosmina	55.0	10.2	3.2	1.7	2.5	1.0	62.5	<0.001	Off>HM, LM
Chydorus	23.6	14.1	27.1	10.6	2.9	0.9	4.7	0.015	HM>LM
Other littoral Cladocera	1.8	0.7	133.1	34.0	7.6	3.1	7.6	<0.001	HM>LM>Off
Predatory Cladocera	0.0	0.0	0.0	0.0	0.1	0.0	1.9	n.s.	
Cyclopoids	73.8	20.7	155.9	35.5	20.6	4.8	15.4	<0.001	Off, HM>LM
Calanoids	6.0	0.9	8.4	4.8	2.0	0.4	2.7	n.s.	
Veligers	1.1	0.3	0.3	0.1	0.1	0.1	10.1	<0.001	Off>HM, LM
Total biomass	390.6	96.9	342.2	68.0	56.1	10.2	23.0	<0.001	Off, HM>LM
Percent by BM									
D. galeata mendotae	37.3	7.5	0.4	0.1	16.1	6.1	38.1	<0.001	Off>LM>HM
Mesocyclops	48.7	10.6	2.3	1.3	8.1	3.5	15.6	<0.001	Off>HM, LM
A. vernalis	16.2	2.9	32.4	6.5	12.2	4.9	2.3	n.s.	
Herb Clad Length (µm)	564	60	364	15	425	39	5.3	0.009	Off>HM
Cyclopoid Length (µm)	535	21	471	19	429	11	7.6	0.002	Off>HM, LM
Calanoid Length (µm)	742	70	616	42	613	32	2.5	n.s.	
% Daphnia >750 µm	60.6	4.0	35.7	18.0	47.2	9.8	18.8	<0.001	Off, LM>HM

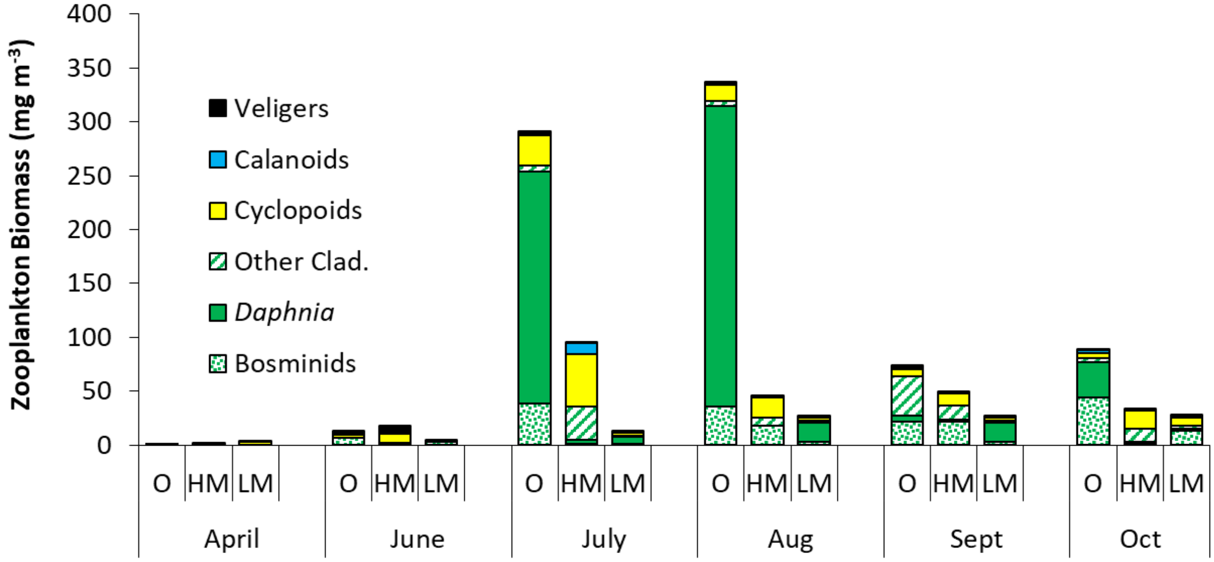

Figure 18. Seasonal patterns in biomass (mg m^{-3}) of dominant zooplankton groups for the Big Bay, Bay of Quinte Nearshore Offshore survey in 2001. O represents the mean of 3 offshore stations, HM is the mean of 4 high macrophyte nearshore stations, and LM is the mean of 3 low macrophyte nearshore stations.

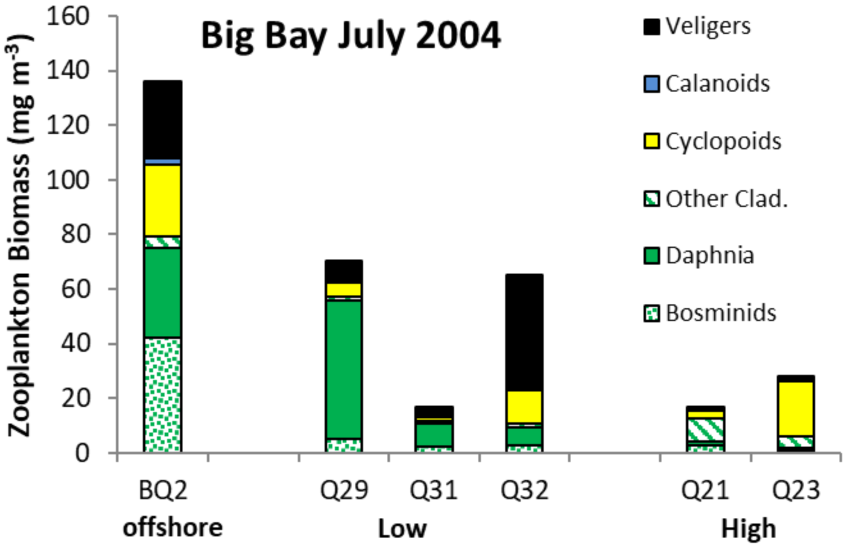

Figure 19. Biomass (mg m^{-3}) of zooplankton groups at an offshore station, three low macrophyte stations and two high macrophyte stations in Big Bay, Bay of Quinte in July 2004.

