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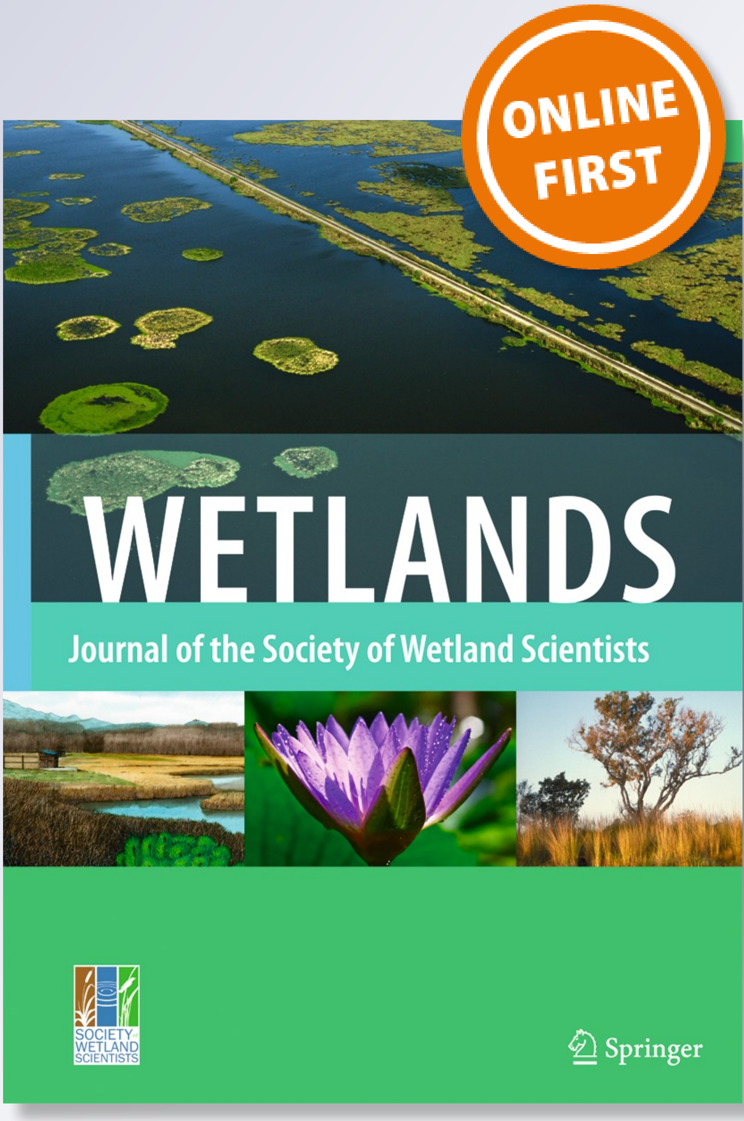

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ORIGINAL RESEARCH

Dry Years Decrease Abundance of American Alligators in the Florida Everglades

J. Hardin Waddle[1] · Laura A. Brandt[2] · Brian M. Jeffery[3] · Frank J. Mazzotti[3]

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Abstract The Everglades has been greatly reduced and is threatened by land use change and altered hydrology. The Comprehensive Everglades Restoration Plan calls for monitoring and assessment of key ecosystem attributes, one of which is abundance of American alligators. We examined 10 years of alligator night spotlight counts from Arthur R. Marshall Loxahatchee National Wildlife Refuge along two canals and in the interior marsh to determine trends and how dry years affect alligator abundance. Alligators showed population response to hydrologic conditions. In particular, there were declines in abundance after dry years followed by an apparent recovery in abundance in subsequent years. Increases in abundance were lower in the marsh than L-40 Canal. In addition, there was evidence that intensity of dry events affected population dynamics with greater declines observed in years with drier conditions. Results revealed that overall population of alligators increased from 2004 to 2013, but that increases varied by survey route. These results demonstrate that dry years cause a decline in alligator abundance proportional to the intensity of the dry event, and that it is important to make a distinction between canals and marsh when measuring alligator response to hydrology.

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Introduction

The Everglades is the largest subtropical wetland in the United States and the focus of one of the world's largest wetland restoration efforts. This once vast peatland covered over 1 million ha in southern Florida, but has been reduced to less than half its original size and is threatened by a number of environmental disturbances including altered hydrology, land use change, and invasive species (Chimney and Goforth 2001). Compartmentalization for flood protection and water supply has created a landscape that is much different from the original condition of the Everglades (Light and Dineen 1994). Remaining wetland areas in Everglades National Park and the Water Conservation Areas are influenced by water management practices and often do not experience a natural hydropattern. This alteration of the natural hydrology led to many consequences that were recognized in the 1990s and resulted in the Central and South Florida (C&SF) Project Restudy to develop a plan for Everglades restoration. A focus of that plan (the Comprehensive Everglades Restoration Plan; CERP) is to restore hydrology to a more natural pattern to improve ecosystem function.

To track progress towards this goal, a system-wide monitoring and assessment plan (MAP) was developed (RECOVER 2001). The MAP established a series of performance measures (metrics associated with specific management objectives) to be monitored and assessed over the 50 year duration of CERP to determine ecosystem responses and if implementation of the CERP was meeting specific goals. For each performance measure, priorities were to document

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status and trends, as well as development of pre-CERP reference states that described natural variability and relations to patterns of change to hydrologic drivers. Because of their strong ties to hydrology, American alligators (*Alligator mississippiensis*) were one of the indicator species selected for monitoring (Mazzotti et al. 2009). In addition, relative abundance of alligators is one of the CERP performance measures.

