VARIATION IN BODY CONDITION OF *ALLIGATOR MISSISSIPPIENSIS* IN FLORIDA

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ABSTRACT

We examined body condition (using Fulton's K with snout-vent length and weight) for 482 American alligators (*Alligator mississippiensis*) collected from 14 aquatic sites in Florida in 2011 and 2012. An information-theoretic approach using Akaike information criterion (AIC) was used to select the best models for alligator body condition from a suite of seven candidate models created using combinations of trophic state (oligotrophic, eutrophic, hypereutrophic), sex, and alligators/km. Our top model included trophic state and alligators/km indicating that alligator body condition from sites classified as hypereutrophic and eutrophic (2.43 ± 0.07 and 2.45 ± 0.05, respectively) were greater than alligator body condition at oligotrophic sites (2.14 ± 0.01). Alligator body condition was lower at sites with a higher density of alligators ≥ 1.25 m. Across all sites, average alligator body condition ranged from 1.94 ± 0.054 (SE) to 2.78 ± 0.121(SE). This was a 43% difference in alligator body condition between the site with the highest alligator body condition (Lochloosa Lake, a hypereutrophic lake in north-central Florida) compared to the site with lowest body condition (Water Conservation Area 3B, an oligotrophic marsh in the Everglades). Across all sites, average alligator body condition was 12% greater at eutrophic and hypereutrophic sites compared to oligotrophic sites which was consistent with patterns observed in other studies for fish standing stock (highest in eutrophic lakes and lowest in oligotrophic marshes in the Everglades). The same patterns occur in alligator stomach content volume (higher in lakes in north-central Florida, Louisiana fresh, intermediate, and brackish marshes compared to the Everglades). Our results illustrate that variation in alligator body condition is consistent with patterns of aquatic site productivity and is a useful parameter for describing differences in aquatic site ecological condition.

Key words: *Alligator mississippiensis,* estuary, Everglades, Fulton's K, lake, marsh, productivity, trophic state.

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INTRODUCTION

American alligators (*Alligator mississippiensis*) occur throughout the southeastern United States and are common in most aquatic habitats. Densities and life history traits vary throughout the range (Abercrombie, 1989; Mazzotti and Brandt, 1994), and show latitudinal and habitat differences (Elsey et al., 1992; Lance, 2003). Numerous environmental factors influence life history traits including temperature, rainfall, environmental seasonality, and food availability. In Florida, based on night-light surveys used to measure relative density, alligator populations are generally considered to be stable or increasing (Florida Fish and Wildlife Conservation Commission, unpublished data). Although alligator populations have increased in Florida, there is variation in population densities and health across the state. Evert (1999) correlated densities of alligators with lake characteristics including size, water quality (total phosphorus, total nitrogen), chlorophyll *a*, percentage of area covered with macrophytes, and fish biomass. His data supported predictions of Fretwell (1987) who suggested that as nutrient levels increase among systems, the abundance of top predators also increases. In the Everglades, a generally oligotrophic ecosystem, alligators have lower growth rates, higher age specific mortality, delayed sexual maturity, smaller clutche sizes, and reduced nesting frequency (Dalrymple, 1996; Mazzotti and Brandt, 1994). Jacobsen and Kushlan (1989) suggested that slow growth rate of alligators in the Everglades was a result of limited food resources in this oligotrophic system and increased maintenance costs because of relatively warm year-round temperatures.

Body condition is an indication of how well an animal is coping with environmental stressors (Murphy et al., 1990; Taylor, 1979). It is related to overall fitness and may affect reproduction, growth, and population density. Alligator body condition is affected by diet, prey density, alligator density, habitat, ambient temperatures, or other factors (Taylor, 1979; Delany et al., 1999; Zweig, 2003). Body condition is a measure of the relationship between length and mass and has been examined for alligators in various locations using a variety of indices (Brandt, 1991; Dalrymple 1996; Fujisaki et al. 2009). Previous studies have examined alligator body condition in relation to captive reared versus free-ranging (Elsey et al., 1992), habitat (Rootes et al., 1991), diet (Delany et al., 1999; Rice et al., 2007), season (Dalrymple, 1996; Barr, 1997), water depths (Fujisaki et al., 2009), and fluctuations in water depth and over time (L.A. Brandt, unpublished.). In general, these studies indicate that site conditions, wetland productivity, food resource type, and availability can influence alligator body condition suggesting that alligators in areas with higher quality or quantity food bases have higher body condition. Based on these studies we hypothesized that alligators in lower productivity sites will have lower average body condition than alligators at higher productivity sites. We evaluate this hypothesis by comparing average alligator body condition in 14 aquatic sites in Florida during 2011 and 2012, and discuss the patterns in relation to site productivity and alligator density.

