Received: 16 August 2021 | Accepted: 15 September 2021

DOI: 10.1002/ecs2.4030

ARTICLE

Coastal and Marine Ecology

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

Evaluating temporal and spatial transferability of a tidal inundation model for foraging waterbirds

Marisa T. Martinez[1] | **Leonardo Calle**[2] | **Stephanie S. Romañach**[3] | **Dale E. Gawlik**[4]

[1]Department of Biological Sciences, Florida Atlantic University, Boca Raton, Florida, USA

[2]Department of Ecology and Institute on Ecosystems, Montana State University, Bozeman, Montana, USA

[3]U.S. Geological Survey, Wetland and Aquatic Research Center, Fort Lauderdale, Florida, USA

[4]Environmental Science Program, Florida Atlantic University, Boca Raton, Florida, USA

Correspondence
Marisa T. Martinez
Email: marisamartin2015@fau.edu

Present address
Leonardo Calle, Regrow, 15 Newmarket Rd., Durham, New Hampshire 03824, USA

Dale E. Gawlik, Harte Research Institute for Gulf of Mexico Studies, Texas A&M University Corpus Christi, 6300 Ocean Drive, Unit 5869, Corpus Christi, Texas 78412, USA

Funding information
American Ornithological Society; The Everglades Foundation; Friends of Gumbo Limbo; The Waterbird Society; U.S. Geological Survey, Grant/Award Number: G15AC00303

Handling Editor: Debra P. C. Peters

Abstract

For ecosystem models to be applicable outside their context of development, temporal and spatial transferability must be demonstrated. This presents a challenge for modeling intertidal ecosystems where spatiotemporal variation arises at multiple scales. Models specializing in tidal dynamics are generally inhibited from having wider ecological applications by coarse spatiotemporal resolution or high user competency. The Tidal Inundation Model of Shallow-water Availability (TiMSA) uniquely simulates tides to empirically derive a time-integrated measure of availability for a shallow-water depth range defined by the user. To evaluate temporal and spatiotemporal transferability, we employed TiMSA at the development site in the Florida Keys and at novel subsites in the Florida Bay (application site) under a different time period (application period). We used foraging little blue herons (*Egretta caerulea*) as the ecological unit with which to constrain the model's "water depth window," that is, range of water depths to estimate shallow-water availability. At the development site, temporally consistent water depth windows contrasted with interannual variation in shallow-water availability, which revealed short-term changes in Little Blue Heron foraging habitat. At the application site, water depth accuracy varied by subsite and was correlated with spatial error in bathymetric elevation. Although TiMSA parameters were sensitive to environmental temporal variation and uncertainty in spatial data, a spatially explicit water depth window generated reliable estimates of shallow-water conditions over space and time at the development and application sites. By exploring the contributing factors to model error, we provide solutions to reduce uncertainty of TiMSA parameters at potential application sites and recommendations for addressing bathymetric inaccuracy in digital elevation models. Accurately quantifying spatiotemporal changes of shallow water has implications for monitoring habitat conditions for tidally influenced species and projecting future changes to coastal ecosystems in response to anthropogenic stressors and natural disturbances such as sea level rise.

KEYWORDS
bathymetry, digital elevation model, Florida Bay, Florida Keys, foraging, hydrologic model, intertidal ecosystem, Little Blue Heron, Tidal Inundation Model of Shallow-water Availability, transferability, waterbirds

INTRODUCTION

The development of an ecosystem model requires judicious designation of temporal and spatial scales to ensure utility and reproducibility (Getz et al., 2018). The ability to transfer the model to contexts different than those for which it was created is imperative (McGarity & Wagner, 2003; Randin et al., 2006; Wenger & Olden, 2012). Model transferability demonstrates performance, transparency, and proper application to potential model users and critics (Klemeŝ, 1986; Moon et al., 2017). Modeling dynamic ecosystems is complicated by mechanisms of biotic and abiotic processes spanning numerous spatial and temporal scales. The intertidal zone, the transition between marine and terrestrial ecosystems, is the most spatiotemporally dynamic of the marine habitats primarily due to the tides (Bearup & Blasius, 2017). While tidal variation arises at multiple timescales from hours to epochs, spatial variability of the intertidal zone is shaped by bathymetry, geomorphology, coastline configuration, and local ecotone structure.

Hydrologic models that consider the spatiotemporal dynamics of tides are often physical-based ocean models (e.g., Regional Ocean Modeling System [ROMS; Shchepetkin & McWilliams, 2005], Oregon State University Tidal Inversion Software [Egbert & Erofeeva, 2002], Hybrid Coordinate Ocean Model [HYCOM; Wallcraft et al., 2009], Code aux Eléments Finis pour la Marée Océanique [Le Provost et al., 1998], General Estuarine Transport Model [Burchard & Boldin, 2002]), which are not specialized for the intertidal zone. In Florida, several hydrologic models have been developed specifically for the coastal wetland transition zone between the Everglades, an expansive freshwater wetland on the mainland, and Florida Bay. The Southern Inland Coastal System model (Swain et al., 2004) and the Tides and Inflows in the Mangrove Ecotone (TIME) model (Langevin et al., 2005) quantify freshwater flow and solute transport between the southern Everglades and northeastern Florida Bay. The Biscayne and Southern Everglades Coastal Transport model (Swain et al., 2019) builds on TIME and the Biscayne model (Lohmann et al., 2012) to account for additional hydrologic attributes of the southern Florida peninsula and surrounding tidal water bodies. Like the physical ocean models, these mechanistic models operate at spatial and temporal resolutions appropriate for evaluating longer-term hydrologic conditions and broader-scale ecosystem patterns. However, they are too coarse to account for the variation of bathymetry and water depths within the model grid-cell (Swain et al., 2019). Second, simplistic models that provide a framework for a wide range of phenomena may serve a broader function for intertidal ecosystems, over exhaustive, costlier models that do not amply address spatiotemporal variation (Bearup & Blasius, 2017). Third, complex, physical models come with operational challenges due to data-rich input criteria and computational constraints.

The Tidal Inundation Model of Shallow-water Availability (TiMSA) is distinct from the aforementioned hydrologic models first as an empirically based model. It integrates point source data to approximate the magnitude and timing of water level change over the tidal cycle (Calle, 2021). Second, it estimates the spatiotemporal availability of a range of water depths defined by the user. This time-integrated measure of resource availability is fundamental to modeling intertidal system processes in which abiotic and biotic drivers have nonlinear effects on the magnitude and/or duration that resources are accessible (Calle et al., 2018). For instance, tides cause fluctuations in food and refugia for nekton, which influence their behavior (Gibson, 1992), movement (Burrows et al., 1994; Sogard et al., 1989), and abundance patterns (Castellanos & Rozas, 2001; Reis-Filho et al., 2011), which influence accessibility of prey for birds foraging on tidal mudflats (Gibson, 2003; Matsunaga, 2000; Powell & Powell, 1986). As such, TiMSA was originally developed as an application to examine shallow-water foraging habitats of two species of wading birds in an intertidal ecosystem, the Little Blue Heron (*Egretta caerulea*) and Great White Heron (*Ardea herodias occidentalis*; Calle et al., 2016, 2018). Wading birds are constrained to forage in water depths relative to their leg length (Gawlik, 2002) and, thus, strongly influenced by daily tidal cycles which restrict the duration and magnitude of foraging habitat to the low tide when water depths are shallow (Martins et al., 2016; Matsunaga, 2000; Powell, 1987; Raposa et al., 2009).

While TiMSA demonstrated high confidence in estimating water depth and shallow-water availability (Calle et al., 2016), the model has not been validated outside its calibration time period and geographical area. Tidal Inundation Model of Shallow-water Availability's simple data assimilation approach makes it theoretically transferrable

to sites that meet minimal input data criteria. Therefore, the objective of our study was to apply TiMSA under different temporal and spatial conditions to evaluate model transferability. For the temporal transfer, we applied TiMSA to a new time period (application period) at the site for which it was developed (development site). The development site resides within the Great White Heron National Wildlife Refuge, which encompasses over 50,000 ha of land and water within the Florida Keys National Marine Sanctuary in the Lower Florida Keys (Figure 1). This coastal region is characterized by benthic habitat types such as seagrass, bare sand, hard-bottom, and nearshore and midchannel patch reefs. Nearshore water circulation is driven by exchange between the eastern Gulf of Mexico and the Atlantic Ocean, primarily from water moving south from the Florida Shelf (Boyer & Jones, 2002). Tides are mixed semidiurnal with a mean range of 0.56 m, and mean sea level varies by 0.24 m through the year with maximum tides between May and October (Stumpf & Haines, 1998).

For the spatiotemporal transfer, we applied TiMSA at a novel site (application site) for the same application period as the temporal transfer. We selected Florida Bay as the application site because we expected the system to operate under similar hydrologic processes as the development site due to their physical proximity (~67 km apart). Selecting an application site in the vicinity of the development site provided an assurance of model transfer feasibility based on spatial autocorrelation and contextual similarity (Klemeŝ, 1986; Rosenberger & Phipps, 2007). Florida Bay is a 220,000-ha triangular-shaped estuary bound by peninsular Florida to the north, the Florida Keys Archipelago to the east and south, and the Southwest Florida Shelf and eastern Gulf of Mexico to the west (Figure 1). Florida Bay is morphologically characterized by a widespread network of shallow carbonate mudbanks and adjacent basins with an average water depth of 1.4 m (Lee et al., 2006). Water circulation is mainly restricted by mudbanks, which attenuate tidal energy, particularly in the central and northeastern portions, and cause the astronomical tides to vary across the east–west orientation (Wang et al., 1994).

Both Florida Bay and the Florida Keys are coastal regions of high ecological importance (Ortner et al., 2014) occupying the largest documented seagrass beds in the world (~587,770 ha; Sargent et al., 1995). However, these regions were ranked the lowest in ecosystem health by the U.S. Army Corps of Engineers, scoring 38% out of 100% on the Everglades Report Card

