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**Key Points:**

- Spatial and temporal variability in the biogeochemistry of ponds makes it difficult to estimate their contributions to salt marsh functioning
- Pond water oxygen levels swing from supersaturation to anoxia over daily cycles, causing successive shifts in redox-sensitive metabolisms
- Biogeochemical processes reflect localized conditions and do not scale with dimensions or vary predictably with marsh spatial properties

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# Salt Marsh Pond Biogeochemistry Changes Hourly-to-Yearly but Does Not Scale With Dimensions or Geospatial Position

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**Abstract** Shallow ponds are expanding in many salt marshes with potential impacts on ecosystem functioning. Determining how pond characteristics change over time and scale with physical dimensions and other spatial predictors could facilitate incorporation of ponds into projections of ecosystem change. We evaluated scaling relationships across six differently sized ponds in three regions of the high marshes within the Plum Island Ecosystems-Long Term Ecological Research site (MA, USA). We further characterized diel fluctuations in surface water chemistry in two ponds to understand short-term processes that affect emergent properties (e.g., habitat suitability). Primary producers drove oxygen levels to supersaturation during the day, while nighttime respiration resulted in hypoxic to anoxic conditions. Diel swings in oxygen were mirrored by pH and resulted in successive shifts in redox-sensitive metabolisms, as indicated by nitrate consumption at dusk followed by peaks in ammonium and then sulfide overnight. Abundances of macroalgae and *Ruppia maritima* correlated with whole-pond oxygen metabolism rates, but not with surface area (SA), volume ($V$), or SA:$V$. Moreover, there were no clear patterns in primary producer abundances, surface water chemistry, or pond metabolism rates across marsh regions supplied by different tidal creeks or that differed in distance to upland borders or creekbanks. Comparisons with data from 2 years prior demonstrate that plant communities and biogeochemical processes are not in steady state. Factors contributing to variability between ponds and years are unclear but likely include infrequent tidal exchange. Temporal and spatial variability and the absence of scaling relationships complicate the integration of high marsh ponds into ecosystem biogeochemical models.

**Plain Language Summary** The spatial extent of shallow ponds is expanding in many salt marshes, due to hydrologic management practices and sea-level rise, among other factors. Accounting for ponds in ecosystem biogeochemical models is important for predicting how marshes may change in the future. It is impractical to characterize every marsh pond because they can account for a large fraction of the landscape. Developing predictive relationships between pond properties and easily measured attributes, such as dimensions or distance from marsh landscape features, could facilitate integration of ponds into ecosystem models. We found that pond biogeochemistry changes dramatically day to night, reflecting a combination of primary production and heterotrophic (i.e., microbial) respiration. However, abundances of primary producers, and their effects on whole-pond oxygen metabolism, did not change predictably with pond surface area or volume. Pond properties also did not vary according to location within the marsh. Instead, each pond was unique. The processes affecting pond development are therefore highly localized and might reflect long periods of tidal isolation in the high marsh.

## 1. Introduction

Shallow ponds are natural features of salt marsh landscapes, but their spatial extent and density have increased in recent decades due to factors including rising sea levels and certain hydrologic management practices (Adamowicz & Roman, 2005; Watson et al., 2017; Wilson et al., 2014). Dieback of emergent vegetation and subsequent pond formation result in landscape fragmentation, increased potential habitat for aquatic invertebrates, juvenile fish, and water birds, and lower rates of ecosystem production and carbon storage (Bolduc & Afton, 2004; Hunter et al., 2009; Spivak et al., 2017). Characterizing how ponds contribute to marsh ecosystem functioning, and determining whether pond biogeochemical processes are stable over time and can be predicted from simple field or geospatial measurements, could potentially inform predictions of ecological and biogeochemical change under future climate and disturbance scenarios (Marani et al., 2010; Mariotti et al., 2020; Wang & Temmerman, 2013). Such efforts are hampered, however, by limited characterizations of pond biogeochemistry and the factors contributing to spatial and temporal variability.

Salt marsh ponds, also known as pools, potholes, and rotten spots, are shallow (<1 m), permanently inundated depressions that range in size from a few square meters to over several thousand (Adamowicz & Roman, 2005; Harshberger, 1916). They can occupy as much as 60% of the marsh platform (Schepers et al., 2017) and are supplied with saltwater by a sinuous network of estuarine rivers, tidal creeks, and mosquito ditches (Figure 1). Ponds perched in the high marsh often only receive new saltwater inputs on spring and storm tides (Figure 1b).

Limited exchange between ponds and the tidal network during short windows of connectivity makes these shallow systems semi-isolated habitats (Spivak et al., 2017). Without the moderating influence of regular tidal exchange, ecological and biogeochemical properties may diverge between ponds, increasing heterogeneity across the marsh landscape. Even over short diel cycles, tidal isolation can lead to extreme swings in pond biogeochemistry due, in part, to the changing balance between autotrophic and heterotrophic metabolisms (Beck & Bruland, 2000; Kearns et al., 2017; Rigaud et al., 2018; Spivak et al., 2017). These oscillations provide information about the responsiveness of microbial communities and how the dominant redox-sensitive metabolisms change over short time scales (e.g., hours). Daily, rapid changes in the activity and interactions of different microbial metabolisms may create instability and contribute to both longer-term changes within a single pond and divergence between ponds. Characterizing how pond biogeochemistry changes over hourly-to-annual time scales is therefore useful in understanding how ponds contribute to marsh functioning as well as the suitability of these shallow systems as habitat for animals and insects.

Ponds in mesotidal to macrotidal systems can have a dynamic life cycle whereby they deepen and expand until connecting with the tidal network and draining (Mariotti, 2016; Mariotti et al., 2020; Wilson et al., 2014). The composition of primary producer and animal communities likely changes as ponds expand, reflecting habitat suitability and the outcomes of ecological interactions. Sediments may become more vulnerable to resuspension as ponds widen and the potential for wind-driven waves increases (Mariotti, 2016). Multiple ecological and biogeochemical properties may therefore scale with certain physical attributes, such as surface area (SA), volume ($V$), and SA:$V$. Scaling relationships may be complicated, however, by geospatial characteristics. The composition of tidal water reaching ponds could change with distance from the estuary and residence time in channels and creeks. Differences in elevation and distances from creekbank edges affect tidal connectivity. Ponds located near terrestrial borders could be more strongly influenced by runoff and groundwater (MacKenzie & Dionne, 2008; Noël & Chmura, 2011). Consequently, identifying geospatial relationships may improve predictive understanding of pond biogeochemistry (Mariotti et al., 2020).

Here, we aimed to characterize diel changes in pond surface water chemistry and determine whether biogeochemical properties remain stable over time and vary predictably with pond dimensions or geospatial attributes. We expected nighttime respiration to consume surface water dissolved oxygen (DO), lower pH, and catalyze a succession of anaerobic metabolisms, which would be reversed during the day when primary producers were actively photosynthesizing. We further expected that pond biogeochemistry would vary between years. We tested three hypotheses regarding relationships between pond biogeochemistry, dimensions, and geospatial position in the marsh. Primary producer abundances and whole-pond metabolism rates would (1) increase with pond surface area, volume, and SA:$V$, (2) reflect geospatial conditions in different regions of the high marsh (e.g., tidal creek length, distance from upland or creekbank), or (3) vary by pond. Support for the first two hypotheses would indicate that pond properties follow predictable patterns while support for the third hypothesis would suggest that ponds are isolated habitats with unique trajectories. To accomplish these goals, we characterized diel and interannual changes in two ponds, due to the logistics of high-resolution sampling and the availability of similar data from prior years, but tested the three hypotheses in a broader set of six ponds distributed across three regions of a temperate salt marsh.

