Estuaries and Coasts (2016) 39:1561–1569
DOI 10.1007/s12237-016-0084-2

SHORT COMMUNICATION

Spatial and Temporal Variability in Estuary Habitat Use by American Alligators

Ikuko Fujisaki[1] · **Kristen M. Hart**[2] · **Michael S. Cherkiss**[2] · **Frank J. Mazzotti**[1] ·
Jeff S. Beauchamp[1] · **Brian M. Jeffery**[3] · **Laura A. Brandt**[4]

Received: 1 July 2015 / Revised: 24 February 2016 / Accepted: 26 February 2016 / Published online: 10 March 2016

Abstract Estuarine habitat occupied by *Alligator mississippiensis*, a primarily freshwater species, is spatially and temporally heterogeneous largely due to a salinity gradient that fluctuates. Using long-term night light survey data, we examined seasonal patterns in alligators' habitat use by size classes in midstream and downstream estuary zones of Shark River, Everglades National Park, in southern Florida. We observed predominantly large-sized alligators (total length ≥ 1.75 m); observations of alligators in the small size classes (0.5 m ≤ total length < 1.25 m) were rare especially in the higher-salinity downstream zone. The density of alligators in the downstream zone was lower than that of the midstream zone during the dry season when salinity increases due to reduced precipitation. Conversely, the density of the large size alligators was higher in the downstream zone than in the midstream zone during the wet season, likely because of reduced salinity. We also found a significant declining trend over time in the number of alligators in the dry season, which coincides with the reported decline in alligator relative density in southern Florida freshwater wetlands. Our results indicated high adaptability of alligators to the fluctuating habitat conditions. Use of estuaries by alligators is likely driven in part by physiology and possibly by reproductive cycle, and our results supported their opportunistic use of estuary habitat and ontogenetic niche shifts.

Keywords Habitat use · Nightlight survey · Population abundance · Salinity · Size class

Introduction

Estuarine habitat, at the ecotone between freshwater and marine conditions, is important for a wide range of species of ecological, recreational, and commercial importance. The quality of estuarine habitat is highly variable, both spatially and temporally, due to fluctuating salinity and water levels from tidal cycles and input from upstream freshwater flows. Salinity patterns in an estuary are partially driven by the volume, timing, and location of freshwater flows. Because salinity is a major driver of the ecosystem functionality in estuaries, these changes can affect the distribution and the abundance of aquatic species (e.g., Attrill 2002).

Estuaries throughout the world have been affected by human development and use resulting in changes in freshwater flows and salinity regimes. In the Greater Everglades, FL, upstream draining, channelization, and management actions have altered freshwater flows over the last century (Marshall et al. 2011; Light and Dineen 1994). As a result, system-wide hydrology was modified in both wetlands and estuaries influencing various ecological attributes in the estuary (Davis et al. 2005). A key part of the Everglades restoration is improvement in the timing, distribution, quality, and amount of freshwater flows through the ecosystem, with an explicit goal of restoring the conditions in the southern estuaries to more natural patterns. These improvements will result

✉ Ikuko Fujisaki
ikuko@ufl.edu

[1] Ft. Lauderdale Research and Education Center, University of Florida, Davie, FL, USA

[2] US Geological Survey, Wetland and Aquatic Research Center, Davie, FL, USA

[3] Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville, FL, USA

[4] US Fish and Wildlife Service, Davie, FL, USA

in a more functional estuary defined by key ecosystem attributes including mangrove forest production, coastal lake submerged aquatic vegetation, mangrove fish communities, wood stork and roseate spoonbill nesting colonies, and estuarine crocodilian populations (Davis et al. 2005).

The American alligator (*Alligator mississippiensis*) is primarily a freshwater species that uses estuaries throughout its range (Neil 1958; Gibbons and Coker 1978; Rootes and Chabrec 1991; Mazzotti and Brandt 1994). Because of its ecological importance, the alligator is being used as an indicator of progress toward the Everglades restoration (Mazzotti et al. 2009). Historically, alligators were abundant in the continuous freshwater wetlands and estuarine mangrove zones in the Greater Everglades in southern Florida (Craighead 1968; Rice et al. 2005). However, due to overhunting, droughts, and changes in land use and land covers as a result of water management, their current distribution and abundance is much different than it was historically (Rice et al. 2005). This is particularly apparent in the freshwater tributaries of the southern estuaries where Craighead (1968) reported that alligators were relatively abundant in 1950 but estimated a 99 % decline in the southern Everglades by mid-1960s (Rice et al. 2005). More recent surveys also indicated the declining density of alligators, especially in small size class, in multiple wetland compartments in southern Florida (Fujisaki et al. 2011). Alligator use of estuaries is related to salinity because of their limited osmoregulatory capabilities (Dunson and Mazzotti 1989). Small alligators are relatively intolerant to salinity above 10 psu whereas larger alligators can withstand longer periods of higher salinity because of their lower surface to volume ratios (Lauren 1985) especially when they have access to lower salinity water for brief periods. A study reported that alligator nests were not observed in moderate–high salinity areas in coastal marshlands, suggesting that salinity also influences their nest site selection (McNease and Joanen 1978). Therefore, altered salinity by changes in freshwater flows into estuaries likely affects the location of alligators (Rice et al. 2005). Studies by satellite and acoustic tracking documented estuarine habitat use by alligators in the Everglades and showed that individual alligators exhibit movement patterns (movement rate, location, and duration) that are related to season, salinity, temperature, and size (Rosenblatt and Heithaus 2011; Fujisaki et al. 2014). Some alligators made frequent excursions to mouths of rivers in near-marine conditions, presumably for foraging, whereas others were sedentary in low-salinity upstream zones (Rosenblatt and Heithaus 2011; Fujisaki et al. 2014). The varied physiology by size class may create ontogenetic niche shifts in the alligators in an estuary habitat, that is, ontogenetic differences in mobility, salinity tolerance, metabolism, and reproductive cycles lead different size classes to use different estuary habitats. Such ontogenetic shift in the alligator has been evidenced in seasonal wetlands and riverine systems (Subalusky et al. 2009), and it may explain the movement variability in the estuary. The restoration of natural freshwater flows to the southern estuaries may result in decrease in salinity, which may also change alligator density in the estuary. Knowledge on ontogenetic niche shift of a species is important to understand ecosystem wide changes in density and habitat use.