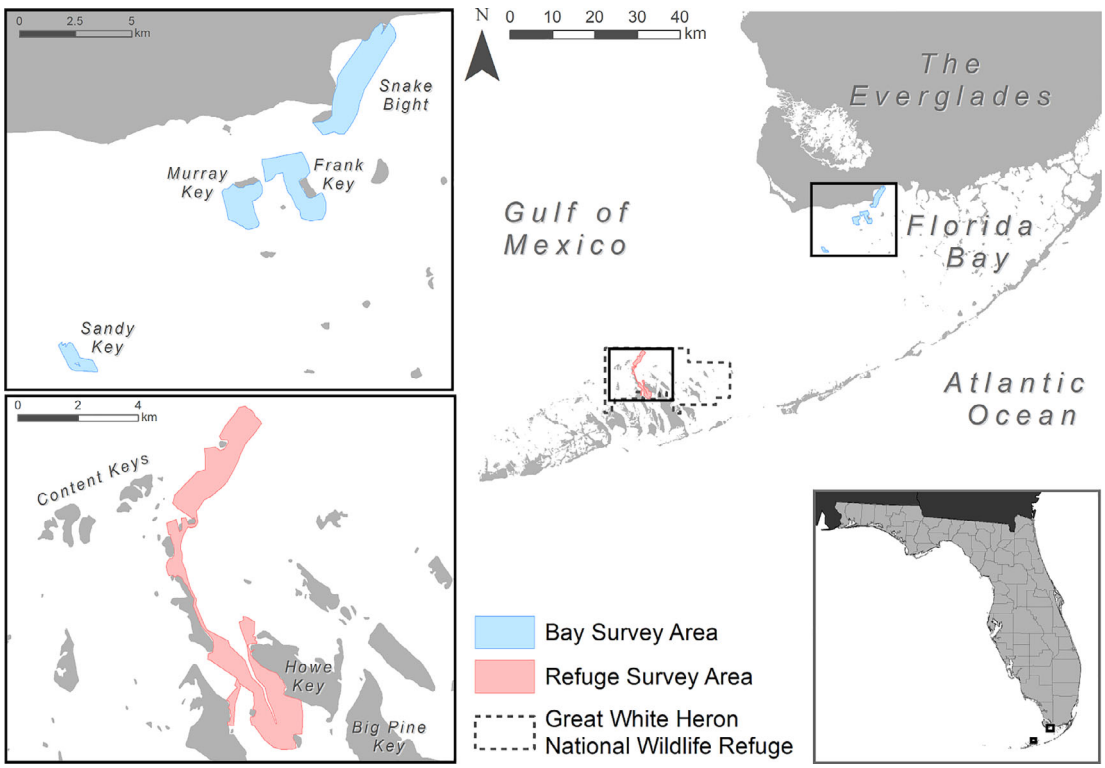

FIGURE 1 Great White Heron National Wildlife Refuge (Refuge) in the Lower Florida Keys and Florida Bay (Bay) showing the location of the model development site and the model application site, respectively, used in this paper. The red and blue shaded regions show where little blue herons were surveyed from 2016 to 2018. Inset shows study area locations on the southern coast of Florida, USA

as part of the Comprehensive Everglades Restoration Plan (CERP; USACE, 2019). A primary aim of the Florida Bay and Florida Keys Feasibility Study under CERP is the "development and application of interrelated modeling tools" for benthic habitats and upper trophic levels including bird species (USACE and SFWMD, 2002). Despite the high ecological importance and management priority of the coastal ecosystems, no fine-scale hydrologic model exists for simulating changes in water levels and assessing spatiotemporal tidal dynamics on ecological phenomena for Florida Bay.

We used the Little Blue Heron as the model's ecological unit with which to constrain the range of water depths and estimate shallow-water availability, keeping consistent with Calle et al. (2016). We compared model output parameters between the development and applications periods, and between the development site and the application site, to investigate temporal and spatial patterns of water depth estimates and shallow-water availability simulations. To advise on the use of TiMSA as a transferrable tool for natural resource management and broader coastal ecosystem research, we provide various applications for evaluating spatiotemporal variation of shallow-water habitats, explore potential sources of error in model estimations, and suggest field and modeling-based solutions to reduce uncertainty in model input and output data.

METHODS

TiMSA application site

Due to the larger area of Florida Bay compared to Great White Heron National Wildlife Refuge, we selected four subsites to perform the spatiotemporal model transfer. Sandy Key, Murray Key, Frank Key, and Snake Bight are intertidal mudflats naturally delineated by deep channels and geomorphology (Figure 1). Sandy Key lies in the western margin of Florida Bay where water exchanges with the Gulf of Mexico and tides are mixed semidiurnal with a mean range of 0.61 m (Fourqurean & Robblee, 1999). Murray Key, Frank Key, and Snake Bight are in central Florida Bay where mean water depths vary up to 0.30 m over the year with greatest water depths from August to November and shallowest from February to May due to changes in net freshwater flux. From January to May, the net freshwater flux is negative when evaporation exceeds precipitation, and becomes positive from June to September during the wet season (South Florida Natural Resources Center and National Park Service, 2012).

TiMSA input data

Bathymetric digital elevation model

The spatial extent and resolution of TiMSA are defined by bathymetric elevation data or digital elevation model (DEM). For the development site, we used the Key West Florida Coastal DEM developed as part of the National Oceanographic and Atmospheric Administration (NOAA) Tsunami Inundation Project. We converted the vertical datum from the North American Vertical Datum 1988 (NAVD88) to the mean lower low water (MLLW, the lowest of the two low tides per day averaged over a 19-year period) using the VDatum tool (Milbert, 2002). The Coastal DEM has a 1/3arc-second (approx. 10 m) horizontal resolution and an estimated vertical accuracy of 0.10 m in shallow waters or 5% of water depth in deeper waters (Grothe et al., 2010). The spatial coverage of the Coastal DEM did not overlap with the application site, and thus, we acquired two distinct DEMs with Florida Bay-wide coverage to compare precision of TiMSA water depth estimates. The Estuarine Bathymetric DEM (EBDEM) was derived from hydrographic survey data collected in 1995 by NOAA and National Ocean Service and has a 3arc-second (approx. 90 m) horizontal resolution. The estimated vertical accuracy is 2% of the depth or 1 m for depths greater than 20 m, and 2% of depth or 0.20 m for depths shallower than 20 m. The Continuously Updated DEM (CUDEM) was developed by NOAA's National Center for Environmental Information (NCEI) to rapidly integrate tiles of bathymetric and topographic data as they become available, as recently as 1 February 2018 for the application site (CIRES, 2014). No quantitative vertical accuracy analyses have been performed on the CUDEM tiles since the vertical accuracy of bathymetric data is dependent on a variety of factors (acquisition sensor/platform, post-processing, environmental conditions, and surveyed depth range). We merged CUDEM tiles with 1/9 arc-second (approx. 3.4 m) resolution for complete coverage of the application site and resampled the grid resolution to 10 and 30 m for our simulation purposes.

Point source water level

Tidal Inundation Model of Shallow-water Availability-estimated water depths are restricted to the spatial and temporal extent of point source water level input data. The spatial extent is divided into individual Thiessen polygons whose boundaries delineate the area closest to each point source, relative to all other point sources within the spatial extent. The polygons function as basins and allow for variation in water level dynamics (e.g., amplitude and wave

period) between polygons dictated by the nearest point source. Point source water level data were derived from 11 tide gauges maintained by NOAA and nine water monitoring stations maintained by the National Park Service (NPS, Table 1). We acquired heights and times of low tides from NOAA tide gauges and fit a sine curve between data points to approximate the rate of change in tidal environments (Calle et al., 2016). For the two NOAA tide gauges at the application site, East Cape and Flamingo, we transformed the tide heights from MLLW to NAVD88 using the VDatum tool to match CUDEM's vertical datum. We acquired 6-min water level data from the NPS water monitoring stations which we linearly interpolated to 1- and 5-min intervals for our simulation purposes.

Foraging bird locations

To constrain the estimation of shallow-water depths to an ecologically relevant range, we acquired locations of foraging little blue herons. We conducted biweekly surveys via motorboat along intertidal mudflats at, or near, low tide between sunrise and sunset. We stopped the boat at 500-m intervals along a predetermined survey transect and two observers scanned the mudflats for waterbirds using 10 × 42 binoculars. We recorded the number of little blue herons within 600 m of the boat and took the bearing and distance to each individual or flock with a compass and range finder from a GPS-referenced location. Employing the double-observer method to identify little blue herons within 600 m reduced the chance of double-counting birds (Nichols et al., 2000) and resulted in high confidence of complete detection (Calle et al., 2016). We avoided surveying under periods of heavy rain or winds exceeding 28 km/h for visibility and safety reasons. At the application site, we performed surveys at each subsite within three successive days to minimize variation of survey conditions from the tidal cycle and weather. We spatially referenced and collocated GPS locations of foraging birds from the development site onto the Coastal DEM and locations from the application site onto the EBDEM and CUDEM in ArcGIS 10.6.1 (ESRI, 2011). Continuously Updated DEM-derived elevations at bird locations were shallower by ∼1 m than those

TABLE 1 Names and coordinates of water level data sources used in the Tidal Inundation Model of Shallow-water Availability for Florida Keys and Florida Bay study areas

Name	Study area	Agency	Latitude	Longitude
Big Spanish Key	Florida Keys	NOAA	24.78833	−81.41166
Howe Key Northeast Point	Florida Keys	NOAA	24.75833	−81.42833
Big Torch Key East	Florida Keys	NOAA	24.73666	−81.44333
Water Keys South End	Florida Keys	NOAA	24.74667	−81.45000
Content Key Content Passage	Florida Keys	NOAA	24.79000	−81.48330
Raccoon Key	Florida Keys	NOAA	24.74166	−81.48333
Howe Key South End	Florida Keys	NOAA	24.72500	−81.40670
East Cape	Florida Bay	NOAA	25.11670	−81.08330
Flamingo	Florida Bay	NOAA	25.14170	−80.92330
Johnson Key	Florida Bay	NPS	25.05254	−80.90448
Buoy Key	Florida Bay	NPS	25.12111	−80.83356
Garfield Bight	Florida Bay	NPS	25.16723	−80.80130
Little Rabbit Key	Florida Bay	NPS	24.98158	−80.82570
Whipray Basin	Florida Bay	NPS	25.07209	−80.73511
Terrapin Bay	Florida Bay	NPS	25.15734	−80.72479
Peterson Key	Florida Bay	NPS	24.91806	−80.74680
Bob Allen	Florida Bay	NPS	25.02663	−80.68137
Little Madeira	Florida Bay	NPS	25.17580	−80.63269
Butternut Key	Florida Bay	NPS	25.08668	−80.51904
Duck Key	Florida Bay	NPS	25.18009	−80.49001

Note: Data from nine tide gauges operated by National Oceanic and Atmospheric Administration (NOAA) were acquired from https://tidesandcurrents.noaa.gov/api-helper/url-generator.html. Data from 11 water monitoring stations operated by Everglades National Park of the National Park Service (NPS) were requested from ever_data_request@nps.gov.

derived from the EBDEM. The CUDEM was created to be updated more frequently as data become available, and is therefore considered the best available DEM for this region. For these reasons, we proceeded with the CUDEM for subsequent TiMSA simulations of the application site.

TiMSA output parameters

Instantaneous water depth

Tidal Inundation Model of Shallow-water Availability uses the point source water level data to numerically add to the water level surface in every grid-cell of the DEM. Then, it calculates the instantaneous water depth as the difference between the elevation of the predicted water level surface and the elevation of the benthic surface. We used TiMSA to estimate the instantaneous water depth of the grid-cell for each bird location at the date and time of observation (±10 min). We pooled these water depths by year at the development and application sites and calculated the 10%–90% quantile to delineate the lower (deeper) and upper (shallower) limits of the foraging range per year. We assumed little blue herons forage within similar water depth ranges over time and space. As such, we expected the range and distributions of water depths to be similar between the development and application periods and between the development and application sites.

Shallow-water availability

Tidal Inundation Model of Shallow-water Availability estimates the spatiotemporal availability of shallow water within a range of water depths defined by the user, that is, water depth window. Every minute the water depth of the grid-cell resides within the water depth window, and 1 min is added to that grid-cell. The process repeats over a defined time period (e.g., 365 days) to estimate temporal shallow-water availability for each grid-cell in units of time. Spatiotemporal shallow-water availability is calculated as the product of the total temporal availability and the total grid-cell area, yielding a unit of area-time (e.g., ha-h). We applied the 10%–90% quantile of water depths at bird foraging locations as the water depth window to estimate daily shallow-water availability and then averaged shallow-water availability estimates over each year of the application period. Since we expected Little Blue Heron water depth windows to be similar across years and anticipated the tidal cycle to be similar across years, we predicted similar patterns of shallow-water availability over the application period.