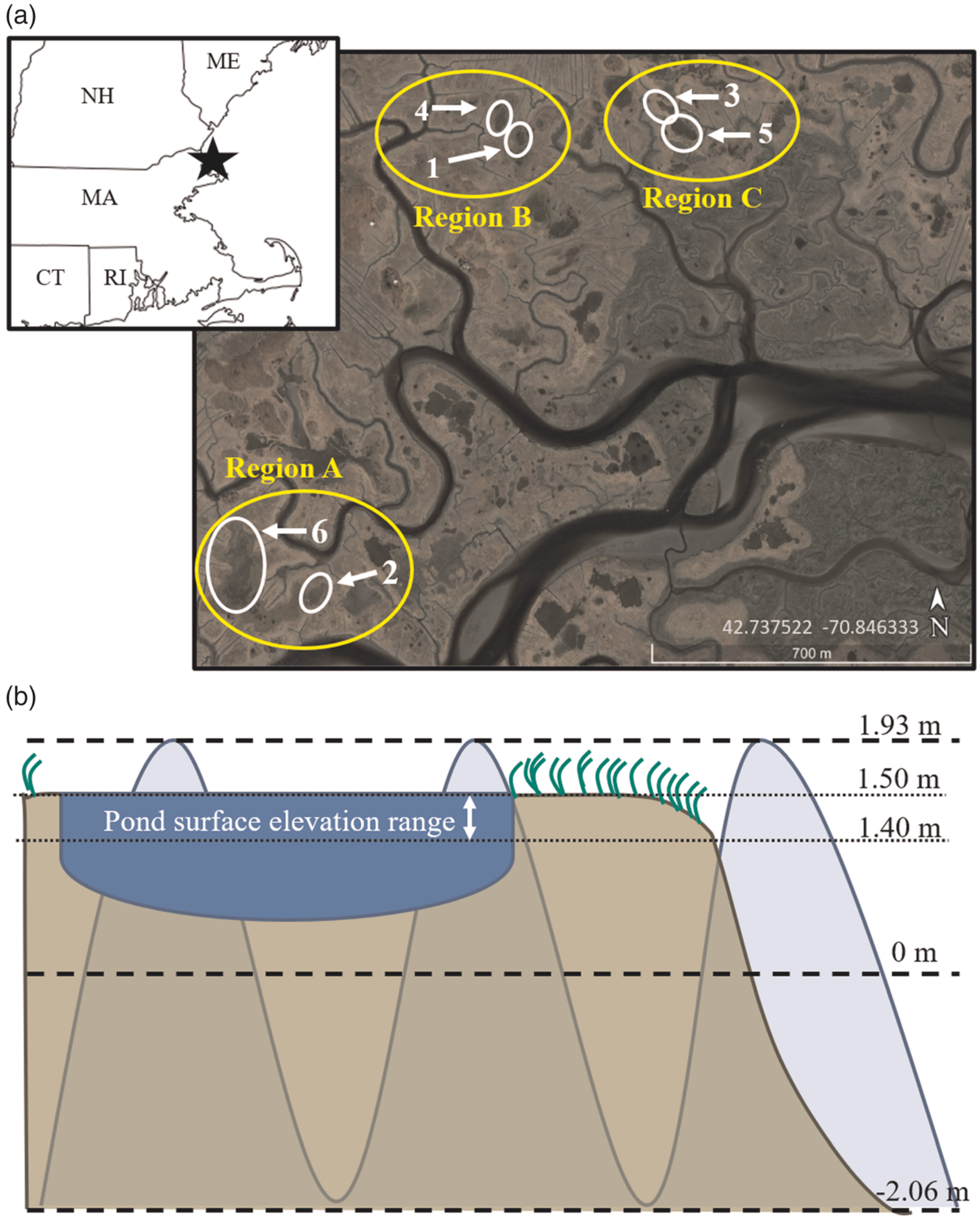

**Figure 1.** (a) The six ponds targeted three regions of the PIE-LTER high marshes. (b) A conceptual marsh profile overlays tidal periods to illustrate pond positions within the tidal frame (1.40–1.50 m) as well as slight differences in duration of tidal connectivity. Heavy dashed lines represent the lowest to highest tides during this study (not to scale). See Table 1 for pond dimensions, elevation, inundation, and spatial characteristics.

## 2. Methods

### 2.1. Study Site

Plum Island Ecosystems-Long Term Ecological Research site has ~12,200 ponds across ~2 km$^2$ of salt marsh (PIE-LTER; Rowley, MA, USA; Millette et al., 2010). We studied six high marsh ponds (1.40–1.50 m above North American Vertical Datum of 1988, [NAVD88]) that span a range of surface areas (643–3,680 m$^2$) and volumes (162–920 m$^3$; Figure 1 and Table 1) and are surrounded by a peat layer that is 1–6 m deep (Hein et al., 2013; Kirwan et al., 2011; Wilson et al., 2014). This regression design allowed us to evaluate scaling relationships, while the high marsh elevation reduced potential confounding effects due to differences in the duration of tidal connectivity (3% range; Table 1 and Figure 1). This system has semidiurnal tides with a mean range of 2.9 m, and the ponds were supplied by different tidal creek networks that divided them across

**Table 1**
*The Six High Marsh Ponds Were Distributed Across Three Regions Within the PIE-LTER Salt Marshes (Figure 1)*

| Pond identity | Region | Depth (m) | Surface area ($m^2$) | Volume ($m^3$) | SA: *V* | NAVD88 (m) | % time with tidal connectivity | Tidal creek length (m) | Upland border (m) | Creekbank distance (m) |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | B | 0.30 | 643 | 190 | 3.4 | 1.48 | 7.7 | 970–1,170 | 250 | 14 |
| 2 | A | 0.30 | 685 | 207 | 3.3 | 1.40 | 10.1 | 95–968 | 340 | 30 |
| 3 | C | 0.23 | 703 | 162 | 4.3 | 1.50 | 7.1 | 840–930 | 200 | 10 |
| 4 | B | 0.29 | 962 | 274 | 3.5 | 1.44 | 9.2 | 880–1,170 | 195 | 12 |
| 5 | C | 0.24 | 1,823 | 438 | 4.2 | 1.44 | 9.2 | 875 | 270 | 13 |
| 6 | A | 0.25 | 3,680 | 920 | 4.0 | 1.40 | 10.1 | 220–1,090 | 185 | 8 |

*Note*. We used a regression design to examine relationships with surface area, volume, and the ratio between the two. The ponds varied in distance from the main channel, upland border, and creekbank edges. Ranges in tidal creek length reflect the different pathways through which water is delivered to the ponds.

three regions. The ponds were 8–30 m from creekbank edges and separated from the main channel by creeks and ditches that were 95–1,170 m long and from the upland border by 185–340 m (Table 1). The ponds were permanently inundated and had similar depths (0.23–0.30 m) and tidal cycles, with days to weeks of isolation punctuated by spring and storm tides. Flooding tides are the main source of water to the ponds, and we defined periods of connectivity as tides that overtopped the marsh and connected with the ponds based on observations and predicted tide heights. Lateral and ground water inputs through pond walls and bottoms were small, representing ~5–7% of pond volumes per year. This is an upper bound based creekbank seepage rates, which are highest within 3 m of the edge and decline sharply with distance into the marsh (Gardner, 2008; Howes & Goehringer, 1994; Jordan & Correll, 1985).

### 2.2. Diel Changes in Pond Surface Water Chemistry

Diel changes in surface water chemistry were measured over two summer days (25 and 26 July 2016) in Ponds 1 and 4. We focused on these ponds because we had previously characterized primary producer communities, metabolism rates, and organic matter dynamics over tidal stages and seasons (Spivak et al., 2017, 2018).

The ponds were flooded by a high tide shortly before sampling began at 17:45 on 25 July but then remained isolated for the rest of the sampling period, which ended at 12:00 on 26 July. The sun set at 20:15 and rose at 05:30 so the sampling period captured ~9 hr of daylight and darkness. The weather was cloudier on 25 than 26 July, but maximum irradiance was similar on both days (1,671 and 1,750 μmol $m^{-2}$ $s^{-1}$, respectively). Air temperatures and wind speeds ranged from 21.8 to 30.0°C (mean = 24.5°C) and 0.8 to 6.4 m $s^{-1}$ (mean = 3.7 m $s^{-1}$), respectively.

Surface water temperature, DO, and conductivity were recorded by a YSI EXO2 (Pond 1) or HOBO loggers (U26-001; U24-002-C, UA-002-64; Pond 4) that were situated at middepth over bare sediment. The sensors were calibrated according to manufacturer specifications immediately before deployment and recorded data in 15 min intervals. Salinity was calculated from conductivity and temperature data using manufacturer software. DO (mg $L^{-1}$) was calculated from percent saturation, barometric pressure, salinity, and temperature data (Garcia & Gordon, 1992).

Discrete surface water samples were collected every 1.5 hr from two locations in each pond. Samples were collected at middepth (~15 cm), 3 m from pond edges by pulling water through tygon tubing into 60 ml syringes. The tubing was flushed before water was collected for salinity, pH, and concentrations of dissolved nutrients ($NH_4^+$, $NO_3^-$, $PO_4^{3-}$), organic carbon (DOC), and sulfide. Samples were passed through precombusted glass fiber filters and put on ice. Samples for DOC were preserved with hydrochloric acid (HCl, pH 2) and sulfide with a sulfide antioxidant buffer solution. Upon return to the lab, pH and sulfide samples were analyzed immediately with pH and silver/sulfide ion selective electrodes, respectively, while the remaining samples were stored cold (4°C: DOC) or frozen (−20°C: $NH_4^+$, $NO_3^-$, $PO_4^{3-}$). Dissolved inorganic nutrient concentrations were measured on an autoanalyzer using standard methods (Gordon et al., 1994). Surface water DOC was determined by high-temperature combustion (720°C; Lalonde et al., 2014). Salinity was measured using a handheld refractometer. Discrete salinity data are reported because the HOBO conductivity sensor failed.

### 2.3. Pond Primary Producers

Primary producer communities were characterized in all six ponds between 23 June and 23 August 2016. Macrophyte abundances were determined two to three times by visually estimating percent cover in six 1 $m^2$ quadrats placed at three random locations along each of two transects, following Spivak et al. (2017). Surface water was collected for chlorophyll and suspended particulate organic matter (POM) from two locations in each pond into 1 L combusted (450°C) glass bottles and filtered through combusted and preweighed glass fiber filters. Additional samples for surface water chlorophyll were collected during the diel study in Ponds 1 and 4, to provide context for the higher resolution observations. Benthic microalgae (BMA) were collected once from all ponds by placing four replicate, combusted glass slides on surface sediments and then scraping attached material onto combusted glass fiber filters (Spivak et al., 2018; Spivak & Ossolinski, 2016). Surface water and sediment chlorophyll concentrations, as a proxy of microalgal biomass, were analyzed according to Neubauer et al. (2000). POM filters were dried to constant mass (60°C), and concentrations were calculated by normalizing to the volume of water filtered.

