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PRIMARY RESEARCH PAPER

Abiotic factors influence the dynamics of marine habitat use by a highly mobile "freshwater" top predator

James C. Nifong · **Brian Silliman**

Abstract Cross-ecosystem movements of mobile consumers are a primary mechanism by which energy and nutrients are exchanged between disparate ecosystems. While factors influencing variation in bottom–up subsidies between ecosystems have been well studied, much less is known regarding how biotic and abiotic factors influence the dynamics of mobile consumer-driven connectivity. In a literature survey, we found only 14% of studies examined factors contributing to variation in cross-ecosystem marine foraging by freshwater-adapted consumers. Here, we examine the relationships between abiotic factors and cross-ecosystem movements of a highly mobile freshwater-adapted top predator, *Alligator mississippiensis* (American alligator). As alligators lack physiological adaptations to survive in marine environments, we predict this linkage would be affected by factors that modify the ability to cope with high salinities. Our results reveal that multiple abiotic factors (e.g., relative humidity, temperature, total precipitation) are key explanatory variables of the duration of cross-ecosystem foraging trips by alligators, and that the absence of salt glands does not preclude them from performing long forays into marine environments. More broadly, our results expand our understanding of mobile consumer-driven ecosystem connectivity at the land–sea interface by demonstrating connectivity is highest when physical stressors are relaxed, and access to and availability of resources are maximized.

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Introduction

Determining the relative importance of the exchange of energy and organisms between ecosystems is essential to understanding how ecosystem connectivity drives large-scale patterns in community structure and ecosystem functioning (Polis et al., 1997; Huxel & McCann, 1998). Historically, much of the research pertaining to energy subsidies in the form of allochthonous resources (i.e., detritus, carrion,

nutrients) has concentrated on the movement of resources from donor to recipient communities through abiotic processes such as tidal deposition or run-off (Jefferies, 2000; Huxel et al., 2002). However, it is well known that mobile consumers such as top predators can readily cross ecosystem boundaries to exploit resources available in adjacent ecosystems and thus, upon return to recipient communities, can deposit nutrients and energy derived from allochthonous production (Lundberg & Moberg, 2003; McCauley & Young, 2012).

Highly mobile consumers are increasingly being considered substantial vectors of energy and nutrients between ecosystems, and these interactions are hypothesized to have significant implications for food web stability (Lundberg & Moberg, 2003; McCann et al., 2005). One intersection of ecosystems where mobile consumers are known to exploit allochthonous resources is at the land–sea interface. At this ecotone, mobile terrestrial and freshwater-adapted organisms have the capability to travel into near-shore marine and estuarine waters or fringing inter-tidal and marginal habitats (e.g., supralittoral zone) to exploit marine-derived food resources (e.g., mammals-Carlton & Hodder, 2003; reptiles-Lillywhite et al., 2008; ants-Garcia et al., 2011). Lacking any specialized adaptions (e.g., salt glands) or physiological mechanisms (e.g., cloacal urine modification) to mitigate the osmotic stress imposed by saline marine ecosystems, the temporal dynamics of cross-ecosystem movements performed by these consumers are likely to be affected by abiotic and biotic factors that directly impact their osmoregulatory capacity (i.e., temperature, salinity, body size, resource availability). Given the widespread use of these behaviors by a taxonomically diverse set of consumers and potential importance of these interactions for energy flow and nutrient transfer among ecosystems; we first, sought to develop a better understanding of the potential factors determining when and where mobile consumers enhance ecosystem connectivity at the land–sea ecotone.

We reviewed recent literature (studies published between 1930 and 2013, see Table S1 for details) for studies that examined movements of terrestrial- and freshwater-adapted consumers across the land–sea ecotone to evaluate the degree to which potential biotic or abiotic factors driving these behaviors had been identified and examined. We found published records for a total of 74 terrestrial- or freshwater-

adapted species spanning 20 Orders documented to cross-ecosystem forage into marine ecosystems (Table S1). Of the 117 studies, only 17 ($\sim$14% of studies) performed on a total of 20 taxon tested the effects of biotic or abiotic factors on variation in cross-ecosystem foraging behaviors. Nonetheless, some general patterns emerged from our review of these studies. First, resource availability (e.g., primary production, secondary production, carrion biomass) was highly influential in determining when and where consumers employed cross-ecosystem movements (Table S2). Second, abiotic factors that are directly linked to osmoregulation (e.g., temperature, relative humidity, and precipitation) were the main determinates of the frequency and duration of cross-ecosystem movements (Table S2). Third, factors affecting the accessibility and detectability of marine food resources [e.g., island area, tidal stage (low or high), sea ice thickness and cover] impacted the efficacy of cross-ecosystem movements in obtaining food. Last, few studies have employed repeated direct measurements (e.g., GPS tracking) of cross-ecosystem movements by individuals over long time periods (weeks to years).

Motivated by these findings, we analyzed cross-ecosystem movement data collected from a large-bodied, highly mobile top predator, *Alligator mississippiensis* (Daudin, 1801) (American alligator, hereafter alligator), to further examine the potential for particular abiotic factors to affect cross-ecosystem movements patterns of freshwater-adapted consumers.

Alligators are a ubiquitous large-bodied top predator in aquatic ecosystems throughout the southeastern Coastal Plain of the United States. As the most well studied crocodilian worldwide (Ross & Ernst, 1994), much is known about their general ecology, biology, and natural history; however, behaviors associated with the use of marine and estuarine habitats has historically received little attention (McNease & Joanen, 1977; Tamarack, 1989; Rootes et al., 1991). Recent evidence suggests, however, that alligators may serve important roles in coastal ecosystems due to their ability to connect disparate ecosystems (Rosenblatt & Heithaus, 2011; Rosenblatt et al., 2013a; Fujisaki et al., 2014, 2016), cascading effects of their interactions with strongly interacting prey (Nifong & Silliman, 2013), and habitat engineering behaviors (Nifong et al., 2015).

Near-shore marine and estuarine ecosystems provide a unique obstacle for alligators to osmoregulate

and maintain water balance as they lack lingual salt glands which are functionally present in species of true crocodiles (Crocodylidae-Taplin et al., 1982). Consequently, alligators are thought to solely rely on behavioral mechanisms to counteract the osmotic stress imposed by marine environments (Jackson et al., 1996). Repetitive cross-ecosystem movements from high salinity to freshwater ecosystems are hypothesized to be the principal behavioral mechanism by which alligators osmoregulate while exploiting marine habitats and prey (Mazzotti & Dunson, 1989).

Previous studies on movement patterns of coastal inhabiting alligators have concentrated on large-scale movements (10's of km) across an elongated salinity gradient, where boundaries between freshwater and marine ecosystems are constantly changing (Rosenblatt & Heithaus, 2011; Rosenblatt et al., 2013b; Fujisaki et al., 2014, 2016). Thus, disentangling the impacts of abiotic factors (e.g., salinity, temperature) on cross-ecosystem movements is difficult and requires detailed knowledge of the fine-scale spatial distribution of abiotic gradients in the system. Conversely, barrier island systems along the Atlantic coast of the US offer an opportunity to study cross-ecosystem movement patterns of alligators across a truncated, but wide ranging salinity gradient (0 to >35 PSU); wherein, freshwater ponds and wetlands located within the island interior are isolated from the surrounding marine and estuarine habitats (i.e., salt marshes, tidal creeks) but only separated by relatively short overland distances (<2 km). Furthermore, to our knowledge no study has directly assessed the individual and combined effects of multiple abiotic factors such as temperature, salinity, tidal range, precipitation, and humidity on the duration of marine habitat use by alligators. Previous studies have inferred the effects of abiotic factors based on observed differences in movement, habitat use, and abundance patterns among seasons diverging in abiotic conditions (Rosenblatt & Heithaus, 2011; Rosenblatt et al., 2013b; Fujisaki et al., 2014, 2016); however, in these ecosystems many other factors such as prey availability vary seasonally and may influence habitat use patterns. Given the clear differences in abiotic conditions among discrete habitats near barrier islands, we can possibly gain deeper insight into the direction and magnitude of abiotic effects as well as eco-physiological forces driving these patterns as opposed to those insights gained from studying movements along an elongated salinity gradient.

Specifically, using data collected from GPS–VHF telemetry, we set out to answer the following four questions regarding cross-ecosystem movement patterns of alligators inhabiting barrier island systems where freshwater and marine habitats are discrete: (1) What is the frequency and duration of marine and freshwater habitat use by alligators? (2) Which abiotic factors influence cross-ecosystem movements? (3) Does the rate of movement differ between habitats and which abiotic factors affect movement rates? and (4) Do alligator home ranges and core activity areas include marine habitats?

