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# Influence of salinity on SAV distribution in a series of intermittently connected coastal lakes

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## ABSTRACT

Intermittently closed and open lakes and lagoons (ICOLLs) are coastal lakes that intermittently exchange water with the sea and experience saline intrusions. Understanding effects of seawater exchange on local biota is important to preserve ecosystem functioning and ecological integrity. Coastal dune lakes of northwest Florida are an understudied group of ICOLLs in close geographic proximity and with entrance regimes operating along a frequency continuum. We exploited this natural continuum and corresponding water chemistry gradient to determine effects of water chemistry on resident submersed aquatic vegetation (SAV) distributions in these ecosystems. SAV distribution decreased with increases in salinity, but was unaffected by variation in nitrogen, phosphorous, and turbidity. Salinity perturbations corresponding with water exchange with the Gulf of Mexico were associated with reductions in SAV in coastal dune lakes. Potential impacts associated with changes in global climate may increase the frequency of seawater exchange across all coastal dune lakes and potentially reduce the distribution of oligohaline macrophytes among these ecosystems.

## 1. Introduction

Estuarine submersed aquatic vegetation (SAV) is ecologically and economically important. Characterized by dense beds of structurally complex shoots, blades, and rhizomes, SAV acts as critical nursery habitat for juvenile fish and invertebrates by providing food and refugia (Jones and West, 2005). In addition, through reducing water flow via aboveground structures, SAV supports multiple regulating services such as sediment stabilization, nutrient cycling, and erosion control (Barbier et al., 2011). Hence, an understanding of mechanisms driving distribution of SAV is important in preserving ecosystem services and estuarine function (Cullen-Unsworth and Unsworth, 2018).

Intermittently closed and open lakes and lagoons (ICOLLs) comprise a class of estuaries characterized by stochastic, rather than perpetual, water exchanges through a recurrent connection to the sea (Roy et al., 2001; Tagliapietra et al., 2009). Ordinarily isolated from an adjacent sea by a sand dune or berm structure, heavy rains, storm waves, or spring tides occasionally breach the barrier, reverting the lakes to tidal estuaries for brief periods of time (i.e., days to weeks), although in regions with pronounced wet and dry seasons, connections may persist for far longer (i.e., months; Haines et al., 2006; Schallenberg et al., 2010). In

addition, managers commonly increase the frequency or duration of barrier openings mechanically, or initiate sea-ICOLL exchange (Stephens and Murtagh, 2012). Though relatively small (i.e., depth <5 m; surface area <10 km<sup>2</sup>), and uncommon (Haines et al., 2006; but see McSweeney et al., 2017), ICOLLs support high biodiversity (Dye and Barros, 2005), and provide aesthetic as well as economic value (Pollard, 1994; West and Gordon, 1994; West and Morrison, 2004).

Environmental stressors influence community structure in estuaries. In particular, small estuaries are often predominantly influenced by abiotic processes due to substantial fluctuations in physical variables such as water chemistry (Haines et al., 2006; Morris and Turner, 2010; Hyman and Stephens, 2020). Salinity, nutrient concentrations, and light availability shape SAV and phytoplankton community structure in ICOLLs and similar estuary classes such as small, highly pulsed permanently open waterbodies (Livingston et al., 1998; Bachelet et al., 2000; Nozais et al., 2001; Dobberfuhl, 2007; Lamptey and Armah, 2008; Lemley and Adams, 2019). However, SAV responses to water chemistry changes depend on community structure, especially species' physiological tolerances (Bornman et al., 2008; Whitfield et al., 2008; Riddin and Adams, 2010). Moreover, effects of seawater inflows on ICOLL water chemistry are determined by local differences between ICOLL

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water chemistry and seawater, as well as broader regional climate patterns (Nozais et al., 2001; dos Santos et al., 2006; Haines et al., 2006; McSweeney et al., 2017; Hyman and Stephens, 2020).

Linkages between seawater inflows and SAV distributions in ICOLLS may similarly depend on entrance dynamics and regional climate. In semi-arid regions such as South Africa (Taylor et al., 2006; Adams et al., 2016), Australia (Ferguson et al., 2018; Scanes et al., 2020), and the Mediterranean Sea (Largier et al., 1997; Bachelet et al., 2000), effects of seawater exchange on SAV among ICOLLS are well studied. Here, rainfall and corresponding freshwater inputs are rarer and unpredictable (Adams and Van Niekerk, 2020). As a result, effects of seawater exchange depend on abiotic conditions. For example, closed periods coinciding with dry seasons can result in hypersalinity (>35) and desiccation stress (Riddin and Adams, 2008; Largier et al., 1997; Wooldridge et al., 2016), which may be alleviated by connections with the sea. However, while the bulk of ICOLLS studied occur in temperate locations with pronounced dry seasons or hot summers (Peel et al., 2007; McSweeney et al., 2017), whether these patterns extend to ICOLLS in regions with less extreme salinity regimes is as not well understood. This is an important question, as a plurality of ICOLLS occur globally in temperate regions with cooler summers and more consistent rainfall (McSweeney et al., 2017). Even in South Africa, ICOLLS fronting riverine ecosystems with sufficient flow to maintain relatively oligohaline salinity regimes experience shifts in SAV and algal communities following steep increases in salinity coinciding with entrance openings (Riddin and Adams, 2010). It is therefore probable that SAV communities in oligohaline (0–5) to mesohaline (5–10) ICOLLS in non-arid regions may be disturbed by salinity increases associated with seawater exchange.

Salinity is not the only component of seawater distinct from freshwater; other water chemistry variables may influence biological communities (Human et al., 2016) and must also be considered when ascertaining relationships between connectivity and SAV in ICOLLS. For example, seawater exchange can promote SAV in eutrophic ICOLLS through flushing, removing excess nutrients and limiting algal growth (Human et al., 2016).

Coastal dune lakes of northwest Florida are an understudied group of ICOLLS which connect with the Gulf of Mexico (GOM) for brief periods of time. Herein, ‘coastal dune lakes’ is used to differentiate the ICOLLS examined in this study from others globally. Residing in a temperate region characterized by mild summer temperatures and an absence of a pronounced wet and dry season, coastal dune lakes are representative of