### 2.4. Pond Metabolism Rates

Oxygen-based metabolism rates of gross and net ecosystem production (GEP, NEP) and respiration ($R$) were measured in all six ponds between 23 June and 23 August 2016. Sensors recorded DO (% saturation), temperature (°C), and conductivity (mS $cm^{-1}$) in 15 min intervals. We used a combination of sensors and, due to availability, rotated one YSI EXO2 (0–50 $\pm$ 0.1 mg DO $L^{-1}$, −5–50°C, 0–200 $\pm$ 1% mS $cm^{-1}$) two HOBO DO (U26-001, 0–30 $\pm$ 0.5 mg DO $L^{-1}$) and conductivity (U24-002-C, 0.1–55 $\pm$ 0.005 mS $cm^{-1}$) loggers, and HOBO temperature loggers (UA-002-64, −20–70°C) between ponds and did not deploy water level sensors. One of the HOBO DO sensors failed on 28 July, and later data were discarded. Sensors were situated at middepth above bare sediment and regularly inspected, cleaned, and calibrated according to manufacturer specifications. DO concentration and salinity data were calculated as described above. Atmospheric conditions, including wind speed (m $s^{-1}$), temperature (°C), relative humidity (%), barometric pressure (mbar), and photosynthetically active radiation (PAR; μmol $m^{-2}$ $s^{-1}$), were recorded 14 m above the marsh by a meteorological tower, ~1 km north and west of Region C (42.742439–70.830223) (Giblin & Forbrich, 2018).

### 2.5. Data Analyses

For the diel time series, we calculated the means, standard error (SE), and coefficient of variation (CV) of surface water conditions to characterize day versus night differences and variability in the two ponds.

Across the broader set of six ponds, we used a "free-water" diel oxygen approach to estimate GEP, NEP, and $R$ (Spivak et al., 2017; Staehr et al., 2010). Because the sensors do not capture ebullition, we likely underestimated net oxygen production (Howard et al., 2018). Oxygen saturation was calculated using volumetric solubility constants and corrected for salinity, temperature, and barometric pressure (Garcia & Gordon, 1992). Wind speeds measured at 14 m were scaled to 10 m (Smith, 1985). Gas transfer velocities ($k$, m $day^{-1}$) were calculated according to Cole and Caraco (1998) and adjusted using a Schmidt number for oxygen in saltwater (Wanninkhof, 2014). GEP, NEP, and $R$ were estimated from measurements of PAR, water temperature, and DO using an ordinary least squares approach with the LakeMetabolizer package in *R* (Winslow et al., 2016). Rates were not estimated for days with missing data (e.g., maintenance).

We tested our three hypotheses about whether biogeochemical properties vary by pond (1–6), marsh region (A, B, or C), pond dimensions (area, volume, SA:$V$), or geospatial position (distance from upland border or creekbank; Figure 1 and Table 1) by constructing a series of mixed effect models with either region or pond identity as a nested random effect within sampling time point. We accounted for potential differences in sensors measuring temperature and conductivity by including sensor as a nested random effect within sampling time point. We constructed another set of linear mixed effect models to evaluate factors influencing GEP, NEP, and $R$, with potential drivers (water temperature, PAR, and macrophyte abundances) as fixed effects and pond identity as a random effect. For all models, we further specified a first-order autoregressive correlation structure with the same random structure to account for our repeated measures design. By modeling covariances among data points sampled within ponds, a mixed model approach allows us to meet the assumption of independence of errors. We constructed linear mixed effect models using the nlme package for the software *R* (Pinheiro et al., 2016) and, for each model, we calculated the marginal (variance of fixed effects only) and conditional (variance of both fixed and random effects) $r^2$ (in the sense of

Nakagawa & Schielzeth, 2013), using the piecewiseSEM package in *R* (Lefcheck & Freckleton, 2016). Statistical analyses were performed using *R* open-source software (R Development Core Team, 2020). Data were $\log_{10}$-transformed as necessary to maintain homogeneity of variance. Values are presented as means ± SE unless noted otherwise.

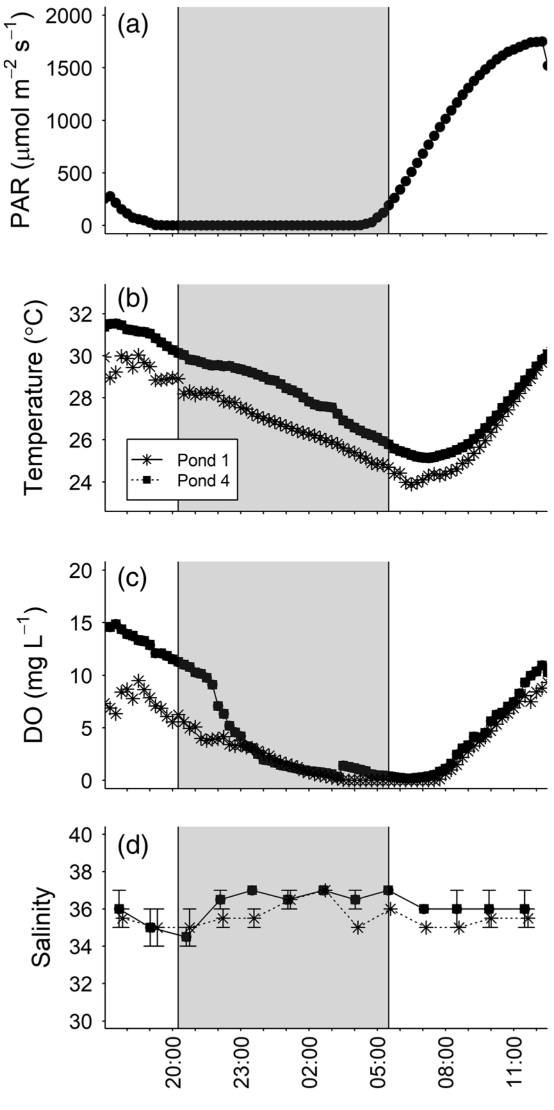

**Figure 2.** Diel environmental and pond surface water properties in July 2016. Photosynthetically active radiation (PAR; a), surface water temperature (b), and dissolved oxygen (DO; c) were low overnight and increased after sunrise, while salinity (d) was relatively constant. Shading denotes hours between sunset and sunrise.

## 3. Results

### 3.1. Diel Changes in Surface Water Chemistry

High rates of primary production and respiration in Ponds 1 and 4 resulted in sharp day-to-night swings in DO and pH but more muted changes in inorganic nutrients, sulfide, and DOC (Figures 2 and 3). Surface water temperatures dipped overnight, while salinity was constant, though Pond 4 was warmer and more saline (Figures 2b and 2d). Pond 4 was slightly more productive than Pond 1, with DO reaching 14.86 and 10.9 mg L$^{-1}$ on 25 July, respectively. DO fell to hypoxic levels by midnight (Pond 4) or 00:30 (Pond 1) and remained at or below 2 mg L$^{-1}$ until 08:30 (Pond 4) or 08:45 (Pond 1) on 26 July (Figure 2c). As a result, pond surface waters were continuously suboxic, or even anoxic, for more than 8 hr. By 12:00 on 26 July surface water DO rose to 10.38 and 8.43 mg L$^{-1}$ in Ponds 4 and 1, respectively.

Day-night changes in productivity were mirrored by pH (Figure 3a). During the day pH reached 9.04 and 8.21 in Ponds 4 and 1, respectively, while nighttime respiration resulted in a 6.50–6.79-fold increase in hydrogen ion concentrations and a ~0.8 unit drop in pH to 8.21 (Pond 4) and 7.36 (Pond 1). DOC was similar in both ponds, and concentrations were slightly higher at night (1,027 ± 84 μmol L$^{-1}$) than during the day (885 ± 40 μmol L$^{-1}$; Figure 3b). Concentrations of $NO_3^-$ and $NH_4^+$ were also similar between ponds but showed different day-night patterns (Figures 3c and 3d). Nitrate was higher during the day (0.11 ± 0.03 μmol L$^{-1}$), particularly just before sunset, than at night (0.06 ± 0.01 μmol L$^{-1}$), while $NH_4^+$ was higher at night (0.14 ± 0.03 μmol L$^{-1}$), peaking just before midnight, and lower during the day (0.08 ± 0.01 μmol L$^{-1}$). The CV values for $NO_3^-$ were similar between ponds and over day (1.53) and night (1.31) periods, while values for $NH_4^+$ concentrations were slightly higher at night (1.06) than during the day (0.41). Phosphate concentrations were similar in both ponds and did not show clear diel patterns (day: 0.24 ± 0.02, night: 0.25 ± 0.05 μmol L$^{-1}$; Figure 3e). Sulfide increased overnight, peaking around dawn (Figure 3f). Sulfate did not become limiting and concentrations were similar during the day (23.44 ± 0.59 mmol L$^{-1}$) and night (22.95 ± 0.13 mmol L$^{-1}$). The muted day-night changes in $NH_4^+$, $NO_3^-$, and sulfide, compared to DO and pH, suggests rapid recycling of electron acceptors and exchange between microbial communities.