Based on previous studies, general findings from our literature survey, and our current understanding of alligator ecology and physiology, we hypothesized that abiotic factors that either influence alligator's ability to osmoregulate (e.g., temperature, salinity, precipitation) or affect resource availability (e.g., water depth, precipitation) will be the most important factors driving cross-ecosystem movement patterns. We compare our findings to studies on other consumer species recovered during our literature survey to synthesize a general understanding of the factors that regulate cross-ecosystem movement of mobile consumers at the land–sea interface. These findings provide an avenue for further research regarding the role of mobile consumers in coastal ecosystems and potential impacts of changing environmental conditions on these interactions.

Materials and methods

Study site

We conducted this study within the domain of the Georgia Coastal Ecosystems Long term Ecological Research (GCE-LTER) station, located on the southeastern US Atlantic coast and encompassing 77,544 ha of near-shore marine, estuarine lagoon, barrier island, and riverine habitats. The study focused on alligators inhabiting Sapelo Island (31.455779°N, 81.256115°W, Fig. 1a), a 6,777 ha barrier island containing 4,411 ha of uplands habitats comprised of maritime forest and scrub habitats speckled with small freshwater ponds and wetlands as well as mosquito ditches. Sapelo Island is bordered by expansive tidal salt marshes and creeks to the west and by the Atlantic Ocean to the southeast; Sapelo Island is separated from the smaller Blackbeard Island to the northeast by a
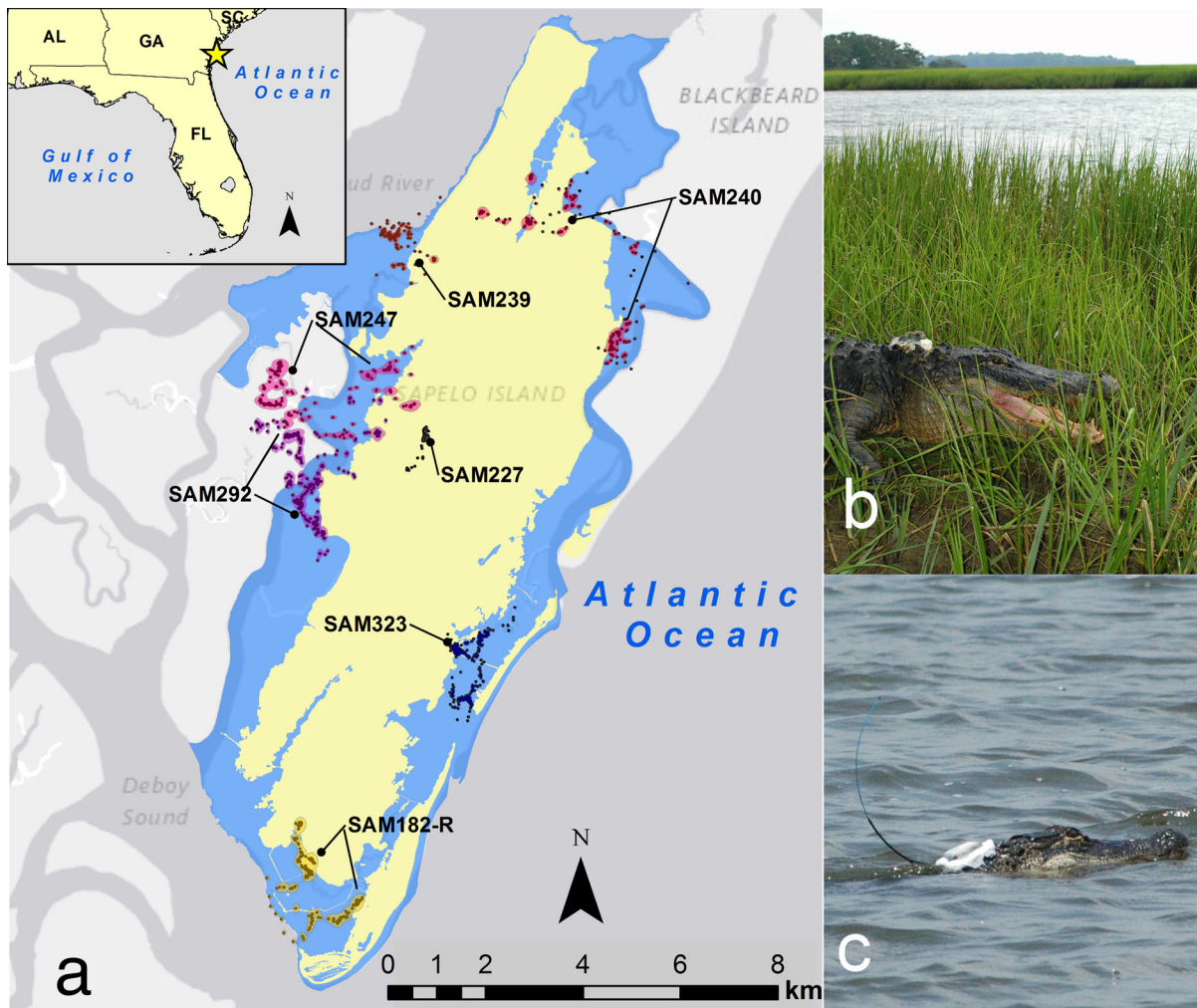
Fig. 1 Map and photos of alligators tracked with GPS–VHF transmitters. **a** Map of Sapelo and Blackbeard Islands, Georgia and surrounding salt marsh habitats. Freshwater habitats located on Sapelo Island are filled *yellow* and adjacent marine habitats filled *blue*. *Colored points* are successful locations logged by GPS–VHF transmitters during all deployments during 2008–2010 (refer to Table 1 for specific dates of deployments and other information on individuals). *Darkened colored polygons* outline the core-use areas (50% KDE) and outer more transparent polygons outline home range areas (95% KDE) estimated from 3D GPS locations recorded by transmitters. The *yellow star* in the *inset* map (*top-left*) denotes the general location of Sapelo Island, GA along the southeastern United States coastline. **b** Photo of adult male alligator with GPS–VHF transmitter attached to nuchal scute cluster. **c** Photo of adult male alligator with GPS–VHF transmitter attached while swimming to illustrate the position of the transmitter while alligators move through aquatic habitats

network of tidal creeks and salt marsh. Water salinity in the surrounding marine habitats is typically within the range of 24–35 PSU, although salinity can be temporarily lowered to 5–15 PSU during periods of heavy rain (GCE-LTER, 2014). The closest source of potential freshwater influx into the marine system other than rainfall is the Altamaha River, located approximately 8 km south of the southern apex of Sapelo Island. Freshwater inputs from the Altamaha River are highly dependent on river discharge, wind, and tidal range; the river only has a significant impact on salinity gradients surrounding Sapelo Island during periods of very high discharge.

GPS–VHF telemetry

We attached dual GPS–VHF tracking units to alligators to record and transmit locational data. The size of

Table 1 Total length, sex, dates of tracking, total days tracked, fix rate, number of cross-ecosystem trips performed, core-use, and home range areas determined from alligators outfitted with GPS–VHF units on Sapelo Island, Georgia during 2008–2010

Individual	TL (cm)	Sex	Dates of tracking	Tracking days (n)	Fix rate (%)	Number trips to or from marine habitats	Core-use area (50% KDE, ha)	Home range area (95% KDE, ha)
SAM227	233	F	5/27/2008–8/29/2008	94	50.7	0	0.02	0.67
SAM239	200	F	6/21/2008–8/06/2008	46	39.1	7	1.64	21.53
SAM240	263	M	4/21/2008–7/30/2008	100	59.0	3	0.79	51.75
SAM247	250	M	7/7/2009–8/31/2009	55	42.9	5	10.29	86.97
SAM292	232	M	6/29/2009–9/8/2009	71	48.8	4	8.00	86.36
SAM182-R	254	M	5/19/2010–6/22/2010	34	56.5	3	9.96	59.45
SAM323	296	M	6/10/2010–9/10/2010	92	79.1	10	0.47	18.80
mean[a]	246.9	–	–	70.3	53.7	5.3	4.45	46.50
SD[a]	29.8	–	–	26.0	13.2	2.7	4.72	33.94

[a] Mean and SD calculations exclude data from one female (SAM227) that remained in freshwater habitats throughout the tracking period

the GPS–VHF units restricted their use to adult individuals (total length [TL] > 183 cm). We conducted deployments and actively tracked individuals between 21 April 2008 and 10 September 2010. We used five pre-programmed units (H.A.B.I.T. Research Ltd., Victoria, BC, Canada) for deployments from 2008 to 2009 and two user-programmable units (Telemetry Solutions Inc., Concord, CA, USA) for deployments in 2010. Telemetry units were attached to the nuchal scute cluster, using methods similar to Kay (2004) (Fig. 1b). Briefly, following capture from boat or land using snag hooks and pole-snares, individuals were immobilized by securing them to a 2.5 m spineboard with VELCRO Spider-straps (Med-tech Resources Inc., Eugene, OR, USA). Prior to adhering each unit, we sanitized the mounting area with 90% ethanol and scrubbed free of debris using sterile gauze pad and administered 1 ml of local anesthetic (lidocaine) at the base of each nuchal scute. Using a drill (Dremel, Racine, WI, USA) one hole (3 mm diameter) was created through each of the four-large nuchal scutes. A consistent application of saline water inhibited tissue from overheating and suffering damage during the drilling process. After being positioned on the nuchal scute cluster, GPS–VHF units were secured in place with shrink-wrapped annealed stainless-steel wire threaded through the scute holes, into PVC channels located at the base of each unit and through the opposing scute hole. Terminal ends of the wires were twisted together and folded under the unit. Lastly, marine-grade epoxy was applied to the base of

the unit, encapsulating the attachment wires to provide a streamline shape and to prevent the unit from snagging on obstructions in the environment (Fig. 1c). Total time of GPS–VHF attachment was roughly 60–90 min and never exceeded 120 min.

