Hydrobiologia (2009) 635:329–338
DOI 10.1007/s10750-009-9925-3

PRIMARY RESEARCH PAPER

Relationship between body condition of American alligators and water depth in the Everglades, Florida

Ikuko Fujisaki · Kenneth G. Rice ·
Leonard G. Pearlstine · Frank J. Mazzotti

Received: 2 April 2009 / Revised: 3 August 2009 / Accepted: 10 August 2009 / Published online: 27 August 2009

Abstract Feeding opportunities of American alligators (*Alligator mississippiensis*) in freshwater wetlands in south Florida are closely linked to hydrologic conditions. In the Everglades, seasonally and annually fluctuating surface water levels affect populations of aquatic organisms that alligators consume. Since prey becomes more concentrated when water depth decreases, we hypothesized an inverse relationship between body condition and water depth in the Everglades. On average, condition of adult alligators in the dry season was significantly higher than in the wet season, but this was not the case for juveniles/subadults. The correlation between body condition and measured water depth at capture locations was weak; however, there was a significant negative correlation between the condition and predicted water depth prior to capture for all animals except for spring juveniles/subadults which had a weak positive condition–water depth relationship. Overall, a relatively strong inverse correlation occurred at 10–49 days prior to the capture day, suggesting that current body condition of alligators may depend on feeding opportunities during that period. Fitted regression of body condition on water depth (mean depth of 10 days when condition-water depth correlation was greatest) resulted in a significantly negative slope, except for spring adult females and spring juveniles/subadults for which slopes were not significantly different from zero. Our results imply that water management practices may be critical for alligators in the Everglades since water depth can affect animal condition in a relatively short period of time.

Keywords Condition index · Alligators · Hydrology · South Florida · Prey abundance

Introduction

As a top predator in Everglades wetlands, the American alligator (*Alligator mississippiensis*) consumes a variety of prey items. Smaller alligators

---

Handling editor: Stuart Anthony Halse

I. Fujisaki (✉) · F. J. Mazzotti
Ft. Lauderdale Research and Education Center,
University of Florida, 3205 College Ave,
Davie, FL 33314, USA
e-mail: ikuko@ufl.edu

F. J. Mazzotti
e-mail: fjma@ufl.edu

K. G. Rice
U. S. Geological Survey, Florida Integrated Science
Center, 7920 NW 71 St, Gainesville, FL 32653-3701,
USA
e-mail: krice@usgs.gov

L. G. Pearlstine
Everglades and Dry Tortugas National Parks, South
Florida Natural Resources Center, 950 N Krome Ave,
Homestead, FL 33030, USA
e-mail: Leonard_pearlstine@nps.gov

generally eat invertebrates such as molluscs, insects, and crustaceans, whereas larger alligators eat vertebrates such as fish, reptiles, mammals, birds, and amphibians (Barr, 1997). However, as alligators are opportunistic predators, their diet changes based on prey availability (Valentine et al., 1972; Wolfe et al., 1987; Platt et al., 1990; Delany & Abercrombie, 1986; Delany, 1990; Barr, 1997). Surface water fluctuations in the Everglades affect populations of various aquatic organisms upon which alligators rely as food sources (Kushlan, 1974, 1980; Loftus & Eklund, 1994). When the surrounding marsh is dry, alligator holes (depressions maintained by alligators that retain water during the dry season) have high prey concentrations because they hold water for aquatic organisms including fish, invertebrates, and reptiles; however, when water depth becomes too low or remains low for a long time, prey becomes scarcer (Kushlan, 1974; Kushlan & Kushlan, 1980; Loftus & Eklund, 1994; Ruetz et al., 2005). Changes in abundance and type of available prey due to surface water fluctuations affect alligators' feeding opportunities, and therefore may affect body condition, relative fatness of animals. Body condition is considered to be an indicator of animal health or how well the animal is coping with its environment (Taylor, 1979; Murphy et al., 1990; Dalrymple, 1996).

The Everglades is considered a harsh environment for alligators (Dalrymple, 1996) because of its prolonged high ambient temperatures, altered natural water flows due to canal construction, and seasonal shortages of food (Kushlan, 1987; Jacobsen & Kushlan, 1989; Mazzotti & Brandt, 1994). In the Everglades, alligators are known to display slower growth rates, smaller sizes at maturity, and longer periods to reach maturity than in other portions of their range (Jacobsen & Kushlan, 1989; Mazzotti & Brandt, 1994). Understanding linkages between body condition of alligators and hydrologic pattern (depth and period of inundation), a key factor affecting prey availability and abundance, is important for conservation of this species in the Everglades. The wet season is an important time for crocodilian feeding and growth in other ecosystems with seasonally fluctuation water depths (Gorzula, 1978; Webb & Messel, 1978; Webb et al., 1982, 1983). However, in the Everglades ecosystem, decreased water levels lead to higher prey concentrations, and thus may increase feeding opportunities and reduce the metabolic cost of foraging. Previous studies examined monthly and seasonal differences in body condition of alligators in the Everglades, but relationships between the condition and water depth have not been directly tested. A study by Dalrymple (1996) of wild-caught juvenile alligators from 1985–1991 found an increase in body condition during dry months when water depth was lower in the Shark Valley region of Everglades National Park; however, since the observed pattern of condition also corresponded to changes in other factors such as ambient temperature, the effect of water depth on condition was not clear. Barr (1997) examined the hypothesis of an inverse relationship between the juvenile condition and water depth by comparing condition in presumably dry months (March 1995 and 1996) to condition in wet months (October 1994 and 1995); he found, however, that mean body condition of juveniles was lower in dry periods, possibly because of atypical water depth (high dry season water levels) during his study period. To date, no studies have explicitly examined the relationship between alligator condition and water depth in the Everglades.