We established a long-term monitoring program to determine trends in relative density of alligators in the Shark River estuary, Everglades National Park (ENP), FL. Our objectives in this study were to (1) determine the spatial and temporal patterns of habitat use by alligators in estuarine habitat by size class and (2) examine the trends in relative density of this species by size class. These results will help us to understand patterns and trends of habitat use by alligators in a spatially and temporally heterogeneous estuarine habitat.

Materials and Methods

Study Area

We established a 24-km survey route covering midstream and downstream zones of the Shark River estuary in ENP, FL, USA (Fig. 1). Shark River is the outflow from Shark Slough, one of the major watersheds and a primary wetland habitat for alligators in ENP, which empties into the Gulf of Mexico. The survey route follows the salinity gradient from low- to near-marine condition (Anderson et al. 2014). Salinity in the estuary, especially in the downstream zone, varies by season with higher salinities during the dry season (November–April) because of less precipitation compared to the wet season (May–October) (Romigh et al. 2006). To delineate the estuary zones, we used the same boundary used in Rosenblatt and Heithaus (2011; Fig. 1). A 16.5-km segment of the route intersects with the midstream zone surrounded by mangrove swamp. The remaining 7.5-km segment is located in the downstream zone and extends near the river mouth. According to hourly measurements from 2009 to 2012 by gages placed in each zone by the US Geological Survey (Anderson et al. 2014), the mean salinity in the midstream (gage TI) was 6.08 psu (range 0.27–28.76 psu) during wet season and 6.33 (range 0.01–24.78 psu) during dry season (Anderson et al. 2014). The mean salinity in the downstream (gage GI) was 3.31 (0.93–34.14 psu) during the wet season and 15.28 psu (1.65–32.63 psu) during the dry season.

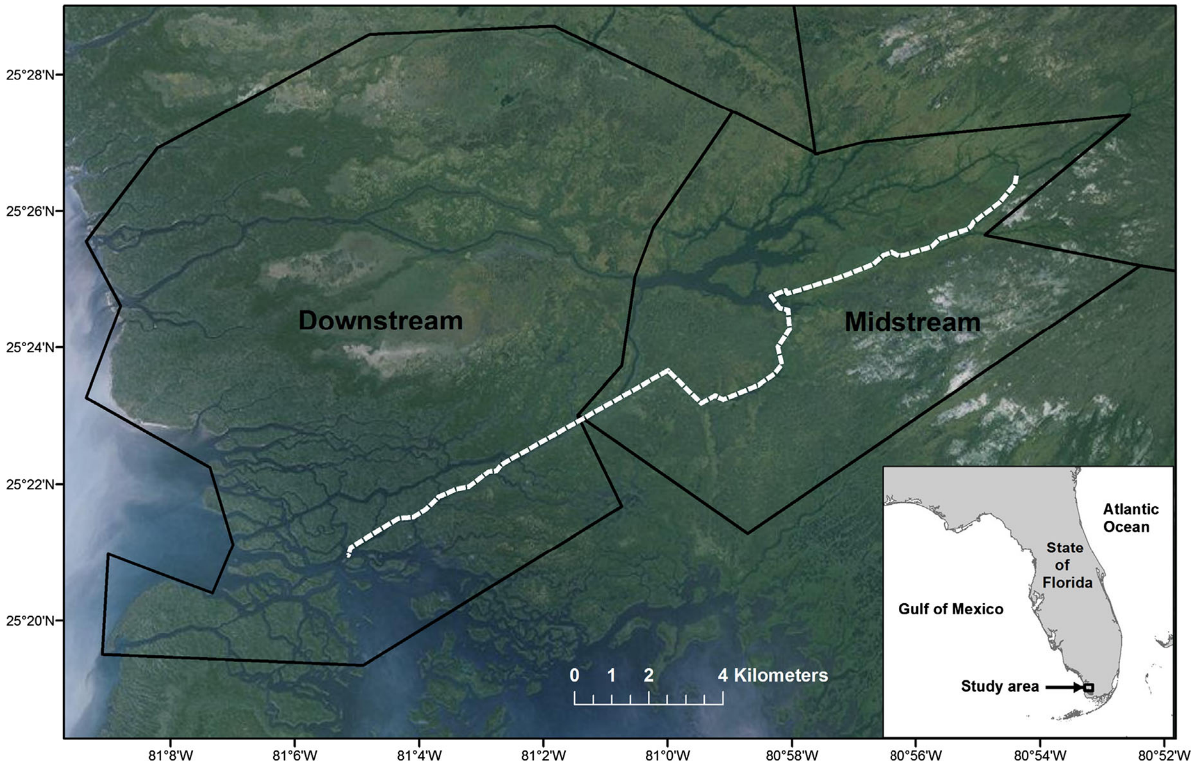

Fig. 1 Location of the survey route (*dashed line*) in Shark River estuary in Everglades National Park, FL. Boundary of the two zones (midstream and downstream) followed Rosenblatt and Heithaus (2011)

Data Collection

We used the data from the alligator surveys conducted from 1998 to 2013 following the protocol described in Fujisaki et al. (2011). In brief, a boat operator searches for alligators using a 200,000 candle watt spotlight along a predetermined route. The location, habitat, and size estimates were recorded by the observer. Alligators were classified into four size categories based on total length: hatchling (<0.5 m), small (0.5≤, <1.25 m), medium (1.25≤, <1.75 m), large (≥1.75 m), and unknown (size could not be determined). Salinity and water temperature are measured at route start and end points. Salinity was measured with a handheld refractometer, and temperature were measured with a Taylor dial thermometer. Both were measured at the water surface. Surveys were not conducted the day of, before, or after a full moon, or when heavy rain or high winds (>24 km/h) occurred. Due to environmental constraints imposed by the weather and the moon, we cannot always perform the survey during the same point in the tidal cycle. After the first one-time survey in 1998, we surveyed again in 2002. Beginning in 2003, we conducted surveys twice in both spring and fall to have independent replications (Woodward and Moore 1990). Although we aimed to conduct the second survey within 2–3 weeks after the first survey, on some occasions, the two surveys were conducted more than 3 weeks apart due to weather conditions and logistics. Replicated surveys were conducted by the same boat driver except for dry season surveys in 2003.