MATERIAL AND METHODS

We took advantage of morphometric data collected from alligators captured for other studies at 14 aquatic sites in Florida (Fig. 1) during spring and fall 2011 and 2012. Sites included emergent marsh associated with lakes and rivers ranging from north-central to southern Florida (lake), freshwater wetlands within the ridge and slough landscape of the Everglades ecosystem (marsh, Ogden, 2005), and one estuarine site where salinity fluctuated from 0 to 35 ppt in western Everglades National Park (estuary). During 2011 and 2012, two of four lake sites were eutrophic and two were hypereutrophic based on Trophic State Index calculated using data from the Florida water atlas (Lake County Water Atlas, http://www.lake.wateratlas.usf.edu/shared/learnmore.%20asp?toolsection=lm_tsi accessed 1/27/16). Lakes with values of 0–59 were classified as oligotrophic, 60–69 as eutrophic, and 70–100 as hypereutrophic. All marshes and the estuary were oligotrophic (Davis, 1994; Childers et al., 2006; Table 1). We

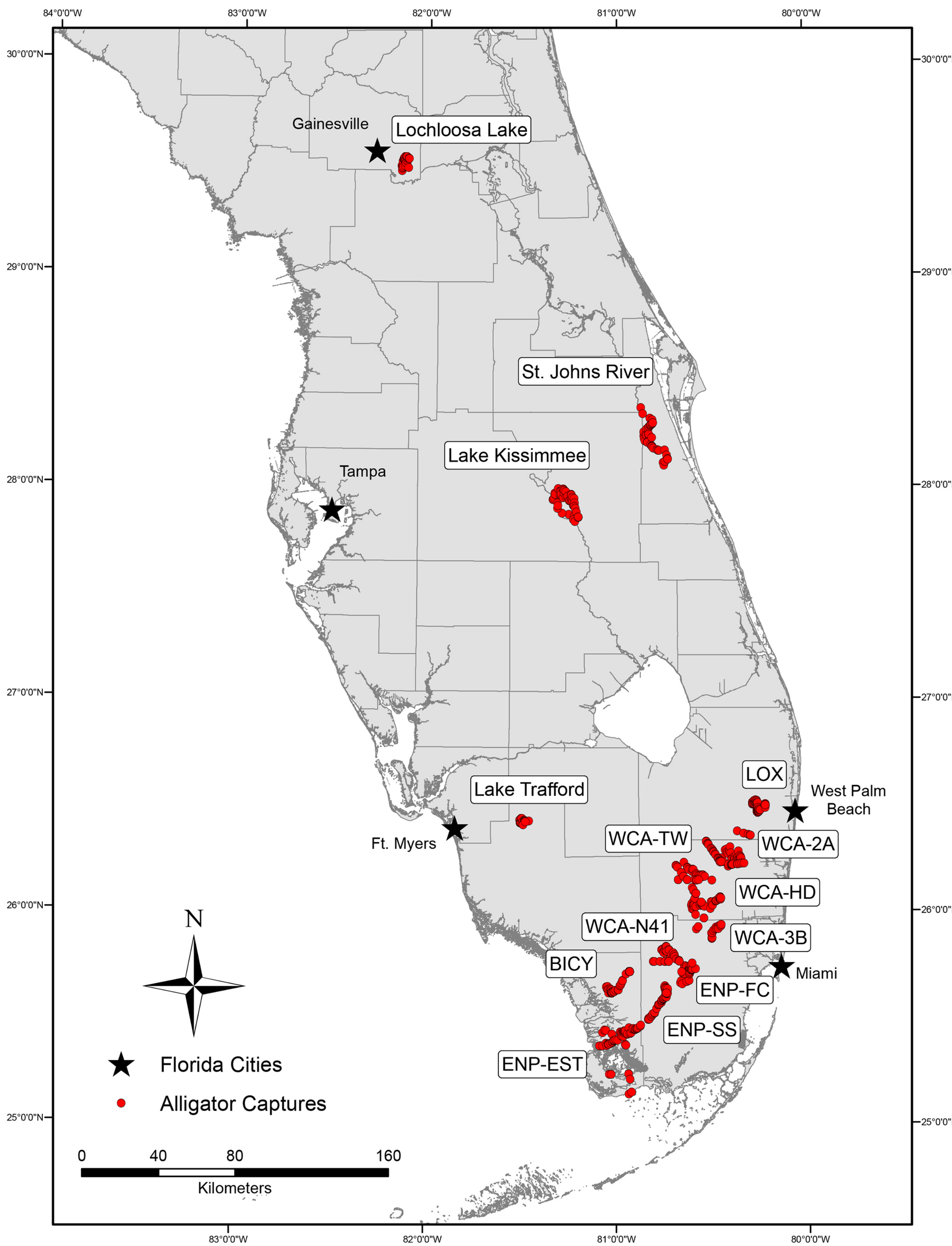

Figure 1. Locations of 14 aquatic sites in Florida used to examine alligator body condition in 2011 and 2012. Red dots are capture locations of individual alligators.

Table 1. Average alligator body condition (Fulton's K using snout-vent length and weight) from samples collected in 2011 and 2012 in 14 aquatic sites in Florida. Trophic states are oligotrophic (O), eutrophic (E), and hypereutrophic (H). Alligators /km are for individuals ≥1.25 m.

