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## International Journal of Sediment Research

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## Original Research

## Relationship between apparent redox potential discontinuity (aRPD) depth and environmental variables in soft-sediment habitats

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## ARTICLE INFO

## Article history:

Received 14 November 2016

Received in revised form

23 March 2017

Accepted 11 September 2017

Available online 14 September 2017

## ABSTRACT

As global temperatures increase and dissolved oxygen (DO) content decreases in marine systems, indices assessing sediment DO content in benthic habitats are becoming increasingly useful. One such measure is the depth to the apparent redox potential discontinuity (aRPD), a transition of sediment color that serves as a relative measure of sediment DO content. We examined spatiotemporal variation of aRPD depth, and the nature of the relationships between aRPD depth and biotic (infauna and epibenthic predators) and abiotic variables (sediment properties), as well as the availability of resources (chlorophyll *a* concentration, and organic matter content) in the intertidal mudflats of the Bay of Fundy, Canada. aRPD depth varied significantly through space and time, and a combination of biotic (sessile and errant infauna, as well as epibenthic predators), and abiotic (exposure time of a plot, sediment particle size, penetrability, and water content) variables, as well as the availability of resources (sediment organic matter content, and chlorophyll *a* concentration) were correlated with aRPD depth. As such, knowledge of both biotic and abiotic variables are required for a holistic understanding of sediment DO conditions. Abiotic variables likely dictate a suite of potential aRPD depth conditions, while biota and resource availability, via bioturbation and respiration, strongly influence the observed aRPD depth. As DO conditions in marine systems will continue to change due to global climate change, elucidating these relationships are a key first step in predicting the influence decreasing DO content may have upon marine benthos.

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## 1. Introduction

Global climate change is increasing water temperatures in marine systems (Houghton et al., 2001; Stachowicz et al., 2002). As warm water holds less dissolved oxygen (DO) than cold water (Kristensen, 2000), aerobic metazoans may be harmed by decreasing DO content in warming oceans (Diaz & Rosenberg, 2008; Ferguson et al., 2013). In fact, hypoxia (low oxygen conditions, exact value varies by species; Vaquer-Sunyer & Duarte, 2008) and anoxia (DO < 0.0 mg/L; Tyson & Pearson, 1991) have already created dead zones, vast areas devoid of life, in many marine systems (Diaz & Rosenberg, 2008; Halpern et al., 2007; Solan et al. 2004). More specifically, DO content of sediment pore

water may represent a limiting resource in benthic marine habitats (Ferguson et al., 2013). In fact, hypoxia/anoxia has been observed to result in infaunal mortality (Altieri & Witman, 2006; Nilsson & Rosenberg, 2000), migration (Sturdivant et al., 2012), and altered bioturbation activity (Nilsson & Rosenberg, 2000; Rosenberg et al., 2001; Sturdivant et al., 2012).

Far from a static parameter, DO content of sediment pore water has been observed to be influenced by sediment aerial exposure in intertidal systems (Cranford et al., 1985; de Goeij & Honkoop, 2002), energy of the water above (Huettel & Gust, 1992; Kristensen, 2000), sediment particle size and porosity (Aller, 1983; Huettel & Gust, 1992), respiration of sediment microbes (Mermillod-Blondin, 2004; Pischedda et al., 2012), bioturbation by epibenthic (Commito, 1982a; Stief & Hölker, 2006), and infaunal animals (Clare et al., 2016; Quintana et al., 2013; Volkenborn et al., 2010), and respiration (Christensen et al., 2000; Jovanovic et al., 2014).

While these variables have the potential to influence sediment pore water DO content, simply obtaining measurements of DO can

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be challenging. The time required to collect DO profiles from intertidal sediment cores is prohibitive for studies conducted on a broad spatiotemporal scale (Gerwing et al., 2015b). One index of sediment pore water DO content is the apparent redox potential discontinuity, or aRPD (Birchenough et al., 2012; Teal et al., 2009). Measuring aRPD depth relies on the assumption that in the absence of DO in sediment pore water, Iron (Fe) and Sulphur (S) are reduced by anaerobic microbial decomposition of organic carbon (Canfield et al., 1993a, 1993b). These ions then precipitate as ferric sulfides, producing a grey/green or black coloration of the sediment (Bull & Taillefert, 2001; Lyle, 1983; Valdemarsen et al., 2009). As DO is usually the most energetically favored electron acceptor in sediment pore water (Kristensen, 2000; Nøhr Glud et al., 1994), ions that induce the grey/green or black color cannot persist for long in the presence of oxygen (Hargrave, 1972; Kristensen, 2000; Revsbech et al., 1980). The aRPD is, thus, located where the sediment changes color from reddish-brown to grey/green or black. Depth of the aRPD has been shown to be a good relative indicator of sediment pore water DO content. Sediment above the aRPD has a higher relative DO content, while sediment below has less (Gerwing et al., 2015b). Thus, aRPD depth can be used to compare sediment DO conditions; a deeper aRPD represents sediment with more available DO in pore water, while a shallower aRPD depth represents sediment with less available DO (Gerwing et al., 2015b). However, as the reactions responsible for sediment color change do not occur instantaneously (Grenthe et al., 1992; Lyle, 1983; Valdemarsen et al., 2010), aRPD depth likely reflects an integrated long-term average of sediment DO and redox (Eh) conditions (Gerwing et al., 2013, 2015b).