Water depth surveys and water depth accuracy

We replicated Calle et al.'s (2016) evaluation of estimated water depth to measure accuracy at the application site. We deployed high accuracy (±0.03 m) HOBO U20L-004 data loggers (Onset Computer Corporation) at 21 sampling locations across the subsites secured at least 500 m apart. At each sampling location, we recorded the GPS coordinates and measured the water depth after a 20-min acclimation period. Data loggers recorded barometric pressure and water temperature every 15 min for at least 24 h from 29 June to 18 July 2017. We collected 960 h of barometric pressure and temperature measurements, which we converted to water depth using HOBOware software and Barometric Compensation Data Assistant (Onset, 2020). We calculated model error as the difference between TiMSA-estimated water depth and water depth measured by the data logger. We expected model error to be similar between the development site and application site.

We investigated temporal and spatial error in the model and examined the effects of bathymetric elevation at the sampling locations and distance to the nearest reference gauge on model error. The three nearest reference gauges were located at East Cape, Flamingo, and Johnson Key (Table 1). We assigned each sampling location a unique identifier and binned time from low tide into 90 levels nested within each sampling location. This approach specified a random slope and random intercept (with respect to time from low tide) for each sampling location. We performed a linear mixed effects model using the *nlme* package (Pinheiro et al., 2020) in R (R Core Team, 2020) for our analyses. We predicted negative effects of bathymetric elevation and distance to reference gauge on model error.

RESULTS

Temporal model transfer at the development site

We acquired 70 foraging locations of little blue herons between March and June of 2016. The 10%–90% quantile range of estimated water depths at foraging locations was 1.128 m (Table 2). In 2017, the 10%–90% quantile range was slightly narrower (0.863 m) for 148 foraging locations acquired between February and June. In 2018, the 10%–90% quantile range was narrowest at 0.335 m for 41 locations acquired between April and June. The narrow range in 2018 is likely an artifact of the smaller sample size of foraging locations compared to 2016 and 2017. Despite the difference in quantile ranges among years,

TABLE 2 Water depth windows (10%, 90% quantiles) and ranges (|90% quantile–10% quantile|) of Little Blue Heron foraging locations, in meters, relative to the water surface at Great White Heron National Wildlife Refuge (Refuge) and four subsites at Florida Bay

Year	Site	Water depth window	Range
2016	Refuge	−0.796, 0.332	1.128
	Sandy Key	−0.943, −0.682	0.261
	Murray Key	−1.151, −0.872	0.279
	Frank Key	−2.044, −1.226	0.818
	Snake Bight	−1.298, −0.110	1.188
2017	Refuge	−0.574, 0.289	0.863
	Sandy Key	−1.025, −0.705	0.320
	Murray Key	−1.077, −0.773	0.304
	Frank Key	−1.990, −0.916	1.075
	Snake Bight	−1.520, −0.049	1.471
2018	Refuge	−0.571, −0.236	0.335
	Sandy Key	−1.020, −0.830	0.190
	Murray Key	−1.033, −0.872	0.162
	Frank Key	−1.856, −1.273	0.583
	Snake Bight	−1.765, −0.101	1.665
Development period	Refuge	−0.550, 0.450	0.900
Application period	Refuge	−0.588, 0.324	0.912
	Sandy Key	−1.020, −0.708	0.311
	Murray Key	−1.080, −0.778	0.302
	Frank Key	−1.965, −0.944	1.021
	Snake Bight	−1.541, −0.071	1.470

Note: Water depth windows and ranges were calculated for each year of the application period (2016–2018) and pooled across years. At the Refuge, the water depth window and range from the development period (2011–2013) are provided for comparison.

the central tendency of the water depth distribution was similar among years (Figure 2), confirmed by nonsignificant pair-wise comparisons at the $\alpha = 0.05$ level. Thus, we pooled water depth estimates across the application period (2016–2018) to compare to the development period (2011–2013). The application period 10%–90% quantile range and water depth window [10% quantile, 90% quantile] was 0.912 m [−0.588 m, 0.324 m], which closely matched that of the development period, 0.9 m [−0.55 m, 0.45 m]. This supports our prediction of similar water depth windows between the developmental and application periods. As the water depth window is empirically derived, it integrates uncertainty across multiple sources of error (e.g., georeferenced bird locations, DEM, and model simulations) and thus differs from the biological range of water depths for a Little Blue Heron (0–0.28 m, Gawlik, 2002) while still providing useful insights into patterns of shallow-water availability.

We applied the water depth window [−0.588 m, 0.324 m] to estimate yearly shallow-water availability at the development site. Total shallow-water availability was similar between 2016 (17,645 ha-h) and 2017 (17,375 ha-h), but the spatial distribution of availability varied between years (Figure 3). Minutes of shallow-water availability per grid-cell were higher on average in the northern portion of the site, depicted by more red and yellow-colored pixels, and lower on average in the southern portion (Figure 3). Total shallow-water availability was greatest in 2018 (25,851 ha-h) with ubiquitous increases per grid-cell across the site. This result conflicted with our prediction of consistent shallow-water availability among years.

To investigate the observed change of total availability of shallow water under a static water depth window, we isolated the effect of water level fluctuations on shallow-water availability. For every 0.1 m between −0.5 and 0.3 m (the minimum and maximum low tide heights, respectively, over the application period), we uniformly subtracted that value from the Coastal DEM and created a binary mask for available shallow water between −0.59 and 0.31 m, the water depth window. As expected, shallow-water availability decreased as water levels increased, but

changes in shallow-water availability were evident at just 0.1-m increments, particularly between the +0.3-m change and +0.2-m change in the northwest and southeast polygons, and between the 0-m change and −0.1-m change in the central and west polygons (Figure 4). This simple simulation demonstrates that even when the water depth window and bathymetry are fixed, large spatiotemporal changes in shallow-water availability emerge from small water level fluctuations.

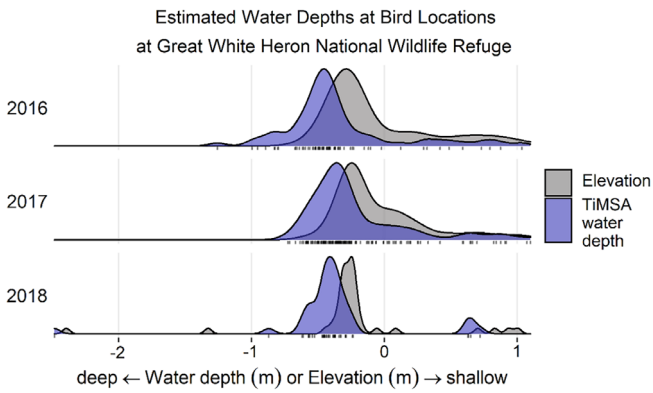

FIGURE 2 Density distributions of water depths (rug marks on *x*-axis) and elevations relative to mean lower low water (MLLW) at Little Blue Heron foraging locations within the Great White Heron National Wildlife Refuge. Water depths were estimated by the Tidal Inundation Model of Shallow-water Availability, and elevations were derived from the Coastal Digital Elevation Model. Density distribution heights are scaled to 1

Spatiotemporal model transfer at the application site

We acquired 58 locations between March and May in 2016 (Sandy Key = 22, Murray Key = 5, Frank Key = 13, and Snake Bight = 18), 334 locations between February and July in 2017 (Sandy Key = 99, Murray Key = 46, Frank Key = 68, and Snake Bight = 121) and 68 locations between March and July in 2018 (Sandy Key = 25, Murray Key = 3, Frank Key = 23, and Snake Bight = 17). Each year, the 10%–90% quantile range and distribution of estimated water depths at foraging locations differed among subsites (Table 2, Figure 5). The 10%–90% quantile ranges and water depth windows were consistently narrow and shallow at Sandy Key and Murray Key and consistently wide and deep at Snake Bight. The central tendency of water depth distribution at Sandy Key, Murray Key, and Frank Key was similar among years (Figure 5), confirmed by nonsignificant pair-wise comparisons at the $\alpha = 0.05$ level. At Snake Bight, however, mean water depth was significantly different in 2018 than in 2016 ($p < 0.05$, $T = -3.589$) and 2017 ($p < 0.01$,

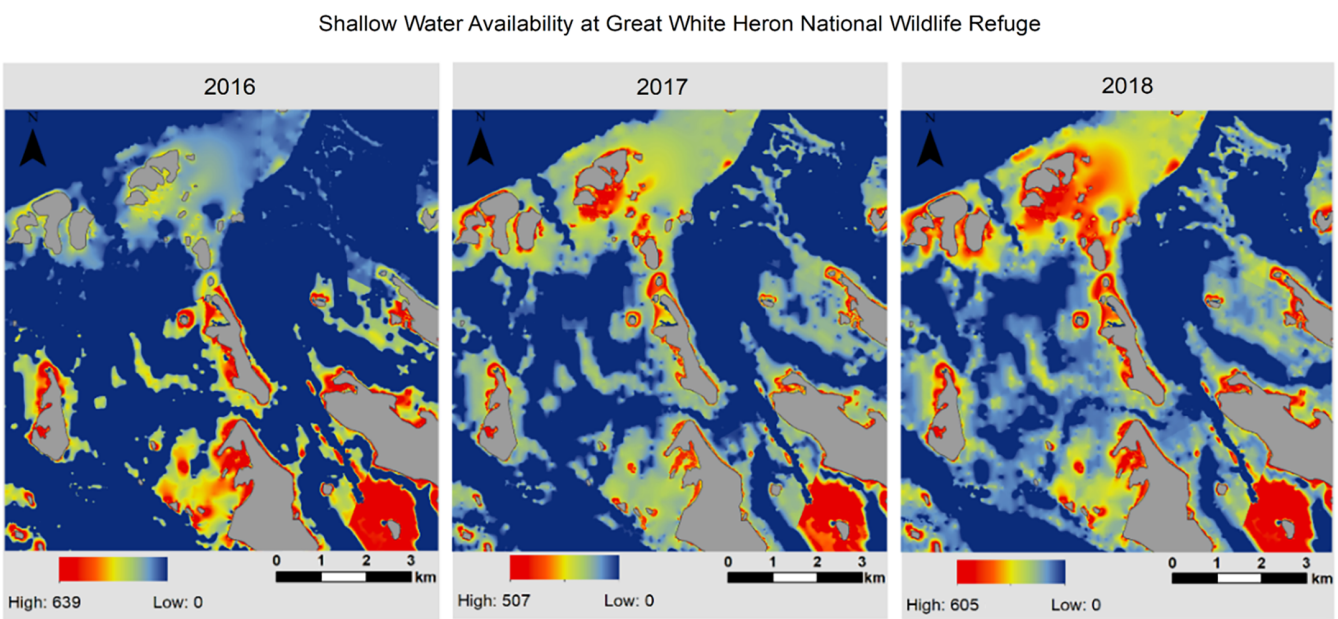

FIGURE 3 Average shallow-water availability at Great White Heron National Wildlife Refuge each year of the application period. Shallow-water availability was estimated by the Tidal Inundation Model of Shallow-water Availability using the water depth window: −0.59 and 0.32 m. The water depth window was derived from the 10%–90% quantile range of water depths at Little Blue Heron foraging locations pooled over the application period. For every minute the grid-cell (10 m × 10 m) occurs within the water depth window, 1 min of availability is added to the grid-cell. The process repeats over the tide to generate an output of shallow-water availability in minutes for each day of the year between sunrise and sunset to account for the diurnal constraint of Little Blue Heron foraging activity