Full Site Name	Site	Trophic State	Habitat	Average body condition	SE	Sample Size	Alligators/ km
Water Conservation Area 3B	WCA3B	O	Marsh	1.94	0.054	10	1.1
Water Conservation Area 2A	WCA2A	O	Marsh	2.07	0.040	24	1.1
Everglades National Park Frog City	ENP-FC	O	Marsh	2.08	0.036	44	0.7
Water Conservation Area 3A North 41	WCA3A-N41	O	Marsh	2.09	0.042	21	2.7
Everglades National Park Shark Slough	ENP-SS	O	Marsh	2.09	0.033	44	0.5
Water Conservation Area 3A Holiday Park	WCA3A-HD	O	Marsh	2.10	0.062	22	1.8
Big Cypress National Preserve	BICY	O	Marsh	2.14	0.046	46	1.0
Arthur R. Marshall Loxahatchee National Wildlife Refuge	LOX	O	Marsh	2.19	0.035	58	5.7
Water Conservation Area 3A Tower	WCA3A-TW	O	Marsh	2.19	0.057	17	0.2
Everglades National Park Estuary	ENP-EST	O	Estuary	2.29	0.042	61	0.7
St. Johns River	St. Johns River	E	Lake	2.43	0.058	33	6.5
Lake Kissimmee	Lake Kissimmee	E	Lake	2.47	0.078	37	5.2
Lake Trafford	Lake Trafford	H	Lake	2.21	0.061	39	43.6
Lochloosa Lake	Lake Lochloosa	H	Lake	2.78	0.121	25	7.8

obtained data on counts of alligators ≥1.25 m for each site from either the Florida Fish and Wildlife Conservation Commission annual surveys (FWC, unpublished data) or the Restoration Coordination and Verification Monitoring and Assessment Plan surveys (F.J. Mazzotti, unpublished data) to use as an index of alligator density.