NEARSHORE ZOOPLANKTON – DISCUSSION

Overall, biomass of total zooplankton, cladocerans and copepods were quite similar at the nearshore and offshore sites in all of the studies outlined here, although there were some taxonomic differences among areas. In the recent 2017 – 2018 study, populations of littoral, macrophyte-associated cladocerans were only marginally elevated at the nearshore sites, suggesting these sites were not deep enough “in the weeds” to show clear taxonomic differences. The nearshore sites chosen in 2017 and 2018 were likely highly representative of the vegetated nearshore zone which accounts for about a third of the upper and middle reaches of the Bay of Quinte. In comparison, littoral taxa were much more important at the 2001 and 2004 shallow high macrophyte sites, which were more characteristic of coastal wetlands found in protected embayments.

Using the 2017 and 2018 data, examination of the zooplankton metrics outlined in Currie et al. (2023a) provided no indication that zooplankton community “health” at the nearshore sites was better relative to the long-term offshore stations. All three nearshore-offshore surveys carried out in the Bay of Quinte over the last two decades showed that there were fewer large zooplankton such as *D. galeata mendotae*, *Mesocyclops edax* and diaptomid copepods in the nearshore relative to the offshore, and that the cladocerans in the nearshore were smaller. This may suggest a higher rate of fish planktivory closer to shore, as larger zooplankton taxa are preferentially consumed by fishes such as Alewife (*Alosa pseudoharengus*), young Yellow Perch and shiners (Brooks and Dodson 1965). Lessening cladoceran size, % *D. galeata mendotae* and % *Mesocyclops* have all been proposed as indicators of high fish planktivory in the Bay of Quinte (Currie et al. 2023a). Both species can be reduced or eliminated when planktivores are abundant (e.g., Chang et al. 2004; Evans and Jude 1986; McQueen and Post 1988). However, electrofishing surveys in the Bay of Quinte do not indicate particularly high levels of planktivorous fishes in these locations and instead might point to foraging by planktivorous centrarchids such as Bluegill Sunfish (*Lepomis macrochirus*) (see Trophic Ratios section of Currie et al. 2023c). Diet studies of these fishes would help to determine if they are preferentially targeting *Daphnia* and *Mesocyclops* in the nearshore. The *Daphnia* that were found in the nearshore in the recent survey also carried fewer eggs. Larger females tend to carry more eggs, and zooplankton carrying pigmented eggs may be more vulnerable to visually feeding predators (Svensson 1992). A clear response between food availability and fecundity has been demonstrated in *Daphnia* (Lampert 1978), and possible higher competition for algal resources in the nearshore may have precipitated the lower egg ratios observed there.

In the upper and middle Bay of Quinte, the offshore planktivorous fish community is comprised largely of Alewife, White Perch (*Morone americana*), Yellow Perch and Gizzard Shad (*Dorosoma cepedianum*) (Hoyle 2018). As obligate planktivores, Alewife, can exert considerable grazing pressure on zooplankton in the Bay of Quinte when they are abundant, as demonstrated in the 1980s (Strus and Hurley 1992). They enter the Bay of Quinte in the spring and early summer to spawn and return to Lake Ontario by late summer (Hoyle 2018). Zooplankton comprise only a portion of the diets of the remaining species, especially as they get older (Schaus et al. 2002; Scott and

Crossman 1973), but these fishes are generally present year-round. Populations of planktivorous centrarchid fishes such as Pumpkinseed Sunfish (*Lepomis gibbosus*) and Bluegill have increased in the upper bay since the early 1990s, especially in the nearshore zone (Brousseau et al. 2011; Hoyle et al. 2012), and these fishes often associate with submerged macrophytes for cover and feeding. Vegetated nearshore areas with medium to high macrophyte densities support higher biomass of Pumpkinseeds and Yellow Perch compared to more homogeneous offshore habitats (Brousseau et al. 2003; Randall et al. 2012). Sunfish and perch, particularly the larger individuals, prefer benthic invertebrate prey and small fishes over zooplankton (Scott and Crossman 1973). However, vegetated areas are important fish nursery habitats, and larvae and young-of-the-year of many wetland fish species often rely heavily on zooplankton, and cladocerans in particular (García-Berthou and Moreno-Amich 2000). In a Lake Erie study, cladocerans comprised of >70% of the diets of both juvenile Yellow Perch and White Perch in June and July, but this dropped to <25% in August and September (Schaeffer and Margraf 1986). However, the habitat utilization of the nearshore zone of the upper Bay of Quinte by YOY fishes is unclear (Erin Brown, MNRF pers. comm.). Proper assessment would require different sampling gear than is used by MNRF for their long-term sampling program. As such, there is little information on both densities of larval or YOY fishes in the Bay of Quinte and their diets, so their impacts on zooplankton are largely unknown.

Given similarities in water quality at the nearshore and offshore sites, there is no reason to believe that water quality stressors are impeding survival and growth of cladocerans more in the nearshore relative to the offshore. Larger zooplankton taxa, and *Daphnia* in particular, are often more sensitive to impaired water quality, including pesticides which were not measured during our sampling (Sprules 1984; Havens and Hanazato 1993). Water clarity plays a role in the ability of many visually feeding predators to catch zooplankton prey. In both the 2001 study and in 2017 – 2018, the calculated 1% euphotic zone depth in the offshore was often less than the depth of the water column, especially in late summer and fall. This means that the bottom waters receive <1% of the available surface light at these times of the year. Offshore zooplankton residing deep in the water column are therefore less vulnerable to visually feeding fish during the day. This light refuge is not available at the nearshore sites where light reaches the bottom, although zooplankton may hide among the macrophytes during the day (Burks et al. 2001; Timms and Moss 1984). It is possible that zooplankton may be particularly vulnerable the nearshore areas with sparser macrophyte growth (as sampled in 2001), thus explaining the low biomass of zooplankton observed in low density macrophyte beds relative to the other areas. Furthermore, in our 2001 study, the low macrophyte nearshore zone was colonized by less structurally complex plants such as tape grass (*Vallisneria* sp.) and Richardson's pondweed (*Potamogeton richardsonii*) which likely offer limited protection. Meerhoff et al. (2007) found that in subtropical lakes where fish predation rates were high, macrophytes offered insufficient refuge for large zooplankton.

Differences in the availability and quality of algal and microbial food resources in the nearshore and offshore could also impact zooplankton populations. In the 2001 study, chlorophyll *a*, total phytoplankton biomass and herbivorous cladoceran biomass were higher in the offshore. Large zooplankton grazers require considerably more food resources than small grazers just for survival (Lehman 1988). However, no significant differences in phytoplankton or the microbial loop were observed between the slightly deeper nearshore and offshore stations in the 2017 – 2018 study, suggesting standing stock food resources were similar among areas. It is possible for submergent macrophyte beds to limit the production of planktonic algae due to the plants competing with algae for both light and nutrients (Scheffer 1998), but this does not appear to be the case in the recent survey since biomass and productivity were not different between nearshore and offshore sites. Filtering activities of *Dreissena* mussels are also expected to play a role in structuring the nearshore planktonic food web (see the Macrophytes and *Dreissena* section below). Despite lower biomass of settled mussels, dreissenid veliger biomass was higher in the offshore in 2001, and while not significant, it also tended to be higher offshore in the recent survey. It is likely that veligers are staying in the water column longer in the offshore, given the lack of suitable substrates for settlement (Wright et al. 1996).