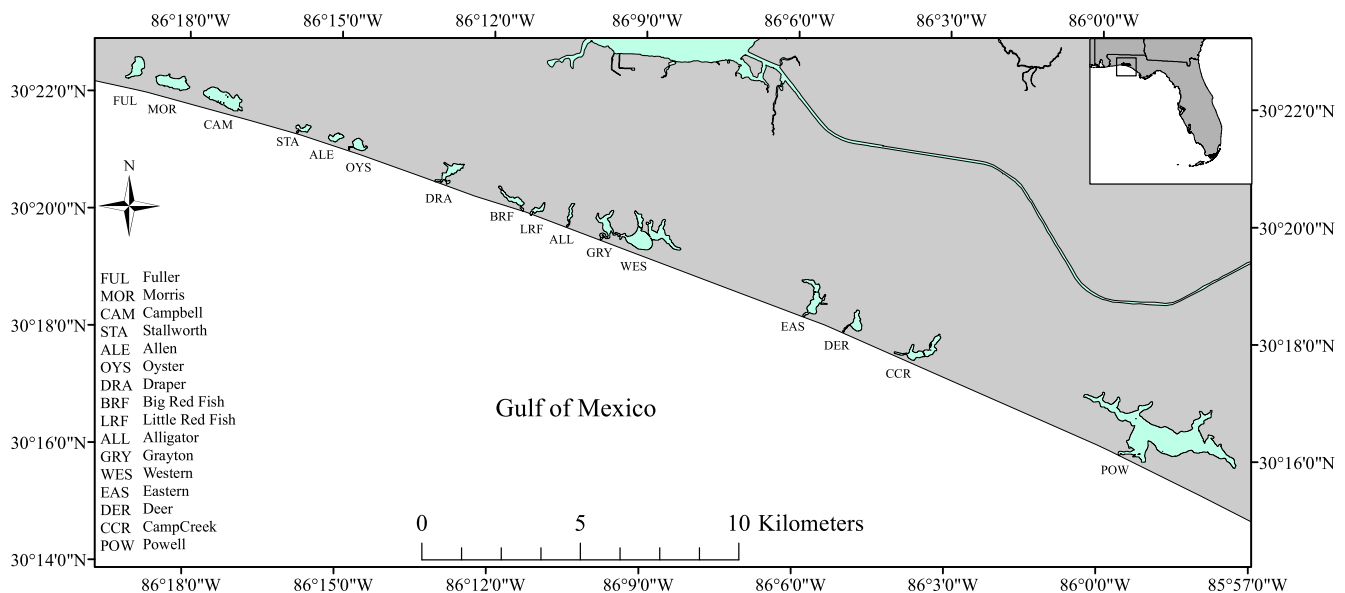
oligohaline (0–5) to mesohaline (5–10) ICOLLS with moderate fluctuations in salinity relative to global counterparts in semi-arid regions. Frequencies of sea-to-lake connections are a function of sea level height and hydraulic gradients between lakes and the GOM (Hyman and Stephens, 2020). Entrance regimes are therefore lake specific; low-perched lakes receive seawater as often as weeks to months, while higher-perched lakes receive seawater as sporadically as once per decade (Hyman and Stephens, 2020). This morphological variation has produced a suite of ICOLLS in close proximity (i.e., within a 30 km stretch of coastline; Fig. 1) with entrance regimes operating along a frequency continuum. We exploited this variation in salinity regimes and nutrient profiles among otherwise similar estuaries to understand patterns in SAV percent area cover (PAC) and community structure in ICOLLS located in temperate regions. We compare these patterns with those of ICOLLS located in arid and semi-arid regions (i.e., South Africa and Australia).

Using these coastal dune lakes as representative study systems, our objective was to evaluate relationships between water chemistry and SAV PAC among ICOLLS in cooler temperate regions without pronounced wet and dry seasons. Understanding that relationships between abiotic variables and SAV are complex, we developed multiple alternative hypotheses  $H_i$  (Chamberlin, 1890) using combinations of salinity, nutrients (i.e., nitrogen and phosphorus), and turbidity as independent variables (Table 1). Effects of salinity, nutrients, and turbidity on SAV

**Table 1**

Akaike's information criterion corrected for small sample size (AICc) for the linear mixed effects models ( $g_i$ ) corresponding to the different hypotheses for PACc.  $\Delta_i$ : difference in the AICc values between model  $g_i$  and the best model;  $w_i$ : probability that model  $g_i$  is the best model in the set; S: Season; Sal: Salinity; N: Nitrogen; P: Phosphorus; T: Turbidity.

Hypothesis	Model	Formula	AICc	$\Delta_i$	$W_i$
$H_0$	$g_0$	S	224.79	13.56	0.00
$H_1$	$g_1$	S + Sal + (S x Sal)	211.23	0.00	0.60
$H_{2a}$	$g_2$	S + N + (S x N)	222.97	11.74	0.00
$H_{2b}$	$g_3$	S + P + (S x P)	233.39	22.16	0.00
$H_{2c}$	$g_4$	S + P + N + (S x P) + (S x N)	235.14	23.91	0.00
$H_{3a}$	$g_5$	S + Sal + N + (Sal x N)	227.60	16.37	0.00
$H_{3b}$	$g_6$	S + Sal + P + (Sal x P)	226.92	15.69	0.00
$H_4$	$g_7$	S + Sal + N + P	218.08	6.85	0.02
$H_5$	$g_8$	S + Sal + N + P + (P x N)	213.32	2.09	0.21
$H_6$	$g_9$	S + Sal + T + (S x Sal)	213.87	2.64	0.16



**Fig. 1.** Geographic location of 16 coastal dune lakes. Adapted from Hyman and Stephens (2020).

distribution must be considered within the context of season due to changes in SAV distributions over the annual cycle. In the following paragraph, we describe and justify the independent variables and corresponding hypotheses (in parentheses).

We expect SAV distribution to be influenced by seasonality ( $H_0$ ), with greater SAV cover in spring and summer relative to fall and winter, following the annual growing season. SAV distribution and community composition are often altered at pulsed higher salinities ( $H_1$ ) corresponding with opening events (Whitfield et al., 2008; Riddin and Adams, 2010; Rodríguez-Gallego et al., 2015; Ferguson et al., 2018; Scanes et al., 2020). Due to natural changes in SAV distribution over annual cycles, salinity and season may also produce interaction effects ( $H_1$ ). SAV distribution may also be enhanced by constraints on phytoplankton biomass by nitrogen ( $H_{2a}$ ) or phosphorus ( $H_{2b}$ ) limitation or both ( $H_{2c}$ ) on microalgal biomass, which may preclude regime shifts from benthic to water column dominance via nutrient over-enrichment (i.e., SAV to phytoplankton; Nozais et al., 2001). Over-enrichment impacts of nutrient concentrations, via either nitrogen ( $H_{3a}$ ) or phosphorus ( $H_{3b}$ ) can also depend on salinity (Fong et al., 1996; Choi et al., 2010; Boustany et al., 2015). Nutrient concentration over-enrichment may affect SAV distribution at low salinities, but not at high salinities when salinity stress outweighs stress attributed to over-enrichment ( $H_{3a}$  and  $H_{3b}$ ). Hypotheses  $H_4$  and  $H_5$  deal with various combinations of the independent variables such as additive effects of salt stress and nutrient limitation ( $H_4$ ) and co-limitation by nitrogen and phosphorus on water column phytoplankton ( $H_5$ ). For instance, we predict a negative relationship between nitrogen concentrations and SAV distribution at high concentrations of phosphorus, but no relationship between nitrogen concentrations and macrophyte distribution at low phosphorus concentrations, once phosphorus limitation outweighs stress from nitrogen limitation for water column phytoplankton, and vice versa. Finally, due to relationships between light attenuation and SAV distribution in waterbodies with turbidity (Livingston et al., 1998; Hoyer et al., 2004; Dobberfuhl, 2007; Frankovich et al., 2011), we predict reduced SAV distribution in lakes with higher turbidity values ( $H_6$ ).