The objective of this study was to examine linkages between the body condition of American alligators in the Everglades and surface water depths at their capture locations. Examining effects of water depth on condition of free-ranging alligators in the Everglades is challenging because of possible time-lagged responses; that is, current body condition of animals likely depends on previous feeding opportunities rather than current prey availability, and thus there may be a stronger relationship between body condition and past water depth in the habitat. In this study, we hypothesized that there was an inverse relationship between body condition of alligators and previous surface water depth. Such time-lagged abundance and fecundity responses have been observed with other wildlife populations (Swart et al., 1986; Laundra et al., 2007); however, daily fluctuation and spatial variability in surface water depth make it difficult to test the time-lagged response hypothesis. To address this problem, we examined our hypothesis by using a spatially explicit daily surface water depth model for the Everglades to obtain previous water depths at capture locations of each animal.

Materials and methods

Study area

The study area is in Shark River Slough within Everglades National Park (ENP) (Fig. 1). Shark River Slough is an extensive long-hydroperiod area of ENP characterized by sawgrass (*Cladium jamaicense*) and club-rush (*Eleocharis cellulosa*) marsh (South Florida Natural Resources Center, 2005). The slough is a broad bedrock depression extending from the northern park boundary along Tamiami Trail (U.S. Highway 41) to outflows in mangrove communities along the southwest Florida coast. Shark River Slough is fed by precipitation and central Everglades inflows. Seventy-five percent of south Florida rainfall occurs during the May–October wet season. Both flood and drought years are common and tropical storms and hurricanes are major contributors to wet season rainfall variability. Everglades National Park inflows are constrained along the northern and eastern boundary at Tamiami Trail and the South Dade Conveyance System by large-capacity control structures, which have reduced and rerouted flows to the sloughs for approximately the last 40 years resulting in overall dryer conditions and apparent peat loss.

Morphometric and water depth measurements

We conducted nighttime spotlight surveys by airboat and caught juvenile/subadult ($\leq$75 cm, $<$180 cm) and adult ($\geq$180 cm) alligators by hand or noose in the Everglades during the spring dry season (February 17–April 28) and the fall wet season (July 19–November 14) from 2000 to 2006. Because of low water levels decreasing accessibility of the study area, fewer animals were caught in 2001. We measured snout-vent length (SVL) and total length (TL) to the closest 0.1 cm and body mass (M) to the closest 0.01 kg. We determined sex by cloacal examination of captured animals. We measured water depth manually using a 2 m-long bar marked at 0.1 cm intervals and recorded geographic coordinates at the capture location of each animal.

Body condition indices, defined by a mass and length relationship, have been used in a number of crocodilian studies (Bagenal & Tesch, 1978; Taylor, 1979; Brandt, 1991; Elsey et al., 1992; Dalrymple, 1996; Barr, 1997; Saalfeld et al., 2008). We used Fulton's condition factor (*K*) as it was previously used in studies of the American alligator (Barr, 1997; Rice et al., 2007). To avoid measurement errors due to missing tail tips, we calculated K using SVL instead of TL:

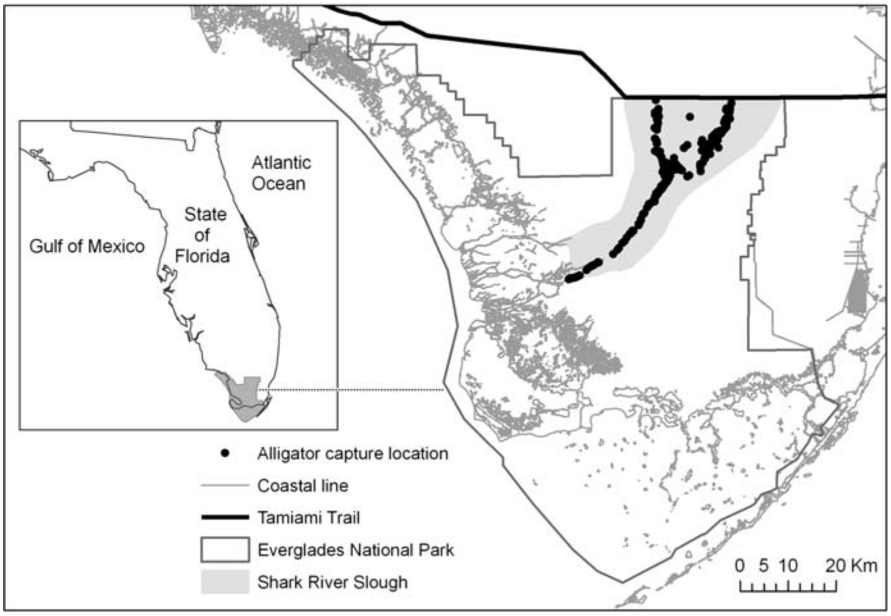

Fig. 1 Map of Everglades National Park and its location within the state of Florida. Capture locations of alligators are indicated with *black dots* and the Shark River Slough area is highlighted in *gray*

$$K = \frac{M}{\mathrm{SVL}^3} \times 10^n$$

where n is a scaling factor which is commonly chosen from integers between 2 and 5 (Cone, 1989). Following a body condition study of American alligators by Rice et al., (2007), we used $n = 5$ since it brought K close to one (Cone, 1989).