In summary, the reduction in large zooplankton, especially *Daphnia* in the nearshore areas suggests that planktivory is high, and competition for available food resources by dreissenid mussels may limit zooplankton production in the nearshore to some degree. Zooplankton biomass may at times be lower in the vegetated nearshore than in offshore waters. This was observed in the LM area in 2001 (Fig. 18), and at both B and HB, nearshore biomass values in 2017 and 2018 were among the lowest observed in the time series (Fig. 13). However, when averaged across the season, there were no significant differences in biomass or secondary production between nearshore and offshore stations. Inclusion of nearshore habitats has not changed the overall findings of the Bay of Quinte zooplankton assessment of Currie et al. (2023b).

MACROPHYTES AND *DREISSENA*

Zebra mussels (hereafter ZM) first arrived in the Great Lakes basin during 1985 – 1986 in Lake St Clair (Hebert et al. 1989), and quagga mussels (hereafter QM) in 1991. Although their source and establishment date in the Bay of Quinte is uncertain, they were established in the upper bay by the late 1990s (Dermott et al. 2012). ZM are filter-feeding organisms and when present in large numbers have the potential to significantly impact phytoplankton abundance through grazing (Fanslow et al. 1995; Horgan and Mills 1997). ZM preferentially settle on hard horizontal surfaces, out of direct sunlight (Marsden and Lansky 2000). Much of the soft bottom substrate of the Bay of Quinte will likely not be an ideal location for settling larval veliger stages of *Dreissena*, even for QM that can tolerate softer sediments (Dermott et al. 2003).

Natural materials (rocks, submerged aquatic vegetation and woody debris) and artificial structures (piers, docks, buoys etc.) provide ZM with increased opportunities for attachment in shallow nearshore areas, as compared to more homogeneous offshore areas in the Bay of Quinte. We hypothesized that there would be increased ZM biomass, and subsequently increased grazing on phytoplankton in heavily vegetated nearshore areas. Macrophyte coverage in the upper Bay of Quinte began to increase in the early 1980s, expanded rapidly in 1996 after the clear phase transition, and was estimated to range from 30 – 50% coverage by 2012 (Leisti et al. 2012; Doka et al. 2016). Given the likely ecosystem effects of increased macrophytes and *Dreissena* in the nearshore, a pilot study was undertaken in 2018 in order to explore the distribution of ZM in the upper Bay of Quinte by comparing the settled ZM on macrophytes in the nearshore areas to the long-term central channel monitoring stations.

At the long-term main stations, B and N, which both have a depth of approximately 5 m, no macrophytes were present. Macrophytes were only found and collected at the paired nearshore stations, which have a depth of approximately 2 m. The lack of macrophytes at the main offshore stations is not unexpected as average light penetration is not sufficient during the summer to reach the bottom, whereas bottom light levels are adequate at the nearshore stations to allow for significant macrophyte growth over the summer (Doka et al. 2016).

The average of the three Ekman sediment samples collected in August 2018 were compared to the sum of all macrophyte-attached zebra mussels within a single rake grab, for both areal abundance and dry weight biomass (Fig. 20 top; Table 8). The majority of the ZM at these upper Bay of Quinte sites were found predominately attached to the macrophytes and not in the sediment (Fig. 20 bottom). A total of 2444 ZM were counted and sized, with the vast majority of individuals being small juveniles with an average length of only 4.3 mm ± 0.01 SE. ZM dry biomass on macrophytes averaged 16.52 g m^{-2} at Bns and 14.29 g m^{-2} at Nns (Fig. 20), whereas corresponding values in the sediments were 0.41 and 2.99 g m^{-2}. The Ekman sediment samples collected at both the main and nearshore stations revealed that while very small numbers of ZM were present at the deeper main stations, the sediments in the shallower, nearshore stations had significantly higher ZM density [$t(9) = -2.88$, $p<0.05$], and subsequently significantly higher biomass.

While macrophyte fronds may provide suitable substrate during the growing season for recently settled mussels, they do not provide stable multi-year substrate as the plant stems usually die off and settle to the bottom during the winter. This is reinforced by the presence of broken shells from previous years in the nearshore zone sediments. Most of the larger mussels (age 1 or older) were found near the base of the plants and on the roots (Fig. 21), where they may have found some protection from winter die-back and ice damage.

The lack of ZM in the sediment is generally expected because soft mud is a poor environment for filtration and lacks strong attachment points for byssal threads (Coakley et al. 2002). Macrophytes, on the other hand, provide firm structure for attachment of settling plantigrade veligers, so in the presence of macrophytes, ZM preferentially choose them as an attachment substrate (Muskó and Bakó 2005). Not only do macrophytes provide increased attachment surface area (some species more than others), but they also provide protection from predators, and an elevated surface which reduces burial risk and higher flow conditions that improve feeding rates.

During this preliminary study, six unique species of macrophytes were found across both sites (*Vallisneria spiralis* - tape grass, *Ceratophyllum demersum* - coontail, *Eriocaulon aquaticum* - pipewort, *Potamogeton strictifolius* - straight pond weed, *Myriophyllum spicatum* - milfoil, and *Elodea canadensis* - common water weed), which represents only a small portion of known macrophyte species in the Bay of Quinte (for a complete species list, see Doka et al. 2016). Macrophyte distributions are known to be patchy (Doka et al. 2016), and the two upper bay sites had very different composition of macrophyte species, with Bns having almost exclusively tape grass, a long flat species with almost no bifurcation beyond the roots, whereas Nns had almost 75% coontail, a highly bifurcated feathery macrophyte species (Fig. 21). The differences in species is due primarily to the limited sampling effort for this pilot study, as only one rake sample was collected at each site, which will underrepresent the species variability at each site. The ZM distribution on macrophytes revealed that at Bns, mussels were only attached to the tape grass which is not surprising given that it represents over 95% of the plant community (Fig. 22). At Nns, ZM preferentially attached to milfoil, even though it was not the most abundant plant species (20%) of the macrophyte community. Though coontail dominated at Nns (74%), no ZM were found on this species, mostly likely because the feathery, breakable structure does not promote successful settlement. Macrophyte morphology, complexity and surface area contribute to settlement rate, which make some species of macrophyte a more preferred settling site for ZM veligers. More complex forms provide more surface area, particularly for small organisms (McAbendoth et al. 2005), and sturdy branching points, such as the node whorls of milfoil, as well as at the root bases of the plants provide suitable habitat for ZM survival, which was observed in this study.