Soft sediments of intertidal mudflats in the Bay of Fundy, Canada, offer a useful setting to examine the myriad of variables that influence sediment pore water DO content. The highly cohesive nature of the fine-grained sediment in this region (Gerwing et al., 2013, 2015a; Sizmurek et al., 2013) restricts penetration of DO-rich water into the sediment (Hargrave, 1972; Huettel & Gust, 1992). This restriction amplifies the importance of bioturbating fauna that contribute to below-surface mixing and oxygen transport (Mermillod-Blondin & Rosenberg, 2006; Mermillod-Blondin et al., 2004). These mudflats support a broad assemblage of potential bioturbators, such as a diverse infaunal community (Gerwing et al., 2015a), epibenthic predators such as flat fish (Risk & Craig, 1976), the Eastern Mudsnail, *Tritia obsoleta* (Cranford, 1988; Galindo et al., 2016), and during the summer months flocks of shorebirds (Gerwing et al., 2016b; Hicklin, 1987).

Mass mortality in marine benthos due to hypoxia (Altieri & Witman, 2006; Diaz & Rosenberg, 2008; Nilsson & Rosenberg, 2000; Pearson & Rosenberg, 1978) may have pronounced global consequences as these habitats are home to a diverse species assemblage (Poore, 1993), and contribute substantially to global primary production (Field et al., 1998; Hargrave et al., 1983). Decreasing densities of benthic infauna will also result in a reduction of their ecosystem services, and decreased bioturbation (Solan et al., 2004). Over long periods of time benthic sediments act as an important sink for carbon (Wenzhöfer & Glud, 2002), and the cycling of organic carbon controls the cycling of atmospheric oxygen (Hartnett et al., 1998). Both of these biogeochemical cycles are greatly influenced by bioturbation activity of benthic infauna (Aller, 1994; Hulthe et al., 1998; Kristensen, 2000; Queirós et al., 2013; Sturdivant et al., 2012). Therefore, the goal of this study was to identify which environmental variables were associated with aRPD depth (a relative indicator of DO content) in soft-sediment intertidal systems in the Bay of Fundy. Specifically, answers to the following questions were sought: 1. Does aRPD depth vary through

space and time? 2. Which environmental variables are associated with aRPD depth?

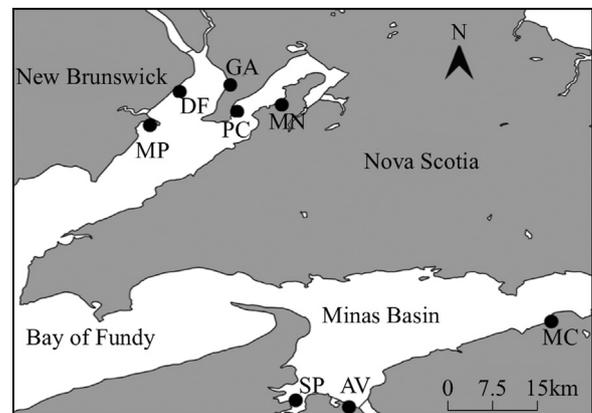
While correlation cannot elucidate cause and effect, the associations identified from the large mensurative dataset used in this paper can form the bases of testable hypotheses. Empirically testing such hypotheses will aid the development of a more detailed understanding of variables that influence aRPD depth, and, thus, sediment DO content. Such an understanding may improve our ability to predict how decreased DO in the world's oceans, as a result of global climate change, will interact with the variables measured here to influence benthic systems.

## 2. Materials and methods

This study combines two datasets: one comprised of aRPD depth and Eh data (Gerwing et al., 2013, 2015a), and another composed of infaunal community composition and environmental properties (Gerwing et al., 2015a, 2016a). Gerwing et al. (2013) described spatiotemporal trends of aRPD depth in the Bay of Fundy, and contrasted aRPD depth with RPD depth as measured by a redox electrode. Gerwing et al. (2015a) described the spatiotemporal variation of infaunal community dynamics and environmental conditions. Building upon these trends, Gerwing et al. (2016a) then investigated the relative importance of biotic and abiotic variables in structuring the infaunal community. The current investigation, however, explores the relationships between biotic/abiotic variables and aRPD depth. This is done using an extensive dataset of biotic and abiotic variables measured from multiple intertidal mudflats in the Bay of Fundy, Canada.

### 2.1. Study sites

This study was conducted on eight intertidal mudflats (hereafter referred to as sites) in the Bay of Fundy, Canada. The Bay of Fundy is comprised of two distinct arms, Chignecto Bay and the Minas Basin (Fig. 1). Mary's Point (MP), Daniels Flats (DF), Grande Anse (GA), Pecks Cove (PC), and Minudie (MN) located in Chignecto Bay, and Moose Cove (MC), Avonport (AV) and Starrs Point (SP) located in the Minas Basin. More information about the biotic and abiotic conditions of these mudflats can be found in Gerwing et al. (2013, 2015a, 2015c).



**Fig. 1.** Study sites (i.e. intertidal mudflats) in the Bay of Fundy, Canada. Site names are Starrs Point (SP), Avonport (AV), Moose Cove (MC), Minudie (MN), Pecks Cove (PC), Grande Anse (GA), Daniels Flats (DF), and Mary's Point (MP).

## 2.2. Mudflat sampling

### 2.2.1. Sampling scheme

Sampling was conducted over two years (2009–2011), and mudflats were sampled every 3 weeks between June and August, and every 6–8 weeks between October and May (Gerwing et al., 2013, 2015a, 2016a). Each sampling round (Round) occurred at the same time each year ( $\pm 1$  week), and sampling was conducted approximately 3 h before to 3 h after low tide. Transects (700–1800 m long depending on mudflat width; 2 transects per mudflat, separated by ~1 km) were stratified into 4 equal zones by length, based upon distance from shore, for random stratified sampling. One sampling location (hereafter referred to as a plot) was randomly selected per zone (for a total of four plots per transect;  $n = 6$ –8 per site, 1021 total) for biotic and environmental sampling.