Daily surface water depth

We used 400 m resolution raster data of model-predicted daily surface water depths in the Everglades from 2000 to 2006, which are freely available from the U.S. Geological Survey at the Everglades Depth Estimation Network website (http://sofia.usgs.gov/eden/). Model-fitted and field-measured water depths have been shown to be highly consistent within the central portion of the Everglades (Volin et al., 2008) (overall RMSE = 3.31 cm). At each location where animals were caught, we extracted daily modeled water depth data for 90 days: the capture day and 89 days prior.

Analysis

We first visually examined the relationship between the mean body condition and mean water depth at capture time of each survey period by season, size class, and sex. Next, we compared condition between spring and fall seasons by sex and size class using one-tailed *t*-tests (with the data pooled for all years) to test a hypothesis that condition is higher in spring than in fall. We then examined the relationship between body condition and model-predicted historical water depth at the capture location of each animal. We calculated correlation coefficients between K and water depth and assessed correlation based on P values, hypothesizing that correlation is significantly different from zero. We averaged the correlation coefficients in 10-day intervals: 0–9, 10–19, 20–29, 30–39, 40–49, 50–59, 60–69, 70–79, and 80–89 days prior to capture. We identified the period with the strongest correlation for each season, size class, and sex combination, and then we used mean water depth during the period to predict body condition by simple linear regression. We used α-level of 0.05 for all analyses.

Results

We caught 289 alligators including two recaptured animals during the study period (Table 1; Fig. 1). With data combined for all 7 years, mean body condition of alligators in spring was consistently higher than in fall for each size class (juvenile/subadult and adult) and sex. Mean spring condition differed from mean fall condition (Δ) by 1.5% for juvenile/subadult females (Δ = 0.03), 1% for juvenile/subadult males (Δ = 0.02), 13.4% for adult females (Δ = 0.27), and 6.6% for adult males (Δ = 0.13). On average, condition was significantly higher in spring (dry season) than fall (wet season)

Table 1 Summary of number, total length, and condition (K) of captured alligators by size class (juvenile/subadult and adult), sex (female and male), and season (spring and fall)

Size class	Sex	Season	N	Total length (cm)				K				t	P	r
				Mean	SD	Min	Max	Mean	SD	Min	Max			
Juvenile/subadult	Female	Spring	56	138.5	27.9	81.5	178.4	2.05	0.27	1.17	2.76	−0.45	0.326	0.189
		Fall	38	137.8	31.6	82.4	178.0	2.02	0.35	0.95	3.20			−0.111
	Male	Spring	26	141.5	27.1	89.9	173.4	2.01	0.15	1.73	2.32	−0.35	0.363	−0.030
		Fall	28	141.3	29.8	78.7	178.5	1.99	0.27	1.56	3.08			−0.107
Adult	Female	Spring	23	203.4	17.6	180.0	253.0	2.29	0.38	1.74	3.00	−2.93	0.002	−0.424
		Fall	35	197.3	15.9	181.0	254.5	2.02	0.30	1.41	2.65			0.160
	Male	Spring	45	221.8	28.3	180.0	283.2	2.10	0.39	1.40	3.34	−1.79	0.037	−0.130
		Fall	38	221.0	23.9	180.0	271.4	1.97	0.24	1.48	2.74			−0.150

P values are based on one-tailed t-test with hypothesis of higher body condition in spring than fall and r is the Pearson's correlation coefficient between the condition and measured water depth at capture location