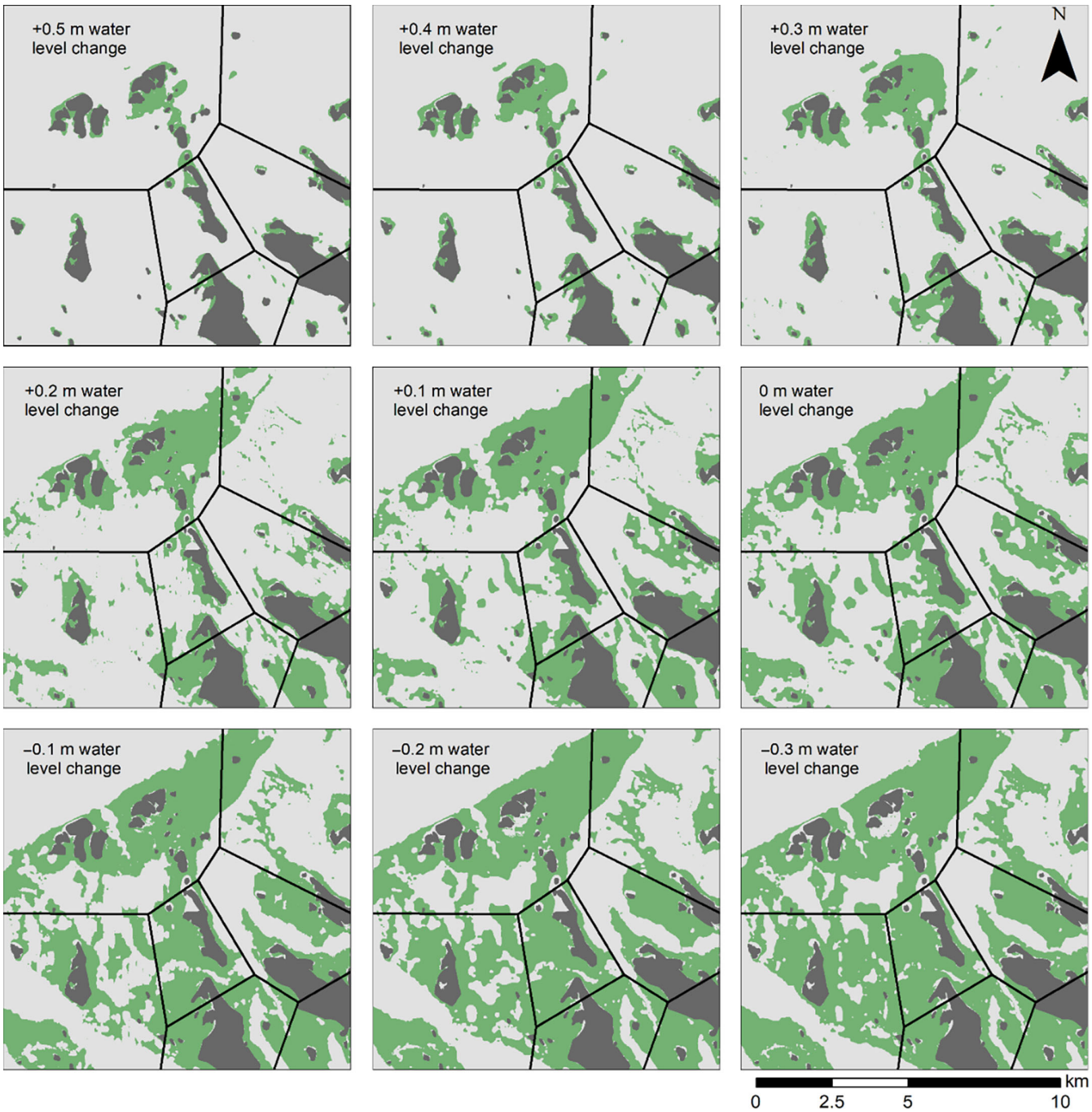

FIGURE 4 Shallow-water availability over a range of water level change at Great White Heron National Wildlife Refuge. For every 0.1 m between −0.5 and +0.3 m (the range of low tide heights for over the application period relative to the mean lower low water [MLLW]), we uniformly subtracted that value from the Coastal Digital Elevation Model and created a binary mask for available shallow water between −0.59 and 0.31 m (the water depth window). The top left output shows visibly less available foraging habitat when water level is +0.5 m (relative to MLLW) compared to the output in the bottom right when water level is −0.3 m (relative to MLLW). The sequence of outputs shows site-wide changes of shallow-water availability resulting from 0.1-m increments of water level change. Black lines represent the boundary of the Thiessen polygons derived from the seven tide gauges used for model simulations

$T = -4.150$). These results conflicted our prediction of similar water depth windows across subsites.

Differences in water depth windows were prominent at Snake Bight where 10%–90% quantile ranges each year was 0.4–1.5 m larger than other subsites. To investigate this further, we performed a focal quality check on bird locations from two separate surveys at Snake Bight in 2017. Locations from each survey were acquired over the

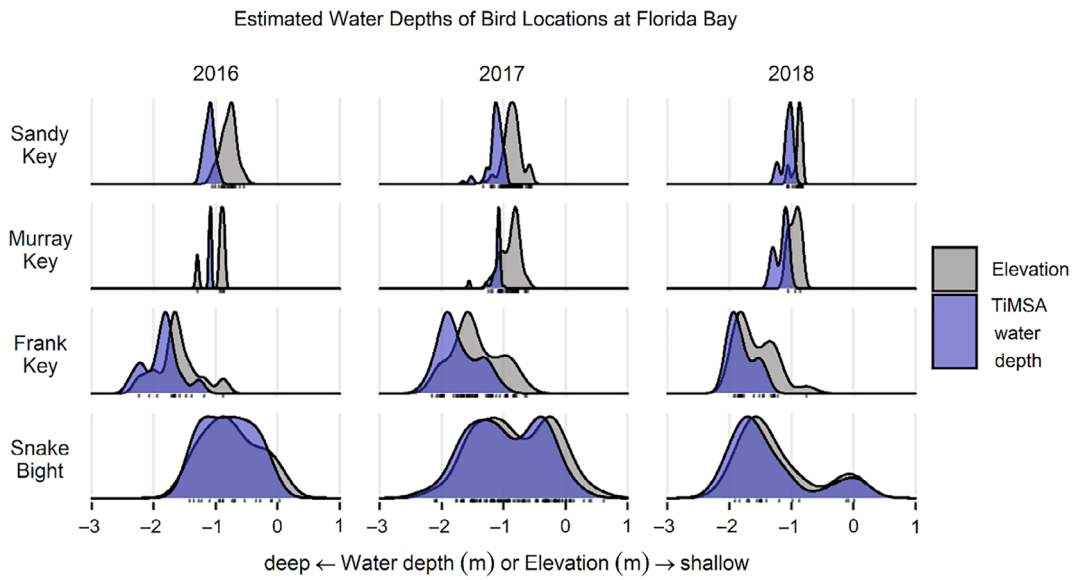

FIGURE 5 Density distributions of water depths (rug marks on *x*-axis) and elevations (relative to North American Vertical Datum 1988) at Little Blue Heron foraging locations from four subsites within the Florida Bay application site. Water depths were estimated by the Tidal Inundation Model of Shallow-water Availability and elevations were derived from the Continuously Updated Digital Elevation Model. Density distribution heights are scaled to 1

duration of 95 and 209 min and a maximum of 4 km apart. Under these survey conditions that held space and time relatively constant, we expected a water level surface at Snake Bight, a planar mudflat with an average water depth of approximately 0.3 m and tidal range of around 0.6 m. We also assumed little blue herons cannot physically forage in water beyond than their leg length; the deepest recorded water depth was 0.28 m (Gawlik, 2002). Thus, we expected elevations at this subset of locations to be within 0.28 m of each other. However, the range in elevation for each survey was 1.534 and 1.818 m, more than five times greater than expected (Figure 6). The only circumstance in which elevation differences of this magnitude could produce water depths within the 0.28 m range of Little Blue Heron foraging depths is by means of a natural or artificial dam. However, no such structure exists at the application site. Therefore, if our assumptions about flat water surface and flat substrate are correct, then the unusually large range of elevations observed must be driven by error in the underlying bathymetric elevation data. This suggests the CUDEM is at fault in this area of the application site and is a source of the error in simulating water depths. We examined this error structure further under "Evaluation of water depth accuracy."

In consideration of this uncertainty in the CUDEM, we pooled water depths across the application period for each subsite separately to calculate subsite-specific water depth windows (Table 2). We applied these water depth windows in TiMSA to estimate total shallow-water availability for the application site. The localized water depth windows generated very different outcomes of shallow-water availability. The Sandy Key and Murray Key water depth windows generated low total shallow-water availability at the application site, which was mainly restricted to the west-central region of the site (Figure 7). These outputs correctly depict zero shallow-water availability within the deep-water channels and within the large, deep basins in the east and south. Outputs also correctly indicated where shallow-water availability is greatest on broad mudflats which surround smaller basins in the west and in the narrow mudflats which form the peripheries of the larger basins to the east. By contrast, the Murray Key and Snake Bight water depth windows generated greater total shallow-water availability distributed across nearly the entire application site, excluding the deepest basins in the south and east of Florida Bay (Figure 7).

Evaluation of water depth accuracy

Among the 21 data logger sampling locations, the average root mean square error (RMSE; min, max, and SD) was 0.784 m (0.068, 1.59, and 0.483 m), which was higher than the 0.21-m average RMSE measured at the development site (Calle et al., 2016). Average RMSE was lowest at Sandy Key (0.357 m), 0.534 m at Murray Key, 0.821 m at Frank Key, and highest at Snake Bight (1.036 m). The spread of error at each sampling location around its