Analysis

We conducted surveys during the dry season (mostly March–April) and wet season (mostly September–October) to understand the seasonal variability in abundance along the survey route. To understand the persistence in habitat use by alligators within a season, we examined the associations in number of observed alligators between the two repeated surveys by size class and zones using Spearman's ρ. For this analysis, we used the data only if the first and second surveys were conducted by the same boat driver to mitigate the effect of varied detection rate by observers. We compared the density of (number of alligators/kilometer) observed alligators in each size class by season and zone using ANOVA F test followed by Tukey's multiple mean comparisons. We also compared the abundance in each zone by season and size class using t test. These analyses were conducted using SAS 9.3 GLM and TTEST procedures.

We examined the temporal trends in relative density as well as the influence of salinity and temperature using a generalized linear model log-link function with alligator count as response variable and year number (in water year), salinity, and water temperature (average of start and end measurements). For salinity and temperature, we used start point measurements for midstream and end point measurements for downstream. This analysis was conducted for each season and size class. The correlation by the same observers conducting multiple surveys was modeled using the generalized estimating equation (Johnston 1996) in the SAS 9.3 GENMOD procedure. In our previous study that examined trends in relative density of alligators in multiple wetland compartments (Fujisaki et al. 2011), the detection rate was accounted for as a function of water depth, because the spatial and temporal variability in water depth in different compartments likely influenced the detection rate. However, the water depth in an estuary fluctuates with tide and there is no estimate of detection probabilities in estuaries (Nifong et al. 2015). Therefore, in this study, we only accounted for varied detection rate by observer differences. All analysis was based on α-level of 0.05.

Results

In total, we conducted 46 surveys in 13 years between 1998 and 2013. All surveys (22) were replicated since 2003. The majority of the replicated surveys were conducted 3 weeks apart, but some replicated surveys were conducted for as long as 34 days (4.5 weeks) apart due to weather conditions or logistics. In the majority of surveys, the start point salinity was zero and the average for wet and dry seasons are 0.95 psu (SD 2.85, range 0–10) and 1.72 psu (SD 3.06, range 0–10) in order (Fig. 2). The mean salinity at the end point was 13.95 psu (SD 9.66, range 0–35) for the wet season and 27.95 psu (SD 6.27, range 11–40) for the dry season. The mean temperature during the wet season at the start and end points were 28.10 °C (SD 1.81, range 24–31) and 28.45 °C (SD 1.57, range 24–31). The mean temperature in dry seasons were 24.51 °C (SD 2.66, range 20–32) at the start point and 24.37 °C (SD 1.85, range 21–28) at the end point.

Based on the data obtained from the 22 replicated same observer surveys (i.e., the same observer conducted two surveys in each season), moderate and significant positive associations between the two surveys were found in the medium size class alligator numbers in the midstream zone ($\rho = 0.471$, $P = 0.027$) and the large size class ($\rho = 0.593$, $P = 0.004$) and the total numbers ($\rho = 0.723$, $P < 0.001$) in the downstream zone (Fig. 3).

Density (number of alligators/km) varied by estuary zone, size class, and season (Fig. 4). The size class difference in alligator density was significant in both seasons and zones. In general, there were more large alligators than medium or small alligators in both estuary zones and both seasons (Fig. 4). The density comparison between the two estuary zones showed a seasonal pattern (Fig. 5). During the wet

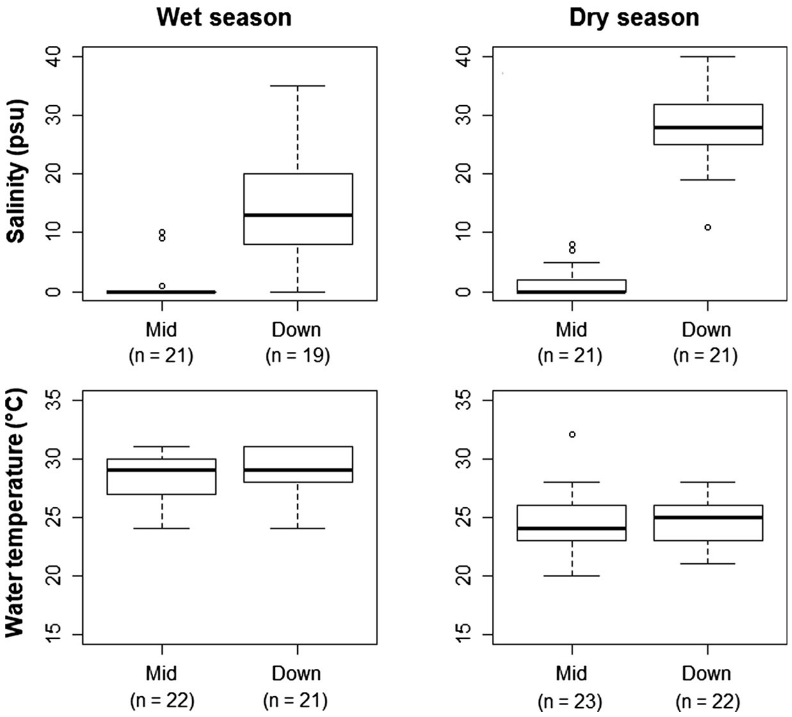

Fig. 2 Box plots of salinity and temperature in the midstream and downstream measured during the wet season (May–October) and the dry season (November–April) surveys in Shark River estuary, Everglades National Park, FL, between 1998 and 2013. The number of observations (*n*) in each plot is the number per each zone

season, the only significant difference between the midstream and downstream zones was observed in the large size class. The large-sized alligator density was greater in the downstream than that in the midstream zone. During the dry season, the zonal difference in alligator density was significant for all size classes; alligator density was consistently greater in the midstream than that in the downstream zone (Fig. 5).