### 2.2.2. aRPD depth

As described in Gerwing et al. (2013), aRPD depth was measured to the nearest 0.5 cm in each plot, in the void left in the sediment following the removal of the 7-cm diameter core for infauna sampling (described in Section 2.2.4). aRPD depth was quantified at a total of 3 randomly selected plots per zone (instead of only one plot per zone as previously described for biotic and environmental sampling;  $n = 10$ –12 per transect, 20–24 per site, 3070 total). These data were used to quantify how aRPD depth varied in space and time; however, because a complete set of biotic and abiotic variables was available from only 1 plot per zone, investigation into which environmental variables correlated with aRPD depth was done using this subset of data ( $n = 3$ –4 per transect, 6–8 per site, 1021 total). Preliminary data analysis revealed that analyses performed on both subsets of data returned similar results when the same variables were used (Gerwing et al., 2015a, 2016a).

### 2.2.3. Other abiotic variables

An index of the time each plot was exposed to air (exposure) was calculated as follows:

$$1 - (\text{plot distance (m) from shore} / \text{total intertidal distance (m)})$$

In each plot, the penetrability of mudflat sediment was assessed by dropping a metal rod (15 cm long, 1.9 cm diameter, 330 g) from 0.74 m, and the depth (mm) that the weight penetrated into the sediment was recorded (Gerwing et al., 2015a). From one plot in each zone, a single sediment sample was collected with a corer measuring 3 cm in diameter and 5 cm deep. Properties of the sediment, including water content, organic matter content, and volume-weighted average particle size, were calculated as in Gerwing et al. (2015a).

### 2.2.4. Biota

At each plot, a 7 cm diameter sediment core was collected, and within 12 h of collection, samples were passed through a 250- $\mu\text{m}$  sieve and preserved in 95% ethanol (Gerwing et al., 2015a, 2016a). Preserved samples were later sorted, and invertebrates were identified and counted under a dissecting microscope. Densities of the amphipod *Corophium volutator*, *Macoma* spp., Harpacticoida copepods (identified to sub-class), Ostracoda (identified to class), and Polychaetes (identified to family) were quantified.

For each plot, the concentration of chlorophyll *a* was assessed from samples of the top 2 mm of sediment as in Coulthard and Hamilton (2011). Chlorophyll *a* is commonly used as an indicator of diatom abundance (Eaton & Franson, 2005), and diatoms form the base of the food web in this system (Trites et al., 2005). The activity/density of three epibenthic predators (sandpipers, fish, and mud snails) were also examined at each plot. The proportion of the plot covered in shorebird (Semipalmated sandpipers (*Calidris pusilla*)) footprints was quantified as an indication of sandpiper habitat use (Robar & Hamilton, 2007) and foraging activity (MacDonald et al., 2012). Abundance of the

Eastern Mud snail, *Tritia obsoletus*, was counted *in situ* (Gerwing et al., 2015a). Flat fish feeding traces (triangular depressions left in the sediment, hereafter referred to as fish bites) were also counted within each plot (McCurdy et al., 2009; Risk & Craig, 1976).

## 2.3. Data analysis

### 2.3.1. Spatiotemporal variation in aRPD depth

PRIMER with the PERMANOVA (Permutational Analysis of Variance) add-on (Anderson, 2001; McArdle & Anderson, 2001) was used to quantify how aRPD depth varied over time and space ( $n = 20$ –24 per site, 3070 total). While a PERMANOVA is appropriate for univariate analysis (Anderson et al., 2008; Clarke & Gorley, 2006), a univariate ANOVA is more commonly used (Underwood, 1997). A multivariate PERMANOVA was conducted in this case, as recent studies from this area have used PERMANOVAs, or similar analyses in PRIMER (Cheverie et al., 2014; Gerwing et al., 2015a, 2015c, 2016a, 2016b) to quantify variables that structure the infaunal community. By using similar methods, these results are as comparable as possible with previous studies in this area.

No transformations of aRPD depth data were required, and its resemblance matrix was constructed using Euclidian distance (Clarke & Gorley, 2006). In the PERMANOVA (999 permutations), Round (8 levels per year), and Year (2 levels; 2009–2010 and 2010–2011) were fixed factors, while Site (8 levels), transect nested within site, and Plot (error term) were random factors. A critical alpha value of 0.05 was used (Beninger et al., 2012) to test interactions and main effects. Due to a significant three-way interaction (Year X Round X Site) each year was analyzed independently.

### 2.3.2. Environmental variables associated with aRPD depth

Prior to analysis, correlations between biotic and abiotic variables were examined by calculating the univariate Pearson's correlation coefficient between all variables. As our goal was to identify relationships that future studies could experimentally evaluate, a threshold of 0.95 (Clarke & Ainsworth, 1993) was used to determine if variables were too correlated to be considered independent. As none of the correlation coefficients exceeded 0.95 (0.84 was the highest observed correlation), all variables were included in the models.