Historically, alligators occurred in virtually all wetland habitats of the Everglades with highest abundance in the wetland habitats peripheral to the deeper slough areas where limestone bedrock was near the surface, and in freshwater mangrove areas (Craighead 1968). Fewer alligators were found in the central slough and sawgrass areas characterized by deeper peat deposits. Spatial patterns of habitat use of alligators have been changed by water management. Today alligators are most abundant in the central slough and canals (Kushlan 1990) and are rare in the peripheral wetlands (Mazzotti and Brandt 1994). Although canals provide nearly permanent access to water, they serve as poor juvenile habitat, offer little protection from predation, and have fewer feeding opportunities because of the lack of cover, and in some cases, steep sides. Canals may function as reproductive sinks for alligators due to a high probability of nest flooding and low hatchling survival (Chopp 2003). Whereas canals may not dry out during periods of low water, periods of low water may affect alligator numbers in canals because animals are concentrated and suffer mortality from fights or cannibalism (Deitz 1979; Delany and Abercrombie 1986).

The interior marshes of the Everglades, which include sloughs, wet prairie, sawgrass, and tree islands, provide nesting and juvenile habitat, but are subject to natural seasonal drying resulting in periodic low water or dry periods, and extreme droughts historically occurring on average every 10 years (Abtew et al. 2006). Alligators in marsh habitat can benefit from moderate low water periods due to high prey concentrations as water becomes limited to small refugia, and alligators have evolved a behavioral mechanism to cope with these dry periods in the marsh through the creation of "gator holes" (McIlhenny 1935; Kushlan 1974; Mazzotti and Brandt 1994). However, extreme or repeated dry periods caused by drought or water management could impact alligator populations through direct mortality (smaller alligators may become desiccated or cannibalized by larger animals), reduction in reproduction (males have a harder time moving around to find females), and reduction in food resources.

There is concern that increasing frequency and intensity of dry events as a result of water management are having negative effects on alligator populations of the Everglades (Mazzotti et al. 2009). Before the era of compartmentalization and water control, extremely low water depths in the Everglades marsh occurred at lower frequency than today (Fennema et al. 1994). During the late 1960s, natural droughts combined with drainage of wetlands resulted in declines of alligators in the Everglades (Carr 1967; Jacobsen and Kushlan 1984; Mazzotti and Brandt 1994). Fujisaki et al. (2011) documented declining trends in small and medium-sized alligators across 8 study areas in the Everglades from 2001 to 2008, and suggested that the 2001 drought may have contributed to this decline. They also suggested that adult alligators may be less susceptible to drought than smaller individuals in these populations. Although there is evidence that extreme dry years, such as those during droughts, may negatively impact alligators, it is not clear to what extent these effects may be exacerbated by a high frequency of dry events over multiple years. We hypothesize that dry events on average of once every 3 to 5 years would support populations of alligators in the Everglades at targeted restoration levels (Mazzotti et al. 2009).

Night spotlight counts of alligators have been the most frequently used method for monitoring abundance of alligators (Wood et al. 1985). The method is used throughout the range of the species. Estimates of abundance from spotlight counts are limited by the same assumptions of any count-based wildlife sampling protocol. To use counts alone as an index of abundance or to determine a trend in abundance over time requires an assumption that the same proportion of the true population of alligators is observed on subsequent visits (Taylor and Neal 1984). This limitation has long been recognized, and various methods have been employed to mitigate the bias of violating this assumption. Most of these approaches involve standardizing survey conditions, time of year, observer, route, and equipment (Wood et al. 1985). Though these methods improve effectiveness of night spotlight count surveys, they must be combined with analytical methods, such as the hierarchical model that Fujisaki et al. (2011) developed, that explicitly models the detection process along with the abundance process.

In this study, we examine count data from 10 years of alligator spotlight counts in marsh and canals at the Arthur R. Marshall Loxahatchee National Wildlife Refuge (LNWR). We employed a hierarchical model of abundance for open populations that estimated annual abundance as well as trends in abundance (Dail and Madsen 2011). Our objectives were to estimate trends in alligator abundance within LNWR; test for differences in trends between marsh (natural) and canal (man-made) habitats; and analyze effect of annual minimum water depth on annual population growth rate to determine effect of dry years on alligator populations. We predicted that alligator abundance would decline after dry years. Based on previous observations we also predicted that alligator detection would decline as water temperature and depth increased (Fujisaki et al. 2011).

Methods

Study Area

The LNWR is a 57,324 ha tract of Everglades wetlands located in Palm Beach County, Florida. It contains all of Water Conservation Area 1 and is managed as one of the U.S. Fish and Wildlife Service's over 540 National Wildlife Refuges under a license agreement with the South Florida Water Management District. Originally this area was a fluvial wetland system that experienced sheet flow during annual high water events, but since the 1950s it has been completely impounded by surrounding canals and levees (Brandt et al. 2000). In the current, post-impoundment condition, the hydrology of LNWR is altered such that there is a north to south gradient in hydroperiod and depth in the marsh with areas in the north drier (shorter hydroperiod and shallower depth) and areas in the south wetter than would have occurred in the natural system (Richardson et al. 1990). Hydrology in the marsh is determined by local precipitation and water management that follows a water regulation schedule (U.S. Army Corps of Engineers 1994) that was developed to benefit ecological conditions in the refuge and allow for greater storage of water within the C&SF system during wet and normal rainfall years. Marsh depths follow a seasonal pattern with highest water depths in the fall (generally October, average maximum depth of 72.5 cm for the last 18 years at the 1–7 gauge) and lowest water depths in the spring (generally May, average minimum depth of 17.6 cm for the last 18 years at the 1–7 gauge) corresponding with the end of the wet and dry seasons, respectively.