Despite the very limited scope of the 2018 pilot study, its findings were in general agreement with earlier upper Bay of Quinte benthic surveys that also typically found much lower mussel biomass at sites deeper than 3 m relative to shallower nearshore sites (Table 8). Ponar results from Dermott et al. (2003) showed that offshore mussel biomass was negligible in the upper bay around Trenton in both 1998 and 2000. However, mean biomass at the offshore Belleville – Big Bay sites were up to three orders of magnitude higher in 1998 and 2000 relative to the offshore stations in 2001 or 2018. In the Dermott et al. (2003) survey, individual ponar grabs were highly variable, and 79% and 50% of offshore upper bay samples contained fewer than 10 mussels in 1998 and 2000, respectively. Invasive round gobies (*Neogobious melanostomus*), which prey heavily of dreissenids, were abundant in the upper Bay of Quinte by the mid-2000s (Taraborelli et al. 2010), and their spread has likely contributed to a decline in mussel biomass in the bay.

In the August 2001 inshore-offshore study, mussel biomass averaged only 0.03 ± 0.01 g m^{-2} dry shell-free biomass in the middle of Big Bay. Nearshore 2001 biomass was higher than we found in the 2018 macrophyte samples, averaging 45.3 ± 12.2 g m^{-2} in the high-macrophyte wetland and 73.9 ± 11.5 g m^{-2} in the rockier, low-macrophyte nearshore area (Fig. 23a). In the earlier study, other benthic invertebrates such as chironomids and oligochaete worms were more important in the offshore relative to ZM (0.5 ± 0.07 g m^{-2} dry weight, using the same conversion factor). Dry biomass of plant-associated invertebrates such as amphipods, isopods, snails, flatworms and insect larvae were highest in the wetland (3.27± 0.33 g m^{-2}) and intermediate in the low macrophyte area (1.66 ± 0.23 g m^{-2}), but these groups were much less dominant than ZM in both areas (Fig. 23a, b).

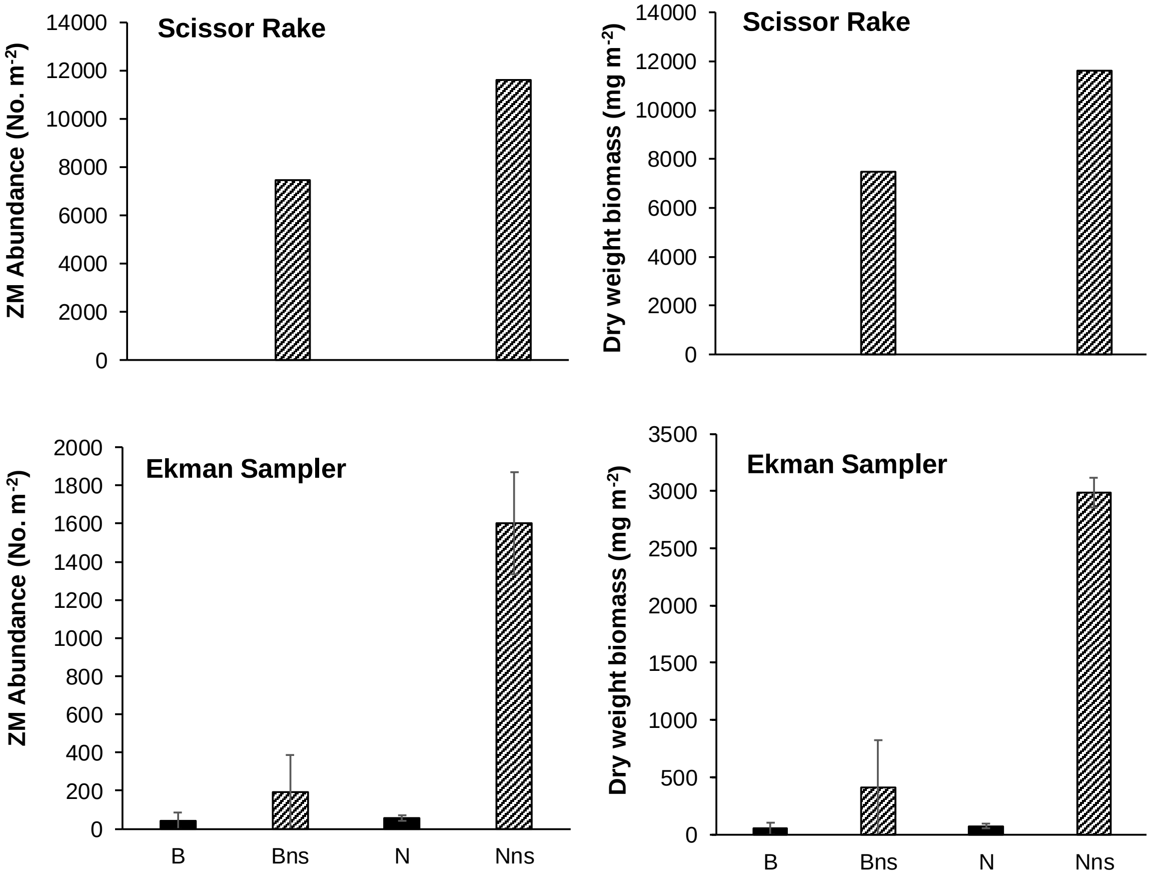

Figure 20. Abundance (left) and dry weight biomass (right; calculated using Eq. 1) of zebra mussels collected from the sediment (Ekman sampler), or attached to macrophytes (scissor rake) at offshore (B, N) and nearshore (Bns, Nns) upper Bay of Quinte stations in August 2018.

Table 8: Dreissena shell-free dry biomass, sample size (N) and standard errors (SE) at nearshore (1 – 3 m depth) and offshore (>3 m) stations in the Upper Bay of Quinte. Dermott et al. (2003) provided 1998 and 2000 data, as well as conversion factors to calculate shell-free dry biomass (0.56 X 0.12 X wet biomass including shells). No macrophytes were found offshore in 2018 for the rake estimates.