We captured smaller alligators by hand when possible and larger alligators with methods commonly used for crocodilians (Chabreck, 1963; Cherkiss et al., 2004). We used fishing poles with snatch hooks to capture wary alligators in open water that were difficult to approach, and locking snares or toggle darts attached to restraining lines to capture alligators that we could approach closely. We measured snout-vent length (SVL) from the tip of the snout to the posterior end of the cloaca, total length (TL) from the tip of the snout to the end of the tail, and tail girth (TG) at the break in scale row immediately posterior to the vent at the third scute row posterior to the rear legs. We measured live animals and animals sacrificed as part of a congruent mercury study or killed by trappers to the nearest 0.1 cm. We marked each live-captured animal by either a unique tail notch or a Florida Fish and Wildlife Conservation Commission web-tag in the right rear foot and released at location of capture. We measured weight (WT) for most alligators to the nearest 0.1 kg. We determined sex by cloacal examination.

Of the 676 individuals in the original dataset, 110 did not include weight. In order to populate the missing values, we performed linear regressions of weight and tail girth that are known to be highly correlated, normalized on a logarithmic scale for the entire dataset and by site. We then performed an analysis of covariance (ANCOVA) that indicated there was a statistically significant difference among the slopes of the regressions by site ($F = 2.338$, $p = 0.0049$). Because of differences among sites, we estimated missing weights of individuals on a per-site basis using the individual regression equations (Appendix 1).

In this study, we used Fulton's K as our body condition index. An assumption of this index is that the weight of an alligator is proportional to the cube of its length. Using 482 alligators from the original dataset without deformities that were ≥1.25 m TL and captured in marsh, lake, or estuary, we calculated the regression slope of the natural log of length on the natural log of weight and tested if it was significantly different from 3 (assumed slope if weight is proportional to the cube of length) using a t-test. The slope was not significantly different from 3 ($t = 0.505$, $p = 0.614$, $df = 479$). Therefore, we used Fulton's K for comparisons of body condition. We used SVL instead of TL to avoid error resulting from tail damage and to make comparisons to other studies. Fulton's K was calculated as $K = WT/SVL^3 \times 10^5$ (Stevenson and Woods, 2006; Zweig et al., 2014).

We used an information-theoretic approach using Akaike information criterion (AIC) to select the best models for alligator body condition from a suite of seven candidate models created using combinations of trophic state (oligotrophic, eutrophic, hypereutrophic), sex, and alligators/km (Table 2). The best model was determined by the lowest AIC value. We used ANOVA to compare average body condition by trophic state and site. Where factors were significant, we used Tukey's Honestly Significant Difference test to identify which groups were different. We used SAS (SAS Institute Inc., 2012) or R (R Core Team, 2014) for analyses. Significance was assessed at $p < 0.05$. We determined site-specific regressions of natural log length vs natural log weight and used this relationship to estimate the weight of a 2 m alligator for comparison across sites and other studies.

RESULTS

The top model included trophic state and alligator density and had a model weight of 0.89. None of the other models had $\Delta AIC < 2$ (Table 2). Alligator body condition from sites classified as hypereutrophic and eutrophic (2.43 ± 0.07 and 2.45 ± 0.05, respectively) were greater than alligator body condition at oligotrophic sites (2.14 ± 0.01) by 12%. Body condition was lower at sites with higher density.

There was a significant difference among sites ($F = 11.48$, $p < 0.001$, $df = 13$) with 43%

Table 2. Seven candidate models ordered by AIC (top) and model output for top model, alligator body condition is a function of trophic state and alligator density.

Variables	AIC	Delta AIC	Model Weight
Density, Trophic	326.2	0	0.89
Density, Sex, Trophic	331.3	5.1	0.07
Density, Trophic, Trophic*Density	332.5	6.3	0.04
Density, Sex, Trophic, Trophic*Density	337.5	11.3	0.00
Trophic	355.7	29.5	0.00
Null	412.9	86.7	0.00
Density	422.5	96.3	0.00

Effect	Trophic	Estimate	Standard Error	DF	t Value	Pr > |t|
Intercept		2.175	0.018	476	118.99	<0.0001
Density		-0.015	0.002	476	-6.44	<0.0001
Trophic	Eutrophic	0.363	0.044	476	8.17	<0.0001
Trophic	Hypereutrophic	0.698	0.078	476	8.90	<0.0001
Trophic	Oligotrophic	0	.	.	.	.

difference in average alligator body condition from the site with highest body condition, Lochloosa Lake, a hypereutrophic lake (2.78 ± 0.121 SE) to the site with lowest body condition, WCA3B, an oligotrophic marsh (1.94 ± 0.054 SE). Average alligator body condition in Lake Kissimmee and St. Johns River, both eutrophic sites, was greater than average alligator body condition from eight oligotrophic marsh sites (Table 1, Fig. 2).

