Sea ice increases benthic community heterogeneity in a seagrass landscape

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Abstract

Sea ice plays an important role in subpolar seagrass meadows. It protects meadows against wave action and extreme temperatures. On the other hand, sea ice destroys seagrass leaves and removes plots of sediments and organics debris, leaving long-lasting ice-made tidal pools of various shapes and sizes within the meadow. The present study aimed at investigating the effect of sea ice on benthic community structure and biogeochemical processes in a subpolar seagrass meadow. Vegetated areas (V), artificially-created (aTP), and natural (nTP) tidal pools were sampled from April to October 2018 in a seagrass meadow located at Manicouagan Peninsula (Québec; 49°5'36"N, 68°12'44"W). aTP and nTP showed similar sediment characteristics with coarser sediment and lower particulate organic carbon and total nitrogen content but also lower NO_x and higher NH_4^+ and PO_4^{3-} porewater concentrations as compared to V. Benthic macrofauna communities showed a strong seasonality with very reduced total density, biomass and species richness during wintertime (from December to April) relatively to summertime (from June to September). Benthic macrofauna communities were also more diversified and abundant in V than in aTP and nTP. Species assemblages in aTP and nTP represented a subset of species assemblages in V with any species found exclusively in tidal pools. However, total biomass was similar among treatments, suggesting that tidal pools sheltered larger individuals than vegetated areas. These results underline the importance of considering the spatial heterogeneity of seagrass meadows when assessing the functioning of these ecosystems.

Keywords: Biodiversity; Macrofauna; Biogeochemistry; *Zostera marina*; Subpolar environment; Tidal pools

1. Introduction

Seagrasses represent a group of marine flowering plants forming vast meadows in estuarine and marine coastal environments from tropical to sub-polar regions (Green and Short, 2003). They are considered some of the most productive and valuable ecosystems worldwide (Barbier et al., 2011; Costanza et al., 1997; Dewsbury et al., 2016). Indeed, their structure enhances habitat complexity, increasing the number of ecological niches in sediment they inhabit (Orth et al., 1984). Their leaves reduce hydrodynamics, providing stable hydrological and sedimentary conditions, and enhancing the sedimentation of organic-rich particles (Fonseca and Fisher, 1986; Hemminga and Duarte, 2000). Together with the degradation of the plant material itself, hydrodynamic reduction enhances sediment organic content, allowing seagrass meadows to sustain complex trophic networks (Boström and Bonsdorff, 1997). Moreover, seagrass meadows provide refugia that ultimately reduce predation pressure as compared to bare sediments (Orth et al., 1984), and play a nursery role for numerous species (Heck et al., 2003). Therefore, seagrass meadows stimulate biodiversity and, for instance, can harbour highly diverse and abundant macrobenthic communities (Boström et al., 2006).

Seagrasses are facing increasing threats resulting from natural (*e.g.,* hurricanes, diseases, heat stress, grazing by herbivores) (Shields et al., 2019) and anthropogenic (*e.g.,* eutrophication, increase in sediment loading, dredging, pollution, maritime infrastructure development) disturbances (Heuvel et al., 2019; Montefalcone et al., 2019; Orth et al., 2006; Shields et al., 2019; Short et al., 2011), which induce a dramatic global loss of seagrasses (Waycott et al., 2009). In turn, the latter results in a significant benthic biodiversity loss (Calizza et al., 2013; Hemminga and Duarte, 2000; Pillay et al., 2010) and associated function (Duffy, 2006) and profound changes in

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biogeochemical exchanges at the sediment-water interface (Delgard et al., 2016; Duarte et al., 2005) with far-reaching consequences at the landscape scale (Duffy, 2006; Heck et al., 2008). Numerous studies have compared components of vegetated and bare sediments to asses and forecast the functional impacts of seagrass loss (*e.g.*, Bernard et al., 2014; Boström and Bonsdorff, 1997; Delgard et al., 2013, 2016; Hughes et al., 2002; Pillay et al., 2010). Our understanding of the consequences of seagrass regression, based on comparisons between habitats is most likely biased as it does not fully account for the variability within seagrass meadows. For instance, an increasing number of studies have highlighted spatial heterogeneity in the structure of macrobenthic assemblages mainly due to physical parameters such as shore height, sediment characteristics and salinity (Barnes, 2010; Barnes and Barnes, 2012; Barnes and Ellwood, 2012; Barnes and Hamylton, 2016, 2013; Blanchet et al., 2004; Boström et al., 2011; Yamada et al., 2007). Considering spatial heterogeneity in seagrass meadows is crucial for understanding ecological processes controlling community structures (Burrows et al., 2009), to undertake effective conservation measures (Airoldi et al., 2008; Larkum et al., 2006) and also to better evaluate the impact of climate change on seagrass distribution (Carr et al., 2012; Wilson and Lotze, 2019).

Sea ice affects more than 250 000 km of the coastline in the northern hemisphere, (Byrne and Dionne, 2002). It represents a unique feature that plays an important role in littoral ecosystems. Sea ice has a stabilizing effect when completely formed and attached to the shore (*i.e.*, ice foot and fast ice) (Anderson, 1983). Indeed, sea ice protects the coast and intertidal areas from wave action, currents and, eventually, drifting ice (Forbes and Taylor, 1994). It also maintains a relatively stable temperature at the seafloor and thus prevents intertidal invertebrates from experiencing lethal thermal stress (Scrosati and Eckersley, 2007). On the other hand, sea ice increases disturbance levels and profoundly impacts benthic communities during its formation and disintegration (*i.e.*, when not attached to the shore) (Barnes, 1999; Carey, 1991; Conlan et al., 1998; Ellis and Wilce, 1961; Gutt, 2001; Gutt and Starmans, 2001; Smale, 2007; Smale et al., 2007). For instance, ice scouring can remove almost all macroalgae and invertebrates of rocky shores in a few days (Petzold et al., 2014). Sea ice also creates original sedimentary structures (Dionne, 1998, 1985; Forbes and Taylor, 1994) and, thus, has an indirect effect on the fauna and flora (Aitken et al., 2008; Conlan et al., 1998). One of the most apparent sedimentary structures in intertidal seagrass meadows are ice-made tidal pools (Dionne, 1985; Fig. 1C). During winter, the sediment column freezes over the first centimeters (Dionne, 1985). Frozen sediments can then bond with ice floes during low tide and be ripped off as tide-level rise. Ice-made tidal pools can be preserved over tens of years or even millennia (Dionne, 1998) thereby increasing landscape heterogeneity not only in space but also in time. Studies on the effects of ice on tidal flats have so far mainly focused on tidal marshes (Dionne, 1989).

The goal of this study was to assess the effects of ice-made tidal pools on the macrobenthic community structure in a subpolar seagrass meadow. Sediment characteristics and benthic communities have been characterized within a seagrass meadow in (1) vegetated areas, (2) first-year tidal pools (artificially created), and (3) multi-year ice-made tidal pools (> 2 years old, determined from aerial images taken in 2016). It was hypothesised that sea ice disturbance would alter the community structure of benthic macrofauna in seagrass meadows. More specifically, it was expected (1) that ice cover sharply reduced total density, biomass and species richness of the overall benthic macrofaunal community during wintertime with different seasonal dynamics between vegetated areas and tidal pools and (2) a decrease in benthic macrofauna biomass and abundance and alteration of diversity patterns in ice-made tidal pools relative to vegetated areas. Such changes would result in a decrease of biodiversity at the local scale (*i.e.,* lower α diversity in tidal pools as compared to vegetated areas) and an increase of (i) species turnover (β diversity) and (ii) biodiversity at the landscape scale (γ diversity) by generating diversified benthic communities depending on the occurrence and the age of tidal pools.

2. Materials and methods

2.1. Study site

This study took place in the Manicouagan peninsula that is located on the north shore of the Lower St. Lawrence estuary (eastern Canada) and is bordered by two rivers (Fig. 1A). The littoral of the Manicouagan peninsula is an open system exposed to currents and waves and ice foot action every winter. This subarctic location has an annual water temperature and salinity range from -2 to 24 °C and 21 to 30, respectively. A semi-diurnal tide characterizes it with an amplitude between 3 and 4.3 m and an intertidal area of 290 km^2. Sediments consist of fine to medium sand with a trend of finer sediments within a large monospecific and perennial *Zostera marina* meadow (Fig. 1B). This meadow covers about 20 % of the intertidal area and is spreading along the shore around the zero-tidal line. It is, therefore, totally emerged only during monthly spring tides. The seagrass meadow is dense (75 to 100 % of coverage) in the middle of the bed (about 15 % of the seagrass bed) and sparse (0 to 75 % of coverage) at its edge (Fig. 1B). The leaf coverage of this meadow is typically limited to five months from May to October, with a maximum leaf biomass reached in August and leaf senescence starting from September. Seeds on fruiting stems have been observed in July and August. During wintertime (typically five months, from December to April), the ice cover destroys most of the remaining seagrass leaves and remove plots of roots and rhizomes leaving long-lasting sandy tidal pools within the meadow. Ice-made tidal pools have characteristics features such as relatively high depth (typically 20 to 30 cm depth relative to the adjacent vegetated sediment) and diameter (typically 2 m but can exceed 10 m) and a micro-cliff of several centimeters at the boundary with the vegetated area (see Fig. 1C). At the study site, there was no evidence of recolonization of ice-made tidal pools by seagrasses. Using an aerial image from 2016 with a resolution of 30 cm (provided by the Canadian Department of Fisheries and Oceans), it has been estimated that within a vegetated area of 7.4 km^2 (corresponding to the dense bed of *Z. marina*), 16.9 % (1.2 km^2) of the surface shows evidences of sea ice disturbance (overall classification accuracy of 91 %; see Appendix A, Table A.1).