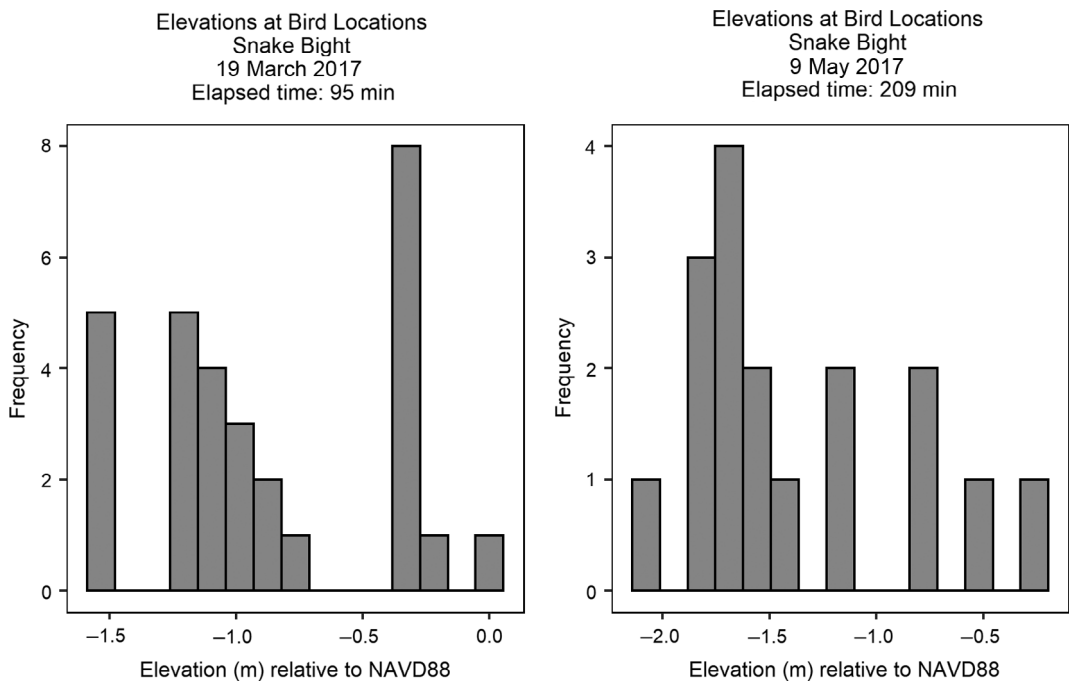

FIGURE 6 The frequency distribution of elevations (relative to North American Vertical Datum 1988) at Little Blue Heron foraging locations acquired on 19 March 2017 and 9 May 2017 at Snake Bight in Florida Bay. The range of elevations were 1.534 and 1.818 m, respectively, more than five times greater than the expected range of 0.28 m for little blue herons

mean represents the temporal error resulting from TiMSA's use of Thiessen polygons to simplify tidal dynamics. Temporal error was similar among subsites (Figure 8) with a mean (min, max) of 0.219 m (0.053 m, 0.286 m), again, higher than the 0.05 m mean temporal error measured at the development site. The spread of error across sampling locations was 0.520 m and represents the spatial error originating from inaccuracies in the DEM. We observed greater deviations from the mean error at Frank Key and Snake Bight where elevations at sampling points were lowest (i.e., toward deeper water depths; Figure 8).

As predicted, elevation had a strong negative effect on model error ($T = -7.564$, df $= 18$, $p < 0.0001$) such that every 1-m decrease in elevation yielded an increase of 1.081 m in total model error (Figure 8). This effect size was more than twice the 0.52 m increase in model error measured at the development site (Calle et al., 2016). Distance from sampling location to reference gauge did not have a significant effect on model error ($T = -0.833$, df $= 18$, $p = 0.416$). This result was unexpected, especially since distances were greater on average at the application site than at the development site. Over time model error tended to rise and fall with the tidal cycle; local error maxima error generally occurred on the flood tides (positive values on x-axis; Figure 9). This pattern was due to predictions of low tide times being out of phase with observed low tide times, as was observed at the development site.

DISCUSSION

Temporal transferability of TiMSA

The agreement in water depth windows between the development and application periods confirms that foraging ranges of little blue herons are temporally consistent over at least a 5-year period. In other words, the water depth window is temporally generalizable at the development site. A water depth window that is robust to short-term temporal gaps (time between the development and application period) means that once it is validated, it can be reliably applied in future TiMSA simulations. The implication for this is that field data collection (Little Blue Heron water depths) and model calibration can occur twice a decade instead of annually, which is considerably more cost and time efficient. It is not clear how agreement in water depth windows will compare for larger temporal gaps (>10–20 years), but we recommend applying [−0.55 to 0.45 m] as a conservative water depth window to estimate shallow-water availability for little blue herons and other small-sized wading bird species as a baseline.

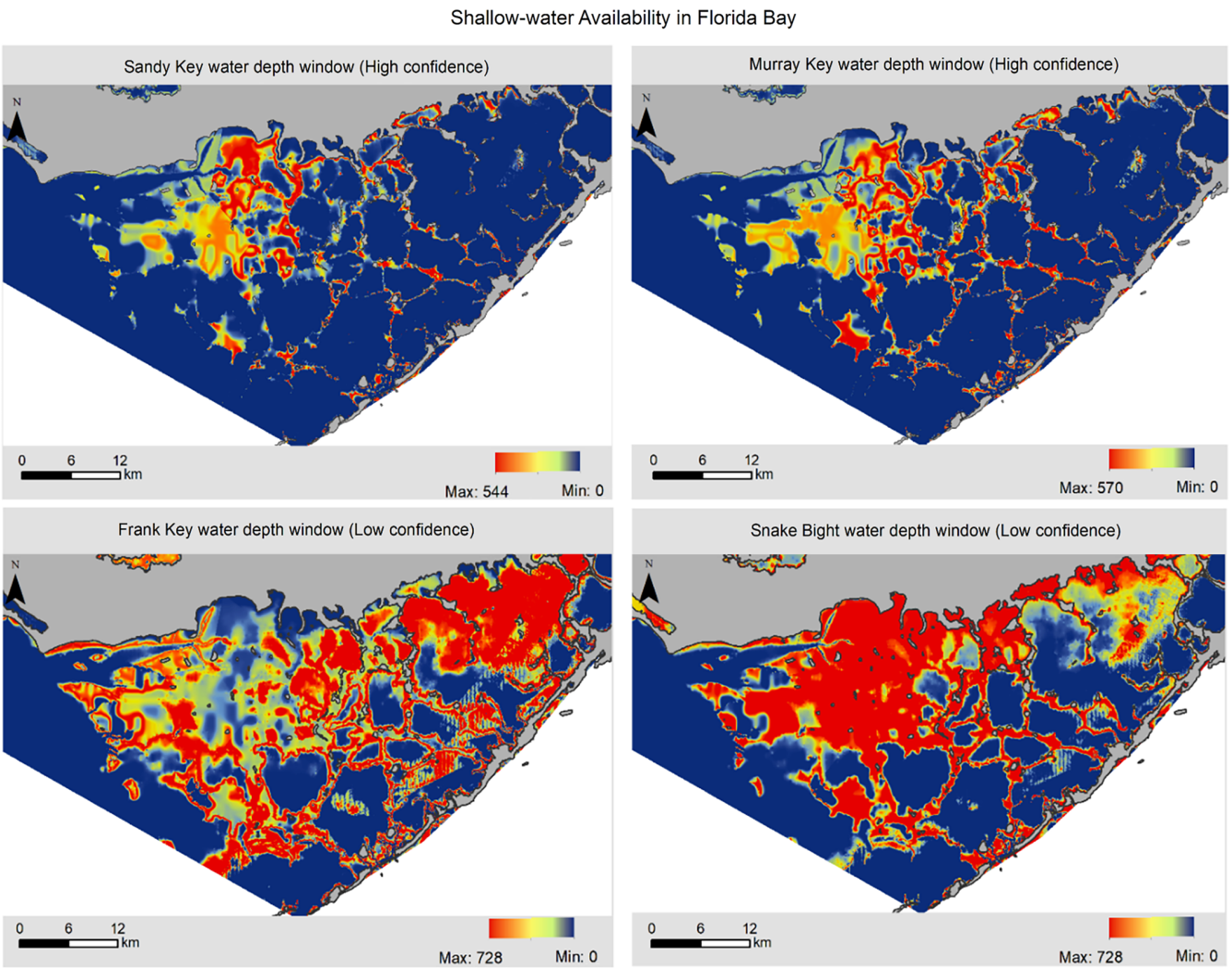

FIGURE 7 Average shallow-water availability at Florida Bay each year of the application period. Shallow-water availability was estimated by the Tidal Inundation Model of Shallow-water Availability (TiMSA) using a subsite-specific water depth window. The water depth windows were derived from the 10% to 90% quantile range of water depths at Little Blue Heron foraging locations at each subsite for each year (see Table 2). For every minute, the grid-cell (30 m × 30 m) occurs within the water depth window, 1 min of availability is added to the grid-cell. The process repeats over the tide to generate an output of shallow-water availability in minutes for each day of the year between sunrise and sunset to account for the diurnal constraint of Little Blue Heron foraging activity. Outputs of shallow-water availability based on the water depth window for Sandy Key and Murray Key reflect narrow ranges of water depth windows (0.311 and 0.302 m, respectively) and delineates available foraging habitat. Outputs of shallow-water availability based on the water depth window for Frank Key and Snake Bight reflect much wider ranges of water depth windows (1.021 and 1.470 m, respectively) and thus delineate uncertain foraging habitat as available. The outputs of shallow-water availability by subsite provide a visual representation of low versus high confidence of TiMSA estimates that are derived from localized water depth windows

The temporal transfer also revealed interannual variation of shallow-water availability over the application period, which was not observed over the development period. Under a temporally stable water depth window, considerable changes in shallow-water availability can occur year-to-year as a result of small annual differences in sea level. These sea level fluctuations reflect interannual differences in tidal period and amplitude. This demonstrates shallow-water availability is temporally explicit parameter that cannot be generalized beyond the tidal conditions specific to the time period of model application. Interpretations made outside the temporal context with which shallow-water availability estimates were generated can lead to inaccurate and misleading inferences.

Short-term gains and losses in Little Blue Heron foraging habitat occur from slight differences in annual tidal cycles. This demonstrates how sensitive shallow-water availability is to sea level fluctuations and the scale at which Little Blue Heron foraging habitat becomes altered as a consequence. Our results directly show TiMSA can