Both types of GPS–VHF units were similar in shape and size (L × W × H, 9 cm × 4 cm × 3 cm and combined with the added marine epoxy weighed approximately 300 g) set in epoxy resin mold with VHF and UHF antennas protruding at a 45° angle from the posterior of the unit (Fig. 1c). Units produced by H.A.B.I.T. Research Ltd. were pre-programmed to attempt hourly GPS fixes for 14 h per day and were dormant for 10 h per day (at randomized intervals), allowing for approximately 120 days of battery life. High-speed data transmission for H.A.B.I.T. units proceeded via a VHF signal and occurred daily during a predetermined time window (1000 to 1200 h). GPS units produced by Telemetry Solutions were programmed to attempt GPS fixes at either 2 h or 1.5 h intervals to conserve battery life, allowing for a predicted battery life of 200–300 days. Data transmission for Telemetry Solutions units proceeded via a UHF (424 MHz) signal anytime the base station was near the unit (usually <1 km depending on clear line of sight). We attempted to download data every 2 weeks throughout each deployment period. Both types of GPS units acquire positional data (i.e., latitude, longitude, vertical height) by communicating with satellites in the NAVSTAR Global Positioning System network; the number of satellites

communicated with for any given attempt to establish a position varied due to environmental conditions and the location of the tracking unit in the habitat.

To download data, study animals were first located with a directional Yagi antenna attached to either an HR2600-DL Osprey receiver unit (H.A.B.I.T., Victoria, BC, Canada) or an R-1000 receiver unit (Communications Specialists Inc., Orange, CA, USA). Then, in the case of H.A.B.I.T. units, data were downloaded through the VHF signal via the Osprey receiver and transferred to a laptop computer. In the case of Telemetry Solutions units, data were downloaded through a UHF signal via a Yagi antenna connected to a base station and PDA, then transferred to a laptop computer. For successfully acquired GPS positions, downloaded data for each location included time of day and date, latitude, longitude, number of satellites used to acquire position, and the horizontal dilution of precision (HDOP, unit-less), a measure of GPS position accuracy (D'eon & Delparte, 2005).

Quantifying movement patterns

All 2D-GPS positions were excluded from analyses due to the decreased accuracy of these data. To quantify the cross-ecosystem movement and habitat use patterns of alligators equipped with GPS–VHF units, we first calculated the frequency and duration of trips made between freshwater wetlands and marine habitats. The start of one trip was defined as the first time, and position an individual was detected in either freshwater or marine habitats after being detected in the opposing habitat. The end of one trip was classified as the last time and position an individual was detected in either freshwater or marine habitat prior to being detected in the opposing habitat. We assumed that individuals did not switch habitats between consecutive points acquired within the same habitat, thus our estimates of the number of trips between habitats are likely conservative.

For each individual, we also calculated the rate of movement (km day^{-1}, distance traveled divided by the time it took to travel that distance) between consecutive GPS locations. Since the two habitat types differed in topology and geomorphology (i.e., winding tidal creeks of marine habitats compared to more homogenous shallow freshwater wetlands and ponds), the calculation of movement rates was performed differently for each habitat. In marine habitats, the

distance between two consecutive points was measured along the mid-stream of tidal creeks or along the marsh edge of open water areas; choosing the most parsimonious route (shortest distance) adjoining two consecutive points. For movements within freshwater wetlands and transitions between habitats, the distance between consecutive points was measured as a straight line connecting the two points. Since additional movements were potentially performed between successful GPS acquisitions, distance traveled as measured here is a highly conservative estimate of the total distance traveled by tracked individuals.

Prior to analyzing movement data, we excluded outliers that were greater than two standard deviations away from the mean for both the duration of occupancy within habitats as well as the rate of movement. To examine the potential effects of abiotic factors on the duration of trips in marine and freshwater habitats, we used generalized linear models (GLM). Our response variable was the number of hours within one habitat before being detected in the opposing habitat. Due to the nature of the data (i.e., counts of hours prior to an event occurring), we used a negative binomial error distribution and log-link function within the 'glm.nb' function of the R package 'MASS' (version 7.3) (White & Bennetts, 1996; Venables & Ripley, 2002). We assessed the effects of abiotic factors on rate of movement, using a GLM with Gaussian error distribution and identity link function within the 'glm' function of the 'stats' package of R (R Core Development Team, 2013). We standardized model input variables following Gelman (2008), using the R package 'arm' (Gelman & Su, 2016). We then selected the best model or implemented model averaging, using the R package 'MuMIn' (Barton, 2016). If the Akaike weight (w) of the top performing model was <0.90, we implemented model averaging to estimate parameters and predict effects for all candidate models with $\Delta AIC_c \leq 2.0$ (Burnham & Anderson, 2002; Grueber et al., 2011). To compare the importance of each covariate, we calculated the Relative Importance of model covariates occurring in all candidate models, calculated as the sum of the Akaike weights (w) from all the models in which the covariate appears (Barton, 2016). To assess individual effects on our model predictions, we assessed whether inclusion of individual effects improved model performance (i.e., lower AIC_c value). Mixed effects GLM analyses (i.e., those including

random effects) were performed using the 'glm-madmb' function in the R package 'glmmADMB' for negative binomial models and the R package'lme4' for Gaussian models (Skaug et al., 2014; Bates et al., 2015).

We concentrated our analyses on abiotic factors which are likely to influence alligator movements based on existing knowledge of this species' physiology and ecology as well as abiotic factors identified in the literature for other cross-ecosystem foragers. To avoid the potential confounding effects of covariation between model parameters, we visually inspected for covariation between predictor variables using the 'pairs' function in R prior to inclusion in our model selection process. We avoided using predictor variables that showed a high amount of covariation ($r > 0.70$). The final set of predictor variables (abiotic factors) included temperature, salinity, humidity, precipitation, maximum water depth, and wind velocity.

As ectothermic vertebrates, the metabolism and consequently, the activity, behavior, and life history of alligators are known to be affected by ambient temperatures (Lewis & Gatten, 1985; Lance, 2003). We hypothesize that the duration of marine habitat use may decrease with increasing temperature, due to increased metabolic demand and water loss. In contrast, we expect that the duration of freshwater habitat use may increase at higher temperatures for the same reasons. Furthermore, alligators lack lingual salt secreting glands and chiefly rely on behavior and morphological adaptations such as a thick integument to mitigate the physiological effects of excess salt loading and increased rates of water loss in high salinity environments (Mazzotti & Dunson, 1984). Thus, abiotic factors such as temperature, salinity, relative humidity, precipitation, and wind velocity can potentially impact both the magnitude and temporal dynamics of the physiological forces (i.e., blood osmolality, rates of evapotranspiration, water deficit.) governing the physio-chemical requirements of alligators. We hypothesize that the duration of marine habitat use will be negatively affected by increasing physiological stress (i.e., higher temperatures, salinities, and wind velocities and lower humidity and precipitation), whereas the duration of freshwater habitat use will be positively affected by increasing stress. We considered maximum water depth as a proxy for tidal amplitude in our study system. In the

marine habitats surrounding Sapelo Island, tidal amplitude varies substantially between spring and neap tidal cycles, ranging from as low as 2 m up to 6 m. Differences in tidal dynamics can potentially affect the distribution and catchability of prey as well as the distance separating freshwater and marine habitats. During spring tides (i.e., high tidal amplitude), the entire salt marsh surface is inundated during high tide, reducing the distance between freshwater and marine habitats and often stimulating the movement of salt marsh organisms. During these dynamic periods, we hypothesize alligators may increase the duration of marine habitat use to reduce energy expenditures and maximize resource intake.