The estimated model parameters indicated negative trends in alligator density except for large-sized class alligators and total number in the downstream zone during wet seasons (Table 1). With both seasons and zones combined, the negative trend was significant only for the large size class. A stronger pattern emerged when we analyzed the data by season and zone. During the wet season, the negative trend was insignificant for all size classes whereas during the dry season, the negative trend was significant for all cases except for the large size class in the downstream. The estimated effect of salinity was significant for total animals in midstream during the wet season and medium size class and total numbers in downstream during the dry season. In all three, the effect was negative (Table 1). The effect of temperature was significant only for medium size class in which the temperature was positively associated with alligator counts.

Discussion

Our results showed population level patterns in habitat use by American alligators. We observed higher densities during the wet season compared to the dry season especially in the downstream zone. This seasonal variation is likely dictated by salinity, reproductive cycle, and temperature. Larger amount of precipitation during the wet season leads to lower salinity and makes the estuary more suitable for alligators. The annual reproductive cycle of alligators is closely related to ambient temperature. For alligators in ENP, dry season comprise courtship time (Ugarte et al. 2013), during which males seek comparably sedentary females in freshwater marshes. During periods of high temperatures, which are associated with wet seasons in our study area, alligators seek deeper water to control their body temperature (Smith 1975). Large alligators may make more frequent excursions to the downstream zone during the wet season because of lower salinity and higher temperature. As a mobile top predator, the alligator transfers energy and nutrients by their movement and foraging activities across ecosystems (Subalusky et al. 2009; Rosenblatt and Heithaus 2011). In our study area, the alligator connects freshwater, estuary, and near-marine zones by their movement and

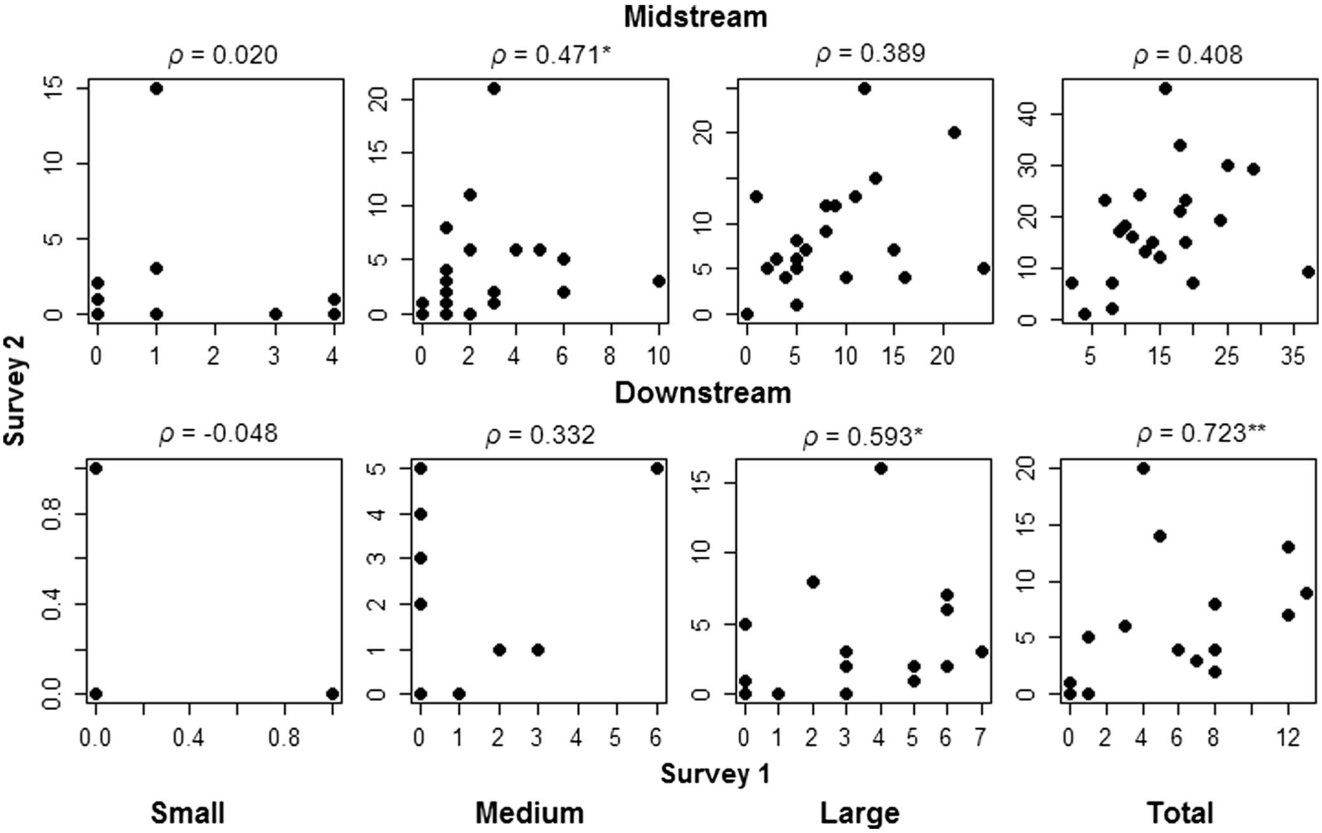

Fig. 3 Plots of number of alligators observed by the replicated nightlight surveys ($n = 22$) in the Shark River estuary, Everglades National Park, FL, by zone (midstream and downstream) and size classes (small, medium, large, and total). The total number includes number of alligators with unknown size class. Spearman's ρ is shown at the top of each plot. *Star marks* indicate significance of the associations (*$p < 0.05$, **$p < 0.01$)