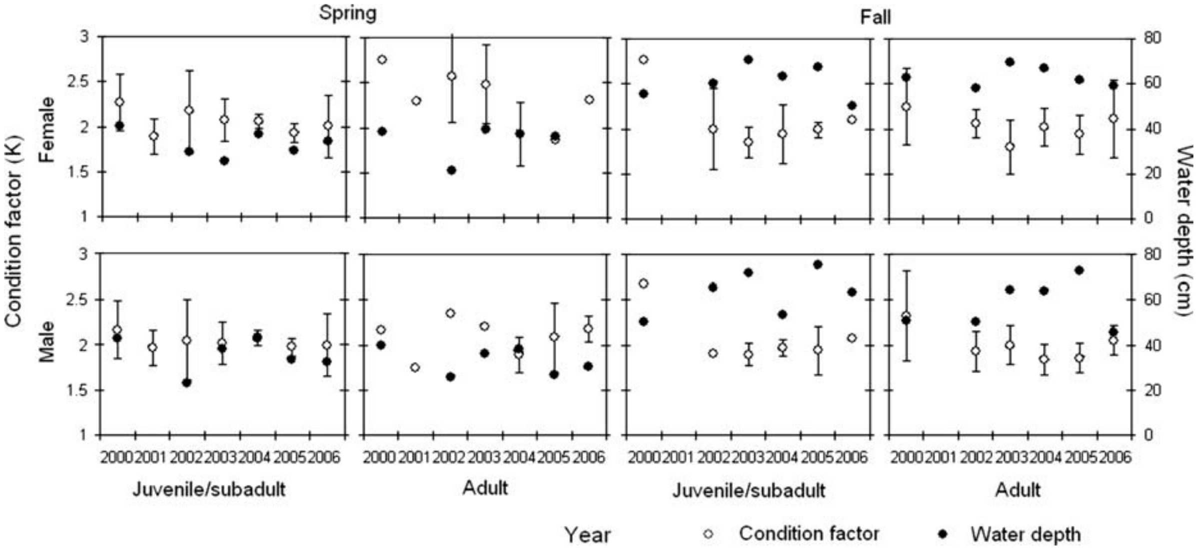

Fig. 2 Plots of mean condition (K) of captured alligators with 95% confidence interval (*open circles*) and average surface water depth manually measured at capture time (*filled circles*) from 2000–2006 by season (spring and fall), sex (female and male), and size class (juvenile/subadult and adult). A *vertical bar* indicating 95% confidence interval was not added when the number of sampled animals was less than three

for adults ($t_{55} = -2.93$, $P = 0.002$ for females; $t_{72} = -1.79$, $P = 0.037$ for males) but not for juveniles/subadults ($t_{90} = -0.45$, $P = 0.325$ for females; $t_{42} = -0.35$, $P = 0.363$ for males).

Overall, correlations between condition and measured water depth at capture time were weak and nonsignificant (r ranged from -0.424 to 0.189) regardless of season, size class, or sex (Table 1). Plots of yearly average condition and measured water depth by season, size class, and sex are shown in Fig. 2. Although each mean condition and water depth represents a small number of animals ($n =$ 1–14), and thus great uncertainty (large confidence interval) exists, there were visible inverse relationships between mean water depth and mean condition in the fall season; this trend was absent in the spring season.

There was moderately high correlation ($r = 0.77$) between measured and model-predicted water depth at raster grids representing capture locations, suggesting relatively strong linear dependence between these two variables. Plots of correlations between condition and model-predicted water depth at capture location for 90 days (capture day and 89 days prior) are shown in Fig. 3 by season, size class, and sex. Correlations between condition and predicted water depth were not significant ($P > 0.05$) on the capture day and 6 days prior for all seasons, size classes, and sexes. In the fall season, there was a pattern of consistently negative correlations between the condition and predicted water depth, implying an inverse relationship between condition and daily water depth prior to capture day for both juveniles/subadults and adults. However, the significance of the correlations (i.e., P value under null hypothesis of no correlation) varied by size class and sex. Inverse correlations were significant for at least 50% of the days for juvenile/subadult males (45 of 90 days) and adult females (55 of 90 days), but rarely significant for juvenile/subadult females (5 of 90 days) and adult males (13 of 90 days). In the spring season, correlation between condition and predicted water depth was not consistent by size class. Juvenile/subadult females and males had very weak (non-significant) positive correlations ($r < 0.2$) between condition and water depth. The correlation was consistently negative for adult females and males in spring. Correlations between adult female condition and predicted water depth were generally similar in spring and fall, but overall correlation was weak and nonsignificant in spring compared to fall. Adult males in spring had significant inverse correlation (74 of 90 days) between condition and water depth that was relatively strong until around 40 days prior to capture.

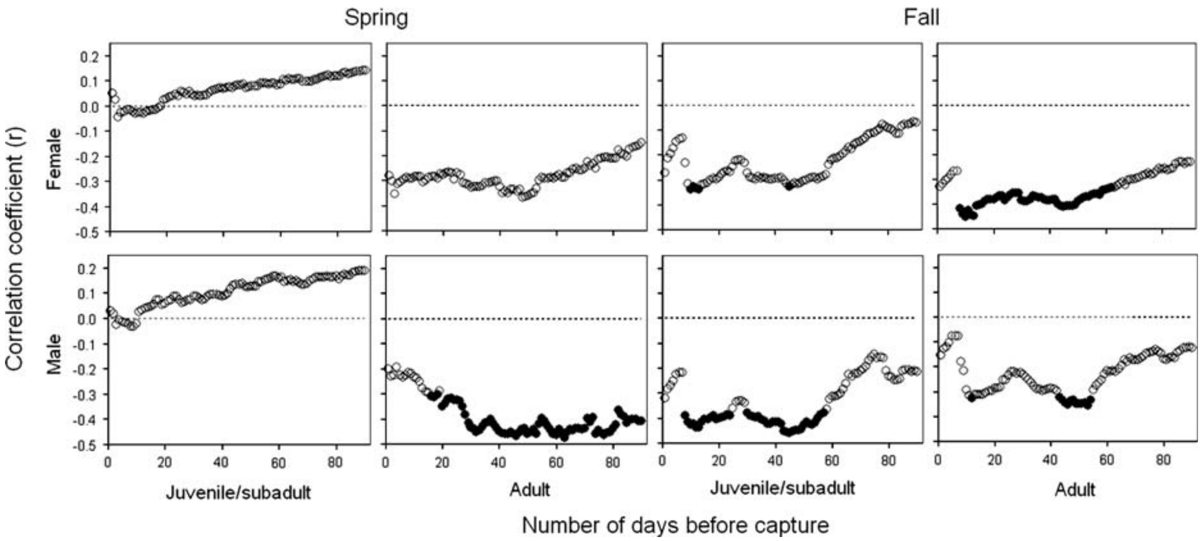

Fig. 3 Plots of Pearson's correlation coefficient (*r*) between condition (*K*) and the model-predicted daily water depth versus number of days before the capture date for sample animals by season (spring and fall), sex (female and male), and size class (juvenile/subadult and adult). *Filled circles* indicate that the correlations are significant at α level of 0.05