## 2. Methods

### 2.1. Sampling

Between January and December 2018, we sampled 14 lakes to assess relationships between water chemistry and SAV composition and distribution across multiple seasons (Fig. 1). Survey seasons were winter, spring, summer and fall. Surveys consisted of i) sonar mapping to assess lake bathymetry and SAV distribution, ii) visual estimates of SAV community composition, and iii) sampling of water chemistry variables.

Sonar surveys assessed lake bathymetry, lake morphology, and SAV areal percent area covered (PAC, a measure of SAV distribution) on each sampling date. Sonar was preferred over aerial imagery due to difficulties estimating SAV distribution in colored or turbid waterbodies (e.g., Wolter et al., 2005). Sonar data were collected using Lowrance hydroacoustic equipment and processed using BioBase cloud-based software (Valley et al., 2015). Lowrance HDS-7 (generation 3) with a 20° side-scan transducer (operating at a frequency of 200 kHz) and Global Positioning System (GPS) were used to estimate water depth and vegetation biovolume (height of SAV in water column relative to total depth). Equipment was attached to either a boat or kayak, depending on lake size, moving between 3 and 13 km h<sup>-1</sup>. Surveys were performed consistently for each lake by first traversing the perimeter to collect information along the lake shoreline, followed by sequential transects across the lake spaced 25 m apart (Fig. S1). In areas where SAV was sufficiently dense to prevent access by vessel, geographic coordinates were recorded manually as 100% biovolume. Sonar equipment produced 20 pings per second (pps), which were used as raw data. Sonar data were uploaded and assessed with BioBase, where ordinary kriging algorithms evaluated acoustic and GPS signals to create a fine-scale (<5

m<sup>2</sup>) map of predicted bathymetry as well as SAV density (Netherland and Jones, 2015; Valley et al., 2015). Bathymetric maps of all coastal dune lakes are included as supplementary material (Fig. S2 – S15). PAC was defined conservatively as the percentage of surface area occupied by aboveground SAV biomass, because belowground biomass could not be detected with sonar, and macrophyte biovolume could artificially fluctuate with changes in water levels following opening events (Radomski and Holbrook, 2015).

Sampling could not be synchronous within each season across all lakes due to logistical constraints. Thus, some unknown variability in the surveys exists, which adds additional uncertainty to seasonal effects. Moreover, in late 2018 Hurricane Michael disrupted sampling in the final season (fall), prohibiting sampling of Grayton, Deer, Eastern, Powell, and Western Lakes.

In July and August, SAV was sampled at five sites within each lake. Sites were selected using a random sampling algorithm from a set of coordinates within areas occupied by SAV based on information from the summer sonar survey. At each site, a large plastic open-ended cylinder (inside diameter 61 cm, sampling area = 0.3 m<sup>2</sup>) was placed over vegetated areas and driven into the lake bottom. The cylinder was staked down on four sides to prevent movement due to currents, wind, or wave action. All aboveground macrophyte biomass was collected from each cylinder and rapidly sealed in a plastic bag, transported on ice, and frozen until processing. SAV from each lake was subsequently identified to the lowest taxonomic level feasible, dried at 50 °C, and measured for dry weight. In three lakes (Deer, Eastern, and Little Red Fish) SAV was not present in any of the randomly selected sampling sites. Deer and Little Red Fish Lakes had almost no recorded SAV in any survey. Meanwhile, Eastern Lake similarly had low PAC values as well as highly patchy and sparse vegetation which, coupled with highly colored and turbid water, resulted in difficulties locating SAV even at locations nearby to randomly selected sites.

Water chemistry measurements were collected at three, open-water stations within each lake at monthly intervals throughout the study. Salinity and turbidity were measured with a Hydrolab HL4 Multiparameter Sonde, calibrated monthly. Water sample collection and in-field measurements were completed by Florida LAKEWATCH and Choctawhatchee Basin Alliance trained citizen scientists following Florida LAKEWATCH sampling and preservation protocols (Hoyer et al., 2012).

Nutrient concentrations were analyzed at the University of Florida Institute of Food and Agricultural Sciences' Florida LAKEWATCH National Environmental Laboratory Accredited Certified (NELAC) laboratory in Gainesville, Florida. Total phosphorus (inorganic and organic) and total nitrogen concentrations were determined following Florida LAKEWATCH Protocol and Standard Operating Procedures (Canfield et al., 1985; Hoyer et al., 2012; Hyman and Stephens, 2020).

### 2.2. Analysis

All data transformations and analyses were performed using R statistical computing language. Collinearity among predictors was assessed using Kendall rank correlation coefficient ( $\tau$ ). Prior to analyses, all predictors were scaled (z-scored) to facilitate parameter estimation among models with interaction terms. Meaningful relationships were evaluated under the accepted threshold for statistical significance ( $\alpha = 0.05$ ).

Lake-specific variation in morphology presented a source of confounding variation in PAC. PAC is a simple ratio of surface area occupied by SAV divided by total surface area of a waterbody. Lakes with larger proportions of bottoms at deeper depths naturally have lower ratios of vegetative cover:surface area compared to shallower lakes due to light attenuation, especially in highly colored or turbid lakes (Canfield et al., 1985). A correction was made to account for this by i) calculating the depth of 98% of all vegetation occurrences (non-interpolated data) across all lakes ( $Z_{max}$ ; Valley et al., 2015), ii) defining the littoral zone in each lake as the surface area of bottom at depths less than or equal to

$Z_{\max}$ , and iii) dividing the surface area occupied by vegetation within the calculated littoral zone by the surface area of the littoral zone in each lake, to yield PAC values standardized for morphology variability (Percent area corrected, or PACc). Analyzing only SAV within calculated littoral zones (where direct evidence of SAV occurrence existed) reduced the likelihood of error attributed to ordinary kriging interpolation (Fig. 2). Finally, water levels of several coastal dune lakes fluctuated with rainfall and opening regimes (i.e., opening events reduced lake water volume). To prevent fluctuating water levels from introducing bias in our data, we conservatively limited analysis to areas which were consistently inundated in all sonar surveys.

SAV communities in each lake were assessed using dry weight as a metric to examine variation in composition. Dry weights of each taxon within a replicate sample were divided by the total dry weight of a sample to estimate relative abundance. Since an obvious depth gradient for species composition was not present within lakes, relative abundances of each taxonomic group were averaged across replicate samples in each lake to estimate lake-specific community composition. Principal component analysis (PCA), a multivariate dimension-reducing technique based on eigenvalue decomposition of an inner-product correlation or covariance matrix, identified SAV community composition patterns among the waterbodies studied. Using PC1 axis scores as a proxy for community composition, scatterplots of salinity and SAV community appeared nonlinear. We fit an asymptotic model (drc package, function `drm`; Ritz et al., 2015) using salinity as a predictor to evaluate nonlinear patterns. Strength of monotonic, nonlinear relationships was evaluated using Spearman's rank correlation test (Spearman's Rho).