Estimated weights of 2 m alligators ranged from 20.1 kg (WCA3B) to 29.0 kg (Lochloosa Lake; Fig. 3; Appendix 2). Estimated weight of 2 m alligators followed a similar pattern as body condition with heavier estimated weights in eutrophic/hypereutrophic lakes compared to oligotrophic marsh sites (Fig. 3). There was a 30% difference in predicted weight between Lochloosa Lake and WCA3B. The predicted weight of a 2 m alligator in the estuary (ENP-EST, 23.3 kg) generally fell between the eutrophic and hypereutrophic lakes and oligotrophic marshes, but was about 20% lower than predicted weight of alligators in estuarine marshes at Rockefeller Wildlife Refuge in Louisiana (28.8 and 30.6 kg, calculated from equations in Rootes et al. [1991] and Chabreck and Joanen [1979], respectively).

DISCUSSION

The overall pattern of body condition described in this study is consistent with the hypothesis that average alligator body condition is higher in higher productivity sites. It also suggests that high alligator density can influence body condition. Across all sites alligator body condition in hypereutrophic and eutrophic sites was 12% greater than in oligotrophic sites. Trophic state along with alligator density appeared in our top model.

Body condition reflects how much food intake exceeds maintenance, reproduction, and growth (Taylor, 1979). A number of factors including prey density, diet, alligator density and temperature affect alligator body condition (Taylor, 1979; Delany et al., 1999; Zweig, 2003). Increased prey density and quality of diet should allow for