A PERMANCOVA (permutational multivariate analysis of covariance), as described in Gerwing et al. (2016a), was used to determine the correlation between total aRPD depth and the following covariates: Abiotic sediment conditions: sediment particle size, penetrability, water content, and plot exposure time. Resources: sediment organic matter content, and chlorophyll *a* concentration. Infauna densities: *Macoma* spp., *Corophium volutator*, Copepoda, Ostracoda, and Polychaetes (Capitellidae, Spionidae, Cirratulidae, Nereididae, Nephtyidae, and Phyllodocidae). Activity of epibenthic predators: density of fish bites, and the proportion of a plot covered in sandpiper footprints. Variance components were also calculated for variables in the PERMANCOVA (Anderson et al., 2008; Searle et al., 1992). The aRPD depth resemblance matrix was calculated as described above, and all covariates were normalized prior to analysis. Sediment particle size, chlorophyll *a* concentration, density of fish bites, *T. obsoletus* density, as well as densities of Phyllodocidae, Nereididae, and Nephtyidae were fourth root transformed prior to normalization to correct skewed distributions (Clarke & Ainsworth, 1993).

Round (8 levels per year) was included as a fixed factor in the PERMANCOVA, while Year (2 levels) and Site (8 levels) were included as random factors. Year, Round, Site, and Plot (the residual) are hereafter referred to as structural factors. Transect was not included in these models, as the plots in this dataset ( $n = 3$ –4 per transect) are far enough apart to be considered independent (Gerwing et al., 2015a, 2016a). To determine statistical significance  $\alpha = 0.05$  was used for the analysis, and we tested for homogeneity of slopes as

**Table 1**

PERMANOVA (permutational multivariate analysis of variance) results investigating whether aRPD (apparent Redox Potential Discontinuity) depth varied over space and time. Due to a significant three-way interaction, PERMANOVAs were conducted for each year. Df = degrees of freedom. MS = mean sum of squares. Pseudo-F = F value.  $p$  =  $p$  value.

| Source                         | Df   | MS      | Pseudo-F | $p$   | Unique permutations |
|--------------------------------|------|---------|----------|-------|---------------------|
| <b>2009–2011</b>               |      |         |          |       |                     |
| Year                           | 1    | 1263.90 | 94.82    | 0.001 | 996                 |
| Round                          | 7    | 61.65   | 1.31     | 0.267 | 998                 |
| Site                           | 7    | 760.11  | 21.49    | 0.001 | 999                 |
| Transect (Site)                | 8    | 35.37   | 8.48     | 0.001 | 998                 |
| Year X Round                   | 7    | 361.28  | 13.20    | 0.001 | 998                 |
| Year X Site                    | 7    | 13.33   | 7.38     | 0.004 | 998                 |
| Round X Site                   | 49   | 47.14   | 7.10     | 0.001 | 998                 |
| Year X Transect (Site)         | 8    | 1.81    | 0.43     | 0.895 | 997                 |
| Round X Transect (Site)        | 56   | 6.64    | 1.59     | 0.003 | 998                 |
| Year X Round X Site            | 49   | 27.38   | 2.45     | 0.002 | 997                 |
| Year X Round X Transect (Site) | 56   | 11.18   | 2.68     | 0.001 | 998                 |
| Residual                       | 2814 | 4.17    |          |       |                     |
| Total                          | 3069 |         |          |       |                     |
| <b>2009–2010</b>               |      |         |          |       |                     |
| Round                          | 7    | 279.50  | 8.68     | 0.001 | 998                 |
| Site                           | 7    | 367.88  | 23.74    | 0.001 | 999                 |
| Transect (Site)                | 8    | 15.49   | 3.39     | 0.001 | 998                 |
| Round X Site                   | 49   | 32.19   | 3.25     | 0.001 | 999                 |
| Round X Transect (Site)        | 56   | 9.92    | 2.17     | 0.001 | 996                 |
| Residual                       | 1406 | 4.57    |          |       |                     |
| Total                          | 1533 |         |          |       |                     |
| <b>2010–2011</b>               |      |         |          |       |                     |
| Round                          | 7    | 143.51  | 3.39     | 0.006 | 998                 |
| Site                           | 7    | 405.39  | 18.71    | 0.001 | 999                 |
| Transect (Site)                | 8    | 21.67   | 5.74     | 0.001 | 999                 |
| Round X Site                   | 49   | 42.35   | 5.36     | 0.001 | 997                 |
| Round X Transect (Site)        | 56   | 7.90    | 2.09     | 0.001 | 999                 |
| Residual                       | 1408 | 3.77    |          |       |                     |
| Total                          | 1535 |         |          |       |                     |

described in Gerwing et al. (2016a). As in Gerwing et al. (2016a), non-significant interactions with covariates were removed from the model, and significant interactions with covariates were interpreted as contributing to the proportion of the population variation accounted for by the involved covariate (Anderson et al., 2008). Because Type I sums of squares was used, and the dataset was mildly unbalanced (3 plots missing), the PERMANCOVA was repeated with independent variables entered in different orders to assess if order of variable inclusion impacted results (Anderson et al., 2008; Clarke & Gorley, 2006). Order of inclusion did not impact variance components or variable significance. Finally, covariates that did not account for any variation in the multivariate data cloud were removed from the PERMANOVA (Fletcher & Underwood, 2002). Pearson's univariate correlation coefficient was then calculated for each variable, to determine the nature of the relationship (positive or negative) with aRPD depth.

### 3. Results

Spatiotemporal variation and environmental variables associated with aRPD depth.

aRPD depth varied significantly by Round, Site, Year, and Transect (Table 1, Fig. 2). aRPD depth was significantly correlated (Table 2) with abiotic sediment variables (particle size: 5.8% of the observed variation; sediment penetrability: 10.2%; sediment water content: 5.2%; and plot exposure time: 2.3%), infauna densities (Phyllodoctidae: 1.4%; Cirratulidae: 1.3%; Capitellidae: 2.9%; *Macoma* spp.: 0.4%; and Copepoda: 1.1%), one epibenthic predator's activity (fish bites: 2.1%), and the availability of resources (sediment organic matter content: 4.9%; and chlorophyll *a* concentration: 2.0%). Overall, abiotic sediment variables accounted for 26.2% of the

variation in aRPD depth, infauna densities accounted for 7.1%, epibenthic predators accounted for 2.1%, and the availability of resources accounted for 4.3%.