					Depth	Dry Biomass (g/m^2)		
Year	**Months**	**Location**	**Habitat**	**Gear**	**(m)**	**N**	**mean**	**SE**
1998	Aug, Oct, Nov	Trenton	nearshore	mini-ponar	0-3	23	39.98	20.52
			offshore		3-5	10	0.01	0.01
1998	Aug, Oct, Nov	Belleville, Big Bay	nearshore	mini-ponar	0-3	17	142.00	45.60
			offshore		3-5	14	63.22	35.80
2000	Oct.	Trenton	nearshore	mini-ponar	0-3	21	62.03	27.1
			offshore		3-5	10	0.05	0.02
2000	Oct.	Belleville, Big Bay	nearshore	mini-ponar	0-3	16	252.9	40.2
			offshore		3-5	14	28.2	18.5
2001	Jun, Aug, Oct	Big Bay	offshore	mini-ponar	6	18	0.03	0.01
			High macro.	mini-ponar	1.5	9	45.3	12.2
			Low macro.	mini-ponar	1.5	9	73.9	11.5
2018	Aug	B	offshore	Ekman	5	3	0.05	0.05
		BNs	nearshore	Ekman	2	2	0.41	0.41
		N	offshore	Ekman	5	3	0.07	0.02
		NNs	nearshore	Ekman	2	3	2.99	0.13
2018	Aug	B	offshore	rake	5	1	N/A	-
		BNs	nearshore	rake	2	1	16.52	-
		N	offshore	rake	5	1	N/A	-
		NNs	nearshore	rake	2	1	14.29	-

*Figure 21. Milfoil (*Myriophyllum spicatum *- top) and tape grass (*Vallisneria spiralis *- bottom) collected during the 2018 macrophyte pilot study from nearshore Bay of Quinte stations. Milfoil has many bifurcation points and a complex leaf pattern which creates a high surface area whereas tape grass is very simple and has a low relative surface area. Note the accumulation of zebra mussels at the roots of the tape grass.*

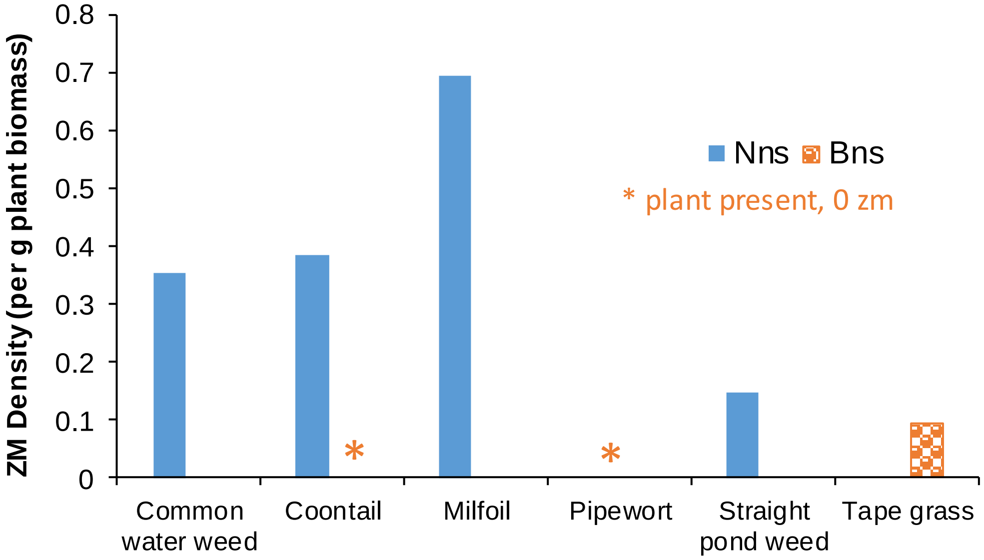

*Figure 22. Density of zebra mussels per unit plant biomass by macrophyte species. The * indicates that the plant species was found at that site, but no mussels were collected from those species.*