### 3.2. Surface Water Temperature and Salinity Across Marsh Regions and Ponds

Surface water temperature and salinity differed between the six ponds (Table 2a; Figure 4). Ponds in Region C had lower salinities and were slightly warmer. The temperature difference could reflect the shallower depths of Region C ponds, but the factors contributing to lower salinities are unclear, since tidal creek length and distances from the upland border and creekbank edges were similar to ponds in Regions A and B (Table 1). Temperature and salinity decreased with increasing volume and SA:*V* ratio ($p < 0.05$), respectively, but neither changed predictably with surface area (Table 2b).

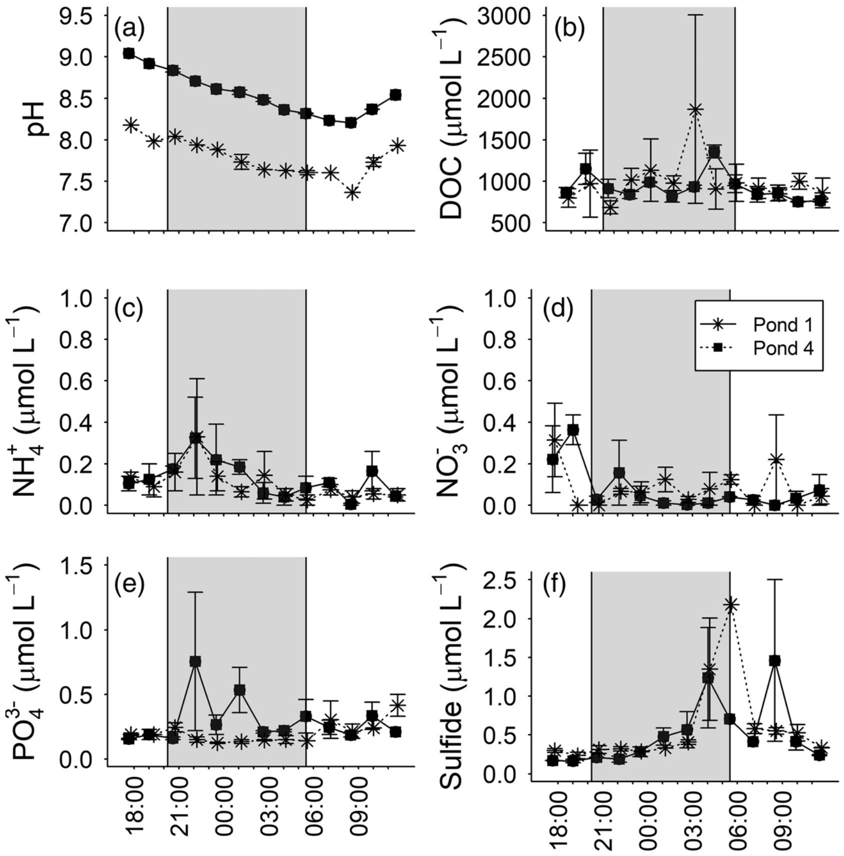

**Figure 3.** Diel surface water chemistry in July 2016. Surface water pH (a) fell overnight, reflecting acidity associated with respiration. Dissolved organic carbon (DOC, b), ammonium ($\mathrm{NH_4}^+$, c), nitrate ($\mathrm{NO_3}^-$, d), and sulfide (f) increased and then fell between sunset and dawn, while phosphate ($\mathrm{PO_4}^{-3}$, e) did not follow a clear diel pattern. Shading denotes hours between sunset and sunrise.

### 3.3. Primary Producers Across Marsh Regions and Ponds

The main primary producers were suspended and benthic microalgae, the macroalgae *Ulva*, and the submerged grass *Ruppia maritima*. Macrophyte abundances and concentrations of BMA and suspended POM varied by pond but did not differ between marsh regions (Table 2a and Figures 5 and 6) or with distances from the upland border or creekbank edge ($p > 0.05$; not shown). Suspended POM and chlorophyll concentrations did not vary with pond dimensions (Table 2b and Figures 5a–5f). Benthic chlorophyll did not change with pond surface area or volume but increased with SA:$V$ (Table 2b and Figures 5g–5i). The latter was largely driven by high concentrations in the shallowest ponds (Region C) which had the highest SA:$V$ ratios (Table 1). Macrophyte communities were dominated by *R. maritima*, with the exception of one pond (Pond 5) in Region C, which had similar abundances of the submerged grass and macroalgae (Figure 6). Abundances of macroalgae and *R. maritima* did not scale with pond surface area, volume, or SA:$V$ (Table 2b).

### 3.4. Pond Metabolism Rates

Whole-pond GEP, NEP, and $R$ were calculated for 20 days in Ponds 2, 4, and 6, and for 39, 14, and 35 days in Ponds 1, 3, and 5, respectively. Differences reflect the goal of capturing at least two isolated and connected tidal stages and omission of days with incomplete sensor data (e.g., maintenance, failure). High tides connected ponds with creeks for 50–67% of days in the study period. Surface water DO concentrations (mg $\mathrm{L}^{-1}$) ranged from anoxia at night to supersaturation during the day (Pond 1: 0–17.2; Pond 2: 0–15.8; Pond 3: 0–15.6; Pond 4: 0–19.5; Pond 5: 0–17.1; Pond 6: 0–14.6). The ponds were hypoxic (<2 mg $\mathrm{L}^{-1}$) on 86–100% of nights.

**Table 2**

*Differences in Pond Surface Water Conditions, Primary Producer Abundances, and Metabolic Rates Were Tested Across Marsh Regions and Pond Identity (a) and as They Related to Pond Dimensions (b) Using Linear Mixed Effect Models*

**a**

| | Marsh region | | | | Pond identity | | | |
|---|---|---|---|---|---|---|---|---|
| | | | $r^2$ | | | | $r^2$ | |
| Response | F | *p* | mar. | cond. | F | *p* | mar. | cond. |
| $\log_{10}$ Temperature (°C) | 5.76 | **0.004** | 0.06 | 0.17 | 4.15 | **0.002** | 0.10 | 0.28 |
| $\log_{10}$ Salinity | 141.85 | **<0.001** | 0.58 | 0.99 | 129.37 | **<0.001** | 0.82 | 0.98 |
| $\log_{10}$ Suspended POM (mg L$^{-1}$) | 1.95 | 0.286 | 0.39 | 0.90 | 7.83 | **0.034** | 0.72 | 0.90 |
| $\log_{10}$ Suspended chlorophyll (μg L$^{-1}$) | 1.20 | 0.455 | 0.26 | 0.70 | 3.05 | 0.108 | 0.39 | 0.77 |
| $\log_{10}$ Benthic chlorophyll (μg cm$^{-2}$) | 5.33 | 0.103 | 0.52 | 0.76 | 3.90 | **0.018** | 0.58 | 0.78 |
| $\log_{10}$ Macroalgae (% cover) | 1.92 | 0.291 | 0.22 | 0.64 | 8.72 | **<0.001** | 0.47 | 0.58 |
| $\log_{10}$ *R. maritima* (% cover) | 0.86 | 0.507 | 0.07 | 0.40 | 3.57 | **0.006** | 0.19 | 0.34 |
| GEP (mg $O_2$ L$^{-1}$ day$^{-1}$) | 0.95 | 0.480 | 0.08 | 0.91 | 5.42 | **0.001** | 0.17 | 0.71 |
| NEP (mg $O_2$ L$^{-1}$ day$^{-1}$) | 4.99 | 0.111 | 0.31 | 0.93 | 10.33 | **<0.001** | 0.44 | 0.84 |
| *R* (mg $O_2$ L$^{-1}$ day$^{-1}$) | 7.86 | 0.064 | 0.35 | 0.93 | 8.39 | **<0.001** | 0.36 | 0.78 |

| | $\log_{10}$ Area ($m^2$) | | | | | $\log_{10}$ Volume ($m^3$) | | | | | $\log_{10}$ SA:*V* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **b** | Est | SE | *p* | $r^2$ | | Est | SE | *p* | $r^2$ | | Est | SE | *p* | $r^2$ | |
| Response | | | | mar | cond | | | | mar | cond | | | | mar | cond |
| $\log_{10}$ Temperature (°C) | −0.02 | 0.01 | 0.075 | 0.02 | 0.19 | −0.03 | 0.01 | **0.027** | 0.03 | 0.20 | 0.12 | 0.08 | 0.111 | 0.02 | 0.13 |
| $\log_{10}$ Salinity | −0.05 | 0.03 | 0.078 | 0.02 | 0.99 | −0.01 | 0.03 | 0.736 | 0.00 | 0.99 | −1.94 | 0.11 | **<0.001** | 0.45 | 0.99 |
| $\log_{10}$ Suspended POM (mg L$^{-1}$) | −0.25 | 0.22 | 0.324 | 0.18 | 0.90 | −0.21 | 0.25 | 0.453 | 0.11 | 0.90 | −2.45 | 0.94 | 0.060 | 0.52 | 0.88 |
| $\log_{10}$ Suspended chlorophyll (μg L$^{-1}$) | −0.71 | 0.31 | 0.083 | 0.35 | 0.71 | −0.76 | 0.33 | 0.838 | 0.35 | 0.72 | −1.19 | 2.87 | 0.699 | 0.02 | 0.76 |
| $\log_{10}$ Benthic chlorophyll (μg cm$^{-2}$) | 0.07 | 0.65 | 0.923 | 0.00 | 0.77 | −0.14 | 0.70 | 0.849 | 0.01 | 0.77 | 6.92 | 1.88 | **0.021** | 0.56 | 0.66 |
| $\log_{10}$ Macroalgae (% cover) | 0.30 | 0.80 | 0.725 | 0.02 | 0.67 | 0.20 | 0.86 | 0.824 | 0.01 | 0.67 | 4.48 | 4.37 | 0.363 | 0.09 | 0.65 |
| $\log_{10}$ *R. maritima* (% cover) | 0.28 | 0.55 | 0.631 | 0.01 | 0.38 | 0.19 | 0.60 | 0.762 | 0.01 | 0.38 | 4.40 | 2.81 | 0.192 | 0.08 | 0.36 |
| $\log_{10}$ GEP (mg $O_2$ L$^{-1}$ day$^{-1}$) | −0.15 | 0.17 | 0.432 | 0.03 | 0.90 | −0.17 | 0.19 | 0.424 | 0.03 | 0.90 | −0.29 | 1.10 | 0.805 | 0.00 | 0.90 |
| $\log_{10}$ NEP (mg $O_2$ L$^{-1}$ day$^{-1}$) | −0.05 | 0.16 | 0.794 | 0.00 | 0.90 | −0.01 | 0.18 | 0.951 | 0.00 | 0.90 | −1.21 | 0.74 | 0.178 | 0.09 | 0.90 |
| $\log_{10}$ *R* (mg $O_2$ L$^{-1}$ day$^{-1}$) | −0.10 | 0.17 | 0.595 | 0.03 | 0.93 | −0.16 | 0.17 | 0.414 | 0.06 | 0.93 | 1.29 | 0.78 | 0.173 | 0.15 | 0.93 |