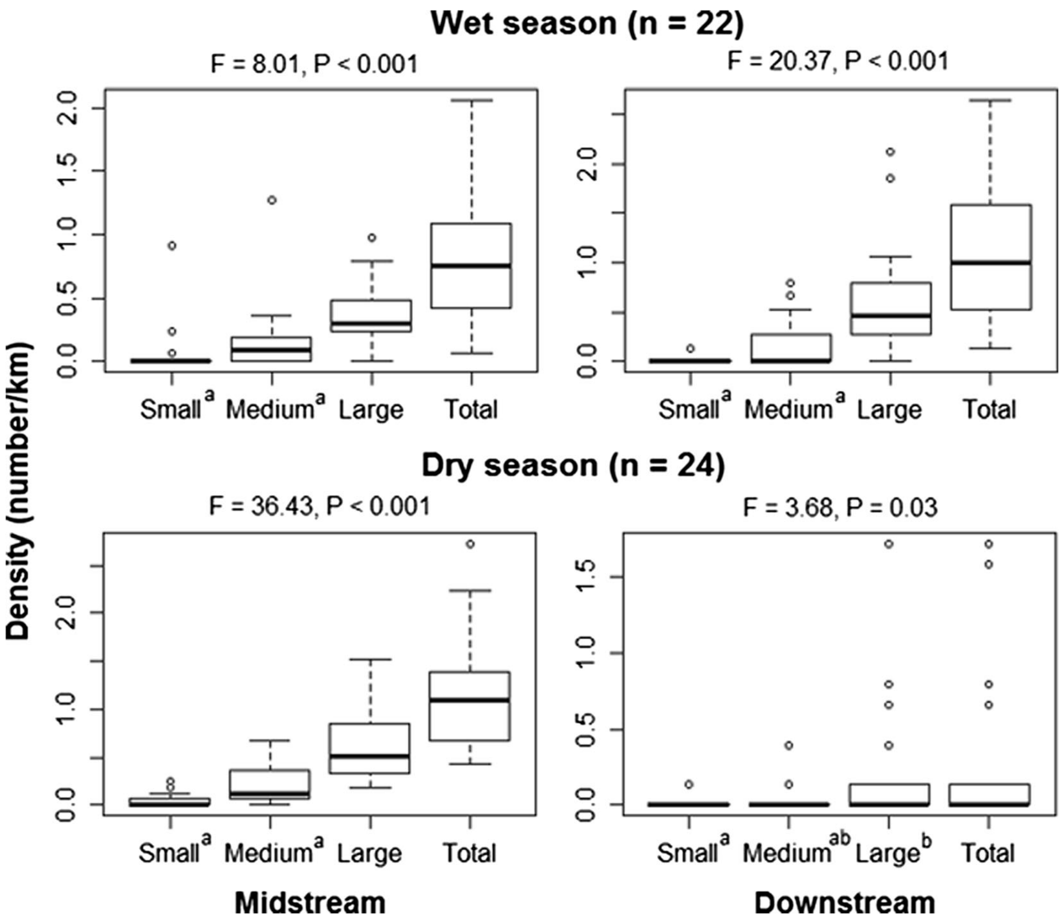

Fig. 4 Box plots showing the density (number/km) of the observed alligators by nightlight surveys conducted between 1998 and 2013 in Shark River estuary Everglades National Park, FL, by size class (small, medium, large, and total), estuary zone (midstream and downstream), and season (wet, May–October; dry, November–April). The total number includes the number of alligators with unknown size class. Test statistics and *P* values from the ANOVA *F* test that compared alligator density by size class (small, medium, and large) are shown at the top of each plot. Group means followed by the same letter are not significantly different based on Tukey's multiple mean comparisons

foraging (Rosenblatt and Heithaus 2011). Reduced precipitation and freshwater flow from the upstream during dry seasons increases residence times of nutrients (Childers et al. 2006). The uneven level of habitat use by alligators during the wet and dry seasons further contributes to create seasonally varied amount of nutrient and energy transfers in the system.

Zonal differences in the relative densities of observed alligators were also elucidated. During dry season, use of the downstream zone was rare for all size classes. This lack of use is particularly apparent in the density of medium- and large-sized alligators, as they are more frequently observed during the wet season. This observation is consistent with an acoustic telemetry study that indicated that adult males spend twice as much of their time in an upstream zone during dry season (Rosenblatt et al. 2013). Higher salinity during the dry season (Romigh et al. 2006) likely makes downstream habitat less suitable even for large-sized class alligators.

The density of alligators differed by size class; the observed alligators were predominantly in the large size class. The observation of the small-sized alligators was extremely rare, especially in the downstream. This was likely due to the larger alligators' ability to tolerate greater salinity environments, as young alligators, particularly hatchlings, are highly sensitive to salt water (Lauren 1985). Juveniles are frequently observed in an ecotone between brackish water and freshwater marshes, but prolonged exposure to a saline environment will result in decreased feeding, loss of body weight, and eventual mortality (Lauren 1985). Our results also agreed with the study in Sapelo Island, GA (Nifong et al. 2014), that reported that alligators caught in an estuarine habitat were of larger size classes than ones caught in freshwater and intermediate habitats. The above study also found that all size class alligators consumed estuary/marine species including mud crabs,