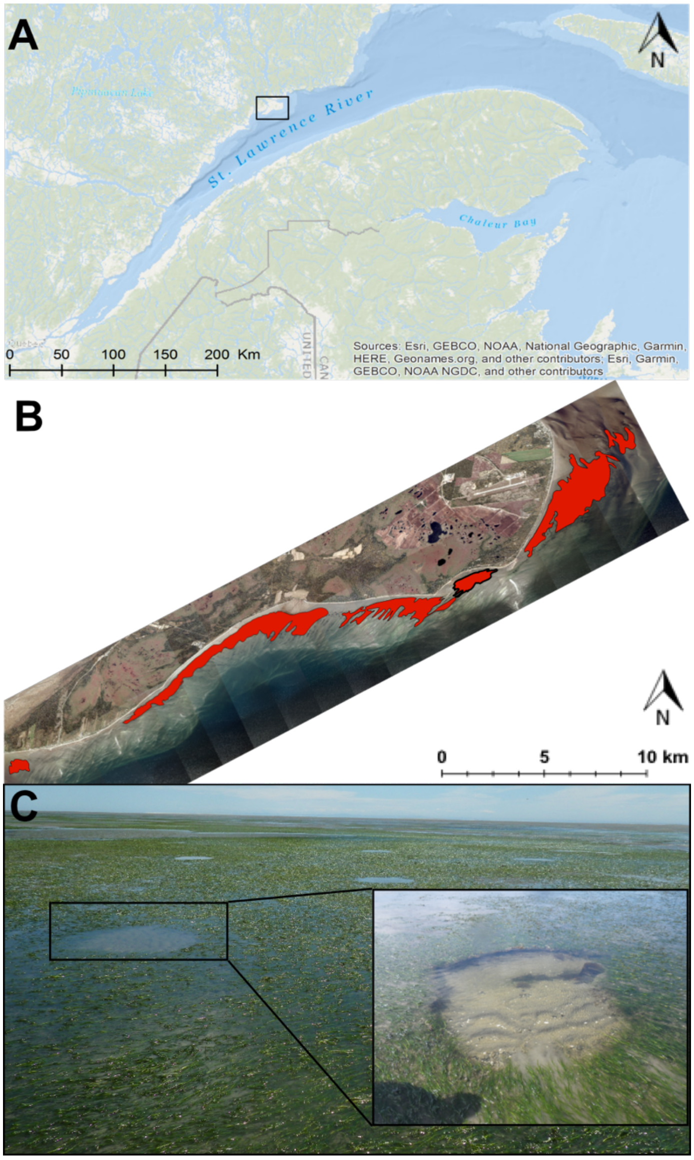

Figure 1: *Study site.* Location of Manicouagan peninsula (Québec, Canada) in the Saint-Lawrence estuary (A), aerial image of the Manicouagan peninsula, its seagrass meadow (highlighted in red) and the sampling area (circled in black) (B) and representative examples of ice-made tidal pools within the studied seagrass meadow (C). Aerial images (B) were provided by the Canadian Department of Fisheries and Oceans (2016).

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2.2. Experimental design and sampling

In April 2018, two days prior the first sampling, 20 artificial tidal pools (aTP; 2 m diameter; 0.20 m depth) were dug around the zero-tidal line in a dense area of the seagrass meadow at the study site “Plage Pointe-Paradis” (49°5.5’ N, 68°12.8’ W; Fig. 1). Another set of 20 natural tidal pools (nTP) of similar diameter and depth (1.74 to 2.37 m of diameter; 0.18 to 0.33 m depth) and at the same tidal level was selected, based on aerial images taken in 2016 (Fig 1C). It was thereby possible to estimate that the nTP selected were at least two-years old. aTP were thus considered as first-year tidal pools and the natural ones as multi-years tidal pools.

All sampling activities were done by hand at low tide, in April, June, August, and October 2018. At each sampling date, five aTP, five nTP, and five areas of vegetated sediment (V treatment) at least five meters away from each other were sampled using sediment cores (2.6 cm inner diameter, 10 cm long) and box cores (20 × 20 cm, 10 cm depth). For each replicate (*i.e.*, 15 corresponding to five V, five aTP and five nTP at each sampling date) five sediment cores and one box core were collected. The sediment cores were collected for sediment grain size, porosity (Φ), organic carbon content (OC) and total nitrogen content (TN), sediment pigments (Chl *a* and phaeopigments), and microbial analyses. Sediment from the box cores was sieved on-site onto a 0.5 mm mesh for benthic macrofauna (mainly infauna and low mobility benthic epifauna) sampling. Whenever necessary (*i.e.*, V treatment), macrofauna and seagrass were separated on-site. Six rhizons (Rhizosphere research products®) were inserted to sample sediment porewater at 0.5, 1.5, 2.5, 3.5, 5 and 7 cm depth in each treatment. Replicate samples were pooled in order to obtain enough porewater for further nutrients analysis. Porosity, OC, TN and porewater nutrient samples were stored at –20 °C until analyses. Macrofauna samples were preserved in 250 mL of a 4 %

buffered (pH 6.5) formaldehyde solution. Microbial (*e.g.*, bacteria) samples were preserved in 10 mL of 1 % filtered (0.2 µm) and buffered (pH 6.5) formaldehyde solution and stored at 4 °C until further analysis. Pigment samples were stored at –80 °C until analysis.

2.3. Sediment characteristics

The median grain size (D_{50}) of the first ten centimeters of the sediment column was assessed by laser diffraction (Malvern Instruments®, 2 µm detection limit). The sediment porosity (Φ) was also assessed by measuring the loss of water after freeze-drying and corrected for sea salt content. The total nitrogen content (TN) was measured on homogenized, freeze-dried samples using a CHNSO analyzer (Costech ECS 4010 CHNSO analyzer®; accuracy < 0.3 %). Organic carbon content (OC) was measured similarly after acidification with 2 M HCl (overnight at 50 °C) to remove carbonates. Pigments of surface sediment (one-centimeter depth) were extracted on two g of subsamples in 10 mL of 90 % acetone for 24 h. Subsamples were then centrifuged at 1000 g for 10 min and analysed fluometrically (Turner Designs10AU®) using an acidification step (5 % HCl) to separate chl *a* and phaeopigments (Riaux-Gobin and Klein, 1992). Sediment porewater samples were analysed for dissolved inorganic phosphate (PO_4^{3-}), nitrite + nitrate (NO_x), and ammonium (NH_4^+) (Coverly et al., 2009) using an AutoAnalyzer 3 HR (Seal-analytical®). Stocks of nutrients were estimated by integrating nutrients concentrations between 0 and 8 cm depth and considering the sediment-water content assessed from sediment porosity. Stocks were computed for a sediment surface of 1 $m^{2.}$

Seagrass leaves and roots/rhizomes were carefully cleaned, separated and dried at 80 °C until constant mass for estimation of above- and below- ground dry biomasses, respectively. Abundances and fluorescence (as a *proxy* of microbial assemblage structure; Bouvier et al., 2007; Schattenhofer et al., 2011) of extractible sediment bacteria were determined. For each sample, three sequential extractions were performed, allowing for the extraction of at least 95 % of extractible bacteria. 2 mL of 100 mM sodium pyrophosphate were added to the subsamples. They were then submitted to sonication (10 min) before being centrifuged for 5 min (3000 g, 20 °C). The supernatants of the three extractions were mixed. Abundances (count mL^{-1}) of extractible bacteria and bacteria fluorescence were then obtained by flow cytometry (CytoFLEX, Beckman Coulter®) following the method of Belzile et al. (2008).

2.4. Macrofauna identification

Macrofauna (epi- and infauna) was sorted and identified to the lowest possible taxonomic level (typically species level) and biomass (wet mass) were determined (± 0.0001 g). Using this macrofauna dataset, total density, total biomass, species richness and Shannon index and Piélou's evenness were calculated. The trophic group was attributed to each species using the biological traits information catalog (MarLIN, 2006).

2.5. Data treatments

Data values are given as mean (± SE). Differences in sediment characteristics (*i.e.*, D_{50}, Φ, OC, TN, OC/TN, Chl *a* and phaeopigments), bacteria abundance and fluorescence and total macrofauna density, biomass, number of species (S), Shannon index (H') as α-diversity and Piéou's evenness between treatments (three levels: aTP, nTP and V) and months (four levels: April, June, August and October) were assessed using two-way PERMANOVAs based on Euclidean distance. The design of statistical analyses consisted of two fixed factors (treatment and month) with a third random factor (replicate; n= 5 per treatment and month) nested within treatment and month. In case

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of a significant effect between fixed factors, pairwise tests were performed to characterize their modalities.

β-diversity was determined using the multivariate dispersion of each combination of treatment × month based on binary Bray-Curtis dissimilarity coefficient (Sorensen dissimilarity) (Anderson, 2006). Differences in spatial β-diversity between treatments for each month was assessed using permutation test. Differences in benthic assemblage structure were assessed using two-way PERMANOVAs (same design as above) based on Bray-Curtis dissimilarity coefficient computed from macrofaunal density and biomass. Taxa observed only once were excluded from the analyses (Clarke and Warwick, 2001). Results of pairwise comparison of PERMANOVAs are given in Appendix B. To visualise the relative differences significant source of variation, non-metric multidimensional scaling ordination (nMDS) plots based on Bray-Curtis dissimilarity coefficient were constructed. The percentage of dissimilarity and the contribution of taxa to the total dissimilarity between groups were calculated using the SIMPER procedure (Clarke, 1993). The statistical significance of the contribution of each taxon to the dissimilarity between groups was assessed using permutation test. Density and biomass data were fourth-square transformed before analyses to minimize the influence of the most dominant taxa. In case of a significant effect between fixed factors, pairwise tests were performed to characterize their modalities. The contributions of environmental factors explaining differences in benthic assemblages (based on density and biomass) were investigated using distance-based redundancy analysis (dbRDA) (Legendre and Anderson, 1999). Environmental data were standardized and checked for co-correlation using Variance Inflection Factor (VIF) values (Environmental factor with VIF < 10 were removed from the environmental data matrix). Stepwise selection was used to build models using

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Aikaike's information criterion (AIC) for variables selection. Species density and biomass were used as response multivariate data set defined using Bray-Curtis distance amongst samples. The significance of dbRDA overall model, terms and axis were tested using permutation tests. Statistical analyses were conducted using R software (ver. 3.5.0) (R Core Team 2018) and relied on "vegan" package (Oksanen et al., 2019).