## 4. Discussion

### 4.1. Seasonal trends in aRPD depth

In general, aRPD depth was deeper in the summer (June to August) than in the winter (October to May). The opposite trend has been observed in other systems, with deeper oxygen penetration observed in winter (Teal et al., 2010), a result of cold water holding more DO than warm water, and microbes consuming less DO in winter (Kristensen, 2000; Thamdrup et al., 1998). The findings of this study were likely a result of low DO diffusion into the highly cohesive sediment (Hargrave, 1972; Huettel & Gust, 1992) of Bay of Fundy mudflats. In such cohesive sediment, the majority of DO penetration deep into sediment may occur via faunal burrows and bioturbation (Mermillod-Blondin & Rosenberg, 2006; Mermillod-Blondin et al., 2004). Faunal densities decrease substantially during winter in the Bay of Fundy (Gerwing et al., 2015a, 2015c), likely removing a pathway for DO to enter the sediment, and resulting in the aRPD moving closer to the surface. At the same time, freezing of the surface sediments may sever the connection between sediment and the oxygenated water above, also resulting in the aRPD moving closer to the surface (Barnes, 1999; Gerwing et al., 2015c).

### 4.2. Environmental variables associated with aRPD depth

aRPD depth was statistically correlated with abiotic sediment variables, infauna densities, resource availability, and the activity

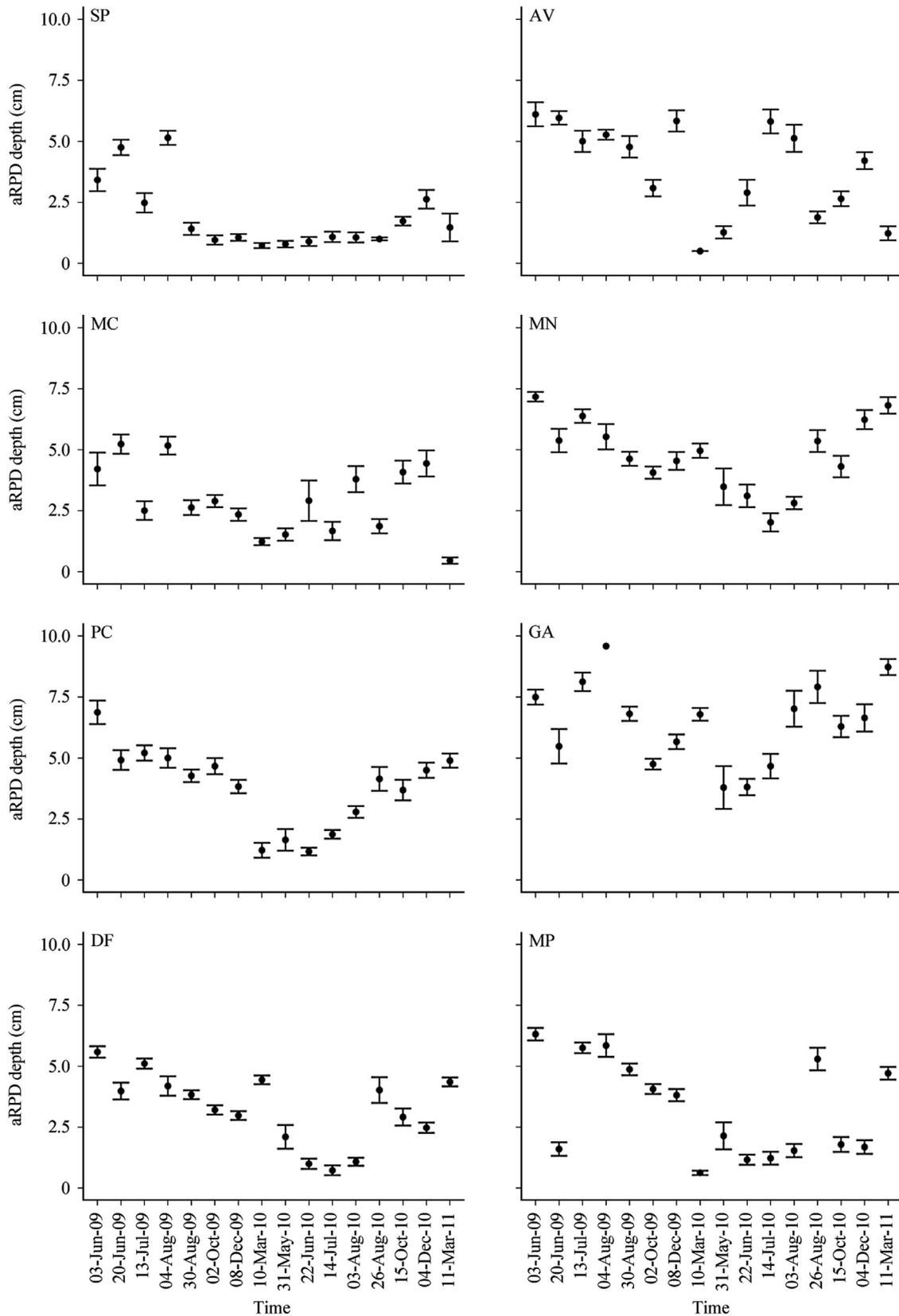


Fig. 2. Apparent redox potential discontinuity (aRPD) depth (mean  $\pm$  SE,  $n = 24$ ) measured at 8 intertidal mudflats within the upper Bay of Fundy, Canada, between June 2009 and March 2011 (SE = standard error, and  $n$  = sample size).