Input variables (abiotic factor data) were measured at GCE-LTER meteorological and hydrological monitoring stations (ML_MET: 31.417845°N, 81.2954 06°W; GCE10_Hydro: 31.482483°N, 81.267917°W; GCE3_Hydro: 31.548264°N, 81.210833°W) near the habitats used by tracked alligators (GCE-LTER, 2014). Meteorological data (air temperature, precipitation, and humidity) were measured every 15 min at the ML_MET station. Hydrological data (salinity, water temperature, and water depth) were measured every 30 min at the GCE3_Hydro and GCE10_Hydro stations (see GCE-LTER, 2014 for specific details on data collection at these monitoring stations). Values of model parameters were calculated as the average of daily mean values over the duration of each discrete trip. If a trip was <24 h, we used the daily mean for the day the trip was made. We used water temperature when assessing effects of abiotic factors on alligator movements within marine habitats and air temperature for freshwater habitats, since no monitoring stations were located within freshwater wetlands.

Home range

Prior to assessment of home ranges through kernel density estimation (KDE), we examined if tracked alligators expressed site fidelity using the 'rhrSiteFidelity' function within the R package 'rhr' (Signer & Balkenhol, 2015). Site fidelity is assessed by calculating two indices, mean squared displacement from centroid (MDC) and linearity index (LI, linear distance between the endpoints of an animal's path divided by the total distance traveled); significant deviation, indicating site fidelity, of empirically derived metrics from simulated metrics is completed

through a bootstrapping procedure using random draws from a uniform distribution. Caution should be taken when estimating home ranges in the absence of site fidelity, as inferences may not be useful and more optimal analytical approaches exist (i.e., Brownian Bridge Movement Models; Signer & Balkenhol, 2015). We applied KDE to all 3D locations recovered from individual tracked alligators. We chose to use the h_{pi} ('plug-in') method to select bandwidth size (i.e., smoothing parameter) to evaluate home range (95% KDE isopleth) and core-use (50% KDE isopleth) areas using the 'rhrKDE' function within the R package 'rhr' version 1.2.909 (Signer & Balkenhol, 2015). We elected to use the h_{pi} method for bandwidth selection, following repeated unsuccessful attempts using the commonly employed h_{LSCV} method, due to convergence failure, and considerable over-smoothing of areas (i.e., KDE contain areas of unsuitable habitat) using the h_{ref} method. These issues are often encountered when attempting KDE using h_{LSCV} and h_{ref} bandwidth selection with large datasets that include discrete habitats (Seaman & Powell, 1996; Seaman et al., 1999; Laver & Kelly, 2008; Campbell et al., 2013). Using the 'rhrAsymptote' function within the 'rhr' package of R, we tested whether KDE estimates were asymptotic, by applying a random permutation procedure to evaluate if and at what sample size (number of positions) an asymptote is reached (Signer & Balkenhol, 2015). If home range estimates never reach an asymptote using the maximum number of empirical observations, then the estimates should be treated as minimum home range areas (Spencer et al., 1990; Laver & Kelly, 2008).

To calculate the proportion of alligator home ranges and core-use areas comprising marine and freshwater habitats, we extracted the 50 and 95% isopleths 'rhrKDE' objects, converted to shapefiles, and performed calculations in ArcMap 10.3. Using the intersect tool, we calculated the area of overlap between alligator home range and core-use areas and two habitat types (freshwater and marine), using a habitat and land cover map (0.5 ha minimum mapping unit) developed for the study area (Madden et al., 2014). Freshwater habitats included all palustrine wetlands as well as upland habitats (e.g., forest, scrub-shrub, herbaceous cover); marine habitats included all lacustrine and estuarine wetlands and marine open waters. In addition, we calculated proportional overlap

among home range and core-use areas of individual alligators. We compared the home ranges and core-use areas of sexes using Mann–Whitney test. Significance was evaluated at $\alpha = 0.05$ for all tests.

Results

GPS–VHF telemetry

We successfully deployed GPS–VHF units on seven adult alligators (2 females and 5 males) for tracking periods ranging from 34 to 100 days (mean = 70 days ± 26 SD; Table 1). Mean fix rate (calculated as the number of successful 3D-GPS positions divided by the total number of GPS position attempts during a tracking interval) was 53% ± 13 SD (Table 1). The horizontal dilution of precision (HDOP) for successfully recorded 3D-GPS locations ranged from 0.8 to 9.9 (mean = 3.0 ± 1.9 SD). The number of satellites used to establish those positions ranged from 3 to 22 (mean = 11 ± 6 SD).

Individuals varied in the frequency and duration of cross-ecosystem trips made between freshwater wetlands and marine habitats. Six out of the seven individuals (86%) performed repeated cross-ecosystem trips. One individual, SAM227, a 2.3 m TL female did not perform any cross-ecosystem trips and was later confirmed to be nesting for the duration of the time she was tracked (5/27/2008–8/29/2008, 94 tracking days). This individual was excluded from further analyses regarding cross-ecosystem movements (i.e., factors driving variation in the duration of marine and freshwater trips). The number of cross-ecosystem trips ranged from 0 to 10 across all individuals for the entire duration of all tracking intervals (mean = 4.5 trips ± 3.2 SD per individual; Table 2).

For alligators that performed cross-ecosystem movements, the mean frequency of trips was 2.26 trips month^{-1} (± 1.52 SD) and ranged from 0.90 to 4.57 trips month^{-1}. The duration of trips within marine habitats ranged from 1.5 to 841.3 h (~35 days) with a mean of 131.7 h (±30.2 SE) (5.5 days ±1.3 SE, $n = 32$; Table 2). Return trips to upland freshwater wetlands ranged from 2.0 to 1751.8 h (~80 days) with a mean of 150.0 h ± 61.1 SE (6.3 days ±2.5 SE, $n = 29$).

Table 2 Duration of occupancy and rate of movement during trips made to marine and freshwater habitats by alligators outfitted with GPS–VHF units on Sapelo Island, Georgia

Individual	Trip duration (h)		Rate of movement (km day^{-1})	
	Marine Mean $\pm$ SD (range)	Freshwater Mean $\pm$ SD (range)	Marine Mean $\pm$ SD (range)	Freshwater Mean $\pm$ SD (range)
SAM227[a]	–	2,071	–	0.18 $\pm$ 0.03 (0.01–2.05)
SAM239	81.2 $\pm$ 38.8 (31.5–136.7)[b]	77.2 $\pm$ 41.0 (23.1–123.9)	0.90 $\pm$ 0.53 (0.27–1.91)	0.40 $\pm$ 0.21 (0.13–0.70)
SAM240	169.5 $\pm$ 65.2 (116.0–242.2)	609.0 $\pm$ 990.3 (2.0–1,751.8)[c]	2.17 $\pm$ 0.38 (1.82–2.58)	0.66 $\pm$ 0.77 (0.15–1.55)
SAM247	148.2 $\pm$ 122.6 (53.0–350.3)	101.5 $\pm$ 125.4 (7.0–291.8)[d]	1.81 $\pm$ 1.00 (0.94–3.37)	0.55 $\pm$ 0.94 (0.01–2.24)
SAM292	334.3 $\pm$ 354.1 (35.0–841.3)[e]	118.8 $\pm$ 43.5 (92.1–168.9)[e]	2.63 $\pm$ 0.96 (1.77–3.97)	0.24 $\pm$ 0.09 (0.15–0.33)
SAM182-R	213.6 $\pm$ 227.9 (76.0–476.7)	18.0 $\pm$ 12.1 (4.0–26.0)[d]	3.08 $\pm$ 0.46 (2.59–3.51)	0.56 $\pm$ 0.46 (0.03–0.93)
SAM323	41.7 $\pm$ 82.6 (1.5–230.9)	123.6 $\pm$ 179.0 (6.0–539.7)	6.11 $\pm$ 3.44 (1.68–10.51)	1.29 $\pm$ 1.27 (0.11–4.25)

[a] Nesting female, confirmed upon recovery of the transmitter

[b] Trip seven to estuary is not included in calculation due to detachment of transmitter at beginning of the trip

[c] Calculations for freshwater trip durations exclude 1 short trip (1 h) likely due to measurement error

[d] Calculations for freshwater trip durations exclude initial period following release

[e] Calculations for marine trip durations exclude initial period following release and calculations for freshwater trip durations exclude the final trip to freshwater prior to recovery of the transmitter

Table 3 Effects and relative importance of parameters on the duration of marine habitat use estimated by model-averaging top performing models ($\Delta AIC_c \leq 2$)

Parameter	Estimate β[a]	Unconditional SE	95% Confidence interval	Relative importance
(Intercept)	4.32	0.21	(−13.88–27.09)	
max.depth	1.40	0.50	(0.69–4.47)	1.00
mean.hum	0.84	0.73	(−0.06–0.21)	0.68
tot.precp	−0.23	0.46	(−1.16–0.70)	0.30

[a] Effect sizes have been standardized on two SD following Gelman (2008)