Mean correlation between condition and predicted water depth was strongest at 10–19 days and 80–89 days prior to capture for fall females (both juvenile/subadult and adult) and spring juvenile/subadult (both female and male) (Table 2). For all others, mean correlation was strongest during the 40–49 days prior to capture. Using mean water depth of these identified periods as an independent variable to predict condition, the slope was negative for all seasons, size classes, and sexes except spring juveniles/subadults (Fig. 4). The negative slope was significant for all fall animals and spring adult males.

Discussion

The relationship between body condition of alligators and water depth varied by size class, season (February–April dry season vs. September–November wet season), and sex. We found consistently higher mean body condition in spring for all size classes and sexes, but the seasonal difference was significant only for adults. The large percentage increase in body condition for spring adult females (13.4%) was likely due, in part, to reproductive behavior, since our spring sample season coincided with the early breeding period in the Everglades. However, male adults also

Table 2 Mean Pearson's correlation coefficient (*r*) between condition factor (*K*) and predicted water depth for nine 10-day intervals prior to capture date by size class (juvenile/subadult and adult), sex (female and male), and season (spring and fall)

Size class	Sex	Season	0–9 days	10–19 days	20–29 days	30–39 days	40–49 days	50–59 days	60–69 days	70–79 days	80–89 days
Juvenile/subadult	Female	Spring	−0.014	−0.009	0.046	0.055	0.078	0.086	0.103	0.113	**0.133**
		Fall	−0.215	**−0.313**	−0.249	−0.294	−0.310	−0.279	−0.181	−0.107	−0.088
	Male	Spring	−0.013	0.050	0.075	0.086	0.122	0.151	0.145	0.162	**0.177**
		Fall	−0.302	−0.412	−0.365	−0.407	**−0.443**	−0.386	−0.259	−0.179	−0.224
Adult	Female	Spring	−0.301	−0.287	−0.291	−0.315	**−0.348**	−0.307	−0.267	−0.221	−0.179
		Fall	−0.338	**−0.406**	−0.368	−0.380	−0.399	−0.363	−0.319	−0.278	−0.243
	Male	Spring	−0.221	−0.292	−0.354	−0.430	**−0.455**	−0.437	−0.447	−0.437	−0.400
		Fall	−0.143	−0.308	−0.244	−0.279	**−0.331**	−0.292	−0.192	−0.152	−0.144

Bold numbers indicate the strongest mean correlation for each size class, sex, and season