Alligator surveys were conducted in three spatially distinct areas: Marsh, L-39 Canal, and L-40 Canal (Fig. 1). Survey routes were a minimum of 1 km from each other to provide independent routes. This distance was based on previous radio telemetry studies that quantified home ranges and straight line movements for alligators in marsh and canal habitats (Morea 1999). Each of these areas was sampled with a single route that was divided into 500-m segments to provide spatial replication. Because the entire route is sampled from one end to the other each sampling occasion, alligators can only be counted once during each survey period. We selected 500 m for the segment length based on radio telemetry data that showed average movement of alligators over 24 h is <500 m (Morea 1999). The 21 km Marsh route is located in the interior of the refuge, and was divided into 42 segments. The L-39 Canal route was 21.5 km and divided into 43 segments. The L-40 Canal route was 10 km, and divided into 20 segments. Surveys were conducted in spring of each year, usually in April. This time period is late in the typical annual dry season of south Florida (Abtew et al. 2006).

Two night-time spotlight surveys (Woodward and Moore 1990; Mazzotti et al. 2010) were conducted from airboats along the established routes each spring from 2004 to 2013. The two surveys were conducted at least 14 days apart to achieve independent counts (Woodward and Moore 1990) and were not done the day of, before, or after a full moon, when water temperature was < 18 °C, when there was heavy rain, or when wind was > 24 km/hr. All surveys were conducted by the same observer (Brandt) using the same airboat and a 200,000 cp spotlight. This sampling regime is effectively a "robust design" where surveys are conducted over successive years (primary periods) with repeat visits within each primary period that spans a short period of time for which population closure may be assumed (secondary periods). Alligators were sampled up to 50 m on either side of the standard transect route, though visibility was sometimes less than that distance in the marsh and was constrained by the width of the canals (35–65 m). Alligators were approached to get a location (using a hand held Global Positioning System, GPS) and size estimate (total length, TL) in 0.25 m increments. If a size estimate could not be made, alligators were classified as small (<1.25 m), medium (≥1.25–<1.75 m), large (≥1.75 m), or unknown. Analysis was performed separately on three groups of size classes: small (0.5–1.25 m), harvestable (≥1.25 m) and non-hatchling alligators (total population≥0.5 m). Hatchling alligators (those< 0.5 m) and alligators of unknown size (<1 % of counts) were not used in the analysis. Although hatchlings are detected on surveys, their survival, even in good conditions, is very low. Thus, including hatchlings would artificially inflate counts. These size classes were selected for analysis because the non-hatchling alligator class is what is used for the CERP performance measure and the harvestable size class is what is used for setting harvest quotas. No harvest of alligators was conducted at LNWR during the time-span of this study. Water temperature at the start and end of the survey was averaged to obtain the water temperature for the survey. Water stage the day of the survey was obtained from the U.S. Geological Survey (USGS) 1–7 and 1-8C gauges to represent stage for the marsh and canal surveys, respectively, for use as a detection covariate. In addition, daily water stage from the USGS 1–7 gauge over the last 10 years was obtained and examined to determine water depth for characterization of each year as wet or dry (see below) for use in the analysis.

Data Analysis

Counts of alligators from spotlight surveys were analyzed using the model developed by Dail and Madsen (2011). This model is a generalized hierarchical *N*-mixture abundance model (Royle 2004), and is appropriate for use for open populations (those where abundance may change over time) and is also suitable for use with "robust design" data. The counts at each segment i (in this case each 500 m increment) from each sample j during each year t are summarized as y_{ijt}. The initial