The 10 statistical models ( $g_0 - g_9$ ) associated with each of the hypotheses  $H_i$  (Table 1) were evaluated within an information theoretic

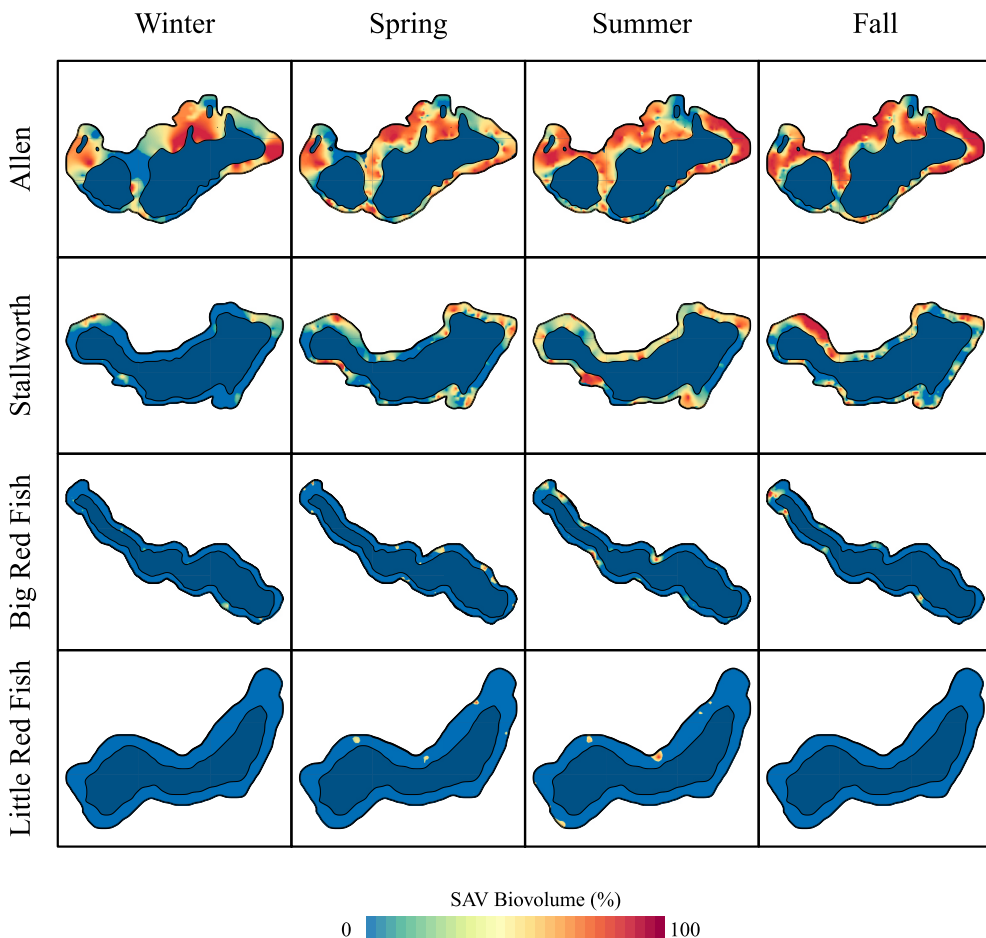
framework (Burnham and Anderson, 2002; Anderson, 2008) to evaluate which predictors were important in explaining variation in PACc. We used Akaike's Information Criterion corrected for small sample sizes (AICc) and weighted model probabilities ( $w_i$ ) based on  $\Delta_i$  values to determine the probability that a particular model was the best-fitting model (Anderson, 2008).

Relationships between PACc and water chemistry variables (salinity, total nitrogen, total phosphorus, and turbidity) were assessed using linear mixed-effects models (`nlme` package, function `lme`; Bates et al., 2015; Pinheiro et al., 2017) with maximum likelihood estimation. PACc was square-root transformed prior to analyses to satisfy normality assumptions. Season was treated as a categorical factor to account for nonlinear patterns in vegetation across seasons. Presumed autocorrelation between repeated measures for individual lakes was accounted for by including a random effect of lake and a first-order autoregressive (AR1) term with lake as a grouping variable. Covariance of random effects (i.e., within-lake dependence) was modeled using an unstructured variance-covariance matrix. Estimated marginal means for main and interaction effects were calculated using Kenward-Roger approximation for degrees of freedom. Pairwise comparisons were evaluated using Tukey's multiple comparison test (`emmeans` package, functions `emmeans` and `emtrends`; Lenth et al., 2018). Model fit was further assessed by conducting log-likelihood ratio  $X^2$  tests and plots of residual vs. predicted values, which appeared random.

### 3. Results

#### 3.1. Percent area covered and macrophyte composition

In total, 51 vegetation surveys were conducted on 14 lakes between



**Fig. 2.** Seasonal submerged aquatic vegetation (SAV) biovolume for four lakes in order of increasing mean salinity: (i) Allen Lake (0.04), (ii) Stallworth Lake (3.98), (iii) Big Red Fish Lake (11.00), and (iv) Little Red Fish Lake (15.17). Lakes displayed here are representative of freshwater, low salinity, intermediate salinity, and brackish lakes and are used to conceptualize variation in PAC with salinity. Colors represent SAV biovolume (red: high; blue: low). Dark blue represents lake surface area outside the calculated littoral zone, where SAV presence was not considered. SAV biovolume is measured as percent of water column occupied by vegetation. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)



January and December 2018. The maximum depth at which SAV occurred among all lakes,  $Z_{\max}$ , was 1.62 m, while lake-specific maximum depth of SAV ranged between 1.22 m (Western) and 1.93 m (Campbell). Estimated littoral zone surface area derived from  $Z_{\max}$  varied between 17 and 63 percent of total lake surface area, attributed to the slopes of the bathymetric profiles (Tables 2 and 3; Fig. S2-S15). The average depth of the littoral zone in each lake was largely consistent: all but three lakes had littoral zones with average depths between 0.7 and 0.9 m (Table 3). The lowest PACc values (0%) occurred in winter, while the highest value (94%) was recorded in fall. However, 50% of lakes had peak PACc values in summer, whereas 35.7% had peak PACc values in spring and 21.4% had peak PACc values in fall. The highest PACc value was recorded in Allen Lake (94%), while lowest PACc values were in Little Red Fish, Fuller, and Eastern Lakes (0%; Table 3).

Four major macrophyte taxa (*Utricularia* spp., *Eleocharis baldwinii*, *Vallisneria americana*, and *Potamogeton pectinatus*) were present in coastal dune lakes, with some variation in species composition. *Utricularia* spp. was present in freshwater ecosystems (Fuller, Morris, Allen, and Campbell Lakes), while *V. americana* and *P. pectinatus* were present in oligohaline and mesohaline systems (Western, Grayton, and Powell Lakes). *Eleocharis baldwinii*—a cosmopolitan species, was dominant in a majority of lakes and was detected in all lakes where vegetation was present, with the notable exception of Allen Lake (Table S1).

Variation in SAV community composition across lakes was examined with PCA (Fig. 3a). Over 89% of total variation in community composition across lakes was accounted for by the first two principal components, with over 67% by PC1. Loadings of *E. baldwinii* with PC1 and PC2 were positive and strong (0.65) or moderate (0.46), respectively. *Utricularia* spp. exhibited a strong, negative relationship with PC1 and a positive relationship with PC2 (−0.75 and 0.37). *Vallisneria americana* exhibited a weak (0.02) positive relationship with PC1 and a strong negative relationship (−0.80) with PC2. *Potamogeton pectinatus* was weakly positively correlated with PC1 (0.07) and weakly negatively correlated with PC2 (−0.03).