of one epibenthic predator (Table 2). The following interpretations of these correlations are premised upon the assumption that variables that consume sediment pore water DO result in a

shallower aRPD depth, while variables that introduce DO into the sediment result in a deeper aRPD depth (Gerwing et al., 2015b). With regard to abiotic sediment variables, sediment particle size,

**Table 2**

PERMANCOVA (permutational multivariate analysis of covariance) determining which variables were associated with aRPD (apparent Redox Potential Discontinuity) depth variation at Bay of Fundy intertidal mudflats in 2009–2011. Significant *p* values are in bold. Only interactions between structural variables and covariates that were significant are presented. The correlation coefficient presented is Pearson's univariate correlation coefficient. Df = degrees of freedom. MS = mean sum of squares. Pseudo-F = F value. *p* = *p* value.

| Source                              | Df   | MS    | Pseudo-F | Unique permutations | <i>p</i>     | Variance components (%) | Correlation coefficient |
|-------------------------------------|------|-------|----------|---------------------|--------------|-------------------------|-------------------------|
| <b>Particle size</b>                | 1    | 464.5 | 195.49   | 997                 | <b>0.001</b> | <b>3.6</b>              | <b>0.18</b>             |
| Particle size X Round               | 7    | 4.6   | 1.95     | 999                 | 0.066        | 0.2                     |                         |
| <b>Particle size X Site</b>         | 7    | 18.1  | 7.64     | 998                 | <b>0.001</b> | <b>2.2</b>              |                         |
| <b>Penetrability</b>                | 1    | 446.6 | 187.96   | 996                 | <b>0.001</b> | <b>5.7</b>              | <b>0.84</b>             |
| Penetrability X Year                | 1    | 8.5   | 3.56     | 999                 | 0.061        | 0.1                     |                         |
| <b>Penetrability X Round</b>        | 7    | 9.8   | 4.11     | 999                 | <b>0.001</b> | <b>0.9</b>              |                         |
| <b>Penetrability X Site</b>         | 7    | 23.7  | 9.97     | 999                 | <b>0.001</b> | <b>3.6</b>              |                         |
| <b>Water content</b>                | 1    | 384.6 | 161.86   | 998                 | <b>0.001</b> | <b>4.1</b>              | <b>0.30</b>             |
| <b>Water content X Round</b>        | 7    | 8.2   | 3.47     | 999                 | <b>0.003</b> | <b>0.6</b>              |                         |
| <b>Water content X Site</b>         | 7    | 5.9   | 2.50     | 998                 | <b>0.02</b>  | <b>0.6</b>              |                         |
| <b>Exposure</b>                     | 1    | 87.0  | 36.61    | 996                 | <b>0.001</b> | <b>0.7</b>              | <b>-0.17</b>            |
| <b>Exposure X Round</b>             | 7    | 10.2  | 4.31     | 998                 | <b>0.001</b> | <b>0.6</b>              |                         |
| <b>Exposure X Site</b>              | 7    | 10.8  | 4.53     | 999                 | <b>0.001</b> | <b>0.9</b>              |                         |
| <b>Organic matter</b>               | 1    | 11.7  | 4.93     | 994                 | <b>0.023</b> | <b>0.2</b>              | <b>-0.47</b>            |
| <b>Organic matter X Round</b>       | 7    | 6.2   | 2.61     | 998                 | <b>0.013</b> | <b>0.9</b>              |                         |
| <b>Organic matter X Site</b>        | 7    | 13.3  | 5.60     | 999                 | <b>0.001</b> | <b>3.9</b>              |                         |
| <b>Chlorophyll <i>a</i></b>         | 1    | 42.0  | 17.66    | 996                 | <b>0.002</b> | <b>0.3</b>              | <b>-0.02</b>            |
| <b>Chlorophyll <i>a</i> X Round</b> | 7    | 18.2  | 7.64     | 998                 | <b>0.001</b> | <b>1.7</b>              |                         |
| <b>Phyllodocidae</b>                | 1    | 131.8 | 55.45    | 997                 | <b>0.001</b> | <b>1.1</b>              | <b>-0.16</b>            |
| <b>Phyllodocidae X Round</b>        | 7    | 6.0   | 2.53     | 999                 | <b>0.016</b> | <b>0.3</b>              |                         |
| <b>Cirratulidae</b>                 | 1    | 121.1 | 50.98    | 997                 | <b>0.001</b> | <b>1.3</b>              | <b>-0.22</b>            |
| Cirratulidae X Site                 | 7    | 4.3   | 1.81     | 998                 | 0.096        | 1.7                     |                         |
| <b>Capitellidae</b>                 | 1    | 29.9  | 12.58    | 996                 | <b>0.003</b> | <b>0.4</b>              | <b>-0.20</b>            |
| Capitellidae X Round                | 7    | 4.9   | 2.08     | 999                 | 0.065        | 0.4                     |                         |
| <b>Capitellidae X Site</b>          | 7    | 5.6   | 2.35     | 998                 | <b>0.032</b> | <b>2.5</b>              |                         |
| <b>Macoma spp.</b>                  | 1    | 51.3  | 21.59    | 997                 | <b>0.001</b> | <b>0.4</b>              | <b>-0.08</b>            |
| Macoma spp. X Site                  | 7    | 3.3   | 1.41     | 999                 | 0.207        | 0.2                     |                         |
| <b>Copepoda</b>                     | 1    | 69.8  | 29.36    | 999                 | <b>0.001</b> | <b>0.6</b>              | <b>0.06</b>             |
| <b>Copepoda X Site</b>              | 7    | 6.5   | 2.72     | 999                 | <b>0.007</b> | <b>0.5</b>              |                         |
| <b>Fish bites</b>                   | 1    | 102.9 | 43.29    | 997                 | <b>0.001</b> | <b>0.8</b>              | <b>0.16</b>             |
| Fish bites X Year                   | 1    | 8.1   | 3.42     | 999                 | 0.067        | 1.1                     |                         |
| <b>Fish bites X Round</b>           | 7    | 7.4   | 3.11     | 997                 | <b>0.01</b>  | <b>0.8</b>              |                         |
| <b>Fish bites X Site</b>            | 7    | 7.0   | 2.93     | 999                 | <b>0.011</b> | <b>0.5</b>              |                         |
| <b>Year</b>                         | 1    | 540.4 | 227.46   | 995                 | <b>0.001</b> | <b>10.0</b>             |                         |
| <b>Round</b>                        | 7    | 24.9  | 10.46    | 998                 | <b>0.001</b> | <b>1.5</b>              |                         |
| <b>Site</b>                         | 7    | 59.2  | 24.90    | 997                 | <b>0.001</b> | <b>4.7</b>              |                         |
| <b>Year X Round</b>                 | 7    | 47.0  | 19.76    | 998                 | <b>0.001</b> | <b>9.3</b>              |                         |
| Year X Site                         | 7    | 4.9   | 2.06     | 999                 | 0.051        | 0.5                     |                         |
| <b>Round X Site</b>                 | 49   | 9.3   | 3.93     | 998                 | <b>0.001</b> | <b>5.8</b>              |                         |
| <b>Year X Round X Site</b>          | 49   | 6.6   | 2.78     | 998                 | <b>0.001</b> | <b>5.8</b>              |                         |
| <b>Residual</b>                     | 727  | 2.4   |          |                     |              | <b>18.8</b>             |                         |
| Total                               | 1002 |       |          |                     |              |                         |                         |