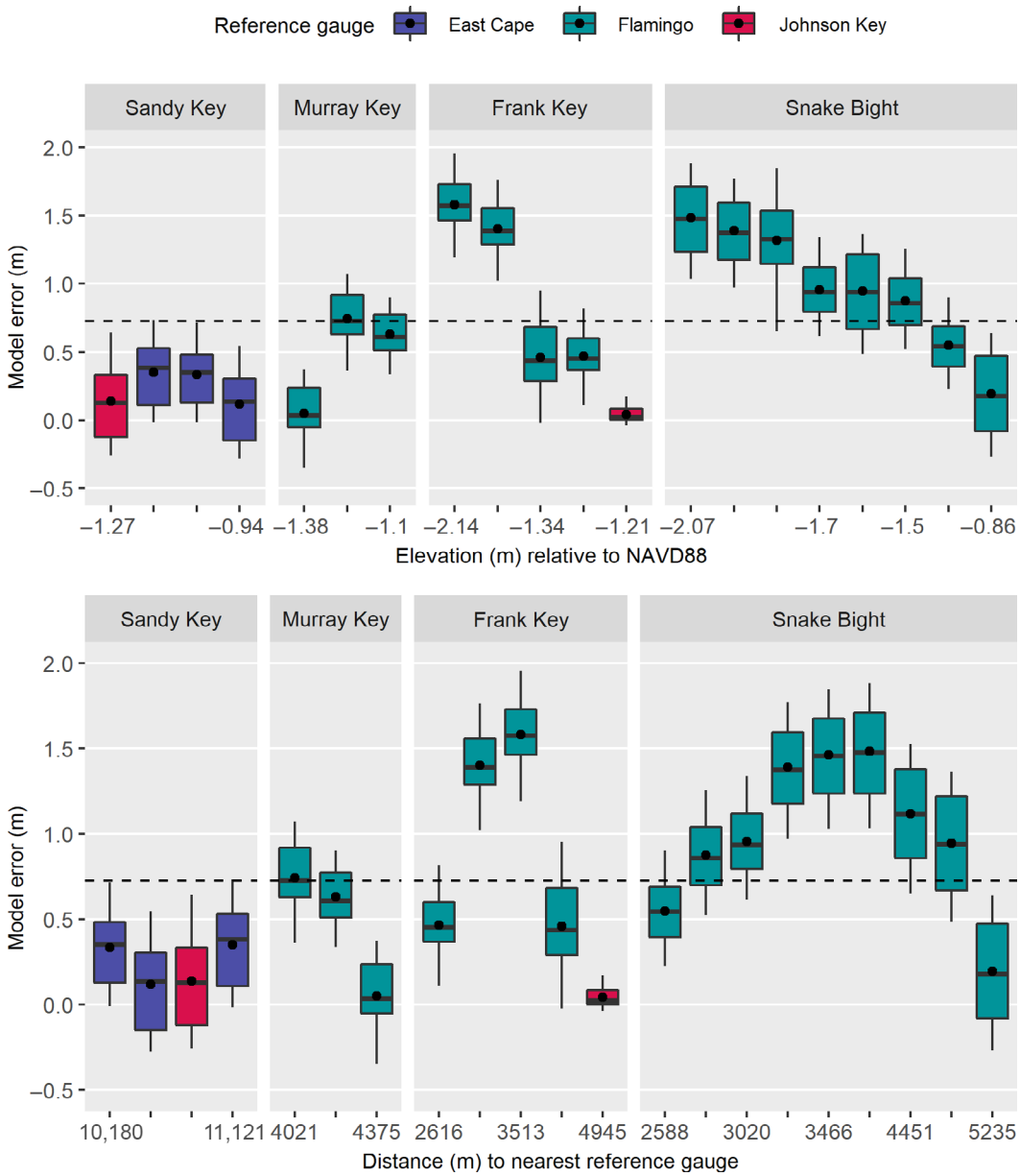

FIGURE 8 Boxplots of model error (water depths predicted by the Tidal Inundation Model of Shallow-water Availability [TiMSA] minus water levels measured by data loggers) for each sampling location ($n = 21$) in Florida Bay. Positive values of model error indicate TiMSA predicted deeper water depths than observed; negative values indicate shallower water depths were predicted. The temporal error (error due to tidal simulation) is demonstrated by the vertical spread at each sampling location (whiskers), while the spatial error (inaccuracies in the digital elevation model) is demonstrated by entire vertical shifts among all sampling locations. Dashed line at $y = 0.72$ represents the mean error pooled across all locations, and dots inside the boxplot represent the local mean error. Elevation (relative to North American Vertical Datum 1988) at the sampling location had a strong negative effect on model error, portrayed by the vertical shifts in the distributions of error among sampling, locations (top panel). Distance to nearest reference gauge did not have an effect on model error represented by the lack of a distinguishable pattern in the distributions of error among sampling locations (bottom panel)

quantify spatial and temporal changes to shallow water that are otherwise imperceptible with tidal data alone. It is not yet known how the mechanisms that drive the relationship between hydrological processes and shallow-water habitat use patterns by birds are expected to change with sea level rise. A habitat suitability model for wading birds using a precursory model to TiMSA projected a loss of nearly 25% of coastal foraging habitat in the Lower Florida Keys by 2050 and a 50% loss by 2075 under three sea level rise scenarios developed by the Intergovernmental Panel on Climate Change (Calle et al., 2012). When coupled with increasing intensity and severity of storms and hurricanes and accelerating rates of sea level rise, large areas of foraging habitat may be at

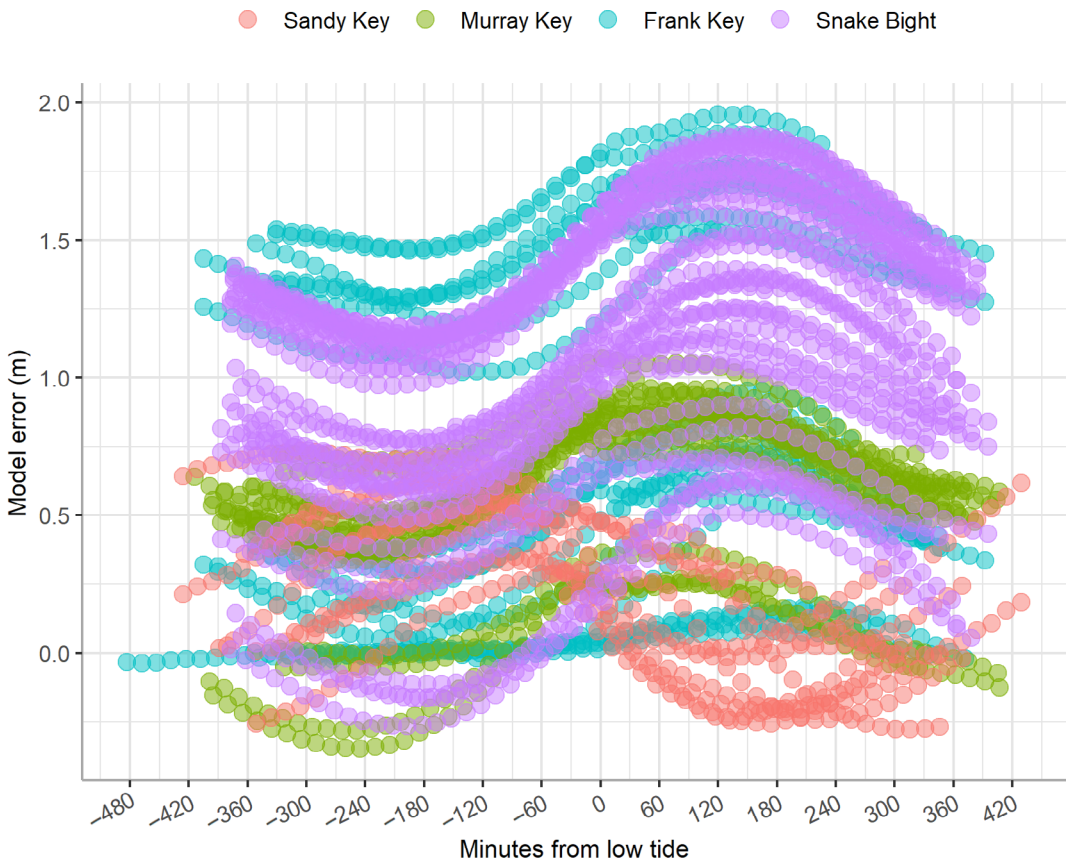

FIGURE 9 Model error (water depths predicted by Tidal Inundation Model of Shallow-water Availability [TiMSA] minus water depths measured by data loggers) for each sampling location ($n = 21$) versus minutes from low tide at Florida Bay. Each circle represents a water depth measurement at a sampling location. Positive values of model error indicate TiMSA predicted deeper water depths than observed; negative values indicate shallower water depths were predicted. Value of 0 on the *x*-axis represents low tide at the nearest reference gauge relative to the sampling location. Negative values represent number of minutes prior to low tide and positive values represent number of minutes after low tide. Model error tended to rise and fall over the tidal cycle due to a temporal offset in which TiMSA-predicted low tide times were out of phase with low tide times at the reference gauge. Local maximums of error generally occurred after low tide

risk of being lost over shorter time periods than previously predicted. Tidal Inundation Model of Shallow-water Availability can serve to evaluate outcomes of hydrologic restoration plans, water management regimes, and sea level rise scenarios on shallow-water resources for ecological (e.g., habitat suitability, species distribution, and resource selection) and anthropogenic needs (e.g., flood risk, coastal resiliency, and vulnerability).

Spatiotemporal transferability of TiMSA

The transfer of TiMSA to a novel site under a different time period revealed the extent to which model parameters are spatially explicit. Water depth windows, and ultimately shallow-water availability, are sensitive to spatial variation in the model's bathymetric DEM layer. Since water depth windows are empirically derived via locally observed data, TiMSA assumes the spatial variation of the DEM and estimates shallow-water availability with the level of confidence proportional to that of the DEM. Water depth windows derived from central Florida Bay spanned a wide range of water depths, signaling uncertainty of the CUDEM in these areas. A consequence of a liberal water depth window is an inflated number of occurrences where water is classified as "available" for the focal organism and an overestimation of shallow-water availability. By contrast, the narrow water depth windows derived from western Florida Bay were representative of biological foraging limits of the Little Blue Heron. Consequently, the outputs of shallow-water availability generated from these spatially explicit water depth windows were reflective of actual foraging conditions in Florida Bay. Hydrologic model parameters that are sensitive to spatial variation are likely to more representative of the water body's intrinsic physical and geographical conditions (Patil & Stieglitz, 2015).

The TiMSA parameter for shallow-water availability has additional advantages over estimated or observed water depth in practice. The units of shallow-water availability in area-time can be scaled to a spatial or temporal context relevant to the user (or organism). As a time-integrated estimate, shallow-water availability accounts for both axes of resource access (area and duration) and provides a more realistic perspective of how an organism interacts and responds to its changing environment. As such, the temporally dynamic and spatially explicit parameter of shallow-water availability is superior to water depth for resource selection studies of wading birds. Shallow-water availability was strongly associated with abundance of little blue herons and Great White Herons (Calle et al., 2016) and explained patterns of foraging habitat selection at multiple spatial scales for both species (Calle et al., 2018). Evaluating shallow-water availability as habitat attribute for waterbirds in other intertidal areas can contribute to our understanding of biotic responses to anthropogenic stressors and natural disturbances and forecast areas with high probability of selection to target for conservation. Beyond waterbirds, water depth windows and shallow-water availability estimates can be generated for other tidally influenced species (Gibson, 2003; Speirs et al., 2002), including taxa of concern in South Florida such as Pink Shrimp (*Farfantepenaeus duorarum*), prey fish, sportfish, and the American Crocodile (*Crocodylus acutus*). It is important to note the quality (and confidence) of the estimations of shallow-water availability depends on the water depth window. A water depth window that reflects the ecology of the species of interest generates more reliable estimates of shallow-water availability, but achieving highest confidence in model outputs requires accuracy of the input DEM. Tidal Inundation Model of Shallow-water Availability-estimated water depths derived from different DEMs produce different water depth windows. Thus, water depth windows are DEM-specific. We strongly recommend evaluating DEM accuracy of multiple DEMs, if available, prior to implementing TiMSA at new application sites to assess feasibility and reliability of a spatio-temporal transfer.

Contributing factors and solutions for improving water depth accuracy

While TiMSA reasonably approximates timing of inundation at timescales of days via integration over time, it is less accurate in estimating inundation times at finer timescales (e.g., min) even though it simulates inundation at 1-min intervals. At the application site, TiMSA predicted earlier inundation times and deeper water depths than were measured by data loggers. This limitation is likely from a lack of a physically based framework in the model to simulate the notorious complexities of bathymetry and hydrology in Florida Bay. The model's simplification of tidal dynamics (i.e., use of Thiessen polygons) likely biased inundation times at grid-cells near physical barriers to flow, such as on the banks of tidal flats. Therefore, it is not surprising TiMSA performed better in areas along the Gulf of Mexico where fluctuations in water levels are tidally dominated, and performed worse in the interior of Florida Bay where water regimes are less tidally influenced. The geomorphology of broad mudbanks in the western Bay dampens tidal forcing toward the central and eastern portions of Florida Bay where water circulation is highly restricted by the Florida Keys. Consequently, the southern and western regions of Florida Bay experience extensive tidal activity, whereas the central-eastern portion of Florida Bay is more sensitive to wind forcing and barometric pressure and experiences a very weak diurnal tide (Wang et al., 1994).