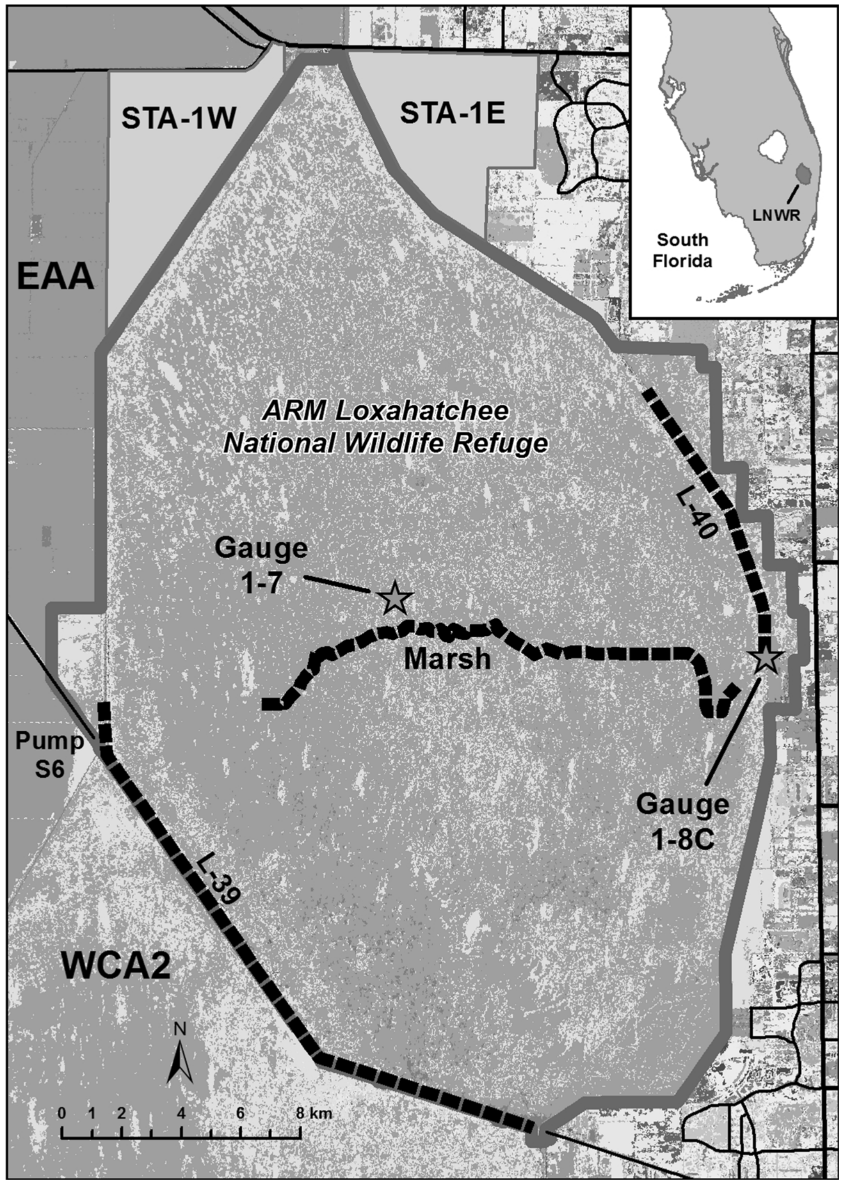

Fig. 1 Location of the three alligator survey routes and the two water level gauges in Arthur R. Marshall Loxahatchee National Wildlife Refuge

abundance (λ), finite rate of increase (γ), and detection probability at each sample (p_j) are modeled with the following hierarchical model:

$$N_{it} \sim \text{Poisson}(\lambda)$$
$$N_{i,t+1} \sim \text{Poisson}(N_{it}\gamma)$$
$$y_{ijt} \sim \text{Binomial}\left(N_{it}, p_j\right)$$

where N_{it} is the abundance and $\gamma>1$ indicates that the population is increasing. Note that λ represents the initial abundance, and each additional year the abundance ($N_{i,t+1}$) is derived from the estimates of the trend over the interval between years and the abundance of the previous year (N_{it}).

The parameters λ, γ, and p may be modeled as a function of covariates as is typical in this type of modeling, with intercept and beta values for the slopes of the covariate effects modeled in the formula for each. Because their range of support spans all positive real numbers, parameters λ and γ are modeled as log-linear functions. Because its range of support is the set of real numbers between 0 and 1, parameter p is modeled as a logit-linear function.

We used two sets of categorical covariates, Route (L-39 Canal, L-40 Canal, and Marsh) and Canal (1=canal, 0=marsh), to model variation in initial abundance. Route, Canal, Year (different value for each interval possible), and Hydrology (dry or wet in the previous calendar year categorical variable) were used as covariates to model variation in the rate of increase. Calendar years were considered dry if any daily value of water stage at the 1–7 gauge was < 4.72 m mean sea level (15.5 ft). Ground elevation at the 1–7 gauge is approximately 4.57 m (15 ft), thus readings below 4.72 m (15.5 ft) represent water depths on the marsh less than

15 cm, a depth at which it is more difficult for alligators to move around. The driest time of a given calendar year occurs after the spring surveys (generally in May or June), so dry year effects are observed in the following calendar year spring survey. This 15 cm depth also represents a drier than average condition in the marsh (average minimum dry season depth during this study was 17.6 cm) but is not synonymous with a drought which is a more extreme event defined regionally.

Water temperature and daily stage on the day of the survey at the 1–7 gauge (marsh) or 1-8C gauge (canal), standardized to have mean 0, were used as covariates of detection probability. We also used the Canal category as a covariate of p to determine if the probability of detection varied between the marsh and canal routes.

Model fitting was done using maximum likelihood methods in the R statistical environment (R Core Team 2012) using the pcountOpen function in the R package "unmarked" (Fiske and Chandler 2011). This function is specifically written to handle the Dail and Madsen model (Chandler and King 2011). The upper bound of the discrete integration parameter (K) was set to 200 (maximum observed count was 45) for all models after trials determined that parameter estimates were insensitive to selection of larger values (Fiske et al. 2010). We used information-theoretic model selection based on Akaike's Information Criterion (AIC) to identify the best model from the set of models representing combinations of covariates we hypothesized to be important to various processes of the hierarchical model. Models were chosen for analysis based on a priori hypotheses about the system. First, λ and γ were held constant while combinations of the covariates on p were tested. Once the appropriate covariates for p were determined, models with covariates on λ and γ were tested. The entire set of models was fit separately for the non-hatchling, small, and harvestable size classes.

We examined effect of low water levels on the marsh population trend by modeling effect of minimum daily stage value for the previous calendar year on the estimate of the finite rate of population increase during the survey year at the marsh transect. This was performed using least squares regression.

Results

From 2004 to 2013 a total of 8340 non-hatchling alligators was counted during spring surveys at LNWR. These counts varied between samples, among sites, and among years (Table 1). Of the 2429 alligators counted at L-39 Canal, only 83 (3.4 %) were in the small category. At the L-40 Canal, 766 of the 3206 (23.9 %) alligators counted were in the small category. The marsh route had the highest proportion of small alligators with 982 of the 2705 (36.3 %) alligators encountered in the small category.