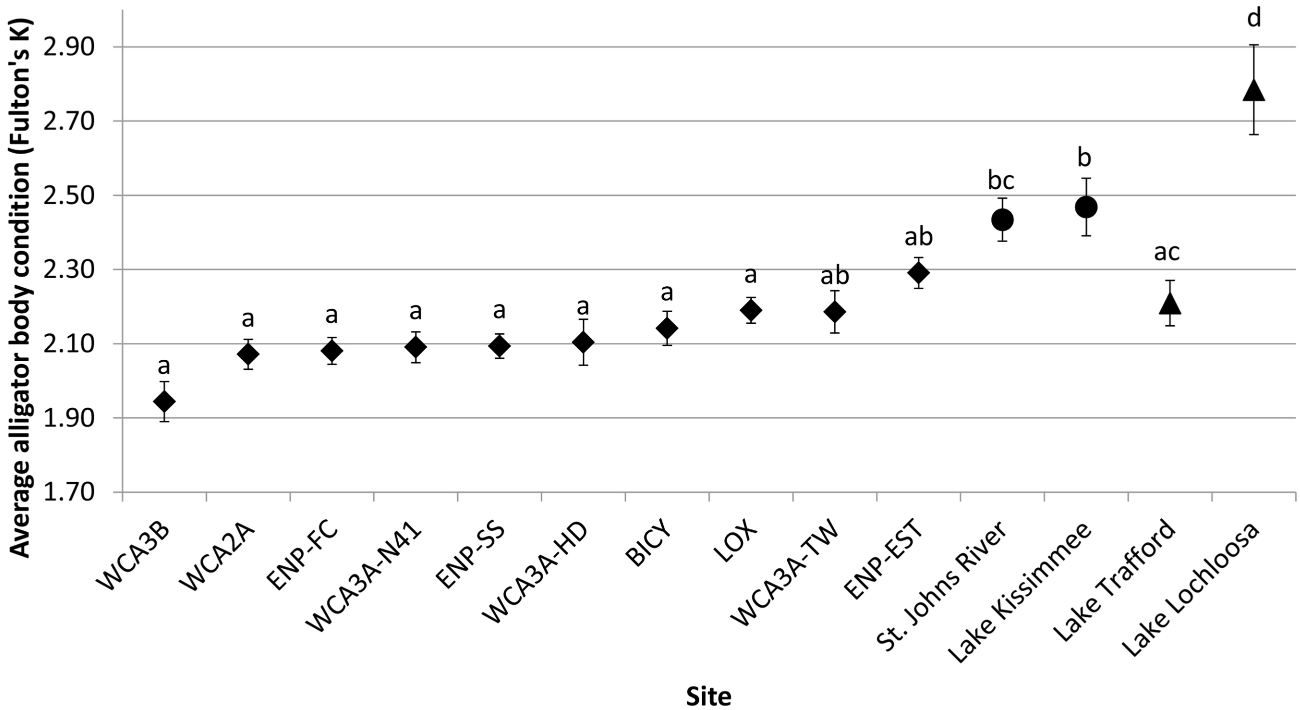

Figure 2. Average alligator body condition (Fulton's K using snout-vent length and weight ± SE) across 14 aquatic sites in Florida during 2011 and 2012. Sites are ordered by trophic state. Diamonds indicated oligotrophic sites, circles eutrophic sites, and triangles hypereutrophic sites.

increases in body condition, while high densities of alligators and higher temperatures may negatively affect body condition via competition for food (high densities) and increased metabolic costs at sites with warmer temperatures.

We used trophic state as an indicator of productivity and hence density of prey. Our results are consistent with patterns observed in studies for fish standing stock (another measure of productivity) and alligator stomach content volume (an indication of food consumption) across sites of different trophic states indicating the merit of this linkage. Turner et al. (1999) summarized results from aquatic sites in Florida and found that fish standing stock was highest in Florida lakes (27.6 g/m^2 to 8.3 g/m^2 [Barnett and Schneider, 1974; Wolfe and Prophett, 1993]) and lowest in oligotrophic marshes of the Everglades (0.2 to 0.7 g/m^2 [Loftus and Eklund, 1994; Turner and Trexler, 1997]). In Louisiana, standing stock of fish in palustrine marsh (9.8 g/m^2 [Turner, 1966 in Rootes et al., 1991[) was less than in mesotrophic estuarine marsh (39.4 g/m^2 [Perry et al., 1976 in Rootes et al., 1991[). Stomach content volume for alligators approximately 2 m in length was higher in lakes in north-central Florida, ranging from 459 g to 594 g (Rice, 2004) to 167 g (Delany and Abercrombie, 1986) and lower in the Everglades, averaging 55 g (Barr, 1997). Overall, stomach content volume of similar size alligators in Florida was lower than in Louisiana's fresh, intermediate, and brackish marsh habitats (552 g, 531 g, 223 g, respectively; McNease and Joanen, 1977), indicating that alligators in the Everglades are eating less than in other areas.

Calculation of predicted weights of alligators from this and other studies also follows this trophic state pattern. Predicted weight of a 2 m alligator in Louisiana palustrine marsh (22.4 kg) was lower than that of a Louisiana estuarine marsh alligator (28.8 kg, Rootes et al., 1991; 30.6 kg, Chabreck and

Joanen, 1979), but higher than predicted weights of alligators at seven of nine Everglades oligotrophic marsh sites in our study (20.1 to 22.2 kg; Fig. 3).

Additional evidence of how food resources affect alligator body condition comes from a study at LOX and WCA3A where Nell (2014) found that alligators captured adjacent to wading bird colonies, where there is substantial food energy provided via nestling carcasses (Nell and Frederick, 2015), had better body condition than alligators captured a considerable distance from wading bird colonies (2.26 ± 0.31and 2.00 ± 0.32, respectively). Therefore, although overall these sites were oligotrophic, body condition of alligators near higher food resources had body condition approaching that observed in eutrophic sites.