Marine habitat use

Following our exclusion criteria (i.e., greater than two standard deviations from the mean), we removed two lengthy trips into marine habitats undertaken by separate individuals (SAM292 and SAM182-R; Table 2). Using the remaining data (30 trips), our set of top performing models (AIC$_c \leq 2.0$) explaining the duration of trips within marine habitats included the effects of three parameters, maximum water depth, relative humidity, and total precipitation (Tables 3, S3). The most important parameter was maximum water depth, occurring in all candidate models, followed by relative humidity and total precipitation (Table 3). The addition of individual as a random effect in the top performing model (Table S3) did not improve model performance

(Table S4); the mean variance explained by the random effect was estimated to be 0.0004 $\pm$ 0.0001 (SD). Effects of each parameter on the duration of marine trips were investigated by first setting all other parameters to their mean and predicting the response using the model-averaged parameter estimates across the observed range of the parameter of interest. Both increasing relative humidity and maximum depth were found to positively affect the duration of trips in marine habitats (Fig. 2a, b). While the general functional form of these parameters' effects was similar, the 95% confidence interval (95% CI) for relative humidity effect size contained zero (Table 3). The effect of total precipitation was estimated to be slightly negative (standardized $\beta \pm SE = -0.23 \pm 0.46$, Table 3); however, the 95% CI for the estimated effect size contained zero.
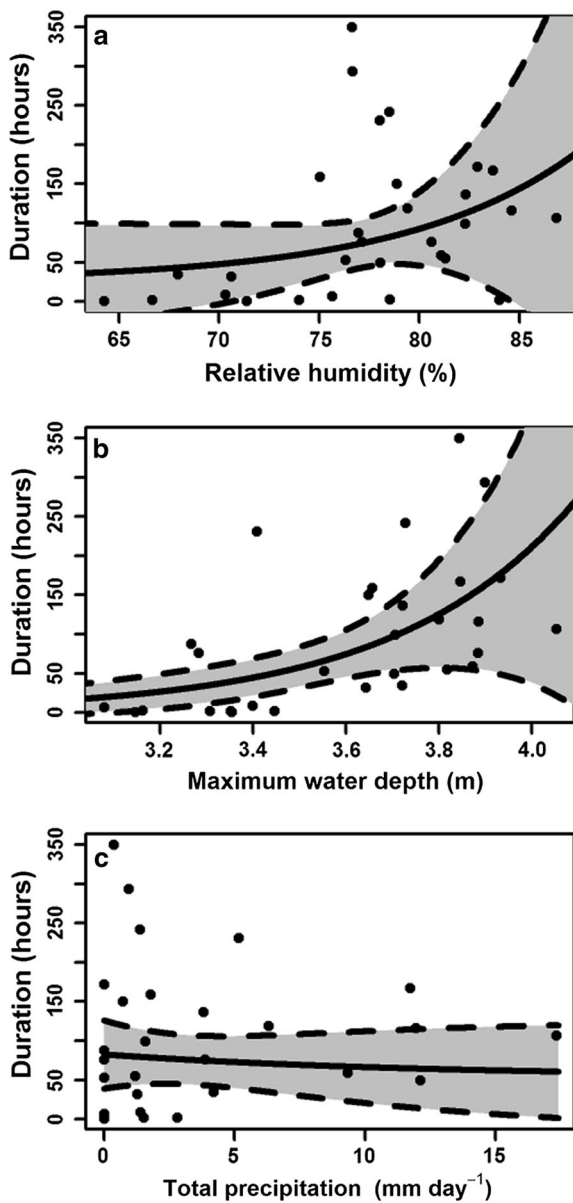
Fig. 2 Model-averaged predicted effects of **a** relative humidity, **b** maximum water depth, and **c** total daily precipitation on the duration of trips by alligators within marine habitats. *Solid black points* are raw data. *Solid lines* are predicted mean values and *dashed lines* bound the 95% confidence interval (*gray*)

Freshwater habitat use

We removed one instance of prolonged occupation within freshwater wetlands (1,752 h) by the individual SAM240, a 2.6 m TL male, from subsequent model fitting exercises. With the outlier removed (28 trips), our best-fit GLM selected for the duration of freshwater trips

included the main effects from air temperature, total precipitation, and wind velocity (Tables 4, S5). The addition of individual as a random effect did not improve model performance (Table S6); the mean variance explained by the random effect was estimated to be 0.0012 ± 0.0002 (SD). We found that duration of trips within freshwater habitats increased as air temperatures increased (standardized $\beta \pm SE = 1.18 \pm 0.36$); this effect was more pronounced as temperatures exceeded 28°C (Fig. 3a). Correspondingly, increasing precipitation had a positive effect (standardized $\beta \pm SE = 1.13 \pm 0.35$) on the duration of freshwater trips (Fig. 3b). The effect of increasing wind velocity on duration of freshwater trips was slightly negative (standardized $\beta \pm SE = -0.79 \pm 0.34$; Fig. 3c). No 95% CIs for parameters in the top model for duration of freshwater trips contained zero (Table 4).

Rate of movement

Rate of movement between consecutive GPS positions logged for all alligators ranged from 0 to 54.97 km day^{-1} (mean = 1.54 km day^{-1} $\pm$ 4.02 SD, n = 3,830). Rate of movement averaged per individual over the duration of trips within marine habitats ranged from 0.27 to 10.51 km day^{-1} (mean = 3.21 km day^{-1} $\pm$ 2.85 SD, n = 32), whereas the per trip average in freshwater habitats ranged from 0.01 to 2.24 km day^{-1} (mean = 0.72 km day^{-1} $\pm$ 0.91 SD, n = 28; Table 2).

Following our exclusion criteria, we removed data for five trips undertaken by two individuals (SAM323, a 2.9 m TL male, and SAM239, a 2.0 m TL female), all within the marine environment (Table 2). Furthermore, we excluded movement data from the one nesting female that solely remained in a freshwater wetland from our analysis. The top performing models include the effects of habitat type, wind velocity, and salinity (Table 5, S7). The addition of individual as a random effect did not improve model performance, and the variance explained by the random effect was indistinguishable from zero (Table S8). The most important parameter was habitat type, occurring in all top performing models (Table 5, S7), followed by wind velocity, salinity, and relative humidity. Using model-averaged parameter estimates and setting all other parameters to their mean values, we estimated the rate of movement within marine habitats to be 2.9× greater than rates within freshwater habitats (freshwater = 1.14 km day^{-1} $\pm$ 0.47   SE   vs.

Table 4 Effects for model parameters on the duration of freshwater habitat use from the best-fit model and Chi-squared test results (*P* value) for reduction of model deviance

Parameter	Estimate β[a]	Unconditional SE	95% Confidence interval	*P* value
(Intercept)	4.24	0.17	(3.93–4.59)	–
Mean.a.temp	1.18	0.36	(0.42–1.93)	0.008
Tot.precp	1.13	0.35	(0.30–2.06)	0.011
Mean.wind	−0.79	0.34	(−1.43 to −0.18)	0.010

[a] Effect sizes have been standardized on two SD following Gelman (2008)

marine = 3.29 km day^{-1} ± 0.25 SE, Fig. 4a). We estimated the effects of wind velocity (standardized β ± SE = 0.06 ± 0.17) and salinity (standardized β ± SE = 0.01 ± 0.04) to be slightly positive and relative humidity to be slightly negative (standardized β ± SE = −0.003 ± 0.016; Fig. 4b–d, respectively). However, the estimated effect sizes for these parameters were two to three orders of magnitude smaller than the effect size of habitat type, and 95% CIs surrounding estimates included zero (Table 5).

Home range

We examined patterns of site fidelity in alligator locational data using two metrics, mean squared displacement from centroid (MDC) and linearity index (LI). We detected robust evidence for site fidelity (both MDC and LI tests significant) in locational data collected from three individuals (SAM182-R, SAM239, and SAM292) and weaker evidence (either MDC or LI tests significant) for data collected from four individuals (SAM227, SAM240, SAM247, and SAM323). Since all individuals expressed site fidelity to some extent, we proceeded to examine core-use and home range areas using KDE. Estimated core-use areas (50% KDE isopleths) for individual alligators, ranged from 0.02 to 10.29 ha (mean = 4.45 ha ± 4.72 SD; Table 1; Figs. 1a, S1). Home range areas (95% KDE isopleths) ranged from 0.67 to 86.97 ha (mean = 46.51 ha ± 33.94 SD). All KDE estimates (50 and 95%) failed to reach an asymptote. Accordingly, these estimates should be considered as minimum core-use and home range areas.