Table 1 Total raw counts of non-hatchling alligators during two spring samples each year 2004–2013 at the L-39 Canal (21.5 km), L-40 Canal (10 km), and Marsh (21.5 km) routes

	L-39 Canal		L-40 Canal		Marsh	
Year	Sample 1	Sample 2	Sample 1	Sample 2	Sample 1	Sample 2
2004	95	143	85	98	111	130
2005	129	89	100	17	126	95
2006	132	159	92	97	121	98
2007	139	195	201	254	149	227
2008	27	52	39	41	67	80
2009	189	173	209	197	164	148
2010	105	131	102	123	96	98
2011	209	123	384	392	281	314
2012	74	59	76	71	107	88
2013	57	149	259	369	82	123

Model selection results for models based on the non-hatchling alligators indicated support for only one model based on AIC model weight (Table 2). In the best model the abundance parameter, λ, was a function of the route (L-39 Canal, L-40 Canal, or Marsh). Whether or not the route was a canal was not a good predictor of abundance at LNWR. The rate of population change, γ, was best modeled as a function of both route and year (i.e., different values for each year of the study). This indicates that both initial abundance and the rate of population growth varied among the three routes, but the parameter estimates for the effect of route on λ include 0 (Table 3). The binomial categorical variable of wet or dry year was not selected based on AIC. All of the detection covariates (water temperature, water stage, and whether or not the site was a canal) were included in the best model. Model selection results for small alligator only and harvestable alligator datasets were qualitatively similar to the non-hatchling alligator dataset. The same model received all of the AIC model weight in all three analyses.

The effect of the canal covariate on detection was positive (0.19; 95 % C.I. −0.20, 0.57). This indicates that alligators had a slightly higher detection probability in canals, but the estimate of the confidence interval of this effect does include 0. The mean detection probability estimate (at mean water temperature and stage) was 0.113 (95 % C.I. 0.084, 0.150) in the marsh route and 0.133 (95 % C.I. 0.111, 0.158) in the canal routes. The beta estimate for effect of water temperature on detection was slightly negative (−0.01) with a 95 % C.I. including 0 (−0.03, 0.02), whereas the beta estimate for effect of stage was negative (−0.16) with a 95 % C.I. that was completely negative (−0.22,−0.10) (Fig. 2; Table 3).

The estimated number of non-hatchling alligators along all LNWR routes combined increased during the period 2004–2013 by 55.0 % from 2684 to 4160. Alligator abundance

Table 2 Model selection results for the abundance model on counts of all non-hatchling alligators at Arthur R. Marshall Loxahatchee National Wildlife Refuge

λ	γ	*P*	No. Par.	AIC	Δ AIC	AIC weight
Route	Route+Year	Temperature+Stage+Canal	18	9446.7	0.0	1.00
Route	Canal+Year	Temperature+Stage+Canal	17	9536.5	89.8	0.00
Route	Year	Temperature+Stage+Canal	16	9543.5	96.8	0.00
Route	Route+Hydro	Temperature+Stage+Canal	11	9721.3	274.6	0.00
Route	Hydrology	Temperature+Stage+Canal	9	9821.6	374.8	0.00
Route	Route	Temperature+Stage+Canal	10	9899.4	452.7	0.00
Route	Canal	Temperature+Stage+Canal	9	9975.1	528.4	0.00
Route	Constant	Temperature+Stage+Canal	8	9982.7	536.0	0.00
Canal	Constant	Temperature+Stage+Canal	7	10011.2	564.5	0.00
Constant	Constant	Temperature+Stage+Canal	6	10027.9	581.2	0.00
Constant	Constant	Temperature+Stage	5	10030.8	584.0	0.00
Constant	Constant	Stage	4	10033.6	586.8	0.00
Constant	Constant	Temperature	4	11213.5	1766.7	0.00
Constant	Constant	Canal	4	11254.0	1807.2	0.00
Constant	Constant	Constant	3	11263.5	1816.8	0.00

declined by 21.4 % at the L-39 Canal, increased by 237.5 % at the L-40 Canal, and increased by 16.7 % at the Marsh route, but the confidence intervals on these estimates were somewhat wide and there was considerable annual variation (Table 4). The average abundance estimates among the 500-m segments along each route was lowest at the L-39 Canal and highest at the L-40 Canal (Fig. 3).

Table 3 Parameter estimates with standard errors and 95 % confidence intervals for the best model from the total alligator dataset

			95 % C.I.	
	Estimate	SE	Lower	Upper
Abundance (λ):				
Intercept	3.30	0.16	2.99	3.61
L39	−0.19	0.19	−0.56	0.17
L40	0.12	0.19	−0.26	0.49
Recruitment (γ):				
Intercept	−0.15	0.06	−0.26	−0.03
L39	−0.06	0.02	−0.09	−0.02
L40	0.13	0.02	0.10	0.17
Year 2005	0.30	0.10	0.11	0.50
Year 2006	0.53	0.08	0.38	0.68
Year 2007	−0.95	0.10	−1.14	−0.76
Year 2008	1.11	0.10	0.92	1.30
Year 2009	−0.12	0.09	−0.30	0.06
Year 2010	0.70	0.10	0.50	0.89
Year 2011	−0.92	0.09	−1.10	−0.74
Year 2012	0.90	0.08	0.74	1.06
Detection (*P*):				
Intercept	−2.06	0.17	−2.40	−1.73
Temp	−0.01	0.01	−0.03	0.02
Stage	−0.16	0.03	−0.22	−0.10
Canal	0.19	0.20	−0.20	0.57

The trend in abundance (i.e., finite rate of population increase γ) was variable from year to year and across routes, and was not explained by our wet/dry hydrology variable (Table 2). Although estimates of γ varied by route, the pattern across routes was similar in any given year (Table 5). A declining trend in alligator populations at LNWR ($\gamma<1$) was detected during intervals after the 2004, 2007, 2009, and 2011 dry season at all three routes. These 4 years were designated as dry based on our criterion of a minimum stage of < 4.72 m (15.5 ft). When the annual population growth rate estimates from the marsh were subjected to linear regression on the minimum daily stage value for the same interval, the model was significant ($F=7.96$, $p=0.0257$) with an R^2 of 0.532 (Fig. 4).