PC1 scores of SAV community composition were strongly related to salinity (Fig. 3b;  $\rho = 0.82$ ,  $p < 0.01$ ). Model estimates indicated a three-parameter asymptotic function adequately described patterns between SAV community composition and salinity, with statistically significant upper and lower limits (46.21 and −74.30, respectively;  $p < 0.01$ ) and a marginally significant rate constant (steepness parameter = 1.62;  $p = 0.07$ ).

### 3.2. Water chemistry

A total of 540 water chemistry samples were collected from 58

**Table 2**

Surface area, average depth, maximum depth, volume, and hydraulic gradients among coastal dune lakes in Florida. Geomorphology values were calculated from kriging outputs of sonar surveys conducted in 2018. Hydraulic gradients, a measure of connectivity with the GOM, were obtained from Hyman and Stephens (2020). Lakes with no direct connection with the GOM are indicated with “—” hydraulic gradient values. Minimum, maximum and (grand) mean values of averages among lakes are reported in the summary row. Bathymetric maps of all lakes are reported in supplemental material (Fig. S2-S16).

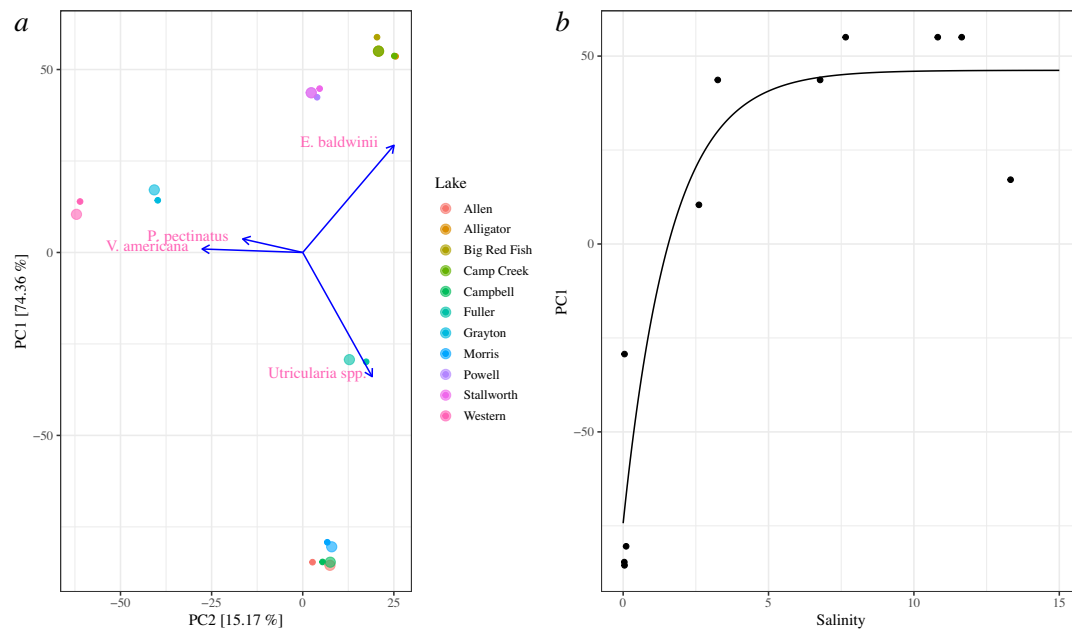
Lake	Lake surface area (m <sup>2</sup> )	Average depth (m)	Max depth (m)	Volume (m <sup>3</sup> )	Hydraulic gradient (cm)
Allen	74,000	1.28	1.85	97,000	—
Alligator	54,000	0.94	1.82	51,000	57.4
Big Red Fish	100,000	1.12	1.81	140,000	20.2
Campbell	430,000	1.39	1.91	360,000	9.5
Camp Creek	260,000	3.54	4.93	1,400,000	106.4
Deer	140,000	2.83	1.99	250,000	41.3
Eastern	270,000	1.74	2.84	530,000	24.4
Fuller	200,000	1.77	2.88	360,000	—
Grayton	180,000	1.42	4.45	330,000	16.2
Little Red Fish	42,000	0.88	1.82	45,000	31.7
Morris	320,000	2.8	4.68	970,000	76.9
Powell	2,700,000	2.54	4.97	7,300,000	7.01
Stallworth	60,000	1.44	2.92	86,000	69.5
Western	710,000	2.04	5.29	1,900,000	—
<b>Summary</b>	<b>370,000 [42,000–2700,000]</b>	<b>1.83 [0.88–3.54]</b>	<b>3.15 [1.81–4.97]</b>	<b>990,000 [45,000–1900,000]</b>	<b>41.89 [7.01–106.40]</b>

**Table 3**

Mean, minimum and maximum values for PACc, littoral zone area, and percent area of littoral zone relative to total surface area among coastal dune lakes in Florida. PACc was calculated from kriging outputs of sonar surveys conducted in 2018. Minimum, maximum and (grand) mean values of averages among lakes are reported in the summary row.

Lake	PACc (%)	Littoral zone area (m <sup>2</sup> )	Littoral area percent of total	Littoral zone average depth (m)
Allen	85.97 [66.17–94.31]	37,000	50	0.72
Alligator	20.8 [2.29–33.03]	34,000	62.96	0.84
Big Red Fish	8.83 [1.65–16.09]	41,000	41	0.82
Campbell	65.44 [42.45–80.51]	76,000	17.67	0.8
Camp Creek	17.45 [2.28–30.89]	84,000	32.31	0.74
Deer	1.96 [0.94–3.21]	51,000	36.43	0.75
Eastern	4.51 [0–11.6]	79,000	29.26	0.78
Fuller	42.41 [0–59.05]	47,000	23.5	0.85
Grayton	5.23 [3.7–7.45]	75,000	41.67	0.8
Little Red Fish	0.43 [0–1.16]	22,000	52.38	0.97
Morris	64.58 [42.92–79.07]	57,000	17.81	0.67
Powell	25.5 [16.9–33.77]	560,000	20.74	0.91
Stallworth	58.36 [16.26–80.99]	23,000	38.33	0.74
Western	74.18 [49.67–86.71]	203,000	28.59	0.85
<b>Summary</b>	<b>36.73 [0.43–85.97]</b>	<b>93,000 [22,000–560000]</b>	<b>34.86 [17.67–62.96]</b>	<b>0.80 [0.67–0.96]</b>

stations in 14 lakes in 2018. Among lakes, mean salinity was 7.2, ranging from 0.04 (Campbell Lake) to 15.17 (Little Red Fish Lake); mean total phosphorus was 13.55  $\mu\text{g/L}$  (10.32–16.81; Camp Creek Lake and Little Red Fish Lake, respectively); mean total nitrogen was 439.94  $\mu\text{g/L}$  (258.33–566.67; Campbell Lake and Fuller Lake, respectively), and mean turbidity was 1.3 NTU (0.17–3.16; Little Red Fish Lake and Stallworth Lake, respectively; Table 4). Nonparametric correlation tests of water chemistry variables indicated limited collinearity. Salinity and phosphorus were moderately positively correlated ( $\tau = 0.40$ ,  $p < 0.05$ ), while correlations for all other pairs of predictors were weak ( $|\tau| <$



**Fig. 3.** PCA ordination of SAV community composition in coastal dune lakes. a) PCA biplot displaying annual mean water chemistry values from each lake. Percent of variation accounted for by each principal component is bracketed. Arrows representing SAV taxa as scaled axes are superimposed. b) Bivariate plot of PCI ordination scores of samples (Fig. 3a) and salinity.