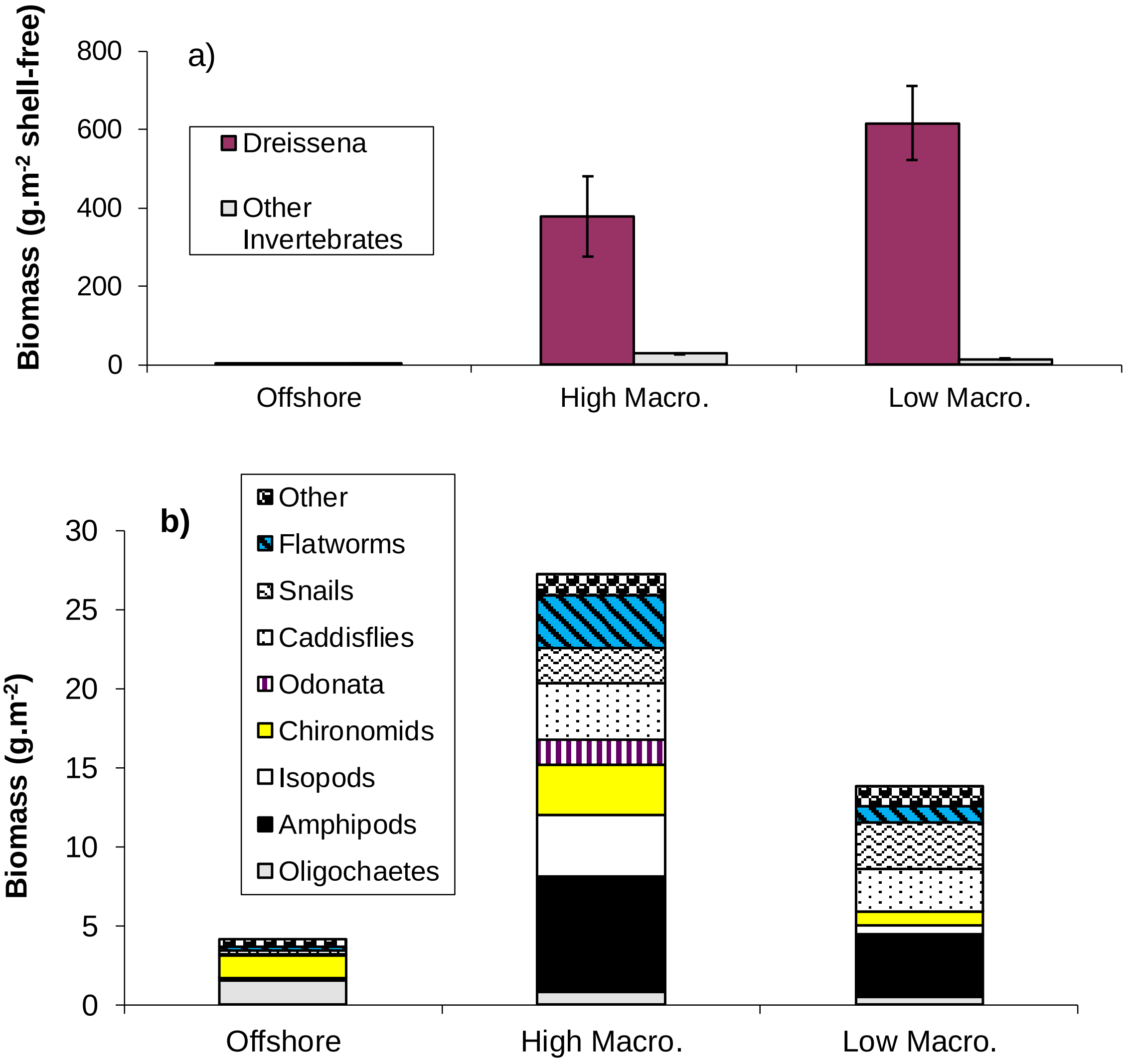

Figure 23. Mean wet shell-free biomass and standard errors of Dreissena and other benthic invertebrate groups collected by Ekman grabs, averaged over June, August and October 2001 in Big Bay, upper Bay of Quinte.

Food Web Implications

The settling of ZM on macrophytes observed in the nearshore waters present an additional phytoplankton grazing pressure which is of course absent from the deeper waters. Furthermore, ZM attached to macrophytes are elevated in the water column and therefore have access to phytoplankton higher in the water column than their sediment-dwelling benthic counterparts. In 2017 – 2018, zooplankton represented 100% of the pelagic grazer biomass at the deeper main stations, due to the complete absence of macrophytes and virtual absence of ZM offshore. However at the nearshore stations, zooplankton represented only 1 to 2% of the grazing biomass compared to the estimated shell-free mussel dry biomass associated with macrophytes. Compared to the much lower estimates of mussels associated with nearshore sediment, zooplankton accounted for 7 to 22% of grazer biomass. Given that macrophytes do not cover 100% of the available nearshore bottom, the actual value is likely somewhere in between.

Regardless, competition between herbivorous zooplankton and mussels for phytoplankton food (especially the smaller, non-colonial, more preferred algal taxa) is undoubtedly greater in the nearshore. ZM could be expected to impact phytoplankton standing crop in this zone, though the vast majority of the settled ZM were small (mean = 3.5 – 4.9 mm) so their resulting filtration rates will be less than 10% of larger mussels (Horgan and Mills 1997). Measurements of clearance (filtration) rates of individual zooplankton were similar before and after *Dreissena* invasion in eutrophic Saginaw Bay, but consumption of algae by zooplankton decreased overall as their biomass declined and was small in comparison to algal growth rates (Bridgeman et al. 1995). Although we did not observe a significant decrease in phytoplankton or herbivorous cladocerans biomass in the high ZM, macrophyte rich areas of the Bay of Quinte in 2017 – 2018, biomass of both groups were lower in this zone in our 2001 survey though this included littoral wetland environments.

In the 2018 pilot study, we were able to confirm that in the upper Bay of Quinte macrophytes facilitated settlement of ZM, and that they are otherwise almost entirely absent in the soft sediment. The nearshore vegetated region accounts for approximately 1/3 of the surface area of the upper Bay of Quinte while the other 2/3 of the upper bay lacks suitable settlement substrate and in this zone ZM are generally lacking. *Dreissena* have been shown to be important grazers of phytoplankton and although small in size, they are present in large numbers in the nearshore. However, despite different densities of ZM between the nearshore and offshore stations, we did not find significant differences in phytoplankton composition or density. This is relevant because the lack of differences in phytoplankton, nutrients or physical properties between the densely vegetated nearshore and offshore suggest there is substantial mixing between these zones in the Bay of Quinte (see Physical and Chemical Parameters section).

In the future, a more targeted project could be developed based on these early finding to investigate the relative grazing rates of *Dreissena and* other benthos found in these areas and compare to the grazing rates of zooplankton. Increased sampling effort would more conclusively determine which macrophyte species mussels prefer, and develop more robust estimates of plant-associated mussel biomass. This could refine mussel population size estimates as density and composition of macrophytes change over time, and shed light on potential impacts of ZM populations.