An exception to the overall pattern of higher body condition in sites with higher trophic state was Lake Trafford, a hypereutrophic lake. This site had lower alligator body condition than expected by its trophic state. It also had the highest relative density of ≥ 1.25 m alligators of all sites with 44 alligators/km compared to the eight alligators/km at Lochloosa Lake, the site with the next highest density. Our model results suggest that high densities may negatively affect body condition. Any benefits of additional food resources were offset by the exceedingly high number of alligators competing for those resources.

Patterns in alligator body condition in Florida are consistent with general patterns of productivity. However, additional work is needed to refine these relationships, including a broader range of sample sites, and factors that might affect body condition such as habitat, concurrent measures of prey availability, and geographic location. Because we took advantage of existing studies, we did not have an equal distribution of sites in each of the trophic states. For example, none of our oligotrophic sites were lakes and all oligotrophic sites were located in the Everglades. In addition, none of our eutrophic or hypereutrophic sites were marshes. Sampling in oligotrophic lake sites, or oligotrophic marshes in other parts of Florida, would help us to understand

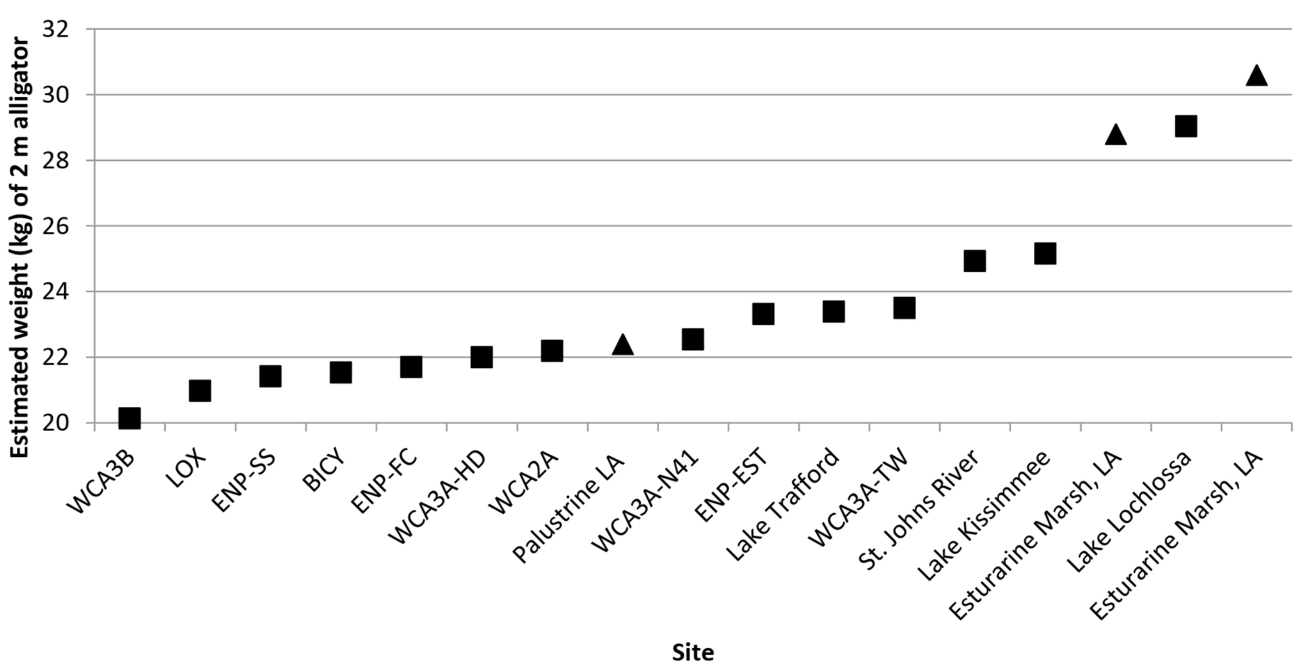

Figure 3. Estimated weights of 2 m alligators from this study (squares) and other studies (triangles). Palustrine and estuarine marsh Louisiana are from Rootes et al. (1991) and Chabreck and Joanen (1979).