3. Results

3.1. Sediment characteristics

The average and standard error values of sediment characteristics are given in Table 1. All sediments consisted of a fine to medium sand (comprised between 145.2 and 293.4 µm) with a lower median grain size (D_{50}) in V (growing season mean value = 162.6 µm), intermediate in aTP (growing season mean value = 185.9 µm) and higher in nTP (growing season mean value = 241.7 µm). Sediment porosity (ϕ) only significantly differed between treatments (Table 2) with higher values in V than in aTP (pairwise test, $p < 0.001$) and in nTP (pairwise test, $p < 0.001$). Organic carbon (OC) and total nitrogen (TN) contents significantly differed between treatments and month with a significant interaction between these two factors (Table 2). Overall, OC and TN content were higher in V than in nTP and higher in August and October than in April. OC/TN ratio significantly differed between months (Table 2) with similar values between April and June (pairwise test, $p = 0.956$) intermediate values in August (pairwise test, August vs. April: $p = 0.029$, August vs. June: $p = 0.004$, August vs. October: $p = 0.019$) and higher values in October (pairwise test, October vs. April and October vs. June: $p < 0.001$). Sediment chlorophyll *a* (Chl *a*) content significantly differed between treatments and months with a significant interaction between these two factors (Table 2). Overall, Chl *a* content tended to increase from April to October and was similar between treatments in April, lower in V than in aTP and nTP in June and August and higher in V intermediate in nTP and lower in aTP in October. Sediment phaeopigments content significantly differed between treatments and months with a significant interaction between these two factors (Table 2). Overall, phaeopigments content increased from April to October with a higher increase for V than aTP and nTP from August to October.

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Table 1: *Sediment characteristics.* Average values of median grain size (D_{50}), porosity (ϕ), organic carbon content (OC), total nitrogen (TN), organic carbon over total nitrogen ratio (OC/TN), chlorophyll *a* (Chl *a*), phaeopigments and above and below-ground seagrass biomass for each studied month (April, June, August and October) and treatments (V: vegetated areas; aTP: artificial tidal pools; nTP: natural tidal pools).

Month	Treatment	D_{50} (µm)	ϕ (volume ratio)	OC (10^{-3} %DW)	TN (10^{-3} %DW)	OC/TN (%/%)	Chl *a* (µg/g)	Phaeopigments (µg/g)	Seagrass biomass (g/m^2)	
									Above ground	Below ground
April	V	181.2 ± 1.2	0.45 ± 0.02	67.8 ± 6.4	12.4 ± 1.7	5.6 ± 0.3	4.5 ± 0.1	1.0 ± 0.1	26.1 ± 1.9	150.6 ± 11.0
	aTP	186.9 ± 1.3	0.36 ± 0.01	58.6 ± 7.3	10.3 ± 1.2	5.7 ± 0.4	4.2 ± 0.3	1.0 ± 0.2	--	--
	nTP	293.4 ± 2.1	0.37 ± 0.01	44.6 ± 8.0	7.3 ± 1.4	6.4 ± 1.6	4.1 ± 0.1	1.0 ± 0.1	--	--
June	V	159.1 ± 1.1	0.48 ± 0.00	87.1 ± 12.8	15.0 ± 1.6	5.8 ± 0.4	6.5 ± 0.2	1.6 ± 0.1	53.7 ± 3.3	172.6 ± 15.6
	aTP	191.4 ± 1.1	0.41 ± 0.01	61.2 ± 8.2	11.3 ± 1.3	5.4 ± 0.3	7.2 ± 0.1	1.6 ± 0.1	--	--
	nTP	231.8 ± 2.1	0.43 ± 0.01	61.3 ± 2.8	10.7 ± 0.5	5.7 ± 0.1	7.7 ± 0.3	1.5 ± 0.1	--	--
August	V	164.9 ± 1.2	0.48 ± 0.01	169.0 ± 11.7	21.5 ± 0.4	7.9 ± 0.5	8.1 ± 0.4	1.9 ± 0.2	229.8 ± 7.8	212.9 ± 10.4
	aTP	177.8 ± 1.3	0.43 ± 0.01	96.8 ± 12.7	14.2 ± 2.9	7.1 ± 0.4	9.1 ± 0.9	1.9 ± 0.3	--	--
	nTP	198.8 ± 1.4	0.41 ± 0.00	93.0 ± 9.2	13.5 ± 1.4	6.9 ± 0.1	8.2 ± 0.3	1.9 ± 0.1	--	--
October	V	145.2 ± 1.0	0.47 ± 0.02	132.0 ± 7.3	16.8 ± 0.6	7.9 ± 0.3	9.1 ± 0.6	3.5 ± 0.4	79.4 ± 16.0	536.1 ± 78.1
	aTP	187.6 ± 1.3	0.40 ± 0.02	85.7 ± 13.9	9.1 ± 1.2	9.4 ± 0.6	6.1 ± 1.0	2.9 ± 0.1	--	--
	nTP	242.6 ± 1.4	0.42 ± 0.01	97.3 ± 7.6	11.3 ± 1.3	8.8 ± 0.8	7.6 ± 0.7	2.4 ± 0.7	--	--

Table 2: *Data treatment.* PERMANOVA results of Treatments and Months effects on sediment characteristics (median grain size (D_{50}), porosity (ϕ), organic carbon content (OC), total nitrogen (TN), organic carbon over total nitrogen ratio (OC/TN), chlorophyll *a* (Chl *a*), phaeopigments, bacteria (Bact.) abundance and fluorescence), univariate index or macrofauna community (Total macrofauna density and biomass, species richness, Shannon diversity index (H') and Piélou's eveness (J)) and multivariate community structure based on macrofauna density and biomass. Values in bold indicate significant effect.

Source	**Treatments**				**Months**				**Treatments × Months**				**Residuals**		**Total**	
	df	SS	F	p	df	SS	F	p	df	SS	F	p	df	SS	df	SS
Sediment characteristics																
D_{50}	2	65954	3279.76	**0.001**	3	12887	427.24	**0.001**	6	14006	232.17	**0.001**	48	483	59	93330
ϕ	2	0.06	40.55	**0.001**	3	0.02	1.954	0.100	6	0.01	1.09	0.374	48	0.03	59	0.12
OC	2	0.02	40.81	**0.001**	3	0.04	51.26	**0.001**	6	0.01	4.8	**0.001**	48	0.01	59	0.08
TN	2	$3.98\ 10^{-4}$	36.91	**0.001**	3	$3.15\ 10^{-4}$	19.51	**0.001**	6	$7.50\ 10^{-5}$	2.32	**0.049**	48	$2.59\ 10^{-4}$	59	$1.05\ 10^{-3}$
OC/TN	2	0.35	0.22	0.824	3	88.55	36.48	**0.001**	6	10.33	2.13	0.068	48	38.83	59	138.07
Chl a	2	14.79	7.05	**0.002**	3	213.55	67.9	**0.001**	6	56.58	9.0	**0.001**	48	50.33	59	335.25
Phaeopigments	2	4.28	5.33	**0.005**	3	20.38	16.89	**0.001**	6	6.47	2.68	**0.025**	48	19.3	59	50.43
Bact. abundance	2	$4.49\ 10^{17}$	19.45	**0.001**	3	$3.18\ 10^{17}$	9.17	**0.001**	6	$4.82\ 10^{16}$	0.7	0.65	48	$5.55\ 10^{17}$	59	$1.37\ 10^{18}$
Bact. fluoresence	2	0.05	23.62	**0.001**	3	0.13	44.36	**0.001**	6	0.005	0.78	0.593	48	0.05	59	0.23
Univariate index																
Total density	2	$1.82\ 10^{7}$	13.61	**0.001**	3	$3.8\ 10^{7}$	18.91	**0.001**	6	$1.45\ 10^{7}$	3.6	**0.007**	48	$3.22\ 10^{7}$	59	$1.03\ 10^{8}$
Toral biomass	2	12037	0.41	0.686	3	185410	4.22	**0.008**	6	42055	0.48	0.828	48	703747	59	943248
Species number	2	0.9	17.38	**0.001**	3	3.04	39.35	**0.001**	6	0.69	4.45	**0.001**	48	1.24	59	5.86
H'	2	3.87	23.07	**0.001**	3	10.19	40.5	**0.001**	6	0.93	1.85	0.110	48	4.03	59	19.02
J	2	0.25	5.36	**0.004**	3	1.04	15.07	**0.001**	6	0.68	4.93	**0.002**	48	1.1	59	3.06
Community structure																
Density	2	2.62	15.75	**<0.001**	3	6.02	24.11	**<0.001**	6	3.38	6.78	**<0.001**	48	3.99	59	16.02

Biomass	2	2.7	13.02	**<0.001**	3	5.62	18.07	**<0.001**	6	2.66	4.27	**<0.001**	48	4.98		59	15.96