Discussion

Alligators at LNWR showed population response to hydrologic conditions. In particular, there were declines in abundance after dry years followed by increases in abundance in subsequent years. In addition, there is evidence that the intensity of dry events affected the population dynamics with greater declines after drier conditions and greater increases after successive years without dry conditions. This overall pattern was similar among sample areas, though the magnitude of responses varied. The impact of slower population recovery rates was particularly apparent following the 2011 dry year (an extreme drought) at L-39 and the Marsh. This illustrates how single year events can affect long-term trends and the value of long-term data to put shorter term changes in context.

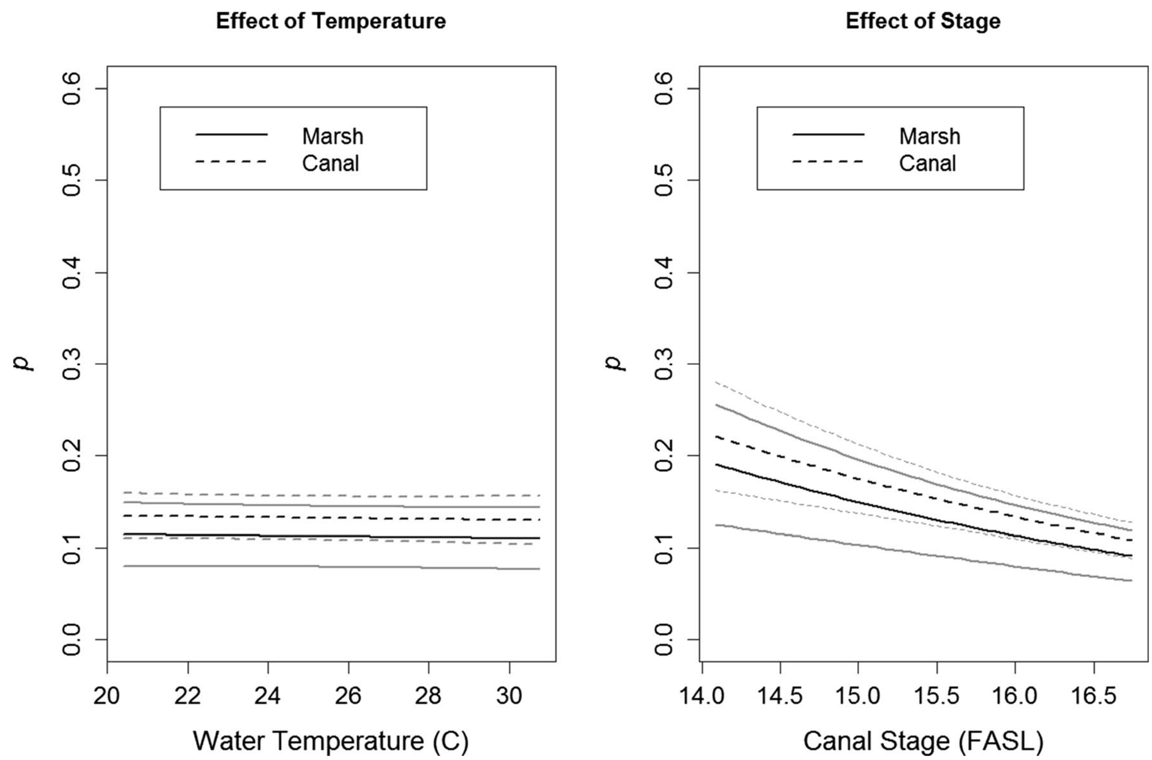

Fig. 2 Effect of water temperature and water stage on detection probability of alligators along marsh and canal routes in Arthur R. Marshall Loxahatchee National Wildlife Refuge 2004–2013. *Light lines* indicate the 95 % confidence interval of each effect

Differences between the marsh site and the canals illustrate the importance of understanding the scope of the population of interest. For example, LNWR is interested in the status of the overall alligator population in the context of a managed alligator hunt. Therefore, knowing the status of the entire (canals and marsh) refuge alligator population is important (increasing in this case). In addition, in the context of Everglades restoration, it is the marsh population that is of interest and the target for hydrologic improvements. Therefore, it is important to consider data from these habitats separately when determining both effects of past hydrologic conditions and in using the information to identify future desired hydrologic conditions. Although the general patterns were the same (declines after dry years followed by recovery), using all of the data together or canal data only to draw conclusions about marsh population dynamics would result in the conclusion that over the last 10 years the population was increasing much more than it actually did.