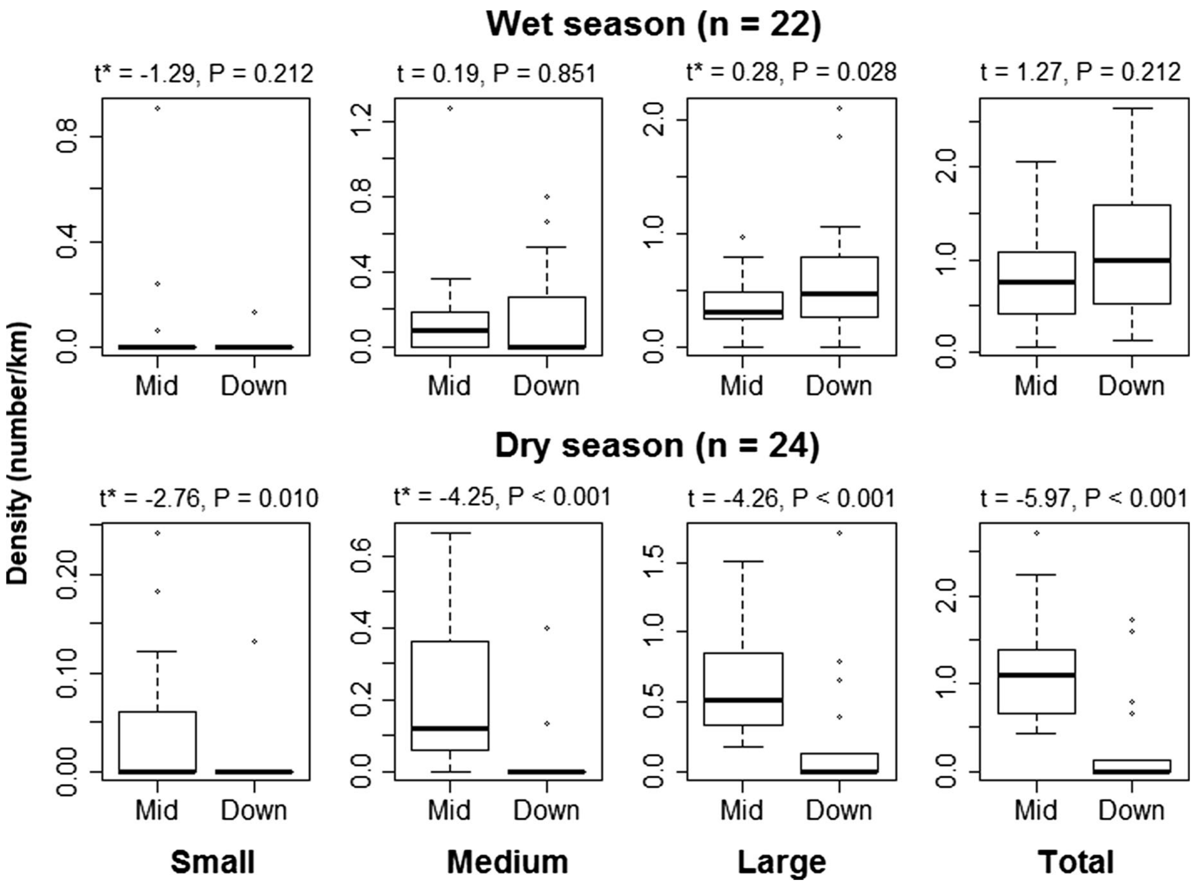

Fig. 5 Box plots showing density (number/km) of observed alligators between 1998 and 2013 by the nightlight survey in Shark River estuary Everglades National Park, FL, by zone (midstream and downstream), size class (small, medium, large, total), and season (wet, May–October; dry, November–April). The total number includes number of alligators with unknown size class. Test statistics and *P* values from *t* test to compare alligator density in the midstream and downstream are indicated at the *top* of each plot

horseshoe crabs, blue crabs, grass shrimp, and fish, but small juveniles consumed estuary/marine prey less frequently than larger-sized alligators (Nifong et al. 2014). Higher salinity in dry season may limit alligators to access such estuary/marine preys, especially for smaller alligators. In our study area, productivity is greater in the downstream than in the midstream (Simard et al. 2006; Rosenblatt et al. 2013) because the oligotrophic system in which we worked receives the limiting nutrient, phosphorus, from the Gulf of Mexico (Childers et al. 2006). With greater salinity tolerance and faster swim speed (Gatten et al. 1991), large-sized alligators have more foraging options, especially in our study area. This high mobility of large-sized alligators was reflected as the lack of strong association in number of observed alligators by the replicated surveys, which likely suggests a large intraseasonal variability in alligator density in the estuary, but we also recognize that this may reflect varied environmental factors, such as tides, because the conditions in the estuary are dynamic.

Previous studies showed that there is a variation in the patterns of decline by size class and among wetland areas related to hydrology and stresses that extreme dry events have on small animals in particular (Fujisaki et al. 2011; RECOVER 2014). The observed declined trend in the number during the dry season coincides with the declined trend of small- and medium-sized alligators in some wetlands in southern Florida, including the adjacent Shark River Slough (Fujisaki et al. 2011; RECOVER 2014). However, in contrast to this study, which found a declined trend of large size class, Fujisaki et al. (2011) reported an increasing trend of large size class in wetlands in southern Florida, including Water Conservation Areas 1, 2A, and 3A in north of ENP. Inconsistent population trend by season in the estuary, that is, absence of significant trend during wet season and declined trend during dry season especially in midstream zone, where the decline in all size classes were found, may be related to the reduced water flow from the freshwater marsh causing an increase in salinity in the estuary.