water content, and penetrability were all positively correlated with aRPD depth (Table 2). This positive relationship suggests that increasing values of these parameters were correlated with a deeper aRPD, an observation that conforms to the current understanding of the dynamics of sediment pore water DO content. Larger sediment particles (sand) allow oxygen-rich water to penetrate further into sediment, when compared to finer-grained sediment (Hargrave, 1972; Huettel & Gust, 1992), resulting in a deeper aRPD. Similarly, sediment that is easier to penetrate (high penetrability values), as well as with high water content (Aller, 1983; Huettel & Gust, 1992), would also allow oxygen-rich water to enter the sediment easier, resulting in a deeper aRPD. The negative correlation between aRPD depth and exposure implies that sediment exposed to the atmosphere for longer periods of time (closer to shore) was associated with a shallower aRPD. While exposed, infauna consume DO in their burrows via respiration (Christensen et al., 2000; Jovanovic et al., 2014; Mermillod-Blondin et al., 2005). Longer periods of exposure may result in increased consumption of DO from sediment pore water via infaunal respiration, resulting in a shallower aRPD.

Sediment organic matter content was negatively correlated with aRPD depth, meaning higher values of organic matter content were associated with shallower aRPD depths. This relationship

was also expected based upon previous studies (Christensen et al., 2000; Mermillod-Blondin et al., 2004; Pischedda et al., 2012). Increased sediment organic matter content will increase bacterial respiration and decomposition activity, consuming DO, therefore, resulting in a shallower aRPD. Conversely, the relationship between chlorophyll *a* concentration and aRPD depth is less clear. Chlorophyll *a* is an indicator of diatom abundance, and diatoms can both produce (photosynthesis) and consume (respiration) DO, increasing or decreasing aRPD depth (Kristensen, 2000). The results of this study suggest that increasing concentrations of chlorophyll *a* were associated with a shallower aRPD depth on these intertidal mudflats, suggesting that diatoms consumed more oxygen than they produced in this system. Conversely, ample resources (high diatom availability) could increase infaunal metabolic activity during digestion, and, therefore, increase consumption of DO, also resulting in a shallower aRPD (Kristensen, 2000). Further study at finer spatiotemporal scales is required to further clarify the exact nature of this relationship.

All of the infauna associated with aRPD depth (errant (Phyllodocidae) and sessile (Capitellidae, Cirratulidae, and *Macoma* spp.)), except for copepods, were negatively correlated with aRPD depth. Infauna can both introduce DO into the sediment via bioturbation (Quintana et al., 2013; Volkenborn et al., 2010), and consume DO via

respiration (Christensen et al., 2000; Jovanovic et al., 2014). The negative correlation observed here can be interpreted in two ways: first, Bay of Fundy infauna were consuming more DO than they introduced into the sediment, resulting in a shallower aRPD depth. Second, infauna aggregated in areas of shallow aRPD depths. The second scenario seems unlikely, as it is doubtful that infauna would aggregate in hypoxic areas; however, future studies conducted at finer spatiotemporal scales are required to further elucidate the nature of these relationships. Copepods were the only infauna positively correlated with aRPD depth. Given their small size, it is unlikely that copepods were bioturbating the sediment enough to greatly impact aRPD depth. It is more likely that copepods tend to aggregate in areas with a deeper aRPD (more available DO in the sediment pore water), but as described above, further study is needed to clarify this relationship. Finally, fish bites, a measure of the activity of an epibenthic predator, were positively correlated with aRPD depth. It is postulated that flat fish are likely acting as surface bioturbators (Commito, 1982a; Stief & Hölker, 2006), whose predatory activity at the sediment surface introduces DO rich water into the sediment, resulting in a deeper aRPD.