Table 4 Annual estimates (with 95 % confidence intervals) of the abundance of non-hatchling alligators along the 3 sampling routes at Arthur R. Marshall Loxahatchee National Wildlife Refuge

Year	L-39	L-40	Marsh
2004	935 (614–1323)	627 (453–835)	1122 (781–1551)
2005	770 (464–1218)	552 (357–816)	958 (596–1469)
2006	914 (571–1448)	711 (476–1045)	1052 (640–1675)
2007	1136 (741–1759)	1323 (992–1765)	1567 (1034–2367)
2008	330 (160–637)	443 (275–681)	562 (315–959)
2009	967 (618–1551)	1283 (935–1753)	1408 (884–2228)
2010	774 (477–1261)	1036 (741–1438)	1043 (632–1696)
2011	989 (639–1544)	2131 (1699–2657)	2162 (1525–3095)
2012	360 (188–653)	738 (518–1023)	768 (476–1209)
2013	735 (426–1279)	2116 (1653–2676)	1309 (806–2102)

The pattern of decreasing trends immediately after dry years followed by increasing trends following subsequent wet years is consistent with hypotheses about the importance of pulse events in wetlands in general and in the Everglades specifically. Although pulse events may result in short-term declines in fish and alligator populations, these events should be maintained in a restored Everglades. Both fish (Loftus and Eklund 1994; Ruetz et al. 2005; Trexler et al. 2005) and wading birds (Frederick and Ogden 2001) show positive responses in years subsequent to droughts that are consistent with the hypothesis that nutrient release during droughts results in increases in primary production in subsequent years. Although we did not have more than 2 consecutive average years after a dry year in this study, these results are consistent with the hypothesis that alligator populations increase under multi-year hydroperiods.

Mortality of all size classes, lower growth rates of hatchlings, and limited reproduction in drier years are likely explanations for decreases in alligator abundance following dry

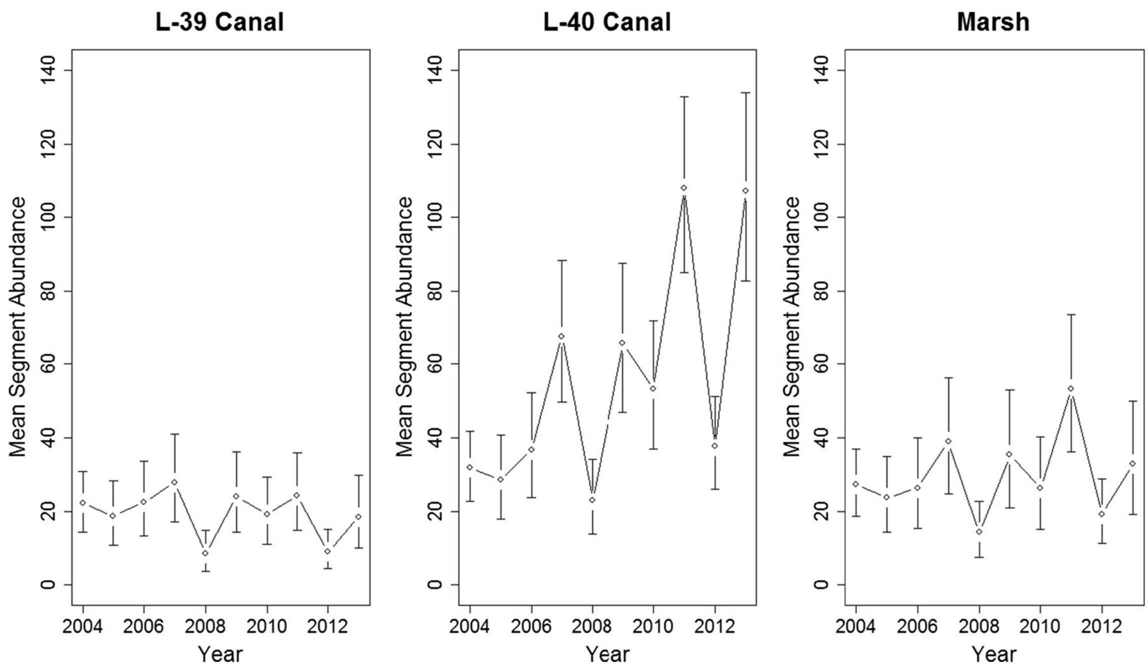

Fig. 3 Mean estimated abundance with 95 % confidence intervals of alligators per 500-m segment along the three routes in Arthur R. Marshall Loxahatchee National Wildlife Refuge 2004–2013

years. Dry conditions can cause mortality of small alligators from desiccation, and alligators of all sizes that take refuge in the remaining wet areas are susceptible to mortality because of interspecific interactions in the crowded conditions (cannibalism and fighting; Deitz 1979; Delany et al. 2011). Harsher conditions where hatchlings are not able to feed because of movement constrained by lower water depths or limitations in food can contribute to lower growth meaning that those animals will not reach 0.5 m by the following spring and so, although present, would not be included in the total count until the following year when they reached 0.5 m. In addition, at lower water levels males expend more energy moving around to find females, and may not be able to breed with as many females, thus decreasing nesting that year (Rice et al. 2004). We have observed a general pattern of more pods of young (indicating more nests) in fall surveys following non-dry springs compared to fall surveys following dry springs (unpublished data).

Increasing trends in years subsequent to dry years may be directly related to increased recruitment from dispersal of animals from areas immediately adjacent to survey routes as well as recruitment from reproduction in previous years. That our analysis of small, harvestable size, and total population showed similar patterns indicates that there are likely multiple mechanisms operating on all size classes resulting in increases in years subsequent to dry years. Dispersal from adjacent areas into our survey areas is very likely in LNWR as the entire refuge has a high density of alligators. Dispersal may not be a contributing factor in other areas of the Everglades such as Water Conservation Area 3 where alligator densities are very

Table 5 The population growth rate (with 95 % confidence interval) over the interval between annual surveys of alligators and the description of each interval as hydrologically wet or dry for the entire Arthur R. Marshall Loxahatchee National Wildlife Refuge and for the marsh route only