*Note*. The estimated slope (Est), standard error of the slope (SE), and *p* value for each predictor variable in the model are presented. The marginal (mar) and conditional (cond) $r^2$ reflect the variance explained by fixed effects alone or by fixed and random effects combined, respectively. Significant *p* values (<0.05) are in bold. Data were transformed as indicated.

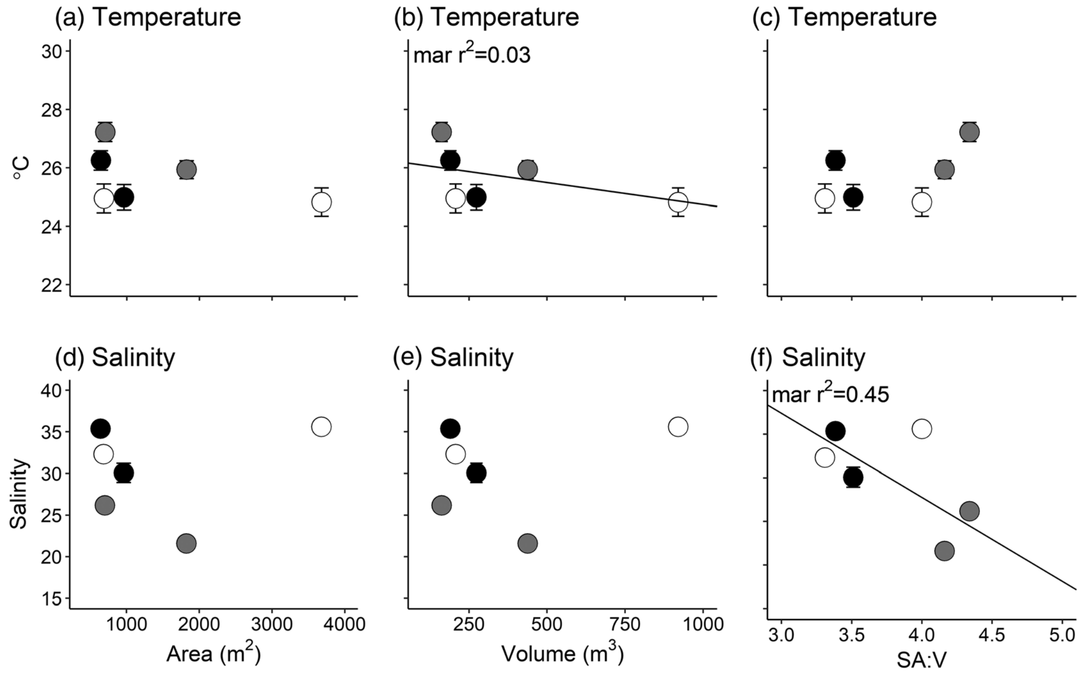

**Figure 4.** Pond surface water properties in summer 2016. Temperature (a–c) and salinity (d–f) were measured in paired ponds within Regions A (white), B (black), and C (gray). Data are mean ± SE. Regression lines and marginal $r^2$ values are included for significant correlations ($p < 0.05$). See Table 1 for pond characteristics and Table 2 for statistical results.

Whole-pond oxygen metabolism rates (mg $O_2$ $L^{-1}$ $day^{-1}$) were consistent with observations in PIE (Johnston et al., 2003; Spivak et al., 2017) and other New England salt marshes (Moseman-Valtierra et al., 2016) and did not scale with area, volume, SA:$V$ (Figure 7 and Table 2b), or with distances to the upland border or creekbank edge ($p > 0.05$, not shown). Region C ponds generally had higher respiration rates (Figures 7g–7i) and were net heterotrophic (i.e., negative NEP, Figures 7d–7f). Autotrophic and heterotrophic processes were more balanced in Region A ponds with NEP near 0. Region B was more variable as one pond had NEP rates near 0 and the other was net autotrophic. Metabolism rates reflected a combination of environmental conditions and macrophyte abundances. GEP correlated positively with water temperature, PAR, and *R. maritima* abundance but negatively with macroalgae (Table 3). Similarly, NEP increased with PAR but decreased with macroalgal abundance, while $R$ increased at higher temperatures. These correlations, while significant, accounted for a small proportion of the variance in the data suggesting that additional factors are likely important.

## 4. Discussion

Shallow ponds are found in salt marshes around the world, from the Chesapeake Bay to the Bay of Fundy, along the U.S. Gulf and West Coasts, south America, western Europe, and Australia (Adamowicz & Roman, 2005; Barnby et al., 1985; Boston, 1983; Miller et al., 2009; Noël & Chmura, 2011; Perillo et al., 1996; Rigaud et al., 2018; Schepers et al., 2017). The six high marsh ponds in PIE had physical and geomorphic characteristics similar to those in other temperate, mesotidal to macrotidal systems (Adamowicz & Roman, 2005; Noël & Chmura, 2011). Summertime surface water temperatures and salinities (Figure 4) were comparable to marsh ponds in Virginia (Layman et al., 2000), New Jersey (Hunter et al., 2009; Smith & Able, 2003), and Maine (MacKenzie & Dionne, 2008). Daily swings in DO from anoxia to supersaturation (0–14.9 mg $L^{-1}$) were also typical of ponds in Virginia (0–20 mg $L^{-1}$; Layman et al., 2000) and New Jersey (0–18 mg $L^{-1}$; Smith & Able, 2003) and likely affect the quality of these shallow systems as habitat for invertebrates, fish, and birds (Bolduc & Afton, 2004). Thus, the six ponds in this study were typical of high marsh ponds in temperate, mesotidal to macrotidal ecosystems.