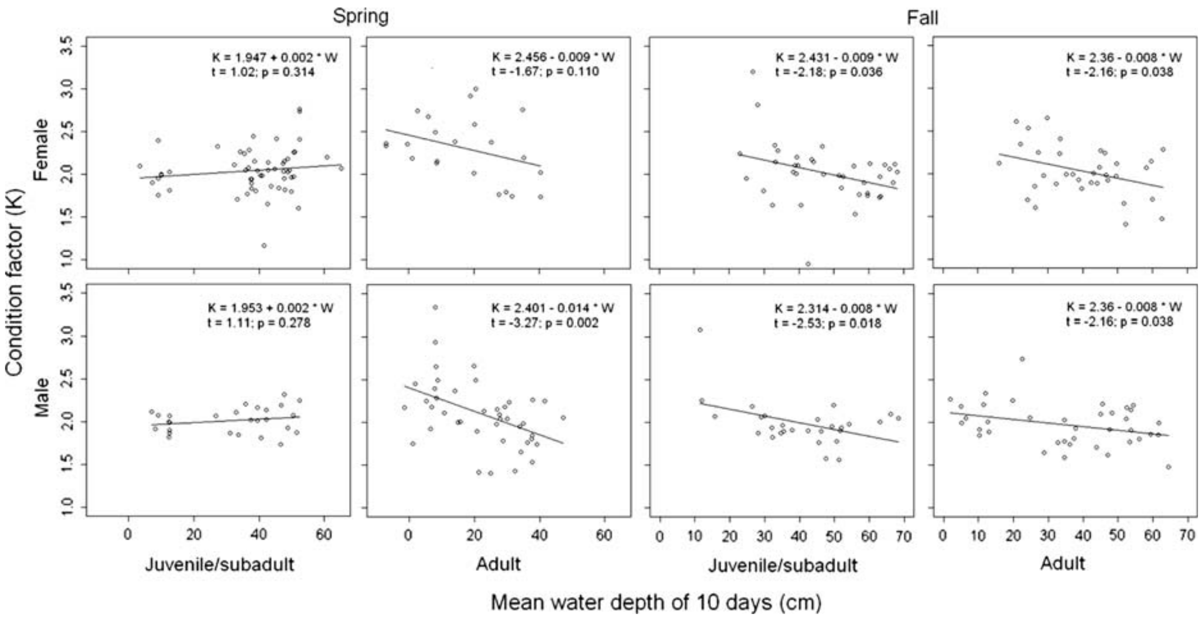

Fig. 4 Plots of condition (*K*) versus mean water depth (W) for 10-day intervals when mean correlation between condition and water depth was the strongest (based on Table 2) by season (spring and fall), sex (female and male), and size class (juvenile/subadult and adult). The regression equations, test statistics, and *P* values for significance of the slope are indicated. Water depth is calculated as predicted water stage minus the digital elevation model of ground elevation relative to the NAVD 88 vertical datum. Water depth is positive if predicted water stage is above ground elevation, zero if stage is at ground elevation, and negative if stage is below ground elevation

had a larger percentage increase (6.6%) in their body condition compared to juveniles/subadults (1.5% for females and 1% for males). Our results were consistent with Dalrymple (1996), who found nonsignificant monthly differences in juvenile condition; nonetheless, he observed a trend of higher body condition in dry season. Although our results did not agree with Barr (1997), who found higher body condition of juveniles in the wet season (October), he noted that water depth was unusually high during one of the dry seasons (March 1995) during his study period from October 1994 to March 1996. Atypical water levels during Barr's study period could have been affected by an El Niño event in winter 1995, which caused above average rainfall and a La Niña event in fall 1995 (Gershunov & Barnett, 1998; Hoerling et al., 1997; Lipp et al., 2001). Our results combined with studies by Dalrymple (1996) and Barr (1997) may suggest that condition is related to water level, rather than season.

Negative correlations between body condition and water depth in fall were consistent with our hypothesis regardless of size class and sex. Negative correlation in fall was relatively strong during the 10–49 days prior to capture. Water depth is generally higher in fall in the Everglades; therefore, reduced water depth may make foraging easier for alligators. Alligators attempt to capture prey more often and are more successful (captures per attempt) when prey are concentrated than when prey are dispersed (F. Mazzotti, unpublished observation). Similar observations were made by Jacobsen & Kushlan (1989), who found that alligators have difficulty in finding and capturing widely dispersed prey in deeper water, and Barr (1997) who found that alligators were more successful at capturing prey on the surface than at capturing actively moving prey underwater.

Unlike fall season, results for spring season varied by size class. Consistent with fall results, adults had an inverse relationship between condition and water depth. This inverse relationship was relatively strong during the 40–49 days prior to capture. Further, adults had higher condition in spring than fall. During spring when water levels are lower, large individuals occupy alligator holes which are an important water source for a variety of aquatic animals. High concentrations of aquatic prey (e.g., fish, reptiles, and invertebrates) that inhabit alligator holes

(Kushlan, 1974; Kushlan & Kushlan, 1980; Loftus & Eklund, 1994), along with the birds and mammals that forage there (Fredrick & Spalding, 1994; Hoffman et al., 1994), provide large alligators access to both variety and quantity of food sources.

Adult female condition relationships with water depth were consistent between spring and fall, but adult male relationships were not (Fig. 3). For males, a negative correlation became stronger from the capture day until around 40 days earlier and remained constant thereafter. This difference between the sexes may be due to a behavioral difference between males and females. Females are more sedentary, while males generally have a larger activity range (Goodwin & Marion, 1979), and thus may have more opportunities to find concentrations of prey.

Contrary to our hypothesis, the correlation between condition and water depth prior to capture was weakly positive for juveniles/subadults. This lack of body condition–water depth relationship may be related to the availability of prey items that juveniles/subadults consume. Adults consume diverse prey depending on availability, whereas juveniles/subadults have less variability in their prey items (Barr, 1997). For example, birds and mammals, which are available during low water conditions, are less important for smaller alligators. In the Everglades, amphibians, reptiles, and gastropods such as apple snails (*Pomacea paludosa*) constituted the largest mass recovered from stomachs of juveniles/subadults (Barr, 1997). Size-mediated habitat selection may also affect feeding opportunities of alligators. Campbell & Mazzotti (2004) found fewer small alligators in alligator holes in the spring dry season (when prey are concentrated in the holes) and more in the fall wet season. Alligator holes may serve as social refugia for small alligators seeking to avoid adults, rather than as locations for foraging on prey concentrations during the spring dry season because small alligators that do not avoid adults may be eaten by them (Delany & Abercrombie, 1986). Further social and behavioral studies of activities and habitat use by alligators may provide an explanation for the differences in condition-water depth relations by season and size class.

Although we hypothesized an inverse relationship between alligator body condition and water depth, this hypothesis is unlikely to be confirmed under extremely low water conditions when aquatic prey become scarcer. Chick et al. (2004) defined a dry-down event, which affects abundance of large fish in the Everglades, as water depth less than 10 cm. Severe drought occurred during our winter–spring 2001 study period and standing water was absent in most of the Everglades until March (Smith et al., 2003), but we do not have a sufficient number of samples to compare alligator body condition in this season to that of others. In all other years, some standing water existed in all capture locations and there was only one observation with measured water depth less than 10 cm.