Nutrient porewater profiles are depicted in Fig. 2. Nitrite + Nitrate (NO_x) porewater concentrations reached maxima values close to the sediment surface (*i.e.*, between 0.5 and 1.5 cm depth) and decrease before to reach relatively constant (between 7.65 and 0.82 µmol L^{-1}) concentrations at 2.5 to 3.5 cm depth. In each treatment, the upper part of the profile of NO_x concentration showed seasonal changes with higher values in April (14.89, 13.60 and 35.65 µmol L^{-1} at 0.5 cm depth in aTP, nTP and V, respectively), a decrease until August (3.43, 1.28 and 5.71 µmol L^{-1} at 0.5 cm depth in aTP, nTP and V, respectively) and an increase (except for aTP) from August to October (3.33, 3.02 and 18.14 µmol L^{-1} at 0.5 cm depth in aTP, nTP and V, respectively). These seasonal changes were more marked in V than in aTP and nTP. aTP and nTP showed similar ammonium (NH_4^+) concentration profiles with minimum concentration at 0.5 cm depth between 0.95 and 14.55 µmol L^{-1} and constant increase with depth to reach a maximum value at 7 cm depth. Seasonal changes in these two treatments were more marked at depth than close to the sediment surface. A decrease of NH_4^+ concentration was observed between April and June (from 92.35 to 57.85 µmol L^{-1} and from 73.38 to 54.68 µmol L^{-1} in aTP and nTP respectively), an increase to reach maximum concentration in October (131.54 and 144.56 in aTP and nTP respectively). NH_4^+ concentrations in V were lower than in aTP and nTP with values ranging between 0.01 and 0.59 µmol L^{-1} at 0.5 cm depth and between 5.80 and 50.51 µmol L^{-1} at 7 cm depth. NH_4^+ concentration profiles in V also tended to increase with depth but to a much lower extend than in aTP and nTP. Seasonal changes were also less marked in V than in aTP and nTP with higher values at 7 cm depth in April (50.51 µmol L^{-1}) a decrease until August (5.80 µmol L^{-1}) and an increase from August to October (35.19 µmol L^{-1}). aTP and nTP showed similar phosphate (PO_4^{3-}) concentration profiles with minimum and relatively constant concentrations close to sediment surface (between 0.5 and 1.5 to 2.5 cm depth) between 0.43 and 7.48 µmol L^{-1} and constant increase with depth to reach a maximum value at 7 cm depth between 32.61 and 53.65 µmol L^{-1}. There were no clear seasonal changes in these two treatments. PO_4^{3-} concentrations in V were lower than in aTP and nTP with values ranging between 0.71 and 1.88 µmol L^{-1} at 0.5 cm depth and between 7.96 and 29.00 µmol L^{-1} at 7 cm depth. PO_4^{3-} concentration profiles in V also tended to increase with depth but to a much lower extend than in aTP and nTP. However, PO_4^{3-} concentration at 7cm showed seasonal changes in V with higher value in April (29.00 µmol L^{-1}), a decrease until August (7.96 µmol L^{-1}) and an increase from August to October (13.76 µmol L^{-1}).

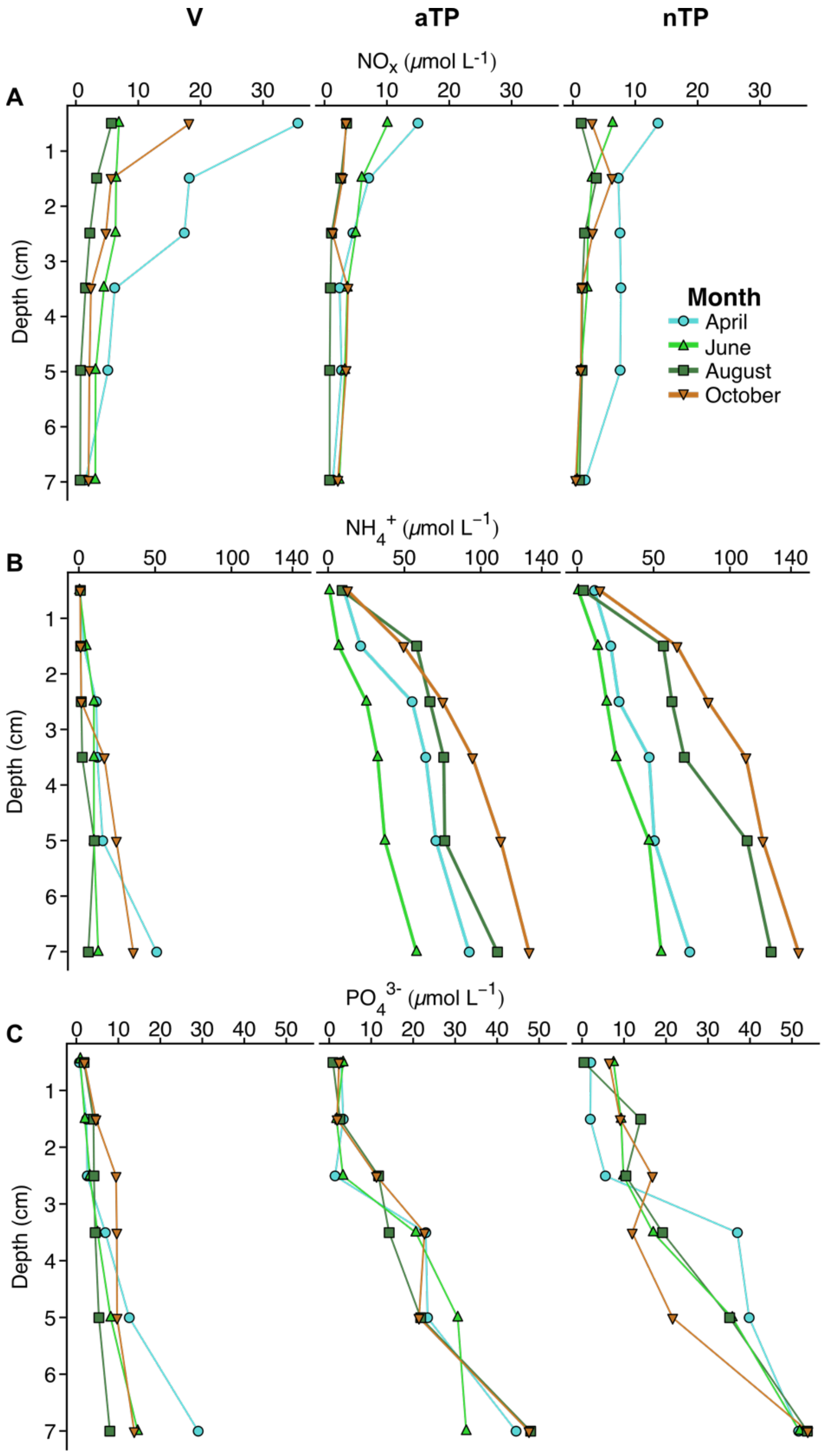

Figure 2: *Porewater*. Depth profiles of NO_x (NO_2 + NO_3^-) (A), NH_4^+ (B) and PO_4^{3-} (C) measured in (V) vegetated sediments, (aTP) artificial tidal pools and (nTP) natural tidal pools.

Sediment bacteria abundance significantly differed among treatments (Table 2) with higher values in V than in aTP (pairwise test, $p = 0.001$) and in nTP (pairwise test, $p < 0.001$) and similar values in aTP and in nTP (pairwise test, $p = 0.052$) (Fig. 3A). Sediment bacteria abundance also significantly differed among months with lower values in April than in June (pairwise test, $p < 0.001$), August (pairwise test, $p = 0.028$) and October (pairwise test, $p < 0.001$). June, August and October did not significantly differ in sediment bacteria abundance (pairwise test, $p > 0.05$ in all cases). Sediment bacteria fluorescence significantly differed between treatments (Table 2) with higher values in V than in aTP (pairwise test, $p < 0.001$) and in nTP (pairwise test, $p = 0.013$) and higher values in nTP than in aTP (pairwise test, $p = 0.009$) (Fig. 3B). Sediment bacteria fluorescence also significantly differed between months (Table 2) with higher values in October (pairwise test, $p < 0.001$ in all cases). Months of April, June and August did not significantly differ in sediment bacteria fluorescence (pairwise test, $p > 0.05$ in all cases).

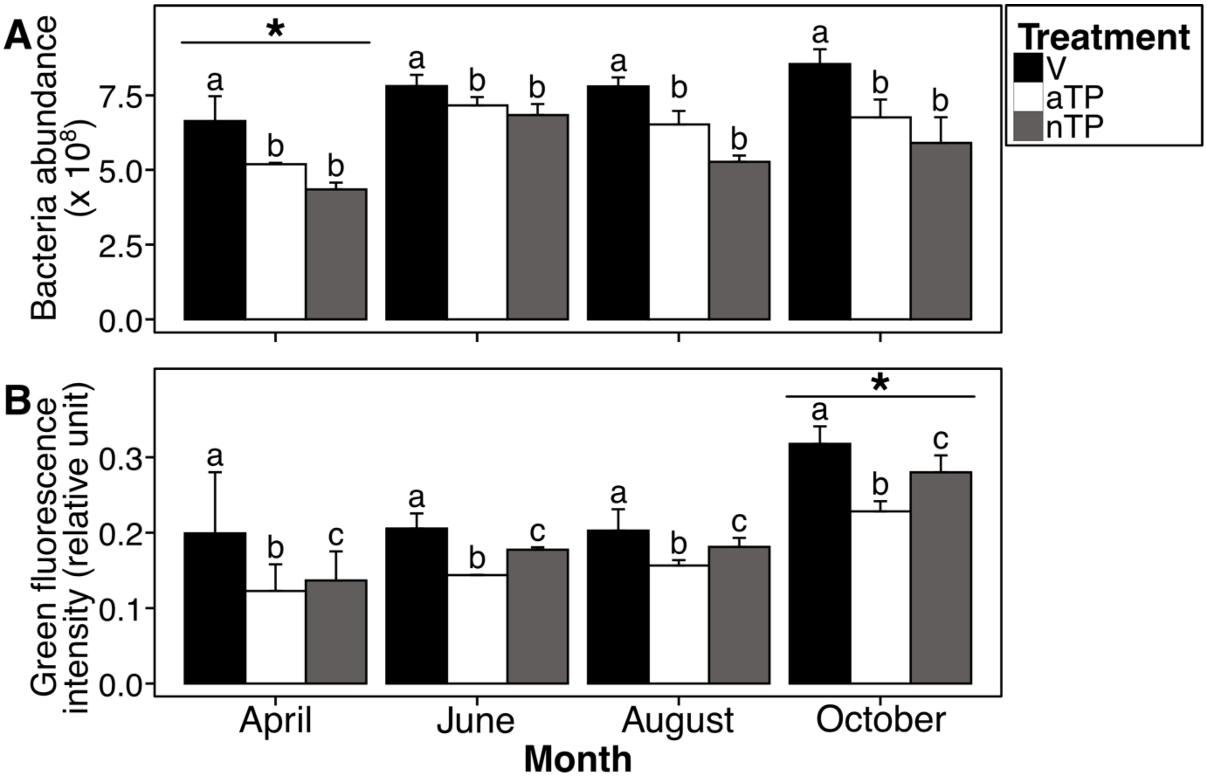

Figure 3: *Bacteria.* Mean (± SE) abundance (count mL^{-1}) (A) and fluorescence (relative unit) (B) of extractible bacteria in the sediment column. V: vegetated area, aTP: artificial tidal pool, nTP: natural tidal pool. Different letters indicate significant (pairwise test. $p < 0.05$) differences between treatments. * indicates significant (pairwise test. $p < 0.05$) differences between months.