Table 1 Estimated slope and standard error (SE) by generalized linear model with log-linear link function to assess temporal (annual) trend and effects of temperature (°C) and salinity (‰) in the number of observed alligators by size class (small, medium, large, and total), zone (midstream and downstream), and season (wet, May–October; dry, November–April) in Shark River estuary, Everglades National Park, FL, between 1998 and 2013

Season	Zone	Size class	Estimate (SE)		
			Year	Salinity	Temperature
Both seasons	Both zones	Small	−0.076 (0.079)	−0.028 (0.340)	0.146 (0.606)
		Medium	−0.066 (0.047)	0.003 (0.021)	0.070 (0.126)
		Large	−0.064 (0.012)**	−0.003 (0.008)	0.011 (0.040)
		Total	−0.025 (0.020)	−0.007 (0.008)	0.022 (0.044)
Wet	Midstream	Medium	−0.027 (0.079)	−0.003 (0.044)	0.095 (0.176)
		Large	−0.053 (0.026)	−0.101 (0.019)	−0.027 (0.029)
		Total	−0.013 (0.040)	−0.083 (0.023)**	0.042 (0.060)
	Downstream	Small	−0.168 (0.170)	0.081 (0.033)	1.202 (0.334)
		Medium	−0.029 (0.060)	−0.032 (0.027)	0.139 (0.101)
		Large	0.007 (0.037)	−0.015 (0.022)	0.132 (0.188)
		Total	0.049 (0.035)	−0.010 (0.023)	0.072 (0.135)
Dry	Midstream	Small	−0.233 (0.092)*	−0.096 (0.031)	−0.014 (0.079)
		Medium	−0.205 (0.060)**	−0.041 (0.026)	−0.059 (0.050)
		Large	−0.082 (0.020)**	−0.004 (0.005)	0.023 (0.026)
		Total	−0.078 (0.027)*	−0.021 (0.099)	−0.042 (0.033)
	Downstream	Medium	−1.381 (0.082)**	−0.235 (0.005)**	0.447 (0.020)**
		Large	−0.223 (0.060)	−0.168 (0.014)	−0.246 (0.166)
		Total	−0.143 (0.041)**	−0.183 (0.001)**	−0.230 (0.122)

Small size class in midstream during wet season and downstream during dry season is not included due to rare detections. The total number includes number of alligators with unknown size class. Star marks indicate significance at α level of 0.05 (*) and 0.01 (**)

In our analysis, the effects of salinity and temperature were rarely significant but this is partially because these factors are associated with season and zone (e.g., higher temperature during the wet season than the dry season and higher salinity in the downstream than in the upstream). Also, our salinity measurements at the start and end points likely did not sufficiently capture the condition of each zone because salinity along the estuary is largely variable (Fujisaki et al. 2014). This is particularly true in the midstream, where the start points were frequently freshwater.

Previous studies have shown individual specialization in alligator's foraging strategy (Rosenblatt and Heithaus 2011; Nifong et al. 2015). Our results indicate that this variability reflects individuals' physiologies, mainly salinity tolerance, and possibly their reproductive cycles. Our seasonal and zonal analysis illuminated population-level patterns in alligator's habitat use and ontogenetic niche shift which is important to understand ecosystem-wide changes in density and habitat use. The observed alligators by our surveys were predominantly in the large size class. With greater salinity tolerance, faster movement speed, and large body size, they have more flexibility in selecting an optimal habitat within heterogeneous habitat quality in space and time. These findings together indicate high adaptability of large-sized alligators to fluctuating habitat conditions; large-sized alligators opportunistically use estuary habitat. This mobility to maximize access to quality resources and to avoid sources of stress coupled with the adaptability makes free-ranging alligators a suitable indicator of the return of more natural freshwater flows to the coastal system. Our expectation with restoration is that alligator density will increase and that more medium and small alligators will be observed as salinity becomes more favorable.

Acknowledgments We acknowledge that K Rice made important contributions to initiate and continue this survey program. We are grateful to G Blakmore, J Brien, M Brien, R Crespo, M Denton, E Larrivee, M Parry, M Squires, and S Williams who conducted the surveys. Coordinates for the estuary zone boundary were provided by A Rosenblatt. This study was funded by the US Army Corps of Engineers and South Florida Water Management District Restoration Coordination and Verification Monitoring and Assessment Plan, the US Geological Survey Priority Ecosystems Science program, the Department of Interior Critical Ecosystem Studies Initiative, and National Park Service (Everglades National Park) through the South Florida and Caribbean Cooperative Ecosystem Studies Unit. The use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US government. The views expressed here do not necessarily represent the views of the US Fish and Wildlife Service.

References

Anderson, G.H., T.J. Smith, III, and K.M. Balentine. 2014. Land-margin ecosystem hydrologic data for the coastal Everglades, Florida, water years 1996–2012. *U.S. Geological Survey Data Series* 853. 38 p.

Attrill, M.J. 2002. A testable liner model for diversity trends in estuaries. *Journal of Animal Ecology* 71: 262–269.

Childers, D., J.N. Boyer, S.E. Davis, C.J. Madden, D.T. Rudnick, and F.H. Sklar. 2006. Relating precipitation and water management to nutrient concentrations in the oligotrophic "upside-down" estuaries of the Florida Everglades. *Limnology and Oceanography* 51: 602–616.

Craighead, F.C. Sr. 1968. The role of the alligator in shaping plan communities and maintaining wildlife in the Southern Everglades. *Florida Naturalist* 41:2–7, 69–74, 94.

Davis, S.M., D.L. Childers, J.J. Lorenz, H.R. Wanless, and T.E. Hopkins. 2005. A conceptual model of ecological interactions in the mangrove estuaries of the Florida Everglades. *Wetlands* 25: 832–842.

Dunson, W., and F.J. Mazzotti. 1989. Salinity as a limiting factor in the distribution of reptiles in Florida Bay: a theory for the estuarine origin of marine snakes and turtles. *Bulletin of Marine Science* 44: 229–244.

Fujisaki, I., F.J. Mazzotti, R.M. Dorazoi, K.G. Rice, M.S. Cherkiss, and B.M. Jeffery. 2011. Estimating trends in alligator populations from nightlight survey data. *Wetlands* 31: 147–155.