Using a habitat and land cover map for the study location, we estimated the proportion of alligator core-use and home range areas comprising marine and freshwater habitats (Table 6; Figs. 1a, S1). On average (across all individuals), core-use areas (50% KDE) were composed of 46.6% marine and 53.4% freshwater habitats, and home range areas (95% KDE) were composed of 69.3% marine and 30.7% freshwater habitats. Composition of core-use areas ranged from 0 to 78.5% marine habitat compared to home range areas that ranged from 0 to 89.9% marine (Table 6). For individuals that exhibited cross-ecosystem movements (excluding SAM227 data), on average 50% KDE's were composed of 54.3% marine habitat and 95% KDE composed of 80.9%. The only overlap between core-use and home range areas of tracked alligators was between two males (SAM247 and SAM292; Figs. 1a, S1). The overlap area of their 50% KDE represented 24.1% of SAM247′s and 35.5% of SAM292′s core-use area. Comparatively, the overlap area of their 95% KDE represented 9.1% of SAM247′s and 8.7% of SAM292′s home range area.

While not statistically significant (Mann–Whitney U test: $U = 9$, $P = 0.19$; for both 50 and 95% KDE), mean core-use and home range areas calculated for the two females (mean 50% KDE = 0.83 ha ± 1.14 SD; 95% KDE = 11.11 ha ± 14.75 SD) were 7.1× and 5.5× smaller, respectively, than core-use and mean home range area estimated for the five males (mean 50% KDE = 5.90 ha ± 4.89 SD; 95% KDE = 60.67 ha ± 28.22 SD; Table 1).

Discussion

During our literature survey, we found alligators to be one of the most studied species of freshwater-adapted consumers documented to perform cross-ecosystem movements into marine habitats (Table S1). However, previous studies to understand the factors contributing to variation in cross-ecosystem movements were performed in systems containing elongated salinity gradients, where boundaries between freshwater and
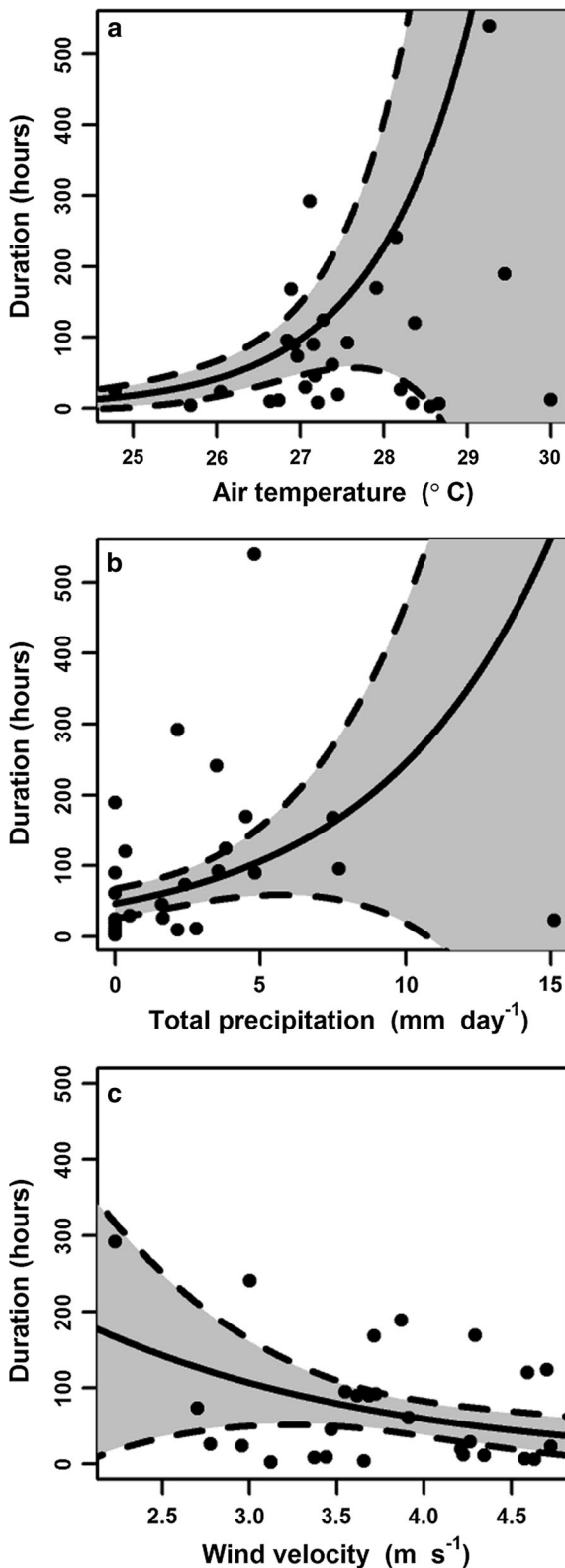
◀ **Fig. 3** Model-averaged predicted effects of **a** air temperature, **b** total precipitation, and **c** wind velocity on the duration of trips by alligators within freshwater habitats. *Solid black points* are raw data. *Solid lines* are predicted mean values and *dashed lines* bound the 95% confidence interval (*gray*)

marine ecosystems are constantly changing (Rosenblatt & Heithaus, 2011; Rosenblatt et al., 2013b; Fujisaki et al., 2014, 2016). We found that adult alligators inhabiting an Atlantic barrier island system, with discrete marine and freshwater habitats, repetitively performed cross-ecosystem movements from freshwater wetlands to forage within marine habitats and that movement patterns were significantly affected by a variety of abiotic factors. Moreover, alligator core-use and home range areas consisted largely of marine habitats. While lacking functional lingual salt glands to mitigate for increased osmotic stresses imposed by marine habitats, alligators could persist in these environments for extended periods of time, in some cases continuously remaining within marine habitats up to 35 days. Our results are the first assessment of cross-ecosystem movement patterns in Atlantic barrier island populations of alligators and one of the few studies which assess the potential for abiotic factors to influence the dynamics of marine habitat use in this species.

Marine habitat use

In our literature survey, we found abiotic as well as biological factors affected the use of marine habitats by terrestrial- and freshwater-adapted consumers (Table S2). Most notably resource availability (biotic), precipitation, and temperature were found to be highly important in determining when and where cross-ecosystem marine foraging occurred.

Of the seven alligators outfitted with GPS–VHF transmitters, six repetitively performed cross-ecosystem forays into marine habitats (Table 1). The one female (SAM227) that did not perform any cross-ecosystem movements was later confirmed to be nest guarding; she was observed to remain near a nest and nursery pond for the duration of the time tracked and hatchlings were observed at the time of GPS–VHF transmitter recovery. Using long-term ecological monitoring meteorological and hydrological data, we

Table 5 Effects and relative importance of parameters on average rate of movement estimated by model-averaging top performing models ($\Delta AIC_c \leq 2$)

Parameter	Estimate β[a]	Unconditional SE	95% Confidence interval	Relative importance
(Intercept)	0.58	1.97	(−3.35–4.51)	
Hab.type[b]	2.15	0.35	(1.45–2.86)	1.00
Mean.wind	0.06	0.17	(−0.28–0.41)	0.24
Mean.sal	0.01	0.04	(−0.07–0.10)	0.17
Mean.hum	0.00	0.02	(−0.04–0.03)	0.16

[a] Effect sizes have been standardized on two SD following Gelman (2008)

[b] Effects of marine habitat

identified three factors including maximum water depth, relative humidity, and total precipitation that significantly contributed to variation in the duration of trips within marine habitats. Below, we discuss probable ecological and biological mechanisms that may help to explain the functional relationships revealed by our analysis.

The most important factor influencing the duration of trips into marine habitats was maximum water depth (Table 3), a proxy for tidal range (i.e., spring, neap). As previously mentioned, this study system experiences semi-diurnal tides averaging 2 m in amplitude; however, during spring tide events amplitudes can exceed 4 m. We found increasing maximum depth to positively affect the duration of trips taken in marine habitats (Fig. 2b); in terms of tidal range this translates into alligators remaining in marine habitats for longer periods of time close to and during spring tide events. We surmise the effect of water depth is primarily driven by two phenomena associated with spring tide events. First, during spring tides, water depths at high tides are maximized and minimized during low tides, producing increased water velocities during ebb and flood tides that often displace common marine prey such as small fish and crustaceans (Diebel, 2003; Nifong et al., 2015). It is possible that alligators devote more time to acquire prey in these periods of increased prey movements. Similar prey-seeking behaviors have been documented for other coastal alligator populations as well as Nile and estuarine crocodiles (Whitefield & Blaber, 1979; Messel et al., 1981, 1982; Tamarack, 1989); wherein, numerous individuals have been observed aggregating in narrow portions of tidal creeks to take advantage of dense schools of migrating fish. Second, the extreme low water depths that accompany spring tide events, isolate and concentrate fully aquatic prey (e.g., shrimp and fish) in shallow pools within tidal creeks during low tides. This increase in the concentration and presumably the catchability of prey may also benefit alligators remaining in marine habitats for longer periods of time as opposed to neap tide periods when prey species can widely disperse across the marsh landscape.