Total seagrass biomass (V treatment) increased from April to October. Seagrass leaves biomass represented 14.8, 23.7, 51.9 and 12.9 % of the total biomass in April, June, August and October, respectively (Table 1).

3.2. Macrobenthic community characteristics

A total of 3 675 individuals, from 60 stations (*i.e.* 3 treatments × 5 replicates × 4 months) were sorted and 24 taxa were identified. After removing taxa observed only once (*Spio cf. theeli, Cistenides granulata*, *Scoloplos* sp. and *Pygospio* sp. corresponding to 17 % of the total number of species) the data matrix still gathered 99.9 % of total abundance. This resulted in a data matrix of 60 stations × 20 species.

3.2.1. Density, biomass, richness and diversity

Means and standard errors of total density and biomass, species richness, and Shannon diversity index of macrobenthic fauna are depicted in Fig. 4. Total density significantly differed between treatments and months with a significant interaction between these two factors (Table 2 and Fig. 4A). Total density was overall higher in V than in aTP and nTP (except in August where values did not significantly differ) (Fig. 4A). Total density within V significantly increased between April and June and then tended to increase from June to October. At each month, there was no significant difference in total density between aTP and nTP (Fig. 4A). Total density within these two treatments significantly differed between months with lower values in April, intermediate in June and October and higher in August (Fig. 4A).

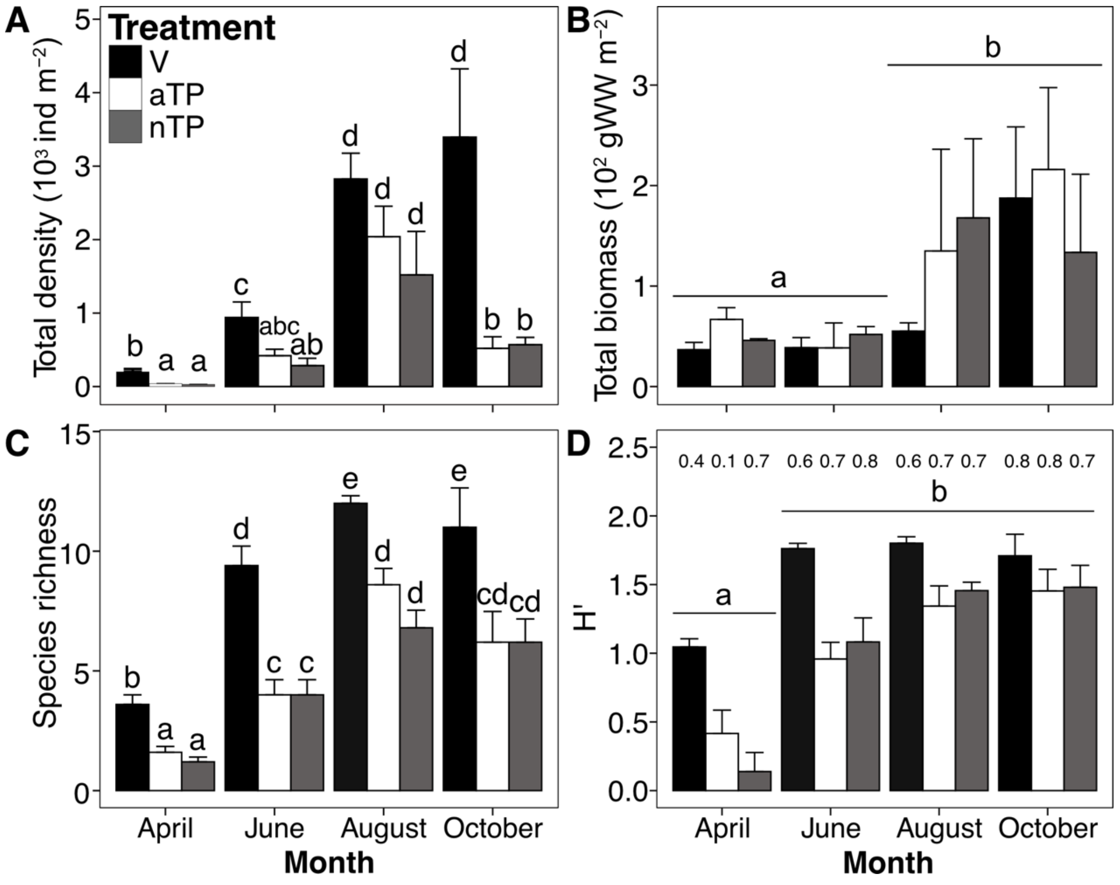

Figure 4: *Univariate descriptors.* Mean (± SE) total density (A). biomass of macrofauna (B). number of species (C) and Shannon index (H') with Piélou's evenness values in each treatment and at each sampling month. Different letters indicate significant (pairwise test. $p < 0.05$) differences between combinations of treatments (V: vegetated areas. aTP: artificial tidal pools. nTP: natural tidal pools) and months. Lines indicate significant (pairwise test, $p < 0.05$) differences between months.

Total biomass only significantly differed between months (Table 2) with higher total biomass in October and August than in April (pairwise test, October *vs.* April: p = 0.014; August *vs.* April: p = 0.043) and June (pairwise test, October *vs.* June: p = 0.006; August *vs.* June: p = 0.046) (Fig. 4B).

Species richness significantly differed between treatments and months with a significant interaction between these two factors (Table 2 and Fig. 4C). Species richness

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was overall higher in V than in aTP and nTP without significant differences between the latter two (Fig. 4C). Species richness tended to increase from April to August and stabilized until October in every treatment (Fig. 4C).

Shannon diversity index (α diversity) significantly differed between treatments and months (Table 2 and Fig. 4D). Shannon diversity index was overall higher in V than in aTP and nTP and it was lower in April than in June, August and October (Fig. 4D). Pielou's evenness index significantly differed between treatments and months with a significant interaction between these two factors (Table 2 and Fig. 4D). Differences were due to relatively low Pielou's evenness index in ice-made tidal pool in April (0.4 and 0.1 for aTP and nTP, respectively) as compared to values (between 0.6 and 0.8) of all other combination of treatments and months (Fig. 4D).

β diversity did not significantly differ between treatments in April (permutation test, F = 2.383, p = 0.137), June (permutation test, F = 0.0097, p = 0.989), August (permutation test, F = 0.9317, p = 0.409), and October (permutation test, F = 0.9444, p = 0.416).

3.2.2. Community structure

The results of non-metric multidimensional scaling (nMDS) based on density data matrix suggested that species assemblages differed between treatments and months (Fig. 5A). PERMANOVA results confirmed this, showing significant interaction effect of treatments and months on the mean species assemblages (Table 4). Overall, there were clear differences between (1) April and the other months for each treatment in terms of mean species assemblage and (2) V and tidal pools (*i.e.* aTP and nTP) (Fig. 5A and Table S3). Macrofauna biomasses also differed between treatments and months (Fig. 5B). This was also confirmed by PERMANOVA results showing significant interaction effect of treatments and months on the mean species assemblage (Table 2).

Macrofaunal biomasses species assemblage showed an overall pattern similar to the one for density (Table S1 and S2).

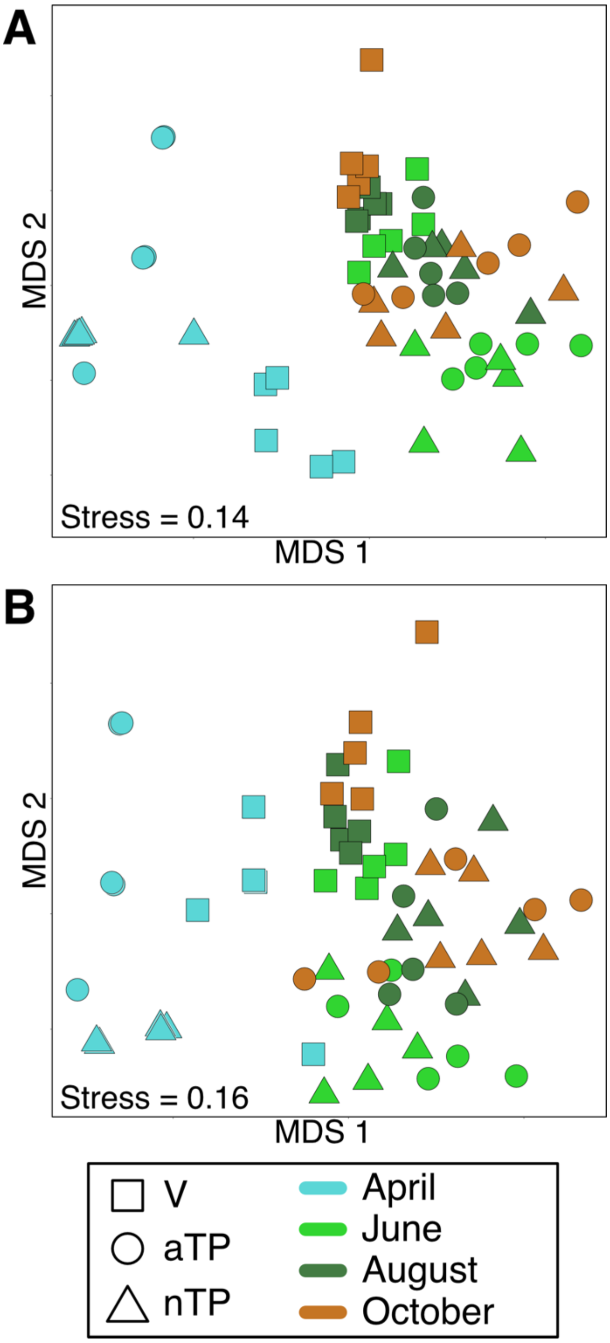

Figure 5: *MDS.* Non-metric multidimensional scaling ordination of macrofauna composition based on fourth rout-transformed data of density (A) and biomasses (B). V: vegetated area; aTP: artificial tidal pool; nTP: natural tidal pool.