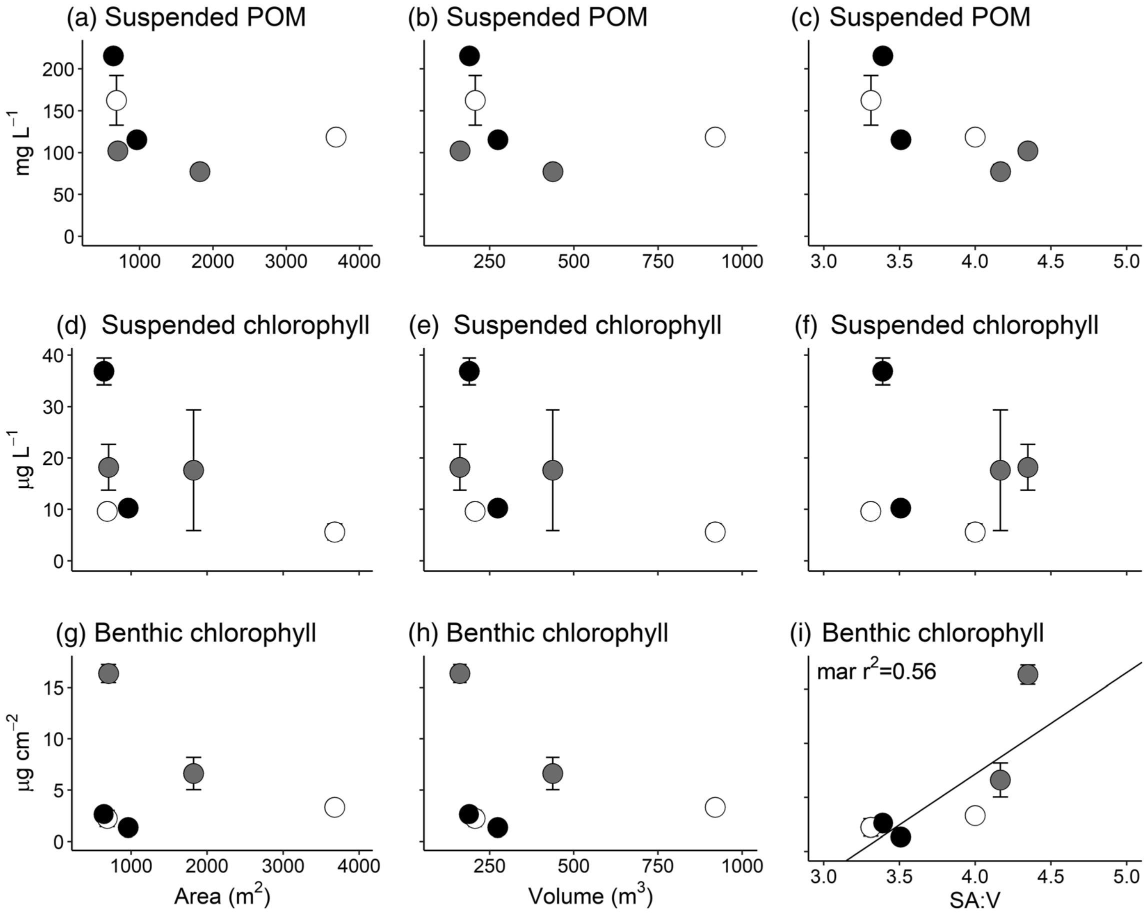

**Figure 5.** Suspended and benthic microalgae in summer 2016. Concentrations of suspended particulate organic matter (POM; a–c) and chlorophyll (d–f) and benthic chlorophyll (g–i) in the paired ponds of Regions A (white), B (black), and C (gray). Data are mean ± SE. Regression lines and marginal $r^2$ values are included for significant correlations ($p < 0.05$). See Table 1 for pond characteristics and Table 2 for statistical results.

### 4.1. Diel Changes in Biogeochemistry

Dramatic, diel swings in surface water biogeochemistry have been observed in shallow, semi-isolated tidal mudflat pools (Rigaud et al., 2018), rocky intertidal pools (Huggett & Griffiths, 1986; Morris & Taylor, 1983), ephemeral desert pools (Scholnick, 1994), and prairie potholes (Rose & Crumpton, 2006). In the PIE ponds, oxygen generated by primary producers was rapidly consumed at night, leading to a series of changes in redox-sensitive metabolisms (Figures 2, 3, and 8). Higher $NO_3^-$ concentrations during the day suggest that $NH_4^+$ released by decomposition was rapidly nitrified, while lower levels at night could reflect multiple processes, including denitrification and dissimilatory nitrate reduction to ammonium (DNRA; Figure 3d; Porubsky et al., 2009; Risgaard-Petersen et al., 1994; Rysgaard et al., 1994). Falling oxygen levels around nightfall likely inhibited nitrification, and possibly facilitated DNRA, resulting in an accumulation of $NH_4^+$ (Figures 3c, 3d, and 8). The subsequent overnight decline in $NH_4^+$ suggests that it was rapidly consumed, potentially through dark uptake by BMA and/or by anaerobic ammonium oxidation (Andersen & Kristensen, 1988; Clément et al., 2005; Porubsky et al., 2009; Rysgaard et al., 1995). Multiple processes producing and consuming $NH_4^+$ at night resulted in greater variability (i.e., CV), compared to the day. Dynamic but low $NH_4^+$ and $NO_3^-$ concentrations suggest inorganic nitrogen was rapidly recycled. This is consistent with previous calculations that sediment $NH_4^+$ fluxes generally met, but rarely exceeded, BMA demand in marsh ponds (Spivak et al., 2018). Further, low $NH_4^+$ and $NO_3^-$ levels and rapid recycling suggest that inorganic nitrogen released by decomposition in ponds is unlikely to be exported and contribute to coastal eutrophication.

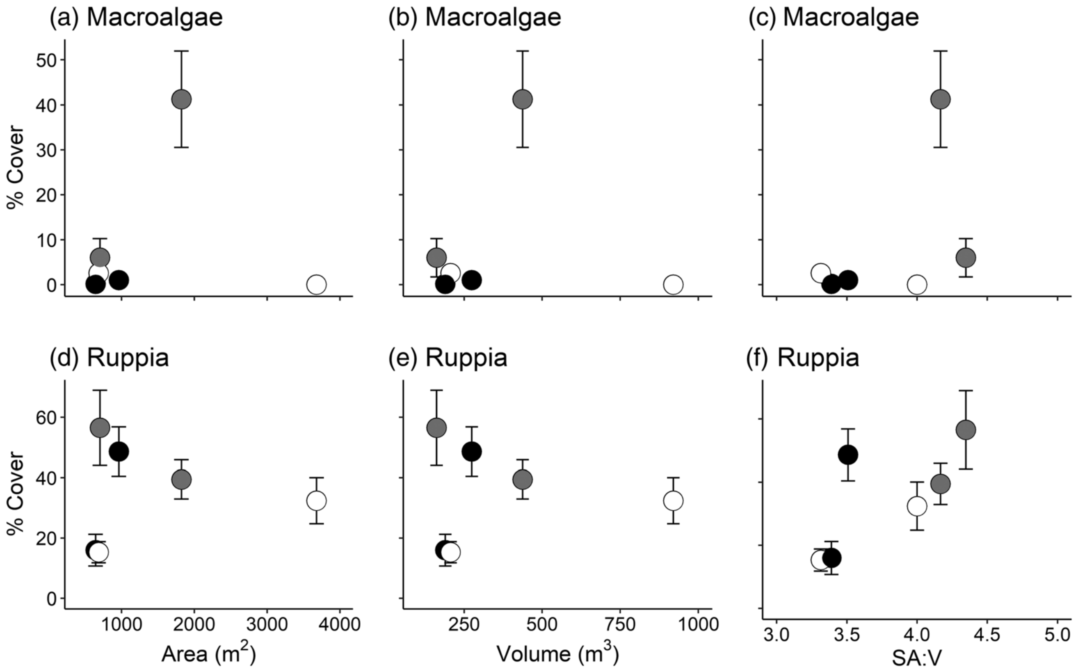

**Figure 6.** Pond macrophyte communities in summer 2016. Abundances of macroalgae (a–c) and *R. maritima* (d–f) in the paired ponds within Regions A (white), B (black), and C (gray). Data are mean ± SE. See Table 1 for pond characteristics and Table 2 for statistical results.

Increased sulfide concentrations, following the $NH_4^+$ peak and during the period of lowest DO concentrations, further indicate that active microbial metabolisms continuously shift overnight (Figures 2c, 3c, 3f, and 8). The sulfide peak likely reflects increased sulfate reduction in surface waters as well as a drop in the oxidation of sulfides diffusing from the sediments. Sulfide concentrations were low, even at their peak, despite abundant sulfate availability and consecutive hours of low DO. This hints that sulfur is rapidly recycled, until the ponds become anoxic, which is consistent with sediment flux measurements (Spivak et al., 2018), pore water dynamics (Rigaud et al., 2018), and the presence of active sulfate reducing and sulfur oxidizing bacterial communities (Kearns et al., 2017; Rao et al., 2016; Salman et al., 2015; Wilbanks et al., 2014). For instance, the activity of bacteria in the orders *Desulfobacterales* and *Chromatiales*, which include members of the pink berry consortia, changed over diel cycles in a nearby PIE pond (Kearns et al., 2017). Thus, the activity of different microbial metabolisms likely peak and ebb during short time frames each day, due to the sharp swings in redox conditions.

Although autotrophic and heterotrophic processes influenced surface water biogeochemistry in a variety of ways, there were only slight differences in DOC between day and night (Figure 3b). This was surprising because we had expected that microbial consumption would lower DOC at night, while exudation of photosynthates would lead to higher concentrations during the day (Maher & Eyre, 2010, 2011; Porubsky et al., 2008; Ziegler & Benner, 1999). However, multiple processes likely produce and consume DOC, resulting in little net change over a diel cycle. Seagrasses, macroalgae, and BMA release considerable fractions of new production as DOC (Evrard et al., 2008; Maher & Eyre, 2010; Wada et al., 2007; Ziegler & Benner, 1999). Decomposition of particulate carbon can produce DOC, and the magnitude of this input may change over diel cycles with the depth of oxygen penetration in surface sediments (Risgaard-Petersen et al., 1994). Photochemical reactions can increase and decrease DOC by oxidizing particulate and degrading dissolved organic matter, respectively (Kieber et al., 2006). Finally, bacterial assimilation can be a strong DOC sink. DOC fluxes in coastal habitats vary with nutrient availability and are often correlated with ecosystem metabolism rates. For instance, adding $NO_3^-$ to BMA-dominated sediments caused a shift from net DOC uptake to release (Porubsky et al., 2008). In a seagrass habitat, DOC fluxes in light and dark benthic chambers were correlated with the ratio of production to respiration and nighttime DO consumption, respectively (Maher & Eyre, 2011). Based on these relationships and assuming marsh ponds are comparable environments, we