how patterns of body condition in the Everglades compare to other oligotrophic sites. Marshes in the Everglades are naturally oligotrophic (Davis, 1994). We expected alligators there to be leaner than alligators in eutrophic sites, hypereutrophic sites, or more northern sites because of limited resources and higher ambient temperatures that result in higher metabolic costs (Jacobsen and Kushlan, 1989). However, because of altered hydrology and altered prey availability, we hypothesize that alligator body condition is lower than it would be in a less altered conditions (Mazzotti et al. 2009). Everglades restoration has the potential to increase alligator body condition by restoring more natural hydrologic patterns leading to increases in prey availability. However, our results indicate that alligator body condition in a restored Everglades (an oligotrophic system) will likely remain lower than alligator body condition in eutrophic and hypereutrophic sites.

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Appendix 1. Site specific regression equations for the relationship between log weight (WT) and log tail girth (TG) for alligators collected in 2011 and 2012 in 14 aquatic sites in Florida. Sites are listed alphabetically.

Site	Sample size: All animals	Sample size: Animals with weights	Regression	R^2	F value	*p*-value
BICY	49	49	y = 2.9383x - 3.3529	0.9383	714.8	<0.001
ENP-EST	63	61	y = 2.5644x - 2.7048	0.8292	286.4	<0.001
ENP-FC	46	46	y = 2.7655x - 3.0716	0.8958	378.2	<0.001
ENP-SS	46	46	y = 2.6996x - 2.9397	0.9064	425.9	<0.001
Lake Kissimmee	52	33	y = 2.8967x - 3.3557	0.9935	4735	<0.001
Lochloosa Lake	38	29	y = 2.7101x - 3.098	0.9924	3521	<0.001
Lake Trafford	48	30	y = 3.0413x - 3.5596	0.9753	1104	<0.001
LOX	78	77	y = 2.6682x - 2.8861	0.8796	547.9	<0.001
St. Johns River	43	26	y = 2.8866x - 3.3529	0.9884	2049	<0.001
WCA2A	72	52	y = 2.918x - 3.3355	0.9912	5656	<0.001
WCA3A-HD	57	43	y = 2.8657x - 3.2553	0.9596	974.5	<0.001
WCA3A-N41	33	27	y = 3.0033x - 3.4408	0.9758	1006	<0.001
WCA3A-TW	37	31	y = 3.1545x - 3.7181	0.9753	1145	<0.001
WCA3B	15	15	y = 2.976x - 3.38	0.9394	201.5	<0.001
All Sites	687	565	y = 2.9461x - 3.3668	0.9543	1.18E+04	<0.001

Appendix 2. Site specific equations used to calculate weight of 2 m alligators based on regressions of natural log of weight and natural log of total length for alligators collected in 2011 and 2012 in 14 aquatic sites in Florida. Sites are listed alphabetically.

Site	Sample size	Regression	R^2	F value	*p*-value
BICY	44	y = 3.357x-14.717	0.9558	973.5	<0.001
ENP-EST	59	y = 3.091x-13.228	0.9247	738.3	<0.001
ENP-FC	42	y = 3.175x-13.745	0.9523	860.2	<0.001
ENP-SS	42	y = 3.226x-14.028	0.948	784.3	<0.001
Lake Kissimmee	35	y = 3.131x-13.364	0.9179	403.7	<0.001
Lochloosa Lake	23	y = 3.435x-14.831	0.9742	907.6	<0.001
Lake Trafford	37	y = 2.944x-12.446	0.9394	590.1	<0.001
LOX	56	y = 2.963x-12.658	0.9646	1552	<0.001
St. Johns River	31	y = 3.142x-13.431	0.9794	1525	<0.001
WCA2A	22	y = 3.294x-14.353	0.9674	683.1	<0.001
WCA3A-HD	20	y = 3.326x-14.531	0.9897	2025	<0.001
WCA3A-N41	19	y = 3.437x-15.095	0.9777	877.9	<0.001
WCA3A-TW	15	y = 3.04x-12.95	0.8948	137.2	<0.001
WCA3B	8	y = 2.968x-12.723	0.9852	599.1	<0.001