Fujisaki, I., K.M. Hart, F.J. Mazzotti, M.S. Cherkiss, A.R. Sartain, B.M. Jeffery, J.S. Beachamp, and M. Denton. 2014. Home range and movements of American alligators (*Alligator mississippiensis*) in an estuary habitat. *Animal Biotelemetry* 2: 8.

Gatten Jr., R.E., J.D. Congdon, F.J. Mazzotti, and R.U. Fischer. 1991. Glycolysis and swimming performance in juvenile American alligators. *Journal of Herpetology* 24: 406–411.

Gibbons, J.W., and J.W. Coker. 1978. Colonization patterns of Atlantic coast barrier islands. *American Midland Naturalist* 99: 219–233.

Johnston G, 1996. Repeated measures analysis with discrete data using the SAS system. Proceedings of SAS User Group International (SUGI), March 10–13, Chicago, Illinois.

Lauren, D. 1985. The effect of chronic saline exposure on the electrolyte balance, nitrogen metabolism, and corticosterone titer in the American alligator, *Alligator mississippiensis. Comparative Biochemistry and Physiology* 1985(81A): 217–223.

Light, S.S., and J.W. Dineen. 1994. Water control in the Everglades: a historical perspective. In *Everglades: the ecosystem and its restoration*, ed. S.M. Davis and J.C. Ogden. Delray Beach: St. Lucie Press.

Marshall, F.E., D.T. Smith, and D.M. Nickerson. 2011. Empirical tools for simulating salinity in the estuaries in Everglades National Park, Florida. *Estuarine, Coastal and Shelf Science* 95: 377–387.

Mazzotti, F.J., and L.A. Brandt. 1994. Ecology of the American alligator in a seasonally fluctuating environment. In *Everglades: the ecosystem and its restoration*, ed. D. Davis and J. Ogden, 485–505. Delray Beach: St. Lucie Press.

Mazzotti, F.J., G.R. Best, L.A. Brandt, C.M. Cherkiss, B.M. Jeffery, and K.G. Rice. 2009. Alligators and crocodiles as indicators for restoration of Everglades ecosystems. *Ecological Indicators* 9S: S137–S149.

McNease, L., and T. Joanen. 1978. Distribution and relative abundance of the alligator in Louisiana coastal marshes. *Proceedings of Annual Conference of Southeast Association of Fish and Wildlife Agencies* 32: 182–186.

Neil, W.T. 1958. The occurrence of amphibians and reptiles in saltwater areas, and a bibliography. *Bulletin of Marine Science* 8: 1–97.

Nifong, J.C., R.L. Nifong, B.R. Silliman, R.H. Lowers, L.J. Guillette Jr., J.M. Ferguson, M. Welsh, K. Abernathy, and G. Marshall. 2014. Animal-borne imaging reveals novel insights into the foraging behaviors and diel activity of a large-bodied apex predator, the American alligator (*Alligator mississippiensis*). *PLoS ONE* 9, e83953.

Nifong, J.C., C.A. Layman, and B.R. Silliman. 2015. Size, sex and individual-level behaviour drive intrapopulation variation in cross-ecosystem foraging of a top-predator. *Journal of Animal Ecology* 84: 35–48.

RECOVER. 2014. 2014 system status report. restoration coordination and verification, c/o United States Army Corps of Engineers, Jacksonville, FL, and South Florida Water Management District, West Palm Beach, FL. Available online at: http://www.evergladesplan.org/pm/ssr_2014/ssr_main_2014.aspx.

Rice, K.G., F.J. Mazzotti, and L.A. Brandt. 2005. Status of American alligator in southern Florida and its role in measuring restoration success in the Everglades. In *Amphibians and reptiles: status and conservation in Florida*, ed. W.E. Meshaka Jr. and K.J. Babbitt, 145–153. Malabar: Krieger Publishing Company.

Romigh, M.M., S.E. Davis, V.H. Rivera-Monroy, and R.R. Twilley. 2006. Flux of organic indent here carbon in a riverine mangrove wetland in the Florida Coastal Everglades. *Hydrobiologia* 569: 505–516.

Rootes, W.L., and R.H. Chabrec. 1991. Growth rates of American alligators in estuarine and palustrine wetlands in Louisiana. *Estuaries* 14: 489–494.

Rosenblatt, A.E., and M.R. Heithaus. 2011. Does variation in movement tactics and trophic interactions among American alligators create habitat linkages? *Journal of Animal Ecology* 80: 786–798.

Rosenblatt, A.E., M.R. Heithaus, F.J. Mazzotti, M. Cherkiss, and B.M. Jeffery. 2013. Intra-population variation in activity ranges, diel patterns, movement rates, and habitat use of American alligators in a subtropical estuary. *Estuarine, Coastal and Shelf Science* 125: 182–190.

Simard, M., K. Zhang, V.H. Rivera-Monroy, M.S. Ross, P.L. Ruiz, E. Castañda-Moya, R.R. Twilley, and E. Rodriguez. 2006. Mapping height and biomass of mangrove forests in Everglades National Park with SRTM elevation data. *Photogrammetric Engineering & Remote Sensing* 72: 299–311.

Smith, E.N. 1975. Thermoregulation of the American alligator, *Alligator mississippiensis. Physiological Zoology* 48: 177–194.

Subalusky, A.L., L.A. Fitzgerald, and L.L. Smith. 2009. Ontogenetic niche shifts in the American alligator establish functional connectivity between aquatic systems. *Biological Conservation* 142: 1507–1514.

Ugarte, C.A., O.L. Bass, W. Nuttle, F.J. Mazzotti, K.G. Rice, I. Fujisaki, and K.R.T. Whelan. 2013. The influence of regional hydrology on nesting behavior and nest rate of the American alligator. *Journal of Wildlife Management* 77: 192–199.

Woodward, A.R., and C.T., Moore. 1990. Statewide alligator surveys. Florida Game and Fresh Water Fish Commission Final Report, Tallahassee, Florida, USA.