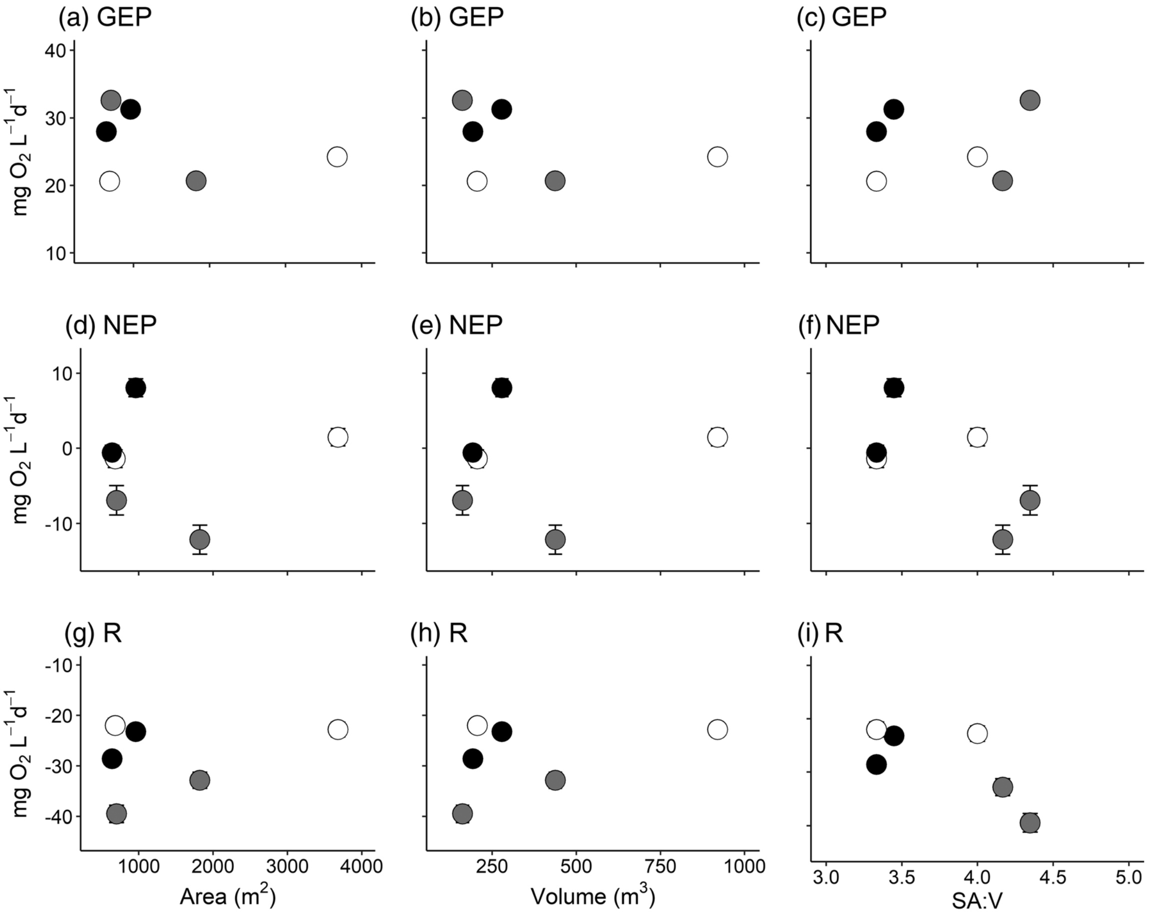

**Figure 7.** Whole-pond oxygen metabolism in summer 2016. Gross ecosystem production (GEP; a–c), net ecosystem production (NEP; d–f), and respiration ($R$; g–i) were calculated from daily swings in DO, measured in paired ponds within Regions A (white), B (black), and C (gray). Data are mean ± SE. See Table 1 for pond characteristics and Table 2 for statistical results.

might have expected a nighttime DOC uptake of −1,900 to −2,500 μmol m$^{-2}$ hr$^{-1}$ and daytime efflux of 1,500–2,000 μmol m$^{-2}$ hr$^{-1}$. These rates are similar to other benthic habitats (Porubsky et al., 2008; Ziegler & Benner, 1999) and, scaled across 24 hr, would have had a small net impact on the DOC reservoir (264–294 mmol m$^{-2}$). Consequently, multiple consumptive and productive processes, along with low dissolved inorganic nitrogen availability, may have contributed to smaller than expected diel DOC oscillations.

Successive, overnight changes in compounds produced and consumed by redox-sensitive metabolisms indicate that microbial communities both respond to and drive pond biogeochemistry (Figure 8). This is

**Table 3**

*Correlations Between Pond Metabolism Rates (GEP, NEP, R) and Potential Environmental (Temperature, PAR) and Biological (Primary Producer Abundance) Drivers*

| | Water temperature (°C) | | | PAR (μmol m$^{-2}$ s$^{-1}$) | | | Log$_{10}$ *R. maritima* (% cover) | | | Log$_{10}$ macroalgae (% cover) | | | $r^2$ | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Response | Est | SE | $p$ | Est | SE | $p$ | Est | SE | $p$ | Est | SE | $p$ | mar | cond |
| GEP (mg O$_2$ L$^{-1}$ day$^{-1}$) | 0.90 | 0.34 | **0.009** | 0.03 | 0.01 | **<0.001** | 10.27 | 3.84 | **0.009** | −4.52 | 2.27 | **0.049** | 0.37 | 0.93 |
| NEP (mg O$_2$ L$^{-1}$ day$^{-1}$) | −0.55 | 0.31 | 0.079 | 0.04 | 0.00 | **<0.001** | 2.46 | 3.86 | 0.525 | −8.16 | 2.82 | **0.005** | 0.45 | 0.95 |
| $R$ (mg O$_2$ L$^{-1}$ day$^{-1}$) | −1.39 | 0.31 | **<0.001** | 0.01 | 0.00 | 0.052 | −6.74 | 3.89 | 0.086 | −5.00 | 2.97 | 0.095 | 0.31 | 0.94 |

*Note.* The estimated slope (Est), standard error of the slope (SE), and $p$ value for each predictor variable in the model are presented. The marginal (mar) and conditional (cond) $r^2$ reflect the variance explained by fixed effects alone or by fixed and random effects combined, respectively. Significant $p$ values (0.05) are in bold. Data were transformed as indicated.

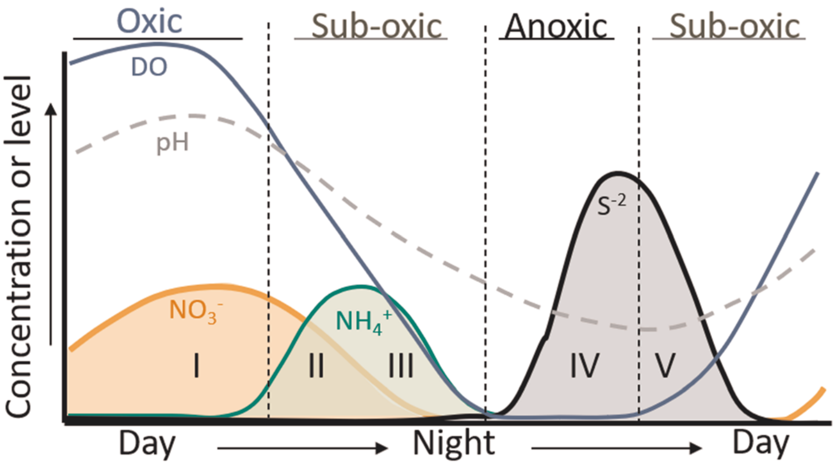

**Figure 8.** Day-night shifts in compounds involved in redox-sensitive metabolisms. I: Primary production supplies oxygen that supports nitrification. II: As oxygen levels decline at night, $NO_3^-$ consumption, potentially by denitrification and DNRA, outpaces nitrification. Inhibition of nitrification allows ammonium from decomposition, and potentially DNRA, to accumulate. III: Dark algal uptake of ammonium and other consumptive processes reduce concentrations. IV: Sulfide peaks during anoxic hours, reflecting sulfate reduction and inhibition of oxidative processes. Respiration increases DIC, causing pH to drop. V: Increasing PAR stimulates primary production, leading to increases in DO, pH, nitrification, and sulfide oxidation.

consistent with the few studies that have examined diel changes in marsh ponds and tidally restricted systems (Beck & Bruland, 2000; Kearns et al., 2017; Rigaud et al., 2018). Sulfate reduction is a low-yield metabolism, and the accumulation of sulfides after consecutive hours of low DO hints that other, more energetically favorable electron acceptors may be actively cycled and contribute to pond metabolism. For instance, Beck and Bruland (2000) and Rigaud et al. (2018) observed increased dissolved manganese concentrations in pond surface waters when DO fell at night. Beck and Bruland (2000) also observed a small increase in dissolved iron overnight but no change in sulfide, suggesting that the system was not anoxic, while Rigaud et al. (2018) did not detect iron in surface waters but measured increasing sulfide levels in pore waters. They hypothesize that interactions between iron and sulfur cycles limited the release of iron into surface waters. Further exploration of electron acceptor recycling, including manganese and iron, is important for understanding microbial responsiveness and interactions over short time scales as well as for further constraining pond contributions to ecosystem-level metabolism and biogeochemistry.