**Table 4**

Mean, minimum and maximum values for salinity, total phosphorus, total nitrogen, and turbidity among coastal dune lakes in Florida. Water chemistry values derived from monthly monitoring.

Lake	TP ( $\mu\text{g/L}$ )	TN ( $\mu\text{g/L}$ )	Salinity	Turbidity (NTU)
Allen	12.38 [4–19]	535.41 [320–710]	0.05 [0.04–0.05]	1.45 [0.53–2.73]
Alligator	13.93 [5–23]	415.19 [120–700]	10.87 [0.93–25.52]	2 [0.57–3.8]
Big Red Fish	16.7 [6–37]	427.84 [200–770]	11 [4.18–26.14]	1.05 [0.13–1.77]
Campbell	10.72 [6–45]	258.33 [190–330]	0.04 [0.04–0.04]	1.05 [0.23–2.37]
Camp Creek	10.32 [7–21]	485.71 [220–820]	11.4 [0.25–34.04]	1.29 [0.54–2.47]
Deer	12.57 [4–28]	438.65 [190–700]	11.35 [0.42–32.16]	0.48 [0–1.13]
Eastern	15.38 [8–36]	330 [220–520]	14.76 [3.1–28.46]	1.04 [0–2.17]
Fuller	12.67 [7–21]	566.67 [320–770]	0.05 [0.04–0.05]	1.75 [0.73–3.5]
Grayton	16.63 [11–28]	414 [280–590]	12.63 [2.76–33.4]	1.42 [0.53–3.07]
Little Red Fish	16.81 [7–28]	504.38 [250–670]	15.17 [5.75–28.97]	0.17 [0–0.6]
Morris	12 [7–31]	470.51 [360–660]	0.11 [0.09–0.14]	1.45 [0.57–1.97]
Powell	15.73 [5–29]	445.38 [230–790]	8.91 [2.62–17.21]	0.97 [0.23–1.93]
Stallworth	13.93 [4–22]	338.81 [240–440]	3.78 [2.16–9.39]	3.16 [2–4.88]
Western	11.47 [7–18]	410.62 [230–620]	4.24 [1.11–12.7]	0.96 [0.62–1.18]
<b>Summary</b>	<b>13.55 [10.32–16.81]</b>	<b>439.94 [258.33–566.67]</b>	<b>7.2 [0.04–15.17]</b>	<b>1.3 [0.17–3.16]</b>

0.20).

### 3.3. Linear mixed-effects models

Based on AICc model comparisons, PACc was best explained by an additive model with season and salinity as main effects as well as a season  $\times$  salinity interaction effect ( $g_1$ ), which had the highest weighted probability (0.60; Table 1). All other models except  $g_8$  and  $g_9$  had weighted probabilities  $<0.05$  and thus were eliminated from further consideration (Table 1). Model  $g_1$  significantly reduced the residual deviance over model  $g_8$  and was a superior model (likelihood ratio  $X^2$  test;  $p = 0.0145$ ). The additional predictor, turbidity, in model  $g_9$  did not significantly reduce residual deviance compared to model  $g_1$  (likelihood ratio  $X^2$  test;  $p = 0.37$ ). Thus, we selected model  $g_1$  as the most parsimonious model accounting for variation in PACc. Model  $g_1$  significantly reduced residual deviance over the null model  $g_0$  (likelihood ratio  $X^2$  test;  $p < 0.01$ ). Residual vs. predicted plots did not indicate heterogeneity of variance or severe departures from normality.

Log-likelihood estimates and AICc scores of model  $g_1$  were nearly identical to an unscaled version using the same parameters, which did

not contain correlated predictors. As a result, the unscaled version is reported here to facilitate interpretation of model coefficients. Parameter estimates of model  $g_1$  were statistically significant (Table 5), with PACc decreasing with salinity (Figs. 2 and 4). Contrast statements (held at constant salinity) indicated PACc was significantly lower for lakes in winter than fall but did not differ between spring, summer, and fall (Table S2). Interaction effects between salinity and season were significant (Table 5; Fig. 4). Linear relationships between salinity and PACc were statistically significant among all seasons (Table S3). However, the magnitude of the relationship between salinity and PACc in winter was lower than fall (Table S4). Although the random effects term in the model (Lake) explained less than 1% of residual variation, the auto-correlation estimate associated with each lake was strong (0.74).