Our study focused only on relationships between alligator body condition and water depth in the Everglades; however, we should note that there are other factors that may affect condition such as habitat, animal density, and ambient temperature (Taylor, 1979; Coulson & Hernandez, 1983; Lewis & Gatten, 1985; Seebacher et al., 2003; Rice et al., 2007). Studies that examine linkages between body condition and other environmental factors, such as ambient temperature and local differences in site productivity, may help us understand whether there are other determinants of body condition for free-ranging alligators.

Usefulness of alligators as an indicator of ecological responses to ecosystem restoration is dependent on our ability to link responses to suitability of environmental conditions and hydrologic change (Mazzotti et al., 2009). Correlations between ecological responses and hydrologic changes may permit assessment of positive or negative trends in restoration. Although data presented here support hypotheses for effects of diminished freshwater flow on condition of alligators, they do not prove a direct relationship. Additional studies are needed to evaluate condition of alligators in relation to hydrology, habitat, temperature, and food supply.

Acknowledgments This study was funded by the U.S. Army Corps of Engineers Comprehensive Everglades Restoration Plan Monitoring and Assessment Program, the U.S. Geological Survey Priority Ecosystems Sciences program, and the U.S. National Park Service Critical Ecosystem Science Initiative. We thank M. Cherkiss, K. Lodligue and both anonymous reviewers for making helpful comments, D. DeAngelis, H. Chen, K. Hart, and D. Ogurcak for reviewing the manuscript, and J. Frost and R. Harvey for providing editorial assistance.

References

Bagenal, T. B. & F. W. Tesch, 1978. Age and growth. In: Bagenal T. B. (ed) Methods for Assessment of Fish Production in Freshwater, 3rd edn. IBP Handbook No. 3. Blackwell Scientific Publications, Oxford: 101–136.

Barr, B., 1997. Food habits of the American alligator, *Alligator mississippiensis*, in the southern Everglades. Ph. D. Dissertation, University of Miami, Coral Gables, Florida.

Brandt, L. A., 1991. Growth of juvenile alligators in Par Pond, Savannah River site, South Carolina. Copeia 1991: 1123–1129.

Campbell, M. R. & F. J. Mazzotti, 2004. Characterization of natural and artificial alligator holes. Southeastern Naturalist 3: 583–594.

Chick, J. H., C. R. Ruetz & J. C. Trexler, 2004. Spatial scale and abundance patterns of large fish communities in freshwater marshes of the Florida Everglades. Wetlands 24: 652–664.

Cone, R. S., 1989. The need to reconsider the use of condition indexes in fishery science. Transactions of the American Fisheries Society 118: 510–514.

Coulson, R. A. & T. Hernandez, 1983. Alligator metabolism, studies on chemical reactions in vivo. Comparative Biochemistry and Physiology 74B: 1–182.

Dalrymple, G. H., 1996. Growth of American alligators in the Shark Valley region of Everglades National Park. Copeia 1996: 212–216.

Delany, M. F., 1990. Late summer diet of juvenile American alligators. Journal of Herpetology 24: 418–421.

Delany, M. F. & C. L. Abercrombie, 1986. American alligator food habits in north central Florida. Journal of Wildlife Management 50: 348–353.

Elsey, R. M., T. Joanen, L. McNease & N. Kinler, 1992. Growth rates and body condition factors of *Alligator mississippiensis* in coastal Louisiana wetlands: a comparison of wild and farm-released juveniles. Comparative Biochemistry and Physiology 103A: 667–672.

Fredrick, P. C. & M. G. Spalding, 1994. Factors affecting reproductive success of wading birds (Ciconiiformes) in the Everglades ecosystem. In Davis, S. M. & J. C. Ogden (eds), Everglades: the Ecosystem, its Restoration. St. Lucie Press, Delray Beach, FL: 659–691.

Gershunov, A. & T. P. Barnett, 1998. ENSO influence on intraseasonal extreme rainfall and temperature frequencies in the contiguous Unites States: observations and model results. Journal of Climate 11: 1575–1586.

Goodwin, T. M. & W. R. Marion, 1979. Seasonal activity ranges and habitat preference of adult alligators in a north-central Florida lake. Journal Herpetology 13: 157–164.

Gorzula, S. J., 1978. An ecological study of *Caiman crocodilus crocodilus* inhabiting savanna lagoons in the Venezuelan Guayana. Oecologia 34: 21–34.

Hoerling, M. P., A. Kumar & N. Zhong, 1997. El Nino, La Nina, and the nonlinearity of their teleconnections. Journal of Climate 10: 1769–1786.

Hoffman, W., G. T. Bancrof & R. J. Sawicki, 1994. Foraging habitat of wading birds in the water conservation areas of the Everglades. In Davis, S. M. & J. C. Ogden (eds), Everglades: the Ecosystem, its Restoration. St. Lucie Press, Delray Beach, FL: 585–614.

Jacobsen, T. & J. A. Kushlan, 1989. Growth dynamics in the American alligator (*Alligator mississippiensis*). Journal of Zoology 219: 309–328.

Kushlan, J. A., 1974. Observations of the role of the American alligator (*Alligator mississippiensis*) in the southern Florida wetlands. Copeia 1974: 993–996.

Kushlan, J. A., 1980. Population fluctuations in Everglades fishes. Copeia 1980: 870–874.