### 4.2. Interannual Changes in Pond Ecology and Biogeochemistry

Snapshot-to-seasonal characterizations of salt marsh ponds describe functioning over short time scales, but interannual data are needed to more fully understand pond dynamics. Comparisons between two ponds in 2014 (Ponds 2 and 1 in Spivak et al., 2017, 2018) and 2016 (Ponds 1 and 4, respectively; this study) indicate that the systems are not in steady state. We previously found that pond plant communities and biogeochemistry are largely similar between flooding and isolated tidal stages, with a few exceptions (Spivak et al., 2017, 2018). For instance, high primary production rates in the summer deplete DIC more strongly during isolated tidal stages and alter carbon isotope systematics (Spivak et al., 2018). Seasonality, in contrast, drives large changes in suspended organic matter, microalgal and macroalgal abundances, and surface water oxygen metabolism rates (Spivak et al., 2017). Sediment respiration rates are similar between seasons and supported, in part, by decomposition of old peat, which drives pond deepening (Spivak et al., 2018). Somewhat surprisingly there was considerable variability between ponds, which motivated us to explore scaling relationships and characterize how biogeochemical processes change over hours to years.

Between 2014 and 2016, surface water salinity and DOC increased 23–26% and 31–60%, respectively, while $NH_4^+$ fell 96% and abundances of *R. maritima* and macroalgae shrank by 42–69% and 93–98%, respectively. Higher salinities likely reflect lower precipitation in 2016 (9.6 cm) compared to 2014 (24.1 cm), rather than differences in average summer air temperatures (2016: 24.4°C; 2014: 22.5°C) or tidal inundation (~2% greater in 2016; NOAA tide gauge 8,443,970). *Ruppia maritima* can tolerate a wide salinity range, from nearly freshwater to hypersaline, but levels greater than ~28, observed in 2016, may inhibit flowering and slow growth (Kantrud, 1991). Falling $NH_4^+$ between 2014 and 2016 and low surface water dissolved inorganic nitrogen-to-$PO_4^{3-}$ ratios (0.8–1.92) may have further limited macroalgal and *R. maritima* growth (Pedersen & Borum, 1997; Pulich, 1989; Thursby, 1984). It is unclear why $NH_4^+$ decreased between years, particularly since *R*, which includes aerobic decomposition, increased from 2014 ($-15.8$ to $-17.9$ mg $O_2$ $L^{-1}$ $day^{-1}$) to 2016 ($-23.2$ to $-28.6$ mg $O_2$ $L^{-1}$ $day^{-1}$), but identifying the causes would be important since macrophytes affect pond metabolism rates (Table 3). A caveat is that surface water nutrient data from this study represent a single diel cycle and measurements throughout the growing season would better capture variability and be more representative of conditions affecting macrophytes. Despite shrinking macrophyte abundances, GEP increased 30–36% while NEP was similar between 2014 and 2016, suggesting that much of the additional production was respired. Comparisons between 2014 (Spivak et al., 2017, 2018) and 2016 (this study) reveal that ponds are dynamic over hourly to interannual time scales, which may complicate integration of these shallow systems into ecosystem biogeochemical budgets.

### 4.3. Spatial Patterns in Pond Biogeochemistry

Pond expansion contributes to landscape fragmentation and could impact habitat usage by resident and migrating animals as well as rates of ecosystem metabolism and carbon storage (Bolduc & Afton, 2004; Spivak et al., 2017, 2018; Trocki & Paton, 2006). Conducting detailed ecological and biogeochemical surveys is time intensive and likely impractical since numerous ponds are scattered across the landscape (Millette et al., 2010; Schepers et al., 2017). Developing scaling relationships between pond dimensions and properties could reduce the need for detailed field surveys since geospatial data products, like LIDAR, are rapidly improving. However, we found few relationships between pond properties and surface area, volume, or SA:*V* (Figures 4–7 and Table 2). Average daily water temperatures decreased slightly with increasing pond volume, likely reflecting differences in heat capacity. Correlations between SA:*V* and salinity (negative; Figure 4f) and benthic chlorophyll (positive; Figure 5i) largely reflect Region C ponds (Ponds 3 and 5). Low salinities in Region C ponds, which were the shallowest (Table 1) and among the warmest (Figure 4), suggest that evaporation was not important. Region C ponds were similar distances from the upland border (200–270 m) and creekbank edges (10–13 m) as those in Regions A (border: 185–340 m, creekbank: 8–30 m) and B (border: 195–250 m, creekbank: 12–14 m) making it unlikely that differences in freshwater runoff or tidal connectivity contributed to salinity differences (Table 1). Greater groundwater inputs, either directly or indirectly, via adjacent ditches and creeks or subsurface stratigraphy, could have contributed to lower salinities in Region C but were not captured by our sampling (Table 2).

There were no clear patterns of microalgal and macrophyte abundances across marsh regions (Figures 5 and 6 and Table 2). Near-complete turnover of water in channels and creeks during tidal cycles likely minimizes differences in delivery of suspended particles, including algal propagules and seagrass seeds. Somewhat surprisingly, there were greater differences in primary producer communities between ponds within a region than across regions. In Region B, for instance, only 37 m separate Ponds 1 and 4, but the former had higher suspended POM and chlorophyll concentrations, while *R. maritima* was more abundant in the latter (Figures 5a–5f and 6d–6f). Similarly, there are 12 m between Region C ponds, but benthic chlorophyll and macroalgae were more abundant in Ponds 3 and 5, respectively (Figures 5g–5i and 6a–6c). Different abundances between nearby ponds within a region suggest that tidal exchange may be too limited to effectively disperse seeds and propagules and that ponds may differ in terms of habitat suitability. Local differences in seed banks and propagule production affect the potential species pool, while pond-specific (e.g., habitat suitability) and species-specific (e.g., growth rates) factors influence colonization, establishment, and development of primary producer communities (Lotze et al., 2000; Van der Heide et al., 2009; van Katwijk et al., 2009). Small differences in colonization sequences, timing of spring emergence, and grazing resistance can affect ecological interactions, such as competition, that influence primary producer community composition (Barranguet et al., 2005; Lotze et al., 2000; Zhang & Zhang, 2007). Thus, the identity of species initially colonizing ponds may be more useful in predicting future primary producer communities than pond dimensions, location within the marsh, or the composition of nearby ponds.

Metabolism rates reflected ecological and environmental factors rather than pond dimensions or geospatial characteristics (Tables 2 and 3). For instance, GEP correlated positively with *R. maritima*, water temperatures, and PAR (Table 3). In contrast, NEP was lower when macroalgae were more abundant (Table 3). It is unclear why macroalgal coverage would negatively affect the balance between autotrophy and heterotrophy, since *Ulva* can be highly productive in shallow, coastal systems (Teichberg et al., 2010). However, positive correlations between NEP and PAR suggest that higher light levels may have stimulated the production of other autotrophs, such as microalgae (Table 3). Respiration increased with surface water temperatures, which is consistent with the metabolic theory of ecology (Allen et al., 2005; Hopkinson et al., 2012; Yvon-Durocher et al., 2010), and implies that the ponds may become more heterotrophic as the climate warms (Table 3). Correlations between oxygen metabolism and multiple environmental, surface water, and primary producer community properties underscore the complexity of biogeochemical interactions in ponds.

We did not find support for our second hypothesis as pond properties did not reflect their position within the landscape. Tidal creek length was not a useful predictor since distances were similar between the six ponds, owing to multiple, winding pathways (Table 1). Distances from the upland border and creekbank edge also could not explain differences between ponds ($p > 0.05$; not shown). For instance, Ponds 2 and 6 in Region A were the farthest and shortest distances, respectively, from the upland border and creekbank edge (Table 1) and had similar temperatures and salinities (Figure 4), microalgal and macrophyte abundances (Figures 5 and 6), and metabolism rates (Figure 7). Our findings contrast Hutchings et al. (2019), who found iron-rich and sulfide-rich ponds at different distances from creekbank edges in an East Anglian (UK) marsh. Thus, the usefulness of geospatial position as a predictor of pond biogeochemistry may differ by marsh system and response variable.

Patterns in surface water conditions, primary producer communities, and metabolic rates provide support for our third hypothesis, that ecological and biogeochemical properties varied by pond (Figures 3–7). The lack of directional relationships between pond properties and dimensions or geospatial position is consistent with the idea that many complex ecological and biogeochemical processes are not easily scaled up (Schindler, 1998; Spivak et al., 2011). Long stretches of tidal isolation likely support the development of divergent plant community and biogeochemical characteristics, even in ponds located in close proximity. Increased frequency of tidal connection, at lower elevations or as sea levels rise, could lead to greater similarities across ponds. We focused on high marsh ponds because low marsh ponds are less abundant in PIE. However, future comparisons between high and low marsh ponds could be useful in understanding how marshes may change with expected increases in tidal inundation.

## 5. Conclusions

Pond expansion in some salt marshes may contribute to ecosystem state shifts from one dominated by emergent vegetation to an open water environment (Marani et al., 2010; Mariotti & Fagherazzi, 2013; Watson et al., 2017). Thus, directional relationships between pond properties and dimensions would be useful in refining predictions of how marsh biogeochemistry may change. However, we found that ponds are dynamic over time scales of hours to years and that variability between ponds is not clearly attributable to dimensions or geospatial position (e.g., tidal creek length and distance from upland or creekbank). Many factors may contribute to between-pond differences (e.g., seed banks and colonization order), but isolation from regular tidal inputs is likely important. The extreme swings in redox-sensitive biogeochemical processes likely reflect the condition of being a semi-isolated system and may become more muted if emergent marshes tip toward open water environments.

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## Data Availability Statement

Data are archived in the PIE-LTER data catalog (Spivak, 2020a, 2020b, 2020c, 2020d).

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