Intertidal morphology, distribution of channels, and bathymetry also strongly determine the response of shallow tidal basins to wind forcing (Defina et al., 2007; Fagherazzi et al., 2006), with elevation having a critical role on the magnitude of said response (Fagherazzi & Wiberg, 2009). We found the relationship between water levels and local wind parameters could not be easily modeled with a time series regression due to complex seasonality (Martinez, unpub. data), and likely, additive or multiplicative effects of other environmental and meteorological variables (Defina et al., 2007; Fagherazzi et al., 2006; Fagherazzi & Wiberg, 2009) not measured in this study. These mechanisms likely contributed to the temporal offset between the TiMSA-predicted and observed inundation times (temporal error). Nonetheless, the model's temporal error was eclipsed by the spatial error driven almost exclusively by nonsystematic biases of accuracy in CUDEM. Model error was highest in areas with lower values of elevation (i.e., deeper water depths) revealing hotspots of CUDEM error in central Florida Bay. Therefore, the largest obstacle toward achieving greater accuracy in TiMSA estimates of water depth at Florida Bay was DEM accuracy.

Despite the limitations posed from the DEM and the physical complexities of Florida Bay, TiMSA is appropriate for predicting total and relative inundation time rather than the precise timing and point value of water depths. Yet, there are possibilities for improving the latter. First, TiMSA can directly integrate water level data from the Water Monitoring Station Network within Florida Bay, which implicitly considers nontidal sources of water inputs and losses (i.e., rain, freshwater outflow, precipitation, and

lateral flow). Second, TiMSA as an open-source tool can be validated against other hydrodynamic physical models (e.g., ROMS, HYCOM, and Bay Assessment Model [BAM]) to trace differences in water depth estimates and identify other hotspots of inaccuracy. Bay Assessment Model decomposes Florida Bay into 54 basins based on the geomorphology of the landscape and bathymetric features whose boundaries impose upon simulated flow between basins (Park et al., 2016). Third, the spatial arrangement of these basins can be used to inform the boundaries of the Thiessen polygons in TiMSA to improve accuracy at the polygon borders. In contrast to BAM, ROMS and HYCOM use a terrain-following approach for shallow coastal regions, which result in smoother transition in water levels and their rates of change, but typically have coarser spatial resolutions requiring re-interpolation of outputs for applications at smaller spatial scales. Yet, even these more advanced models rely on an accurate DEM as the foundation for water depth estimates.

Sources of error in bathymetric DEMs and suggestions to address uncertainty

Building bathymetric DEMs is rife with challenges that introduce errors across various stages of development (Eakins & Grothe, 2014; Hare et al., 2011). National Center for Environmental Information builds their coastal DEMs using estuarine bathymetric data that originate from various sources (NOAA and NCEI, n.d.). These data are subject to error particularly in shallow-water depths. With the advent of the propeller on motorized boats, soundings were no longer collected at depths <0.5 m due to operational risks of running aground. This results in wide areas, particularly tidal flats, where interpolation is based on a marginal depth profile model and estimated for areas without measurements or with dated legacy data (NOAA and NCEI, n.d.; Hare et al., 2011). Second, the bathymetric data were partly generated using triangulated irregular networks known to interpolate depths with relatively large uncertainty for areas with shoreline (NOAA and NCEI, n.d.). Third, data sources span numerous epochs that are subject to long-term sea level fluctuations and erosion and deposition of the benthic surface. The bathymetric changes increase errors near shore where the benthic surface is more dynamic (Dorst, 2005). Fourth, source data were converted from different horizontal and vertical datums, which introduces additional uncertainty. All of these sources of error disproportionately affect the quality and accuracy of bathymetric data in intertidal zones, which severely impede DEM coverage and application for these ecosystems. From our study of shallow-water tidal flats at Florida Bay, we suspect those errors heavily contributed to the inaccuracy of water depth estimates. Thus, improvements to the accuracy of the DEM for this coastal region and potentially others would provide critical advancements in modeling shallow water.

We suggest field-based and modeling validation methods to narrow the range of uncertainty in bathymetric data, particularly for shallow-water areas. To survey areas inaccessible by conventional waterborne surveys, the elevations at the peripheries of permanent flow paths (i.e., channels) and at shallow tidal flats can be obtained via physical measurements or via automated procedures (Giordano et al., 2015). An error surface could be estimated via stratified systematic samples, gridded at ~500-m resolution. At this resolution across Florida Bay for instance, such effort would necessitate 5720 samples, 130 columns from west to east, and 44 rows from north to south. From such coverage, the vertical error could be estimated along the grid and an error surface applied to bias correct any DEM for the region. This procedural option is considerably less expensive than lidar retrievals (Allouis et al., 2010; Fernandez-Diaz et al., 2014). Alternatively, satellite-derived elevation models based on waterline extraction can achieve high accuracy in tidal flat environments approaching that of lidar and can yield high-quality elevation estimates to improve existing DEMs (Bishop-Taylor et al., 2019). Lastly, contributing factors to DEM uncertainty can be combined to estimate total propagated uncertainty for the vertical (depth/elevation) component and its corresponding horizontal position (Hare, 1995), which can then be incorporated into quantifying hydrologic modeling uncertainty (Hare et al., 2011). These recommendations can support best practices in addressing uncertainty when using bathymetric DEMs in coastal ecosystems in future studies.

ACKNOWLEDGMENTS

Financial support for this work was provided by the U.S. Geological Survey's Greater Everglades Priority Ecosystem Science (Cooperative Agreement # G15AC00303), Everglades Foundation, American Ornithological Society, The Waterbird Society, and Friends of Gumbo Limbo. We thank former graduate student Emilie Kohler, and technicians Michelle McInnis and Emilie Chen for their significant contributions to data collection, and to numerous graduate students, technicians, and volunteers for their assistance in the field. Kevin S. Kalasz and two anonymous referees provided useful feedback which greatly improved the manuscript. Field methods were conducted under the National Oceanic and Atmospheric Administration permit numbers FKNMS-2015-154 and FKNMS-2016-142, and under U.S. Fish and Wildlife Special Use Permit numbers FY15-33 and FY17-3.

All research activities were carried out in accordance with relevant guidelines and regulations. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Martinez et al., 2022a) are available from Dryad: https://doi.org/10.5061/dryad.bnzs7h4ch.

TiMSA code (Calle, 2021) is available from Zenodo: https://doi.org/10.5281/zenodo.5167984. Additional code (Martinez et al., 2022b) is available from Zenodo: https://doi.org/10.5281/zenodo.6327693.

ORCID

Marisa T. Martinez https://orcid.org/0000-0002-1915-6019
Leonardo Calle https://orcid.org/0000-0002-0269-6115
Stephanie S. Romañach https://orcid.org/0000-0003-0271-7825

REFERENCES

Allouis, T., J. S. Bailly, Y. Pastol, and C. Le Roux. 2010. "Comparison of LiDAR Waveform Processing Methods for Very Shallow Water Bathymetry Using Raman, Near-Infrared and Green Signals." *Earth Surface Processes and Landforms* 35: 640–50.

Bearup, D., and B. Blasius. 2017. "Ecotone Formation Induced by the Effects of Tidal Flooding: A Conceptual Model of the Mud Flat-Coastal Wetland Ecosystem." *Ecological Complexity* 32: 217–27.

Bishop-Taylor, R., S. Sagar, L. Lymburner, and R. J. Beaman. 2019. "Between the Tides: Modeling the Elevation of Australia's Exposed Intertidal Zone at Continental Scale." *Estuarine, Coastal and Shelf Science* 223: 115–28.

Boyer, J., and R. Jones. 2002. "A View from the Bridge: External and Internal Forces Affecting the Ambient Water Quality of the Florida Keys National Marine Sanctuary (FKNMS)." In *The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook*, edited by J. Porter and K. Porter, 609–28. Boca Raton, FL: CRC Press.

Burchard, H., and K. Boldin. 2002. *GETM, a General Estuarine Transport Model*. Technical report EUR 20253. European Commission. https://publications.jrc.ec.europa.eu/repository/handle/JRC23237.

Burrows, M., R. Gibson, and A. MacLean. 1994. "Effects of Endogenous Rhythms and Light Conditions on Foraging and Predator-Avoidance in Juvenile Plaice." *Journal of Fish Biology* 45: 171–80.

Calle, L. 2021. "Tidal Inundation Model of Shallow Water Availability." Zenodo. https://doi.org/10.5281/zenodo.5167984.

Calle, L., D. E. Gawlik, Z. Xie, L. Green, B. Lapointe, and A. Strong. 2016. "Effects of Tidal Periodicities and Diurnal Foraging Constraints on the Density of Foraging Wading Birds." *The Auk* 133: 378–96.

Calle, L., D. E. Gawlik, Z. Xie, and B. Johnson. 2012. *Feasibility of Evaluating the Impacts of Sea Level Rise on Foraging Habitat of the Little Blue Heron in the Great White Heron National Wildlife Refuge*. Boca Raton, FL: Florida Atlantic University.

Calle, L., L. Green, A. Strong, and D. E. Gawlik. 2018. "Time-Integrated Habitat Availability Is a Resource Attribute That Informs Patterns of Use in Intertidal Areas." *Ecological Monographs* 88: 600–20.

Castellanos, D. L., and L. P. Rozas. 2001. "Nekton Use of Submerged Aquatic Vegetation, Marsh, and Shallow Unvegetated Bottom in the Atchafalaya River Delta, a Louisiana Tidal Freshwater Ecosystem." *Estuaries* 24: 184–97.

Cooperative Institute for Research in Environmental Sciences (CIRES) at the University of Colorado Boulder. 2014. Continuously Updated Digital Elevation Model (CUDEM) – 1/9 Arc-Second Resolution Bathymetric-Topographic Tiles. NOAA National Centers for Environmental Information.

Defina, A., L. Carniello, S. Fagherazzi, and L. D'Alpaos. 2007. "Self-Organization of Shallow Basins in Tidal Flats and Salt Marshes." *Journal of Geophysical Research: Earth Surface* 112: 1–11.

Dorst, L. L. 2005. "Optimization of Survey Frequency: The Netherlands Hydrographic Service." *HYDRO International* 9: 6–9.

Eakins, B. W., and P. R. Grothe. 2014. "Challenges in Building Coastal Digital Elevation Models." *Journal of Coastal Research* 30: 942–53.

Egbert, G. D., and S. Y. Erofeeva. 2002. "Efficient Inverse Modeling of Barotropic Ocean Tides." *Journal of Atmospheric and Oceanic Technology* 19: 183–204.

ESRI. 2011. *ArcGIS Desktop: Release 10.6.1*. Redlands, CA: Environmental Systems Research Institute.

Fagherazzi, S., L. Carniello, L. D'Alpaos, and A. Defina. 2006. "Critical Bifurcation of Shallow Microtidal Landforms in Tidal Flats and Salt Marshes." *Proceedings of the National Academy of Sciences of the United States of America* 103: 8337–41.

Fagherazzi, S., and P. L. Wiberg. 2009. "Importance of Wind Conditions, Fetch, and Water Levels on Wave-Generated Shear Stresses in Shallow Intertidal Basins." *Journal of Geophysical Research: Earth Surface* 114: 1–12.