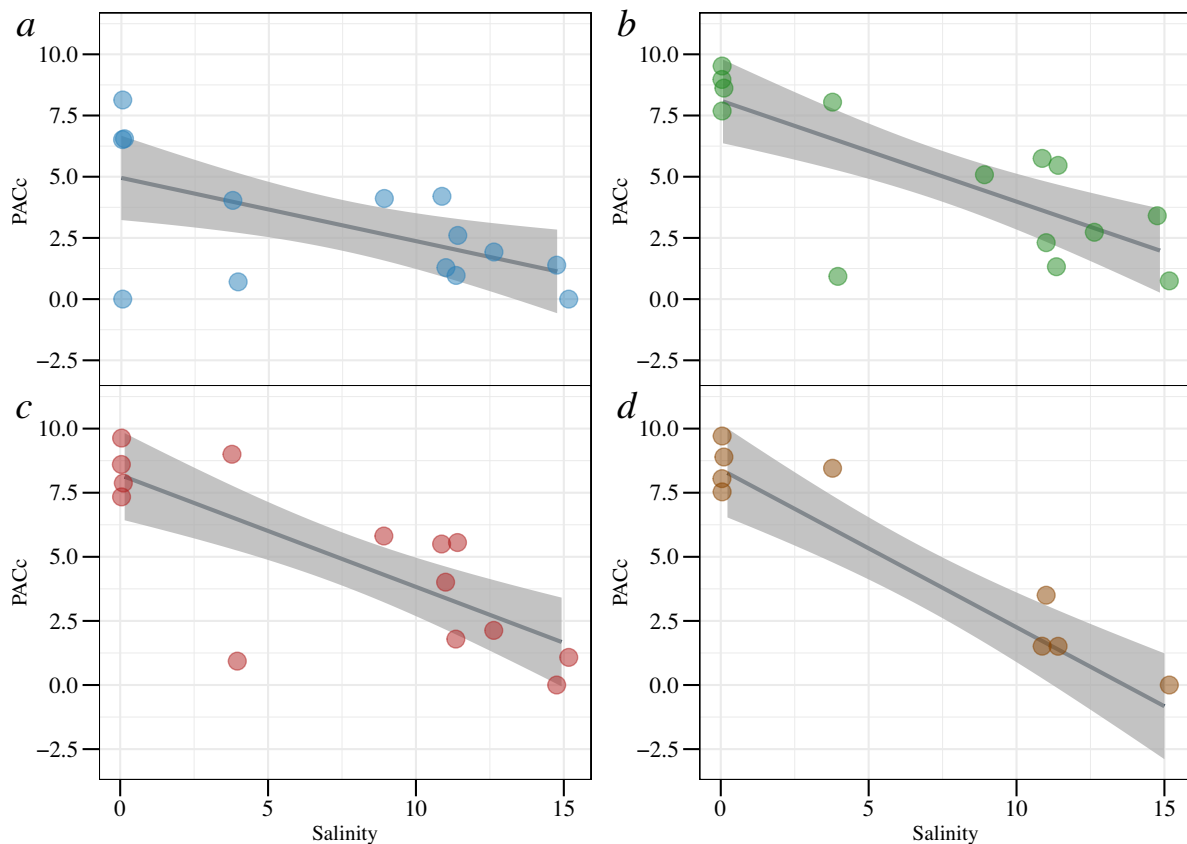
## 4. Discussion

### 4.1. Determinants of SAV in coastal dune lakes

Our study examined relationships between SAV PACc (a metric of SAV abundance and distribution) and water chemistry variables salinity,

**Table 5**  
Parameter estimates from linear mixed effects model  $g_1$ .

Parameter	Variable	Estimate	Standard Error	Degrees of Freedom	t-value	p-value
$\beta_0$	Intercept	4.95	0.94	31	5.28	<0.01
$\beta_{12}$	Spring	3.16	0.67	31	4.71	<0.01
$\beta_{13}$	Summer	3.24	0.88	31	3.66	<0.01
$\beta_{14}$	Fall	3.46	1.04	31	3.33	<0.01
$\beta_2$	Salinity	-0.26	0.1	12	-2.57	0.02
$\beta_{32}$	(Spring x Salinity)	-0.15	0.07	31	-2.14	0.04
$\beta_{33}$	(Summer x Salinity)	-0.18	0.09	31	-1.87	0.07
$\beta_{34}$	(Fall x Salinity)	-0.36	0.12	31	-3.04	<0.01



**Fig. 4.** Linear mixed-effects model outputs with bootstrapped confidence intervals for model  $g_1$ . Relationships between fixed effect salinity and square-root transformed PACc data are displayed for (a) winter, (b) spring, (c) summer, and (d) fall.

total nitrogen, total phosphorus, and turbidity in an understudied group of ICOLLs along the Gulf of Mexico coast of Florida. Our primary goal was to evaluate whether SAV distributions in these oligohaline to mesohaline ICOLLs were best explained by abiotic factors salinity, nutrient availability, turbidity, or combinations of each. Our major finding was that salinity was the strongest predictor of SAV distribution for these subtropical coastal dune lakes, as previously documented for temperate ICOLLs (Scanlan et al., 2020), and that its effects varied with season. A relatively simple model describing SAV PACc as a function of salinity and seasonality best explained observed patterns, rather than variation in nutrient availability or turbidity. The largest SAV PACc consistently occurred in lakes with low salinities and minimal variation in salinity, while PACc was lowest in lakes with higher average salinities and variable salinity regimes. These findings permit generalization of the hypothesis that magnitude and variation in salinity control SAV distributions among temperate ICOLLs in mild (cool summer, consistent rainfall) conditions as well as in dryer, hotter locations. Specifically, in the subtropical climates of Florida, sporadically high salinity appears to be a major constraint on SAV in oligohaline-mesohaline ICOLLs.

SAV PACc varied seasonally, as also documented for SAV biomass (Fernández-Aláez et al., 2002; Steinman et al., 2002; Havens et al., 2004). Winter PACc values were depressed compared to spring, summer, and fall values. A sharp peak in SAV distributions (Hillmann et al., 2019) was not apparent in our study, such that high PACc values were protracted through summer and fall. This may be attributed to longer growing seasons in Florida aquatic ecosystems (Havens et al., 2004). Alternatively, the absence of a sharp peak was potentially a function of the environmental conditions in 2018 relative to years prior such as precipitation, temperature, and storm frequency.

Significant interactions between salinity and seasons necessitated inference on the relationship between salinity and PACc to be made within season. While the negative relationship between salinity and PACc was consistent across seasons, the slope of the relationship varied by season. The weakest relationship between salinity and PACc occurred in winter, while the strongest occurred in fall, with intermediate slopes in spring and summer. This is potentially due to the stronger effects of salinity during the annual growing cycle in lakes characterized by higher salinity regimes (Hillmann et al., 2019).



Despite a negative relationship between turbidity and SAV distribution, turbidity was not a strong predictor of SAV distributions in the coastal dune lakes. This was surprising, as SAV generally has high light requirements (Blanch et al., 1998; Havens et al., 2004; Frankovich et al., 2011; Shields and Moore, 2016). However, turbidity did not vary substantially among the lakes considered within this study and may not have been sufficient to influence SAV distributions.

#### 4.2. SAV community composition

SAV taxa in the coastal dune lakes were limited to relatively few oligohaline species. Moreover, dominant taxa in almost all lakes were either *Utricularia* spp. in four lakes with salinity at or near 0, or *E. baldwinii* in lakes with salinity above 3. *Eleocharis baldwinii* accounted for greater than 50% SAV communities by aboveground biomass dry weight in most lakes and was detected in all coastal dune lakes except Allen Lake. *Utricularia* is a freshwater genus of carnivorous plants. While literature on upper salinity limits is sparse, evidence suggests this genus cannot tolerate salinity above 2.5 (Brock and Lane, 1983). *Vallisneria americana* and *P. pectinatus* have upper salinity tolerances of approximately 15 (Kraemer et al., 1999; Boustany et al., 2015) and 7.5 (Verhoeven, 1975), respectively, while *Eleocharis* spp. can tolerate salinities as high as 10 (Visser et al., 1998, 2000; Howard and Mendelssohn, 1999). No macrophyte taxon observed in the coastal dune lakes can tolerate sustained salinity above 15 (Boustany et al., 2015), which may explain the strong patterns between salinity and SAV distributions observed in this study. Such negative responses of oligohaline macrophytes to increasing salinity stress are common in other aquatic ecosystems (Hoyer et al., 2004; Frazer et al., 2006; Shields and Moore, 2016; Douglass et al., 2020).

SAV community composition shifted across a salinity gradient in the coastal dune lakes. Oligohaline lakes were occupied by dense beds of *E. baldwinii* and *Utricularia* spp., whereas *V. americana*, *P. pectinatus*, and *E. baldwinii* were found in mesohaline lakes. The majority of variation was associated with community dominance by *Utricularia* spp. (negative effects) and *E. baldwinii* (positive effects). As salinity increased, SAV composition rapidly shifted from domination by *Utricularia* spp. to domination by *E. baldwinii*, which likely reflects physiological tolerances of these taxa to salinity.