Variables not statistically correlated with aRPD depth (Infauna: *C. volutator*, ostracods, Spionidae, Nereididae, and Nephtyidae; Epibenthic Predators: sandpiper footprints and *T. obsoletus* densities) could represent a true lack of correlation, insufficient resolution to detect correlation, or interactions between factors obscuring the ability to identify these relationships. For instance, it is likely that Semipalmated Sandpipers, although voracious predators upon Bay of Fundy infauna (MacDonald et al., 2012), do not greatly impact aRPD depth or sediment DO content during their brief stay in Atlantic Canada (~3–4 months). Similarly, it is unlikely that small ostracods had a large impact upon aRPD depth. The Mudsnailed, *T. obsoletus*, on the other hand, could both introduce DO into the sediment via surface bioturbation (Pischedda et al., 2008), or decrease DO entering the sediment by predation upon infauna (Commito, 1982b), or other negative inter-species interactions (Clare et al., 2016). An interaction between introducing and consuming DO in the sediment could have obscured the ability to detect a correlation between *T. obsoletus* densities and aRPD depth. On the other hand, surface bioturbators like Mudsnaileds have been observed to have less of an impact upon sediment conditions than species that burrow deep into the sediment (Pischedda et al., 2008). *C. volutator*, the most abundant single species present in Bay of Fundy soft sediment (Gerwing et al., 2015a), also could have introduced DO into the sediment via bioturbation, or consumed DO via respiration (Christensen et al., 2000; Jovanovic et al., 2014). Clare et al. (2016) observed that increasing densities of a bivalve (*Scrobicularia plana*) in the Mersey Estuary (UK) decreased densities of *C. volutator*, resulting in a shallower aRPD depth. Similar interactions between *C. volutator* and other species in Bay of Fundy soft sediment, as well as interactions between introduction and consumption of DO into the sediment, may have decreased the ability to detect correlations between *C. volutator* and aRPD depth. The predatory polychaetes in the families Nereididae, and Nephtyidae could also introduce DO into the sediment via bioturbation, as well as decrease DO content via respiration or by predated upon other infauna. More study is required to determine if the lack of correlations observed here is the result of insufficient resolution (aRPD depth is only a relative indicator of sediment DO content), interactions obscuring relationships, or a true lack of correlation between these variables.

#### 4.3. Hierarchy of factors influencing aRPD depth

A previous study examining the relationship between sediment organic carbon content, chlorophyll *a* concentration, other environmental conditions, and mixing depth (an analog of aRPD depth)

subtidally in the North Sea, found that aRPD depth is more a product of recent carbon inputs and associated biogenic mixing, than longer term processes (Teal et al., 2010). While our study did not examine long-term processes like carbon or oxygen cycling, the findings do expand upon the short-term factors that influenced aRPD depth. It was observed that abiotic sediment properties accounted for the majority of the observed variation in aRPD depth (26.2%), when compared to infauna (7.1%), epibenthic predators (2.1%), and resource availability (4.3%). As such, a hierarchy of factors that influence aRPD depth (and thus DO content of sediment pore water) is posited for the intertidal mudflats of the Bay of Fundy, Canada. First, abiotic site-level factors such as sediment properties (e.g., particle size, penetrability, and exposure time), as well as exposure to waves and storms determine the potential range of aRPD depths possible at a site. Infauna, epibenthic predators, and resource availability at a site then interact with each other and abiotic factors, resulting in the actual, or observed aRPD depth.

## 5. Conclusions

As global warming continues to raise the temperatures of the oceans (Houghton et al., 2001; Stachowicz et al., 2002), a better understanding of the processes that influence aRPD depth and sediment pore water DO content, may aid predictions of how climate change will impact benthic systems beneath this water. Understanding how climate change will influence the benthos is important, as benthic habitats contain diverse biological communities (Poore, 1993), contribute substantially to global primary production (Field et al., 1998; Hargrave et al., 1983), and over long periods of time, play an important role in the biogeochemical cycles of carbon and oxygen (Aller, 1994; Hulthe et al., 1998; Kristensen, 2000; Queirós et al., 2013; Sturdivant et al., 2012). This study represents a key first-step in attempting to predict how changing DO content in seawater will influence intertidal benthic communities, by presenting a baseline of processes that are associated with aRPD depth, and, therefore, sediment pore water DO content. While these relationships are correlational (due to the mensurative nature of this dataset), they do suggest testable hypotheses, that when empirically examined, may elucidate variables (cause and effect) that influence aRPD depth. Future studies can build upon this information by clarifying these relationships, as well as investigating how the relationships presented in this study vary with DO content and temperature of the water column, bacterial activity (Kristensen, 2000), and concentration of sediment electron acceptors (Teal et al., 2010).

## Acknowledgements

The authors thank M.A. Barbeau, D.J. Hamilton, D. Drolet, and other members of the mudflat ecology group at the University of New Brunswick (UNB), Mount Allison University, and Carleton University for insightful discussions. The authors would also like to thank K. Lewis (University of Northern British Columbia) for providing support and laboratory space. Collection of the data analysed in this study was funded by the Natural Sciences and Engineering Research Council of Canada (a Strategic Project Grant and Discovery grants to M.A. Barbeau and D.J. Hamilton), New Brunswick Wildlife Trust Fund grants to M.A.B., and Mprime (a Canadian Network of Centres of Excellence for the Mathematical Sciences). T.G. Gerwing was supported by a MITACS Elevate Postdoctoral Fellowship while analyzing these data.

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