We found the second most important factor, relative humidity (Table 3), to positively affect the duration of trips within marine habitats; durations of trips increased with increasing relative humidity (Fig. 2a). However, we cautiously infer ecological meaning from this relationship, as the 95% CI for relative humidity's effect size contained zero. Hypothetically, as ectotherms, alligators often spend considerable amounts of time basking on land to increase body temperatures in the morning hours (Fish & Cosgrove, 1987). While the integument of alligators is relatively impermeable to water when submerged in saline water (H_2O efflux in 35‰ water = 0.25 mg $100 \ g^{-1} \ h^{-1}$; Mazzotti & Dunson, 1984), evaporative water loss due to cutaneous evapotranspiration in air is quite high (H_2O efflux at 35°C in air = 13.7 mg $100 \ g^{-1} \ h^{-1}$, Davis et al., 1980). The rate of evaporative water loss is directly related to the magnitude of the driving force (the vapor density difference–VDD, defined as the difference in the concentration of water vapor in the body and in the free air beyond the adhering boundary layer next to the skin's surface) and inversely related to the skin resistance. In theory, higher relative humidity (i.e., decreased VDD) would decrease evaporative water loss by alligators when basking on land and thus, may prolong the need to return to freshwater habitats.
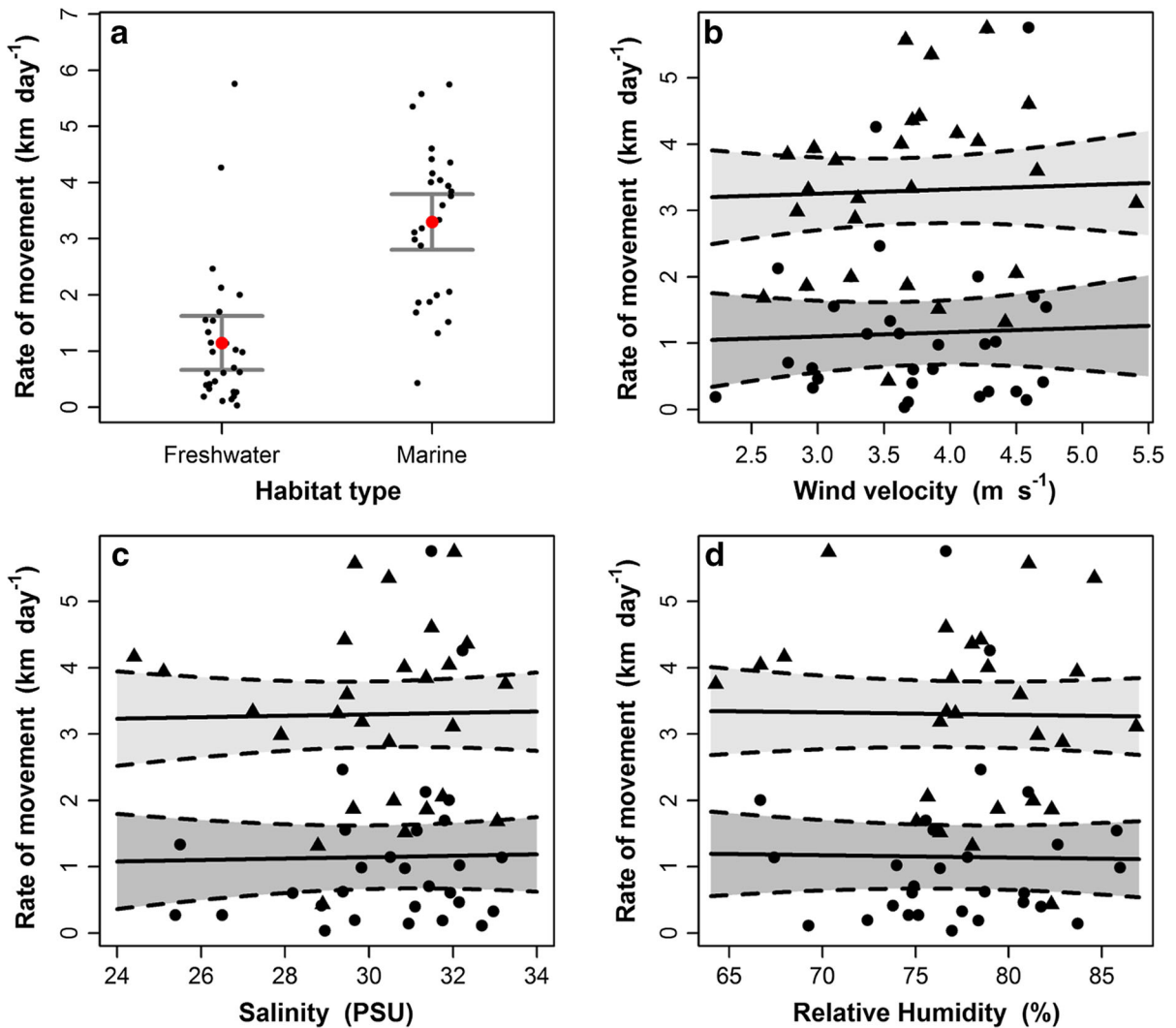
Fig. 4 Model-averaged predicted effects of **a** habitat type (*solid black points* are raw data, enlarged *solid red points* are predicted mean values, and *gray error bars* bound the 95% confidence intervals), **b** wind velocity, **c** salinity, and **d** relative humidity on rate of movement. For panels **b**–**d**, *filled circles* are raw data from freshwater habitats and *filled triangles* are raw data from marine habitats. *Solid lines* are predicted mean values and *dashed lines* bound the 95% confidence intervals (*filled light gray* for predictions in marine habitats and *dark gray* for freshwater habitats)

Table 6 Habitat composition of estimated alligator home range (95% KDE) and core-use (50% KDE) areas	Individual	Core-use area (50% KDE)		Home range (95% KDE)	
		Marine (%)	Freshwater (%)	Marine (%)	Freshwater (%)
	SAM182-R	62.0	38.0	73.3	26.7
	SAM227	0.0	100.0	0.0	100.0
	SAM239	57.0	43.0	86.1	13.9
	SAM240	40.1	59.9	67.7	32.3
	SAM247	68.0	32.0	85.6	14.4
	SAM292	78.5	21.5	89.9	10.1
	SAM323	20.4	79.6	82.6	17.4

We found total precipitation to be the least important factor affecting duration of marine habitat use (Table 3). Using our parameter estimates, we predicted increasing precipitation reduced the duration of marine habitat use (Fig. 2c). However, results show weak support for the inclusion of precipitation and the estimated confidence interval for the effect size included zero. Thus, we do not have enough evidence to draw conclusions as to the underlying mechanisms responsible for these patterns.

Freshwater habitat use

Few studies have assessed factors affecting the duration of return trips to terrestrial and freshwater refugia following movements into marine habitats by cross-ecosystem foragers (Table S1). One can theorize that the effects of abiotic factors on the duration of these return trips should be opposite of the effects on marine habitat use. Our single best-fit model for duration of occupancy in freshwater habitats for alligators included the effects of air temperature, total precipitation, and wind velocity (Table 4, S5).

Air temperature positively affected the duration of freshwater trips (Fig. 3a), and this pattern was likely a consequence of increased freshwater demand experienced by alligators at higher ambient temperatures. As discussed previously, temperature can influence both the metabolic rate and magnitude of evaporative water loss in alligators. During periods of higher temperatures alligators may suffer larger water deficits while using marine habitats, and consequently may need more time to recover upon return to freshwater. In addition, within freshwater wetlands alligators construct extensive underground den complexes which are thought to serve as refugia from extreme temperatures and function as overwintering sites; no such structures have been observed in marine habitats (Wilkinson & Rhodes, 1992).

The effect of total precipitation on the duration of freshwater trips was positive (Fig. 3b). We hypothesize that the increased availability of fresh rainwater likely drives alligators to remain in freshwater wetlands for longer periods of time for two reasons. First, as previously mentioned the only source of freshwater supplying island wetlands is rainwater and thus, when available alligators should maximize their intake to maintain their osmotic balance. Second, elevated water levels within freshwater wetlands can support higher abundances of aquatic prey such as aquatic insects, fish, and crustaceans (Craighead, 1968). It is possible that increased prey availability within freshwater habitats during periods of high rainfall could satisfy the nutritional and energy needs of alligators, thus reducing the need to exploit marine prey.

We found wind velocity to negatively affect the duration of freshwater habitat use (Table 4; Fig. 3c). This finding was surprising and counter to our expectations. Physiologically, we expected increasing wind velocity to positively affect the duration of freshwater habitat use due to increased evaporative water loss experienced while basking on land. Considering the finding of an opposite effect, we hypothesize wind velocity may covary with another important biotic or abiotic factor not measured in this study.