Reproduction and life history strategies, in concert with physiological tolerances, must also be considered when assessing patterns in community structure along environmental gradients. Seeds and clonal propagules produced by aquatic plants vary widely with regard to tolerance of various environmental disturbances, and trade-offs between these alternative reproduction strategies are often species- and context-specific (Eckert et al., 2016). Species in the genus *Utricularia* appear to rely primarily on clonal propagation for reproduction (Kameyama and Ohara, 2006; Porembski et al., 2006). This strategy, coupled with a relatively low adult salinity tolerance, may relegate this species to Allen, Fuller, Campbell, and Morris lakes; coastal dune lakes which rarely experience salinity perturbations. In contrast, *V. americana*, *P. pectinatus* and *E. baldwinii* have both sexual and asexual reproduction strategies (Baldwin et al., 1996; Van Wijk, 1989; French and Moore, 2003; Jarvis and Moore, 2008). Germination of *V. americana* seeds is significantly influenced by salinity, with an upper salinity threshold between 5 and 10 (French and Moore, 2003; Jarvis and Moore, 2008). Meanwhile, *P. pectinatus* seeds can germinate after exposure of up to 6 (Van Wijk, 1989). These upper germination thresholds explain why *V. americana* distributions were expansive in Western Lake but absent in lakes with higher average salinity regimes despite higher salinity tolerance of *V. americana* relative to other SAV taxa. Finally, seeds of *Eleocharis* can germinate in salinities as high as 16 (Baldwin et al., 1996), which may maintain populations in coastal dune lakes with higher average salinity where salinity spikes occur sporadically.

In many estuaries, salinity controls community structure, which in turn defines abiotic stressor-response relationships (Shields and Moore,

2016). Such patterns were evident in our study. Shifts from salinity intolerant *Utricularia* spp. to more salt tolerant taxa may mute relationships between salinity and SAV, which are more striking in other oligohaline ecosystems in Florida (Hoyer et al., 2004). However, *E. baldwinii* dominated macrophyte communities in lakes with mean salinities ranging from 2 to 13, which included a majority of lakes studied and also occurred, although less abundant, in lakes with salinities approaching 0. As a caveat, abiotic relationships that were not significant in our analyses may have been obfuscated by shifts in SAV community composition.

Although not a focus of this study, desiccation stress may also govern SAV community structure, particularly in coastal dune lakes that connect to the GOM frequently. Opening events commonly lower ICOLL water levels and expose SAV to desiccation stress (Riddin and Adams, 2008). While water level changes were not directly measured in our study, opening events of several coastal dune lakes lowered water levels by as much as a meter (A. C. Hyman, pers. obs.), suggesting that desiccation imposes similar stress to SAV. Unlike other species observed, *E. baldwinii* can occupy a broad suite of inundation profiles ranging from inundated to completely exposed (Uchino et al., 1995; Cherry and Gough 2006). In both coastal dune lakes and other ICOLLs, such adaptability is advantageous. Both plant and seed tolerance to desiccation may allow *E. baldwinii* to colonize and maintain distributions in lakes which are uninhabitable by other SAV species less tolerant of fluctuating water levels, such as *V. americana* (Harwell and Havens, 2003). We restricted our study to regions of coastal dune lakes that were consistently inundated throughout our study to control for potential effects of desiccation with regard to PACc. Nonetheless, we acknowledge that desiccation stress, in concert with salinity stress, likely impact community composition and recommend this be explored in future studies.

#### 4.3. Comparisons to local and global counterparts

Globally, effects of seawater connectivity on ICOLL biological communities are complex and regionally specific. In arid regions such as South Africa, Australia, and the Mediterranean, ICOLL SAV may experience salinity stress attributed to hypersaline conditions during ICOLL isolation and evaporation (Taylor et al., 2006; Adams et al., 2016; Russell and Randall, 2017; Ferguson et al., 2018; Scanes et al., 2020). Under these circumstances, connections with the sea can alleviate, rather than aggravate, salinity stress and promote SAV growth, although the frequency of such events is dependent on local environmental conditions (Adams and Van Niekerk, 2020). Alternatively, seawater connections may promote SAV through flushing, which removes excess nutrients and limits algal growth (Human et al., 2016). These effects are often a product of broader environmental conditions, as artificial openings in other locations have led to unintended ecological consequences such as dramatically increased chlorophyll concentrations (Gobler et al., 2005; Schallenberg et al., 2010).

Seawater connectivity in the coastal dune lakes appears to function predominately as a disturbance event to aquatic macrophytes. Among oligotrophic and mesotrophic estuaries with low nutrient concentrations, these findings are consistent with similar studies in Florida and globally. The Florida coastal dune lakes are in a subtropical region with relatively muted seasonal precipitation patterns that do not facilitate hypersaline environments (Peel et al., 2007; Martinez et al., 2012). Instead, seawater inflows increase salinity stress which appear to inhibit, rather than facilitate, oligohaline SAV meadows. Similarly, salinity pulses from seawater in other Floridian estuaries negatively affect SAV (Frazer et al., 2006). However, those pulses are usually attributed to uncommon events such as hurricanes (Frazer et al., 2006) and are generally not considered to constrain SAV growth over long (i.e., annual) timescales. In contrast, frequent salinity pulses in coastal dune lakes are more predictable on an annual timescale (Hyman and Stephens, 2020).

#### 4.4. Management implications

Previous work demonstrated a correlation between hydraulic gradients and seawater connectivity both among the coastal dune lakes as well as global analogs (Hyman and Stephens, 2020; Lill et al., 2013). In the subtropical climates of Florida, entrance regimes—and their associated effects on salinity—appear to be the primary determinant of SAV distribution in the coastal dune lakes. Salinity pulses likely have a stronger influence on oligohaline and mesohaline ICOLs, which harbor SAV communities less tolerant of salinity increases. Effects of seawater connectivity on SAV within coastal dune lakes underscore potential effects of climate change. Both among the coastal dune lakes and ICOLs elsewhere, rising sea levels and increased severe storm frequency associated with warming ocean waters will diminish natural barriers between these ecosystems and the sea, increasing seawater exchange. However, the ultimate effects of these trends, and associated increased connectivity, on SAV largely depend on broader environmental contexts, such as climate, community composition, and catchment processes. Understanding the complex, region-specific relationship between salinity and SAV is important in mitigating broader ecosystem effects associated with these phenomena.

#### 4.5. Concluding remarks

Our work reinforces the understanding that salinity is an abiotic stress in aquatic coastal ecosystems, particularly those with intermittent connections to the sea. However, precise mechanisms driving salinity dynamics differ, and are often dependent on broader physical processes (Haines et al., 2006; Morris and Turner, 2010). While in arid climates evaporation and reduced flow of freshwater strongly influence ICOLL salinity, ICOLL-specific factors such as elevation and hydraulic gradients also dictate entrance conditions, and by extension salinity pulses (Haines et al., 2006). Factors orchestrating relationships between seawater exchange and SAV in ICOLs are region-specific, and efforts to elucidate these relationships at local scales are needed to provide adequate protection and management both at present and in the future.

#### Author statement

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#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### Appendix A. Supplementary data

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