SIMPER analysis based on macrofaunal density showed that, overall, dissimilarities between V and tidal pools (*i.e.,* aTP and nTP) were mostly due to

Oligochaetes, the three polychaetes *Paraexogon hebes*, *Spio filicornis* and *Diplolydora socialis* gr., the two amphipods *Gammarus oceanicus* and *Phoxocephalus holbolli*, the Isopod *Jaera* (*Jaera*) *albifrons*, the two bivalves *Limecola* (as *Macoma*) *balthica* and *Mytilus* sp. and the two gastropods *Littorina obusata* and *L. saxatilis* (Table 3). Overall, dissimilarities between aTP and nTP were mostly due to the polychaetes *Alitta virens* and *Arenicola marina*, the amphipod *G. lawrencianus* and *Wecomedon* (as *Psammonyx*) *nobilis* and the bivalve *L. balthica* (Table 3). SIMPER analysis based on macrofaunal biomasses showed a similar overall pattern relative to the one calculated for macrofaunal density; the exceptions were the Polychaete *A. virens* which contributed significantly to the dissimilarity between V and aTP in addition to the dissimilarity between aTP and nTP, *A. marina* which did not contribute significantly to the dissimilarity between aTP and nTP and *L. balthica* which did not contribute to dissimilarities between treatments (Table 3).

Table 3: *SIMPER analyses*. List of species with their mean density, biomass and contribution to dissimilarity between treatments (aTP: artificial tidal pool. nTP: natural tidal pool. V: vegetated area). The five-dominant species in terms of density. biomass and contribution to dissimilarity (SIMPER analyses) between treatments are in bold. (O): Oligochaete; (P): Polychaete; (A) Amphipod; (I): Isopod; (B): Bivalve; (G): Gastropod; (N): Nemerts; (S): Sipunculids. e indicates epifauna. other species are infauna. Trophic groups: DF: deposit feeder; P: predator; S: scavenger; G: grazer; SF: suspension feeder. * indicates significant contribution

Taxon	**Trophic group**	**Density (ind. m^{-2})**			**Biomass (gWW m^{-2})**			**% contribution to dissimilarity between groups** **Density (fourth-root)**						**Biomass (fourth-root)**					
		V	aTP	nTP	V	aTP	nTP	V *vs.* aTP	p	V *vs.* nTP	p	aTP *vs.* nTP	p	V *vs.* aTP	p	V *vs.* nTP	p	aTP *vs.* nTP	p
Oligochaetes (O)	DF	**293.8**	32.5	36.3	0.1	0.0	0.0	8.4	*	8.5	*	7.2		2.98	*	3.05	*	2.18	
***Parexogone hebes* (P)**	P	48.8	15.0	0.0	0.0	0.0	0.0	4.6	*	4.3	*	2.5		1.42	*	1.35	*	0.64	
***Alitta virens* (P)**	P	48.8	8.8	2.5	**3.8**	**10.3**	0.0	5.5		5.3		7.4	*	8.84	*	6.83		9.14	*
***Nephtys caeca* (P)**	P	22.5	11.3	1.5	**16.8**	**11.7**	**13.2**	4.8		4.9		6.3		11.34		11.74		12.15	
***Spio filicornis* (P)**	DF	12.5	1.3	2.5	0.0	0.0	0.0	4.1	*	4.2	*	1.3		1.59	*	1.67	*	0.52	
***Eteone longa* (P)**	P	25.0	8.8	13.8	0.1	0.0	0.1	4.1		4.2		4.2		2.57		2.84		2.51	
***Arenicola marina* (P)**	DF	2.5	5.0	8.8	1.1	**15.5**	**12.8**	2.6		4.0		7.7	*	5.85		8.94		4.06	
***Dipolydora socialis gr.* (P)**	DF	6.3	0.0	0.0	0.0	0.0	0.0	1.2	*	1.2	*	0.0		0.57	*	0.59	*	0	
***Gammarus lawrencianus* (A)^{e}**	S	52.5	**368.8**	**175.0**	0.11	1.2	0.6	7.6		6.7		13.1	*	5.88	*	9.15		7.47	*
***Gammarus oceanicus* (A)^{e}**	G	**156.3**	0.0	0.0	**5.4**	0.0	0.0	7.1	*	7.1	*	0.9		8.74	*	5.31	*	0.4	
***Wecomedon nobilis* (A)^{e}**	S	5.0	**82.5**	**56.3**	0.1	**7.8**	**4.9**	7.0		6.3		10.9	*	9.27		7.88		11.38	*
***Phoxocephalus holbolli* (A)^{e}**	S	11.2	0.0	0.0	0.0	0.0	0.0	1.3	*	1.3	*	0.0		0.78	*	0.8	*	0	
***Jaera (Jaera) albifrons* (I)^{e}**	G	**80.0**	0.0	0.0	0.0	0.0	0.0	3.4	*	3.4	*	0.0		1.31	*	1.33	*	0	
***Limecola balthica* (B)**	DF	**563.8**	**85.0**	**165.0**	**9.0**	2.6	**2.6**	9.3	*	9.4	*	11.7	*	8.11		8.09		8.71	
***Mytilus sp.* (B)^{e}**	SF	58.8	36.3	21.3	**35.3**	1.0	0.7	6.8	*	7.1	*	5.4		8.37	*	8.63	*	4.32	
***Mya arenaria* (B)**	SF	55.0	**57.5**	**56.3**	1.8	**61.5**	**68.9**	5.5		5.5		9.3		7.97		9.05		14.89	
***Littorina saxatilis* (G)^{e}**	G	**330.0**	**37.5**	**47.5**	1.9	0.2	0.5	8.7	*	8.8	*	7.0		6.67	*	6.84	*	4.24	
***Littorina obusata* (G)^{e}**	G	62.5	2.5	5.0	0.4	0.0	0.5	6.5	*	6.5	*	2.7		3.73	*	4.15	*	2.31	
Nemerteans (N)	P	3.8	1.3	0.0	1.5	3.2	0.0	0.9		0.4		1.2		3.38		0.93		3.83	
Sipunculans (S)	DF	1.3	1.3	2.5	0.0	0.1	0.1	0.6		0.9		1.3		0.63		0.83		1.25	

After verification of co-correlation using VIF and a stepwise analysis, only the variables Chl *a*, NOx, seagrass biomass, PO_4^{3-} and NH_4^+ were used in the model to construct the dbRDA based on macrofaunal density (Permutation ANOVA, $F = 11.534$, $p < 0.001$). This model explained 49.1 % of the total variation and the first two axes of dbRDA explained 47.3 and 28.6 %, respectively, of the variation of fitted model (Fig. 6A). The highest sources of variability were Chl *a* followed by NO_x on the axis dbRDA 1 and seagrass followed by PO_4^{3-} on the axis dbRDA 2, showing the importance of these variables for density-based species assemblages.

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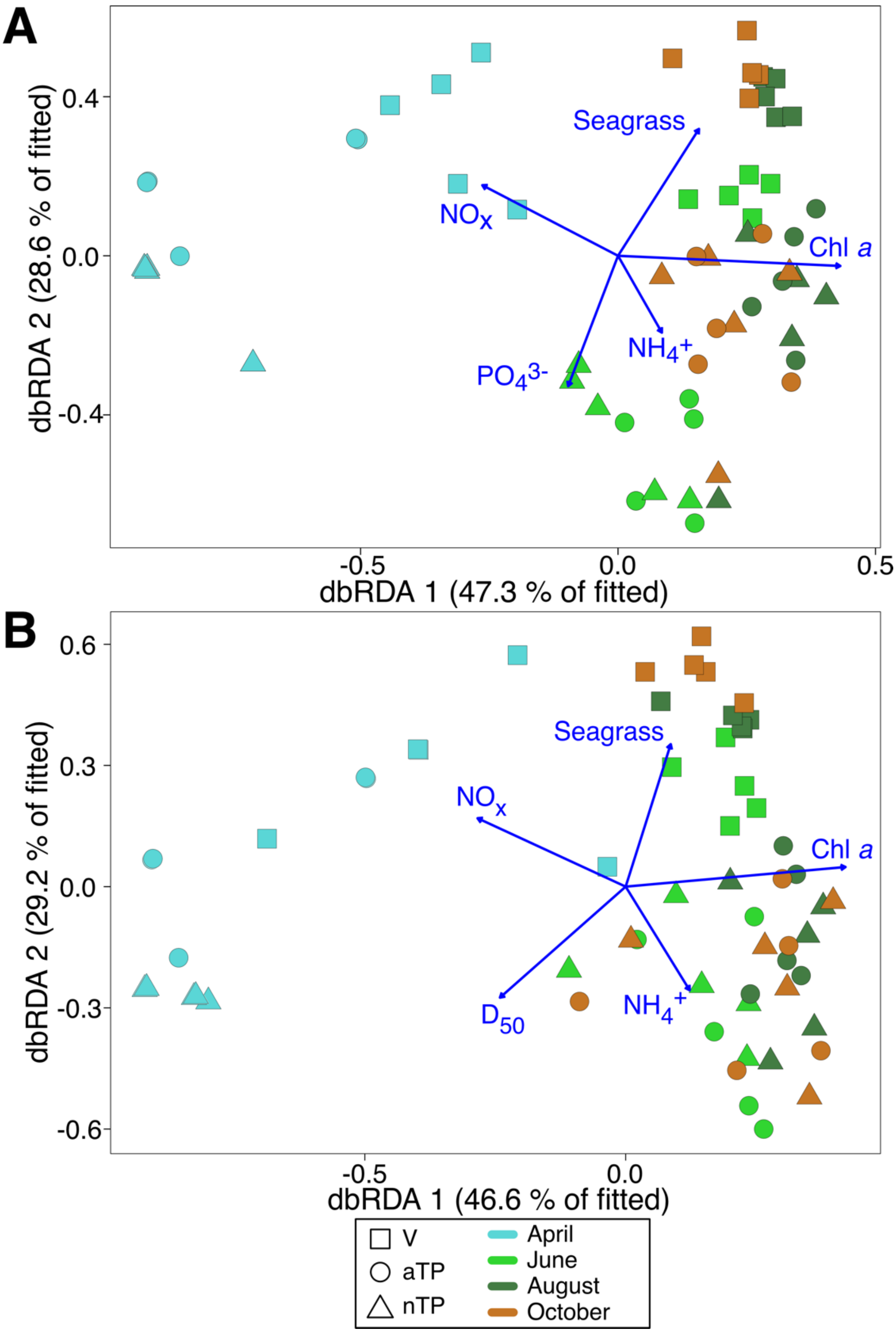