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APPENDICES

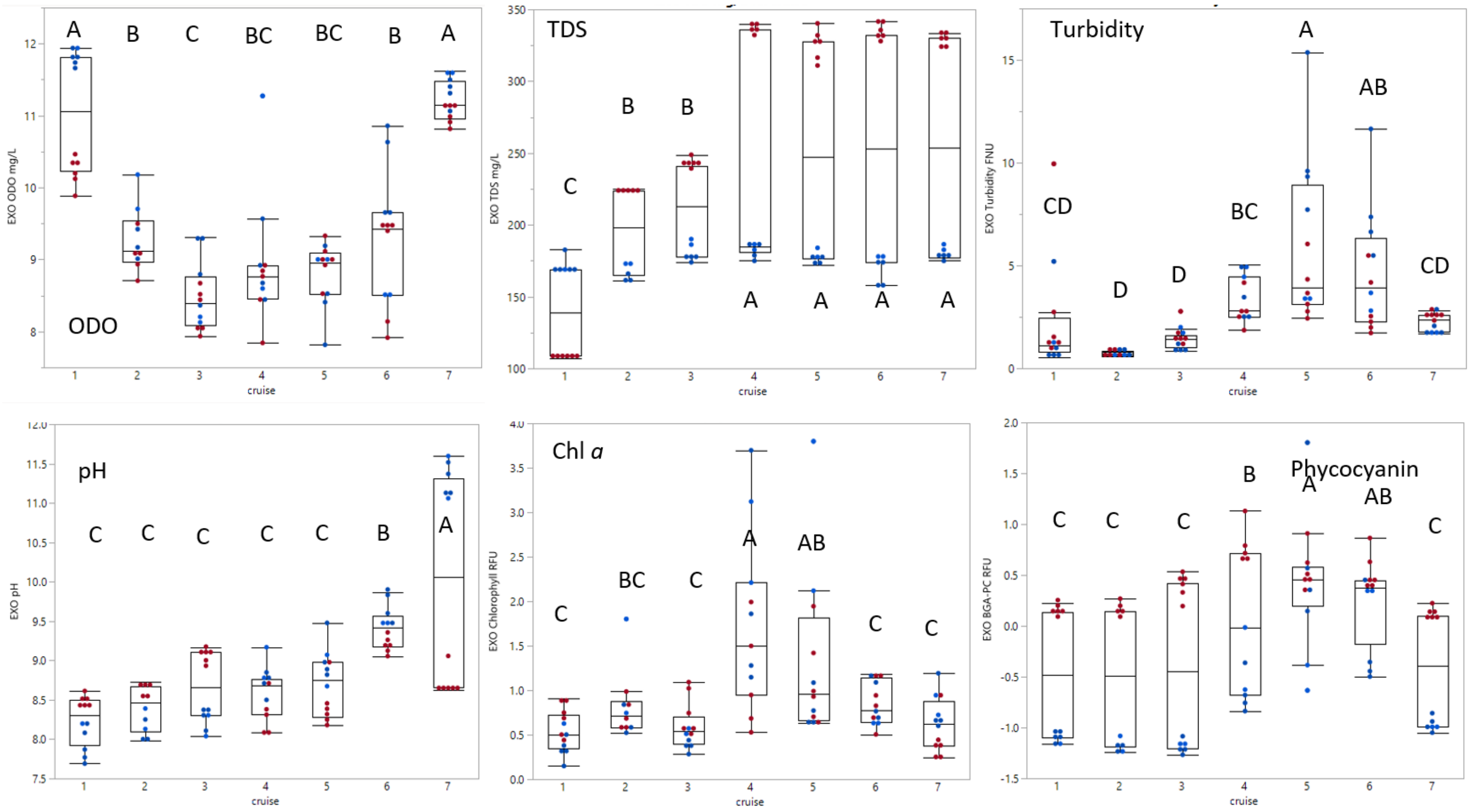
*Appendix 1. Average physical and chemical properties of the Bay of Quinte observed in 2017 and 2018. * no kd data in Aug 2018 and ** no TKN data from HB in Sep 2018. Temp = Temperature, Kd = Vertical (Light) Attenuation Coefficient, Chl a = Chlorophyll a, DIC = Dissolved Inorganic Carbon, DOC = Dissolved Organic Carbon, TKN = Total Kjeldahl Nitrogen, TP = Total Phosphorus.*

		Surface Temp. (°C)	**Kd (m^{-1})**	**Chl a (µg L^{-1})**	**DIC (mg L^{-1})**	**DOC (mg L^{-1})**	**TKN (µg L^{-1})**	**TP (µg L^{-1})**
2017	Count	6	6	6	6	6	6	6
May 3	Mean	12.24	1.11	4.09	21.73	6.05	350.00	17.97
	SE	0.16	0.12	0.34	0.39	0.17	8.14	1.90
June 7	Mean	18.08	0.93	5.44	22.95	6.38	424.33	31.20
	SE	0.56	0.07	1.02	0.51	0.26	14.80	6.30
July 11	Mean	24.10	1.08	8.69	25.92	6.70	433.83	29.50
	SE	0.10	0.04	1.21	0.23	0.28	8.60	1.39
Aug. 8	Mean	22.94	1.08	15.46	25.22	7.72	496.50	41.95
	SE	0.22	0.04	1.93	0.09	0.11	16.03	2.99
Sept.6	Mean	20.68	1.23	9.96	25.13	7.03	438.50	35.10
	SE	0.28	0.13	1.07	0.32	0.29	10.12	2.69
Oct. 2	Mean	19.95	1.17	12.50	24.62	6.83	443.67	39.63
	SE	0.32	0.16	1.20	0.16	0.22	8.90	2.94
Nov. 7	Mean	9.29	0.96	4.17	24.90	6.20	440.50	21.10
	SE	0.07	0.05	0.75	0.39	0.24	11.77	1.56
2017 Total	Count	42	42	42	42	42	42	42
	Mean	18.18	1.08	8.62	24.35	6.70	432.48	30.92
	SE	0.80	0.04	0.75	0.24	0.12	7.44	1.71