Kushlan, J. A., 1987. External threats and internal management: the hydrologic regulation of the Everglades, Florida, USA. Environmental Management 11: 109–119.

Kushlan, J. A. & M. S. Kushlan, 1980. Everglades alligator nests: nesting sites for marsh reptiles. Copeia 1980: 1930–1932.

Laundra, J. W., L. HernAndez & S. G. Clark, 2007. Numerical and demographic responses of pumas to changes in prey abundance: testing current predictions. Journal of Wildlife Management 71: 345–355.

Lewis, L. Y. & R. E. Gatten Jr., 1985. Aerobic metabolism of American alligators, *Alligator mississippiensis*, under standard conditions and during voluntary activity. Comparative Biochemistry and Physiology 80A: 442–447.

Lipp, E. K., N. Schmidt, M. E. Luther & J. B. Rose, 2001. Determining effects of El Nino-Southern Oscillation events on coastal water quality. Estuaries 24: 491–497.

Loftus, W. F. & A. M. Eklund, 1994. Long-term dynamics of an Everglades small-fish assemblage. In Davis, S. M. & J. C. Ogden (eds), Everglades: the Ecosystem, its Restoration. St. Lucie Press, Delray Beach, FL: 461–482.

Mazzotti, F. J. & L. A. Brandt, 1994. Ecology of the American alligator in a seasonally fluctuating environment. In Davis, S. M. & J. C. Ogden (eds), Everglades: the Ecosystem, its Restoration. St. Lucie Press, Delray Beach, FL: 485–505.

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

Murphy, B. R., M. L. Brown & T. A. Springer, 1990. Evaluation of the relative weight (Wr) index, with new application to walleye. North American Journal of Fisheries Management 10: 85–97.

Platt, S. G., C. G. Brantley & R. W. Hastings, 1990. Food habits of juvenile American alligators in the upper Lake Pontchartrain estuary. Northeast Gulf Science 11: 123–130.

Rice, A. N., J. P. Ross, A. R. Woodward, D. A. Carbonneau & H. F. Percival, 2007. Alligator diet in relation to alligator mortality on Lake Griffin, FL. Southeastern Naturalist 6: 97–110.

Ruetz, C. R. III, J. C. Trexler, F. Jordan, W. F. Loftus & S. A. Perry, 2005. Population dynamics of wetland fishes: spatio-temporal patterns synchronized by hydrological disturbance? Journal of Animal Ecology 74: 322–332.

Saalfeld, D. T., K. K. Webb, W. C. Conway, G. E. Calkins & J. P. Duguay, 2008. Growth and condition of American alligators (*Alligator mississippiensis*) in an inland wetland of east Texas. Southeastern Naturalist 7: 541–550.

Seebacher, F., R. M. Elsey & P. L. Trosclair III, 2003. Body temperature null distributions in reptiles with nonzero heat capacity: seasonal thermoregulation in the American alligator (*Alligator mississippiensis*). Physiological and Biochemical Zoology 76: 348–359.

Smith, S. M., D. E. Gawlik, K. Rutchy, G. E. Crozier & S. Gray, 2003. Assessing drought-related ecological risk in the Florida Everglades. Journal of Environmental Management 68: 355–366.

South Florida Natural Resources Center, 2005. An assessment of the Interium Operational Plan. South Florida Natural Resources Center, Everglades National Park, Homestead, FL. Project Evaluation Report. SFNRC Technical Series 2005: 2. 60 pp.

Swart, J., M. R. Perrin, J. W. Hearn & L. J. Fourie, 1986. Mathematical model of the interaction between rock hyrax and caracal lynx, based on demographic data from populations in the Mountain Zebra National Park, South Africa. South African Journal of Science 82: 289–294.

Taylor, J. A., 1979. The foods and feeding habits of subadult *Crocodylus porosus* Schneider in Northern Australia. Australian Wildlife Research 6: 347–359.

Valentine, J. M., J. R. Walther, K. M. McCartney & L. M. Ivy, 1972. Alligator diets on the Sabine National Wildlife Refuge, Louisiana. Journal of Wildlife Management 26: 1–27.

Volin, J., Z. Liu, A. Higer, F. Mazzotti, D. Owen, J. Allen & L. Pearlstine, 2008. Validation of Spatial Continuous EDEN Water-Surface Model for the Everglades, Florida. Department of Natural Resources Management and Engineering, University of Connecticut: 55.

Webb, G. J. & H. Messel, 1978. Morphometric analysis of *Crocodylus porosus* from the north coast of Arnhem Land, Northern Australia. Australian Journal of Zoology 26: 1–27.

Webb, G. J., S. C. Manolis & R. Buckworth, 1982. *Crocodylus johnstoni* in the McKinlay River Area, N. T. I: variation in the diet, and a new method of assessing the relative importance of prey. Australian Journal of Zoology 30: 877–899.

Webb, G. J. W., R. Buckworth & S. C. Manolis, 1983. *Crocodylus johnstoni* in the McKinlay River area, N. T. III: growth, movement and the population age structure. Australian Wildlife Research 10: 383–401.

Wolfe, J. L., D. K. Bradshaw & R. H. Chabreck, 1987. Alligator feeding habits: new data and a review. Northeast Gulf Science 9: 1–8.