Figure 6: *dbRDA analyses.* Distance-based redundancy analysis ordinations of the combination of sampled treatments and months based on macrofaunal density (A) and biomass (B). Selected environmental parameters after checked for co-correlation are depicted by blue arrows. V: vegetated areas; aTP: artificial tidal pools; nTP: natural tidal pools

As above, after verification of co-correlation using VIF and a stepwise analysis, only the variables Chl *a*, seagrass biomass, D_{50}, NO_x and NH_4^+ were used in the model to construct the dbRDA based on macrofaunal biomasses (Permutation ANOVA, F = 10.848, $p < 0.001$). This model explained 45.5 % of the total variation, and the first two axes of dbRDA explained 46.6 and 28.2 %, respectively, of the variation of fitted model (Fig. 6B). The highest sources of variability were Chl *a* followed by NO_x on the axis dbRDA 1 and seagrass followed by D_{50} and NH_4^+ on the axis dbRDA 2, showing the importance of these variables for biomass-based species assemblages.

4. Discussion

4.1. Community structure

Mean macrofauna densities (ranging from 316.7 ind. m^{-2} in April to 3 400 ind. m^{-2} in October) and species richness (ranging from 1.6 species m^{-2} in April to 12.2 species m^{-2} in August) of the seagrass meadow of Manicouagan peninsula were consistent with those reported by Lalumière et al. (1994) in seagrass meadows in James Bay (Canada) but relatively low compared to those found for other seagrass meadows of the Northern Atlantic (typically ranging from 2 000 to 30 000 ind. m^{-2} and 10 to 60 species m^{-2}; Blanchet et al., 2004; Boström and Bonsdorff, 1997; Boyé et al., 2017; Orth, 1973; Tu Do et al., 2011). Relatively low species richness and abundance in subpolar and polar areas are mainly due to the short duration of the growing season and the harshness of the climate (Lalumière et al., 1994; Mattila et al., 1999; Setchell, 1935; Virnstein et al., 1984).

The seagrass meadow of the Manicouagan peninsula exhibits a heterogeneous landscape with vegetated areas intercepted by ice-made tidal pools representing almost

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17 % of the meadow's surface as estimated on aerial images (Fig. 1B). Our results showed that species assemblages in tidal pools (aTP and nTP) were significantly different from the ones in vegetated areas. These differences in species assemblages were mainly correlated to the occurrence of seagrass, lower stocks of NH_4^+ and PO_4^{3-} in vegetated areas, and coarser sediments in tidal pools (Fig. 6). Such differences between vegetated areas and tidal pools can be explained by the fact that during the formation of a tidal pool by sea ice, several centimeters of the sediment column are removed as well as seagrass roots and rhizomes. Ice-made tidal pools act then as a small catchment basin for detritus such as seagrass leaves (Figure 7), shells and small pieces of wood (Dionne, 1998, 1985). This probably reduces light penetration and increase the concentration of reduced solutes (*e.g.*, NH_4^+, H_2S) in the sediment through detritus decomposition in tidal pools. Additionally, ice-made tidal pools increase the difference in sediment texture, which becomes coarser than in the vegetated area by getting closer to the adjacent bare surfaces. Altogether, this generates adverse conditions for seagrass growth and seeds germination, preventing tidal pools from recolonization by seagrass. Nutrients consumption by plants can explain lower porewater NH_4^+ and PO_4^{3-} concentrations measured in vegetated areas. Seagrasses have also the ability to transfer oxygen to below-ground tissues (Borum et al., 2006) where radial loss of oxygen from roots occurs (Frederiksen and Glud, 2006), increasing nitrification rates and enhancing the precipitation of iron-oxyhydroxide and associated PO_4^{3-} (Deborde et al., 2008; Delgard et al., 2013). Enhancing nitrification rates is consistent with the higher NO_x and the lower NH_4^+ porewater concentrations in V than in aTP and nTP (Fig. 2A and B) and the precipitation of iron-oxyhydroxyde and associated PO_4^{3-} is consistent with the lower PO_4^{3-} porewater concentration in V than in aTP and nTP. Oxygenated areas around seagrass below-ground tissues also act as a protection against reduced solutes

such as sulfides (Penhale and Wetzel, 1983) which may affect the survival of seagrasses (Holmer and Bondgaard, 2001), sensitive macrofaunal organisms (Kristensen and Kostka, 2005) but also of the bacteria community (Dale, 1974). Thus, our results highlighted the occurrence of two self-sustained habitats within the seagrass meadow (*i.e.*, vegetated areas and tidal pools).

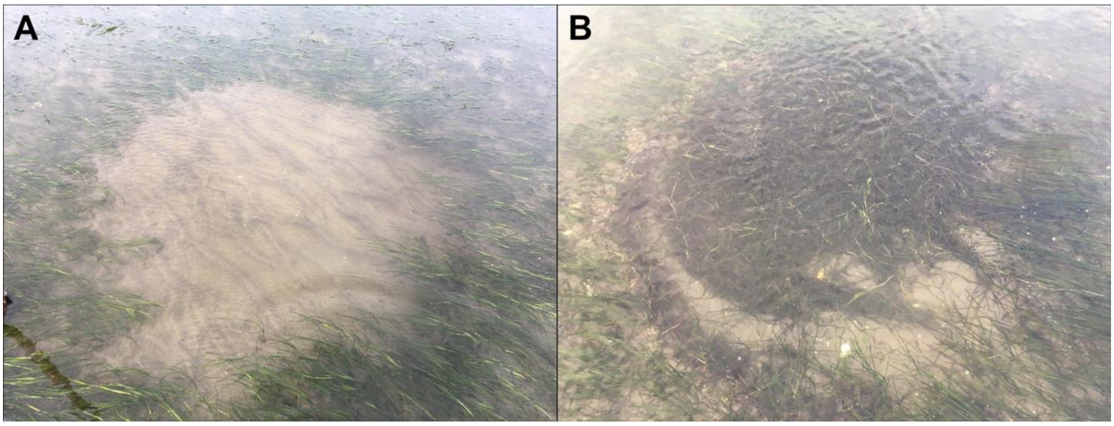

Figure 7: An ice-made tidal pool in June (A) and with seagrass detritus in October (B)

Species assemblages in tidal pools (aTP and nTP) represented a subset of species assemblages of vegetated areas. Indeed, the polychaete *Dipolydora socialis* gr., the amphipods *Gammarus oceanicus* and *Phoxocephalus holbolli* and the isopod *J. albifrons* were found exclusively in vegetated areas, but no species was exclusively found in tidal pools. Therefore, the presence of tidal pools did not affect β- and γ-diversity of macrofaunal at the landscape scale. Scavengers and deposit feeders species such as *Gammarus lawrencianus* and *Wecomedon nobilis* and *Arenicola marina* were, however, found in higher densities in tidal pools (Table 3). This suggests that ice-made tidal pools were preferentially inhabited by scavenging and deposit feeding species. The increase in abundance of scavenging and deposit feeding species is a common response in disturbed areas due to accumulation of detritus (*e.g.*, Callier et al., 2009; Pearson and Rosenberg, 1978; Thrush and Dayton, 2002). It is worth noting that *A. marina* and seagrasses have antagonist effects (*i.e.*, biomechanical warfare) and commonly exclude each other (Philippart, 1994). Indeed, studies have documented that the presence of *A. marina* inhibited the growth of seagrass but also the other way around, that seagrass presence reduced adult lugworm density (Philippart, 1994; Suykerbuyk et al., 2012; Valdemarsen et al., 2011). Therefore, the occurrence of *A. marina* in tidal pools likely contributes to the maintenance of these structures (van der Heide et al., 2012).

Tidal pools also seemed to favor larger organisms. Although macrofauna total density was always higher in vegetated areas, total biomass was not significantly different between treatments and even tended to be higher in tidal pools than in vegetated areas in August (Fig. 4B). This suggests that individual biomass was higher in tidal pools than in vegetated areas. This was particularly obvious for the polychaete *A. virens* and the bivalve *M. arenaria* and to a lower extent for the polychaete *A. marina* (Table 4). These results may be surprising at first since disturbances, especially by ice scouring, usually lead to reduced biomass (Gutt, 2001; Pearson and Rosenberg, 1978). Indeed, Conlan et al. (1998) found that ice scouring in muddy bare sediments removed or impaired large organisms and therefore, leaving ice scours dominated by small polychaetes and crustaceans. Peck and Bullouch (1993) found similar results, with a dominance (86 %) of small individuals of the bivalve *Yoldia eightsi*, at sites of muddy bare sediments exposed to ice scouring, while sites less exposed had only 27 % of individuals smaller than 10 mm in length. Contrary to the studies mentioned above, the present study focused on the seagrass landscape in which seagrasses and large infauna usually tend to exclude each other (Philippart, 1994; Suykerbuyk et al., 2012; Valdemarsen et al., 2011). Indeed, the dense roots and rhizomes of seagrasses prevent large organisms, such as polychaetes and bivalves, from burrowing and greatly decrease their mobility (Brenchley, 1982). Ice-made tidal pools, within seagrass meadows, thus probably act as shelters for larger individuals. Furthermore, because of their structure and location within the seagrass meadow, these tidal pools catch detritus from the adjacent seagrass meadow (see above), thus providing probably sufficient supply in organic material to its inhabitants. The absence of roots and rhizomes may also increase predation pressure by allowing large organisms such as *A. virens* to penetrate more efficiently within the sediment, thereby reducing the abundance of small prey.