Rate of movement

The movement rates in this study were comparable to those measured in other coastal alligator populations (0.05–3.2 km day^{-1}; Rosenblatt et al. 2013b; 0.7–3.2 km day^{-1}; Fujisaki et al., 2014). The most important driver of variation in rate of movement was habitat type (Table 5). Mean rate of movement in marine habitats was nearly 3X greater than in freshwater habitats (Table 2; Fig. 4a). Salt marsh creeks and tidal rivers frequented by alligators in this study system were by far more heterogeneous and expansive than the small isolated freshwater wetlands and ponds located within the island's interior, thus longer distances could be traveled in marine habitats as compared to freshwater. In addition to the ability to perform longer distance movements when navigating within marine habitats, tidal cycles may have also played a role in rate of movement variation among habitats. As previously mentioned, this study system experiences semi-diurnal tides ranging in amplitude from 2 to 4 m. Water velocities during ebb and flood tides are quite high (velocity range = 0.09–0.84 m s^{-1}, Diebel, 2003) and certainly have the potential to facilitate both faster and longer distance movements. In Australia, Campbell et al. (2010) using data from acoustic and satellite telemetry provided evidence that *Crocodylus porosus* Schneider, 1801 (estuarine crocodile) uses surface currents to aid long-distance travel in tidal rivers and

the ocean. Alligators moving in tidal creeks and rivers may also take advantage of directional flow to reduce the energetic costs of aquatic movements.

Our model selection process indicated that wind velocity, salinity, and relative humidity contributed to variation in rate of movement of tracked alligators; however, the magnitude of these effects was minimal when compared to the effect size of habitat type (estimated β's 36–717 times smaller than habitat type β) and all predicted 95% CI's for these factors contained zero (Table 5; Fig. 4b–d, respectively). As such, there is a large amount of uncertainty in the sign and strength of the predicted relationships. The effect of wind velocity was slightly positive. Within marine habitats, increasing wind velocity can dramatically alter water conditions (e.g., wave height, surface currents) and impact tidal movements; it is possible alligators increase their rate of movement in response to these changing environmental conditions. The effect of salinity was slightly positive. When using marine habitats, increased salinity may cause alligators to search for pockets of lower salinity waters. Alternatively, salinity may correlate to biotic factors such as prey availability. Our findings are consistent with Fujisaki et al. (2014), who found increasing salinity to positively influence the daily movements of alligators inhabiting the Florida Everglades. We found relative humidity to be the least important factor affecting rate of movement. The effect size of relative humidity (standardized $\beta = -0.003 \pm 0.016$ SE; Table 5) was very small and while important to the model fitting process, we conclude relative humidity is likely of minor biological significance.

Home range

Our core-use and home range area estimates were comparable to those reported by Lewis et al. (2014) for male and female alligators inhabiting an inland lake in Texas (mean $\pm$ SD, 50% KDE = 20.6 ha $\pm$ 18.5; 95% KDE = 68.9 $\pm$ 31.6). Furthermore, Lewis et al. (2014) found core-use and home range areas of female alligators were 2× and 1.7× smaller than males, for core-use and home range area, respectively. On the contrary, all our core-use and home range areas were much smaller than those estimated by Fujisaki et al. (2014) for alligators inhabiting the Shark River estuary (SRE) within the Florida Everglades (range 50% KDE = 54.0–135.0 ha; range 95%

KDE = 269.0–3311.0 ha). This finding is possibly the result of differences in distribution of freshwater and other landscape characteristics between SRE and the barrier island system studied here. SRE comprises of an expansive network of creeks and channels draining freshwater westerly from the northern reaches of the Everglades to the marine waters of the Gulf of Mexico, with an elongated east-to-west salinity gradient. Conversely, barrier island systems such as Sapelo Island, contain small pockets of freshwater resources isolated from the surrounding marine habitats; essentially, no salinity gradient exists in these systems and alligators are not able to exploit the elongated freshwater wedges characteristic of salinity gradients in riverine systems such as the SRE. It should also be noted that bandwidth selection methods used during KDE analysis differed between our study (h_{Pi}) and the two previously mentioned studies (h_{LSCV}). The greater number of locations per individual in our study, precluded us from using the h_{LSCV} method, due to failure of the algorithm to converge on a solution. KDE estimates using these two methods are comparable when applied to smaller datasets ($n < 200$), with h_{Pi} often outperforming h_{LSCV} (Gitzen et al., 2006). We feel the h_{Pi} method far outperformed the h_{ref} method by producing KDE estimates that chiefly contained suitable habitats versus large areas of unsuitable habitat (Fig. S1).

We found that marine habitats comprise substantial portions of estimated core-use and home range areas for most individuals (Table 6; Figs. 1a, S1). Excluding the nesting female that did not perform cross-ecosystem travel (i.e., ranges comprise 100% freshwater habitats), alligator core-use areas contained smaller proportions of marine habitat relative to home range areas (mean % marine = 54.3 and 80.9% for 50% KDE and 95% KDE, respectively). To date, no studies performed on coastal inhabiting alligators have attempted to quantify the relative habitat composition of core-use and home range areas in terms of marine and freshwater. Fujisaki et al. (2014) reported that one out of five individuals emigrated to fresher upstream marsh habitats following capture in downstream estuarine habitats of the SRE, but did not report habitat composition of the core-use and home range areas. These findings suggest marine habitats are essential for barrier island populations, corroborating similar findings in terms of the importance of marine prey using stomach content and stable isotope

analyses (Nifong et al., 2015; Nifong, 2016). The importance of access to marine habitats should be considered when developing management and conservation plans for coastal alligator populations, especially for those inhabiting barrier islands.

Differences in core-use and home range areas were evident between males and females, with females maintaining core-use and home range areas 7.1× and 5.5× smaller than males, respectively. In other systems (i.e., lakes, freshwater marshes), female alligators are known to occupy smaller home range areas than males, especially while nesting (Joanen & McNease, 1970, 1972). For example, Lewis et al. (2014) found core-use and home range areas of female alligators inhabiting an inland lake of Texas to be 2× and 1.7× smaller than males, respectively. Only one of the five alligators considered by Fujisaki et al. (2014) was female; her core-use and home range area estimates were similar in size to some males and much smaller (2.5× to 16X) than others. While this pattern seems to hold across populations, we believe that more data needed to conclude this pattern is not just the product of the small number of individual females studied.

Conclusion

In terms of understanding the drivers of variation in cross-ecosystem movements by alligators, we found abiotic factors that impacted physiological stress and metabolic processes (i.e., temperature, humidity) were highly important factors influencing the dynamics of marine habitat use. Furthermore, factors that have been shown in past studies to alter environmental conditions (i.e., maximum water depth, precipitation) and the distribution and abundance of commonly occurring alligator prey (e.g., blue crab-Nifong et al., 2012; estuarine fish-Nifong, 2016) were similarly important. The broader implications of our findings for alligator ecology and conservation are two-fold. First, along it's southern and eastern perimeter approximately 4,000 km of alligator's native range is bordered by coastal ecosystems, where individuals have the potential to perform cross-ecosystem movements. Thus, understanding the factors which contribute to variation in cross-ecosystem movements will assist in identifying conservation priorities and lead to more informed management efforts as well as contribute to

our understanding of their ecological impacts to coastal ecosystems (van de Koppel et al., 2015). Second, these data, along with trophic ecology (Nifong et al., 2015; Rosenblatt et al., 2015; Nifong, 2016) and community impact studies (Nifong & Silliman, 2013), reveal alligators are a major component of the coastal marine food webs, whose top–down influence is likely to be dictated by variation in physical (abiotic) factors—a pattern that is emerging from studying top–down control in salt marsh ecosystems (Silliman et al., 2005; Alberti et al., 2010).

More broadly, mobile consumers link disparate ecosystems through the acquisition and transfer of allochthonous production into recipient food webs. These resource subsidies can enhance ecosystem resilience, promote food web stability, and support increased consumer abundances and are increasingly important in recipient ecosystems with low levels of autochthonous production (Huxel et al., 2002; Lundberg & Moberg, 2003; McCann et al., 2005). The cross-ecosystem movement of mobile top predators is of particular significance, as these species are known to have strong effects on ecosystem structure and function through their direct (consumptive) and indirect (non-consumptive) interactions with prey which cascade to lower trophic levels (Peckarsky et al., 2008; Schmitz et al., 2008; Estes et al., 2011). Cross-ecosystem movement of consumers is common at the land–sea interface; however, few studies have addressed the abiotic or biotic factors which influence variation in the use of marine habitat and food resources by cross-ecosystem foragers (see examples in Table S1). Our findings suggest that the frequency and duration of cross-ecosystem marine foraging by terrestrial- and freshwater-adapted consumers can be strongly dependent on multiple abiotic factors. To further our understanding of when and where consumer-driven connectivity may be important to community and ecosystem processes, careful consideration of the factors contributing to variation in these linkage behaviors need to be considered, especially in the face of changing climatic conditions.

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