Fernandez-Diaz, J. C., C. L. Glennie, W. E. Carter, R. L. Shrestha, M. P. Sartori, A. Singhania, C. J. Legleiter, and B. T. Overstreet. 2014. "Early Results of Simultaneous Terrain and Shallow Water Bathymetry Mapping Using a Single-Wavelength Airborne LiDAR Sensor." *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing* 7: 623–35.

Fourqurean, J. W., and M. B. Robblee. 1999. "Florida Bay: A History of Recent Ecological Changes." *Estuaries* 22: 345–57.

Gawlik, D. E. 2002. "The Effects of Prey Availability on the Numerical Response of Wading Birds." *Ecological Monographs* 72: 329–46.

Getz, W. M., C. R. Marshall, C. J. Carlson, L. Giuggioli, S. J. Ryan, S. S. Romañach, C. Boettiger, et al. 2018. "Making Ecological Models Adequate." *Ecology Letters* 21: 153–66.

Gibson, R. 1992. "Tidally-Synchronized Behaviour in Marine Fishes." In *Rhythms in Fishes*, edited by M. Ali, 63–81. New York, NY: Plenum Press.

Gibson, R. N. 2003. "Go with the Flow: Tidal Migration in Marine Animals." *Hydrobiologia* 503: 153–61.

Giordano, F., G. Mattei, C. Parente, F. Peluso, and R. Santamaria. 2015. "Integrating Sensors into a Marine Drone for Bathymetric 3D Surveys in Shallow Waters." *Sensors* 16: 41.

Grothe, P. R., L. A. Taylor, B. W. Eakins, K. S. Carignan, R. R. Warnken, E. Lim, and R. J. Caldwell. 2010. *Digital Elevation Models of Key West: Procedures, Data Sources and Analysis*. Technical Memorandum No. NESDIS NGDC-32. Boulder, CO: National Oceanographic and Atmospheric Administration.

Hare, R., B. Eakins, and C. Amante. 2011. "Modelling Bathymetric Uncertainty." *International Hydrographic Review* 6: 31–42.

Hare, R. M. 1995. "Depth and Position Error Budgets for Multibeam Echosounding." *International Hydrographic Review* LXXII: 37–69.

Klemeŝ, V. 1986. "Operational Testing of Hydrological Simulation Models." *Hydrological Sciences Journal* 31: 13–24.

Langevin, C., E. Swain, and M. Wolfert. 2005. "Simulation of Integrated Surface-Water/Ground-Water Flow and Salinity for a Coastal Wetland and Adjacent Estuary." *Journal of Hydrology* 314: 213–34.

Le Provost, C., F. Lyard, J. M. Molines, M. L. Genco, and F. Rabilloud. 1998. "A Hydrodynamic Ocean Tide Model Improved by Assimilating a Satellite Altimeter-Derived Data Set." *Journal of Geophysical Research: Oceans* 103: 5513–29.

Lee, T. N., E. Johns, N. Melo, R. H. Smith, P. Ortner, and D. Smith. 2006. "On Florida Bay Hypersalinity and Water Exchange." *Bulletin of Marine Science* 79: 301–27.

Lohmann, M. A., E. D. Swain, J. D. Wang, and J. Dixon. 2012. *Evaluation of Effects of Changes in Canal Management and Precipitation Patterns on Salinity in Biscayne Bay, Florida, Using an Integrated Surface-Water/Groundwater Model*. Scientific Investigations Report 2012–5099. Reston, VA: U.S. Geological Survey.

Martinez, M., L. Calle, S. Romanach, and D. Gawlik. 2022a. "Data From: Evaluating Temporal and Spatial Transferability of a Tidal Inundation Model for Foraging Waterbirds." Dryad. Dataset. https://doi.org/10.5061/dryad.bnzs7h4ch.

Martinez, M., L. Calle, S. Romanach, and D. Gawlik. 2022b. "Code From: Evaluating Temporal and Spatial Transferability of a Tidal Inundation Model for Foraging Waterbirds." Zenodo. Code. https://doi.org/10.5281/zenodo.6327693.

Martins, R. C., T. Catry, R. Rebelo, S. Pardal, J. M. Palmeirim, and J. P. Granadeiro. 2016. "Contrasting Estuary-Scale Distribution of Wintering and Migrating Waders: The Potential Role of Fear." *Hydrobiologia* 768: 211–22.

Matsunaga, K. 2000. "Effects of Tidal Cycle on the Feeding Activity and Behavior of Grey Herons in a Tidal Flat in Notsuke Bay, Northern Japan." *Waterbirds* 23: 226–35.

McGarity, T. O., and W. E. Wagner. 2003. "Legal Aspects of the Regulatory Use of Environmental Modeling." *Environmental Law Reporter: News and Analysis* 33: 10751–74.

Milbert, D. G. 2002. VDatum Transformation Tool v4.3.NOAA. https://vdatum.noaa.gov/welcome.html.

Moon, J. B., T. H. Dewitt, M. N. Errend, R. J. F. Bruins, M. E. Kentula, S. J. Chamberlain, M. S. Fennessy, and K. J. Naithani. 2017. "Model Application Niche Analysis: Assessing the Transferability and Generalizability of Ecological Models." *Ecosphere* 8: e01974.

Nichols, J. D., J. E. Hines, J. R. Sauer, F. W. Fallon, J. E. Fallon, and P. J. Heglund. 2000. "A Double-Observer Approach for Estimating Detection Probability and Abundance from Point Counts." *The Auk* 117: 393–408.

NOAA & NCEI. U.S. Estuarine Bathymetric Data Caveats. https://www.ngdc.noaa.gov/mgg/bathymetry/estuarine/faqs.html.

Onset. 2020. *HOBOware*. Bourne, MA: Onset Computer Corporation.

Ortner, P. B., P. J. Fletcher, and C. R. Kelble. 2014. "Introduction to Tools to Support Ecosystem Based Management of South Florida's Coastal Resources." *Ecological Indicators* 44: 2–5.

Park, J., E. Stabenau, and K. Kotum. 2016. *Florida Bay Assessment Model v. 1.0. Hydrologic Model Manual 2016*. 7–27. Homestead, FL: South Florida Natural Resources Center, National Park Service.

Patil, S. D., and M. Stieglitz. 2015. "Comparing Spatial and Temporal Transferability of Hydrological Model Parameters." *Journal of Hydrology* 525: 409–17.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2020. nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-149.

Powell, G. V. N. 1987. "Habitat Use by Wading Birds in a Subtropical Estuary: Implications of Hydrography." *The Auk* 104: 740–9.

Powell, G. V. N., and A. H. Powell. 1986. "Reproduction by Great White Herons *Ardea herodias* in Florida Bay as an Indicator of Habitat Quality." *Biological Conservation* 36: 101–13.

R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Randin, C. F., T. Dirnböck, S. Dullinger, N. E. Zimmermann, M. Zappa, and A. Guisan. 2006. "Are Niche-Based Species Distribution Models Transferable in Space?" *Journal of Biogeography* 33: 1689–703.

Raposa, K. B., R. A. Mckinney, and A. Beaudette. 2009. "Effects of Tide Stage on the Use of Salt Marshes by Wading Birds in Rhode Island." *Northeastern Naturalist* 16: 209–24.

Reis-Filho, J. A., F. Barros, J. D. A. C. D. C. Nunes, C. L. S. Sampaio, and G. B. G. De Souza. 2011. "Moon and Tide Effects on Fish Capture in a Tropical Tidal Flat." *Journal of the Marine Biological Association of the United Kingdom* 91: 735–43.

Rosenberger, R., and T. Phipps. 2007. "Correspondence and Convergence in Benefit Transfer Accuracy: Meta-Analytic Review of the Literature." In *Environmental Value Transfer: Issues and Methods*, edited by S. Navrud and R. Ready, 23–43. Dordrecht, The Netherlands: Kluwer Academic.

Sargent, F. J., T. J. Leary, D. W. Crewz, and C. R. Cruer. 1995. *Scarring of Florida's Seagrasses: Assessment and Management Options*. Technical Report TR-1. St. Petersburg, FL: Florida Marine Research Institute.

Shchepetkin, A. F., and J. C. McWilliams. 2005. "The Regional Oceanic Modeling System (ROMS): A Split-Explicit, Free-Surface, Topography-Following-Coordinate Oceanic Model." *Ocean Modeling* 9: 347–404.

Sogard, S. M., G. V. N. Powell, and J. G. Holmquist. 1989. "Utilization by Fishes of Shallow, Seagrass-Covered Banks in Florida Bay: 2. Diel and Tidal Patterns." *Environmental Biology of Fishes* 24: 81–92.

South Florida Natural Resources Center, and National Park Service. 2012. *Salinity and Hydrology of Florida Bay: Status and Trends 1990–2009*. Technical Series 2012:1. Homestead, FL: South Florida Natural Resources Center.

Speirs, D., S. Lawrie, D. Raffaelli, W. Gurney, and C. Emes. 2002. "Why Do Shallow-Water Predators Migrate? Strategic Models and Empirical Evidence from an Estuarine Mysid." *Journal of Experimental Marine Biology and Ecology* 280: 13–31.

Stumpf, R. P., and J. W. Haines. 1998. "Variations in Tidal Level in the Gulf of Mexico and Implications for Tidal Wetlands." *Estuarine, Coastal and Shelf Science* 46: 165–73.

Swain, E. D., M. A. Lohmann, and C. R. Goodwin. 2019. *The Hydrologic System of the South Florida Peninsula – Development and Application of the Biscayne and Southern Everglades Coastal Transport (BISECT) Model*. Scientific Investigations Report 2019-5045. Reston, VA: U.S. Geological Survey. https://doi.org/10.3133/sir20195045

Swain, E. D., M. A. Wolfert, J. D. Bales, and C. R. Goodwin. 2004. *Two-Dimensional Hydrodynamic Simulation of Surface-Water Flow and Transport to Florida Bay through the Southern Inland and Coastal Systems (SICS)*. Water-Resources Investigations Report 03-4287. Reston, VA: U.S. Geological Survey. https://doi.org/10.3133/wri034287

U.S. Army Corps of Engineers. 2019. 2012–2017 Everglades Report Card. Jacksonville, Florida, USA.

U.S. Army Corps of Engineers, and South Florida Water Management District. 2002. Florida Bay & Florida Keys Feasibility Study, Project Management Plan, Central and Southern Florida Project, Comprehensive Everglades Restoration Plan.

Wallcraft, A., E. Metzger, and S. Carroll. 2009. *Software Design Description for the Hybrid Coordinate Ocean Model (HYCOM) v.2.2*. Mississippi: Naval Research Laboratory. https://www.hycom.org/hycom/documentation

Wang, J. D., J. Van De Kreeke, N. Krishnan, and D. W. Smith. 1994. "Wind and Tide Response in Florida Bay." *Bulletin of Marine Science* 54: 579–601.

Wenger, S. J., and J. D. Olden. 2012. "Assessing Transferability of Ecological Models: An Underappreciated Aspect of Statistical Validation." *Methods in Ecology and Evolution* 3: 260–7.

How to cite this article: Martinez, Marisa T., Leonardo Calle, Stephanie S. Romañach, and Dale E. Gawlik. 2022. "Evaluating Temporal and Spatial Transferability of a Tidal Inundation Model for Foraging Waterbirds." *Ecosphere* 13(4): e4030. https://doi.org/10.1002/ecs2.4030