The effect of tidal pools formation by sea ice extended up to the bacteria compartment. Indeed, bacteria were more abundant in vegetated areas than in tidal pools (Fig. 3). This result is consistent with the particulate organic carbon and total nitrogen content which are also higher in vegetated areas than in tidal pools. Bacteria community structure (based on bacteria fluorescence) significantly differed between vegetated areas and tidal pools. Seagrass meadows are known to shape their associated microbial community for their benefit (Tarquinio et al., 2019), which supports the hypothesis that seagrasses generate positive feedback for their maintenance (see above). Contrary to macrofauna, bacteria communities differed between tidal pools with larger bacteria in nTP than aTP throughout the year. By removing the first centimeters of the sediment, sea ice exposed previously suboxic or anoxic sediment to oxygen and such drastic environmental change (*i.e.* recently exposed sediment to oxygen) could explain the differences between these two treatments. Despite the difference in bacteria communities between aTP and nTP, the similarity in nutrients porewater profiles between these two treatments (Fig. 3B) did not support that they supported different microbial-mediated biogeochemical processes. Further studies using molecular tools are needed to investigate more precisely the impact of sea ice on bacteria communities and the biogeochemical processes they mediate.

4.2. Seasonal changes

Seagrass growth was limited to few months from May to August. During wintertime and springtime (from December to April), not only tidal pools could be created, but sea ice removed most of the seagrass leaves. The leaf biomass was thus minimum in April just after sea ice break-up, and it increased gradually to reach its maximum in August to finally drastically decrease in October. Associated with the increase of leaf biomass, we observed a decrease of sediment grain size and an increase of particulate organic carbon (OC) and total nitrogen (TN) (Table 1). With their dense canopy, seagrass meadows are known to attenuate hydrodynamics and thereby to enhance the deposition of fine organic-rich particles at the sediment surface and preventing their resuspension (Hemminga and Duarte, 2000; van Katwijk et al., 2010). It is worth noting that the depth (10 cm) of the sediment core used in this study probably diluted this effect, which is localised at the sediment surface. Roots and rhizomes biomass increased slightly from April to August and sharply increased from August to October. In a comparative analysis of *Z. marina* meadows in the northern hemisphere, Duarte and Chiscano (1999) found similar values of leaf biomass; however roots and rhizome biomass was higher in the present seagrass meadow. During periods of positive carbon balance, *i.e.*, during summertime when photosynthesis rates exceed the ones of respiration and growth, seagrasses produce carbohydrates (*e.g.,* starch), which are re-allocated to rhizome for long-term storage (Olivé et al., 2007). During winter, the carbon balance becomes negative, and seagrasses only rely on such reserves for their survival (Govers et al., 2015). In the present study, seagrasses have certainly acclimated to accumulate large quantities of carbohydrates in their rhizome to cope with the long (typically six months) and harsh winter season. This hypothesis is coherent with the

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large discrepancy in roots and rhizome biomass between October and April, suggesting that carbohydrates were effectively consumed during wintertime.

Intertidal areas are exposed to a high level of ice scouring during wintertime and springtime, which causes high mortality of benthic organisms. After sea ice collapsed, in April, very few species were found, such as polychaetes (mainly *A. virens*, *N. caeca* and *A. arenicola*), bivalves (*Mytilus* sp. And *M. arenaria*) and the gasteropod *L. obusata*. As a fine crust of ice was partially covering the sampling area, other species (found later in the year) were probably located in more protected areas or deeper within the sediment column. Indeed, macrofauna species developed different strategies to survive the harsh winter season. For instance, polychaetes mainly burrow deep into the sediment (Gordon and Desplanque, 1983) while others, mainly bivalves, can survive being frozen (Gordon and Desplanque, 1983; Medcof and Thomas, 1974). A third strategy for macrofauna is to rest or develop in protected areas (*e.g.*, move farther from the coast to avoid ice, increase the duration of larval stage) during wintertime and to successfully recruit during summertime (Gordon and Desplanque, 1983). During the present study, the recruitment started between April and June and ended between June and August as suggested by the increase in total density and species richness between April and August for both, vegetated areas and tidal pools (Fig. 4A and C). In vegetated areas, the total density remained stable between August and October while it decreased in tidal pools over the same period. This decrease was not associated with a decrease in total biomass nor species richness (Fig. 4B and C) suggesting that, in tidal pools, small individuals were lost during this period. Small individuals may either migrate (if mobile enough) toward vegetated area or died due to adverse conditions in tidal pools or to increase of predation pressure by large organisms (see above).

4.3. Ecological implications

The disturbance generated by sea ice led to tidal pools and results in a reduction of the density and diversity of macrobenthic community as compared to vegetated areas. Although some species preferentially inhabited ice-made tidal pools, none was specific. Contrary to the prediction by the intermediate disturbance hypothesis (*e.g.*, Connell, 1978; Huston, 1979), the formation of tidal pools by sea ice did not lead to an increase of biodiversity at the landscape scale. This was probably because the study site presents rather homogeneous sediments both at the surface and stratigraphically so that the new surface of the ice-made tidal pool is also dominated by sand. Although dramatic, the formation of ice-made tidal pools probably did not affect an area large enough, as compared to the surface of vegetated sediments, to induce a catastrophic shift in community structure. However, it is important to consider ice-made tidal pools in the assessment of community structure or the functioning of seagrass meadows, since they increase the benthic habitat heterogeneity at the landscape scale. Ice-made tidal pools supported, indeed, a different community structure associated with changes in abundances of some macrobenthic species and bacteria communities. For instance, vegetated areas were dominated by bivalves and gastropods while ice-made tidal pools were rather dominated by amphipods (Table 3) and vegetated areas supported more abundant and larger bacteria than tidal pools. This result suggests that, at least at the local scale, vegetated areas and tidal pools supported different food webs and microbial mediated biogeochemical processes, as supposed by the vertical distribution of nutrients within the sediment column. Moreover, ice-made tidal pools supported organisms with a larger size than the ones in vegetated area. Thus, sea ice contributed to enlarge the size spectrum and changed the distribution of biomass of benthic macrofauna species associated to seagrass meadows at the landscape scale. Body size is a “master trait” of organisms and plays a significant role in ecology (Andersen et al., 2016 and references therein). Body size is linked to numerous life-history traits such as metabolism, growth rate, productivity and reproduction. During their growth, large organisms pass through different trophic levels related to their size, increasing food web complexity as compared to small sized organisms (Brose et al., 2017). Larger organisms also allow a more efficient energy transfer through the food web enhancing system stability (Yvon-Durocher et al., 2011). Moreover, larger organisms have a greater impact on sediment bioturbation intensity with far-reaching consequences on ecosystem functioning (Norkko et al., 2013; Séguin et al., 2014; Solan et al., 2004).

Polar and sub-polar ecosystems are characterized by the presence of sea ice, if not permanent, for an extended period of the year. However, sea ice does not occur only in these regions but can also affect temperate ecosystems during cold winters. In this context, it may prove interesting to investigate the effect of such an event on the benthos of temperate seagrass landscape. With the ongoing climate change, several studies have reported a loss of sea ice in the Arctic (Perovich and Richter-Menge, 2009; Stroeve et al., 2014) and a decrease in sea ice thickness increasing the frequency of sea ice formation and disintegration (Lindsay and Schweiger, 2015; Perovich and Richter-Menge, 2009; Stroeve et al., 2014). Therefore, it is likely that ice-made tidal pools are and/or will occur in Arctic with similar effects on the spatial heterogeneity of seagrass meadows. It is worth noting that other disturbances may generate pools, pits or hollows, such as waterfowls foraging (Rivers and Short, 2007; Santos et al., 2012), with potentially similar effects on the benthos as those reported in the present study.

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5. Conclusions

Sea ice has profound effects on the heterogeneity of the benthic community structure of seagrass meadows in time and space. First, the macrobenthic community displayed a strong seasonality with reduced total density, biomass and species richness during the wintertime due to the presence of sea ice cover. Second, sea ice allows the appearance of ice-made tidal pools within the seagrass meadow. These tidal pools had long-lasting consequences on the benthic community structure of seagrass meadows (see graphical abstract). Two months after the appearance of ice-made tidal pools, the benthic macrofauna community structure of first-year tidal pools was similar to one of multi-year tidal pools, suggesting that tidal pools are an alternative stable state of seagrass meadows. At the tidal pool scale, sea ice disturbance resulted in an impoverishment of benthic macrofauna (α) diversity and a change in abundance patterns relative to vegetated areas. Contrary to our expectations, tidal pools supported similar total biomasses as compared to vegetated areas and thus higher individual biomasses. Therefore, the appearance of ice-made tidal pools in the seagrass meadow did not result in an increase of macrobenthic species turnover (β diversity) and γ diversity at the landscape scale but contributed to enlarge the size spectrum of some species with likely far-reaching consequences on ecosystem stability and functioning. In the context of global change and increasing disturbance, it is most likely that vegetated areas and tidal pools will respond differently to disturbances given the difference in community structure. Also, the spatial heterogeneity at the landscape scale will need to be considered to better understand the functioning of seagrass ecosystems and better predict the functional consequences of seagrass loss.

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