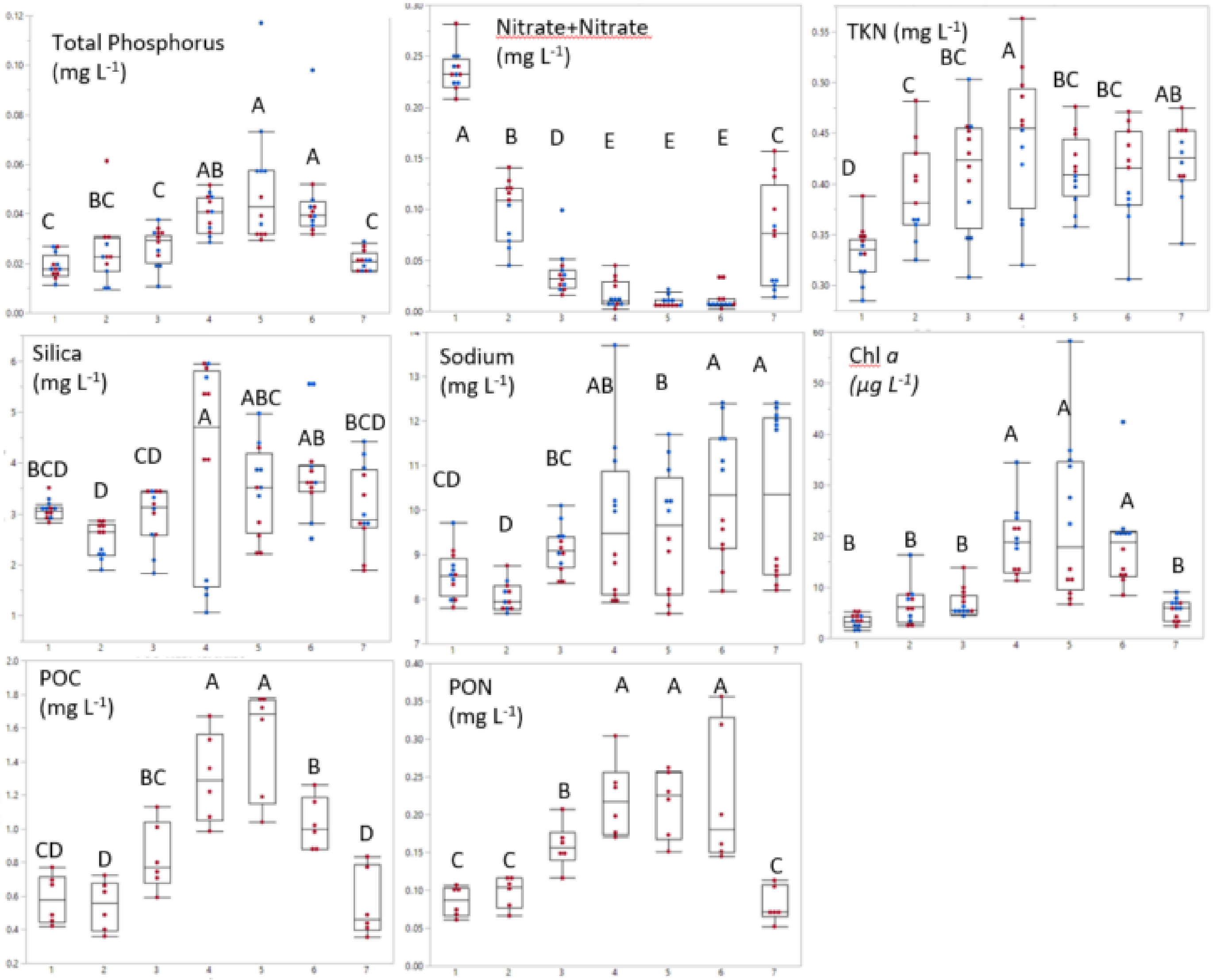
2018	Count	6	6*	6	6	6	6**	6
May 1	Mean	10.08	0.82	2.48	25.12	5.42	313.50	19.52
	SE	0.16	0.02	0.40	0.34	0.25	8.26	2.26
May 29	Mean	21.38	0.89	7.50	23.82	5.92	355.83	30.00
	SE	0.45	0.04	1.97	0.40	0.28	7.76	12.88
June 26	Mean	21.64	0.84	4.87	25.47	5.47	390.33	23.75
	SE	0.39	0.08	0.20	0.61	0.35	30.38	3.94
July 26	Mean	25.13	1.33	22.98	24.52	6.27	391.67	37.90
	SE	0.36	0.12	2.57	0.89	0.73	21.21	3.36
Aug. 22	Mean	23.93		35.59	23.52	5.97	386.33	66.27
	SE	0.09		5.02	0.54	0.27	8.08	11.25
Sep. 19	Mean	23.06	1.43	24.25	19.87	5.58	365.80	49.37
	SE	0.07	0.16	3.62	0.66	0.43	15.43	9.84
Oct. 30	Mean	7.25	0.93	6.99	23.58	5.80	404.00	20.58
	SE	0.33	0.05	0.49	0.53	0.29	14.88	1.71
2018 Total	Count	42	36	42	42	42	41	41
	Mean	18.92	1.04	14.95	23.70	5.77	372.66	35.34
	SE	1.04	0.05	2.04	0.34	0.15	7.51	3.69
2017, 2018	Count	84	78	84	84	84	83	84
	Mean	18.55	1.06	11.78	24.03	6.24	402.93	33.13
	SE	0.65	0.03	1.14	0.21	0.11	6.20	2.04

Appendix 2. Results of the 3 Way ANOVA with Year (2017 and 2018), Cruise, and Habitat (Nearshore or Offshore) as Factors. Only factors that showed no significant effect of station had stations grouped to habitat and are shown in this table. For factors, P values > 0.05 are listed as not significant, "n.s.". ODO = Optical Dissolved Oxygen, TDS = Total Dissolved Solids, Chl = Chlorophyll a, BGA = Blue Green Algae (phycocyanin), NO2+NO3 = Nitrite + Nitrate, Temp = Temperature, TP = Total Phosphorus, TKN = Total Kjeldahl Nitrogen, Kd = Vertical (Light) Attenuation Coefficient, POC = Particulate Organic Carbon, PON = Particulate Organic Nitrogen.

	Overall		**Effect: Year**		**Effect: Cruise**		**Effect: Habitat**	
Parameter	**F(8,73)**	**P**	**F(1,80)**	**P**	**F(6,75)**	**P**	**F(6,75)**	**P**
ODO	32.8	<.0001	17.7	<.0001	41.0	<.0001	0.1	n.s.
TDS	23.6	<.0001	110.5	<.0001	13.1	<.0001	0.03	n.s.
pH	11.1	<.0001	6.5	0.0130	13.7	<.0001	1.1	n.s.
Chl in vivo	6.0	<.0001	2.2	n.s.	7.1	<.0001	2.5	n.s.
BGA	30.7	<.0001	163.6	<.0001	13.5	<.0001	0.1	n.s.
Turbidity	6.6	<.0001	3.6	n.s.	8.2	<.0001	0.005	n.s.
Chl extracted	14.5	<.0001	17.9	<.0001	16.3	<.0001	0.5	n.s.
NO2+NO3	104.9	<.0001	13.9	0.0004	137.1	<.0001	2.7	n.s.
Chloride	6.8	<0.0001	76.3	<0.0001	11.3	<0.0001	4.8	n.s.
Surface Temp	149.3	<.0001	4.9	0.0301	198.2	<.0001	0.4	n.s.
TP	5.8	<.0001	1.7	n.s.	7.5	<.0001	0.02	n.s.
TKN	15.6	<.0001	56.1	<.0001	11.4	<0.0001	0.4	n.s.
Silica	2.6	0.0128	0.5	n.s	3.4	0.0046	0.9	n.s.
Kd	3.5	0.0018	0.05	n.s.	4.6	0.0006	0.2	n.s.
2017 only	**F(7,34)**	**P**	**NA**	**NA**	**F(6,35)**		**F(6,35)**	
POC	16.7	<.0001			19.5	<0.0001	0.03	n.s.
PON	10.1	<0.0001			11.7	<0.0001	0.1	n.s.



Appendix 3. Bay of Quinte nearshore and offshore stations, 2017 (red) and 2018 (blue); EXO sonde measured parameters by cruise, with significant differences noted between cruises. Only parameters with no significant effect of station are shown (see Table 2). Any groups sharing a letter are not statistically different from each other based on post hoc t test from ANOVA in appendix 2.



Appendix 4. Bay of Quinte nearshore and offshore stations (no C), 2017 (red) and 2018 (blue); water chemistry parameters by cruise with significant seasonal differences. Only parameters with no significant effect of station are shown (see Table 2). Any groups sharing a letter are not statistically different from each other based on post hoc t test from ANOVA in Appendix 2.