Interval	L-39	L-40	Marsh	Hydrology
2004–2005	0.81 (0.72–0.91)	0.98 (0.87–1.10)	0.86 (0.77–0.97)	Dry
2005–2006	1.10 (0.98–1.24)	1.33 (1.19–1.49)	1.16 (1.04–1.31)	Wet
2006–2007	1.38 (1.24–1.54)	1.66 (1.51–1.85)	1.46 (1.32–1.62)	Wet
2007–2008	0.31 (0.27–0.37)	0.38 (0.32–0.44)	0.33 (0.28–0.39)	Dry
2008–2009	2.46 (2.11–2.87)	2.97 (2.55–3.47)	2.61 (2.24–3.03)	Wet
2009–2010	0.72 (0.63–0.83)	0.87 (0.76–1.00)	0.76 (0.67–0.88)	Dry
2010–2011	1.63 (1.39–1.92)	1.97 (1.68–2.31)	1.73 (1.47–2.02)	Wet
2011–2012	0.32 (0.28–0.37)	0.39 (0.34–0.45)	0.34 (0.30–0.39)	Dry
2012–2013	2.00 (1.80–2.23)	2.42 (2.17–2.69)	2.12 (1.90–2.37)	Wet

Intervals were designated as dry if the minimum daily value of the stage at the 1–7 (marsh) water gauge during that period was < 4.72 m. Population growth rates <1 indicate a declining population while growth rates >1 indicate an increasing population

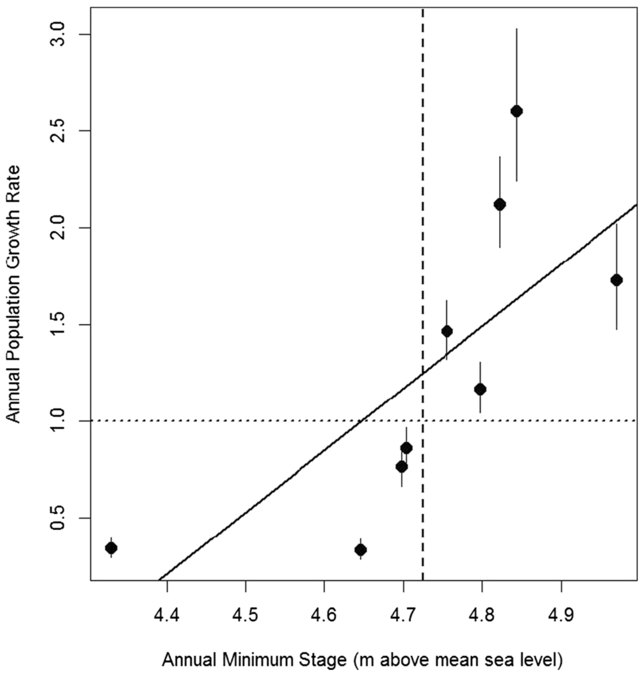

Fig. 4 Annual population growth rates of alligators along the marsh route at Arthur R. Marshall Loxahatchee National Wildlife Refuge (with 95 % confidence interval) and the minimum daily stage value (in m above sea level) measured during that year. The *horizontal dotted line* represents the line below which the population is decreasing. The *vertical dashed line* is the value of stage that represents a water depth of approximately 15 cm on the marsh. The *solid line* is the weighted least squares regression line through the points

low (Mazzotti et al. 2010). It is likely that in these areas alligator populations will recover more slowly from dry events. Another factor that may contribute to the ability of the LNWR marsh population to recover is its deep peat layer that acts as a sponge and buffer. Events characterized as dry may not have as great an impact as in other areas of the Everglades where peat layers are less thick and effects of dry conditions are less buffered.

The L-39 Canal route had a decline (−21.4 %) of alligator abundance whereas the L-40 Canal had a large increase (237.5 %) and the marsh had a small increase (16.7 %) during the 10-year study. The different pattern observed between the two canal routes was somewhat unanticipated as we expected the canal sites to be more similar to each other than to the marsh area. Our results underscore how sites with superficially similar habitat can provide different levels of habitat suitability for alligators even in the face of abiotic events such as droughts that help shape population dynamics in the marsh (Ruetz et al. 2005). Differences in responses may be a result of variation in canal morphology and changes in water flows and nutrients. The L-40 Canal is a narrower canal (approximately 35 m in width) and very distinct along the entire survey route with a border of shrubs between the canal and the marsh. This area of vegetated slightly raised ground provides both cover for smaller alligators and potential sites for nesting. The L-39 Canal is a wider canal (approximately 45–65 m in width) and the route has areas where there is a more direct connection to the marsh through what is primarily cattail (*Typha* spp.), which may not provide juvenile habitat as suitable as that along L-40. In addition, there are places in the south end of L-39 where it is hard to distinguish the location of the canal edge as it is connected to the marsh via open water; therefore, there may be more movement of animals into the marsh where areas may be more suitable for basking and nesting. Thus, that segment of the L-39 Canal route may be in part reflecting marsh population dynamics. The differences in the routes are also reflected in the proportion of small alligators observed, 3.4 % for the L-39 Canal and 23.9 % in the L-40 Canal, as well as our observations of fewer pods of young in L-39 compared to the L-40 Canal (unpublished data), which suggests that little reproduction is happening in the immediate vicinity of the L-39 Canal route. Clearly the distinction between canal and marsh habitat is not the only factor driving differences in abundance and population trend in LNWR among the routes.

Another factor that may have contributed to the decrease in alligators in the L-39 Canal is the stopping of discharges from the S6 pump station in 2001. Prior to that, large alligators often were observed near the outflow both during the day and during night surveys. Although we do not have data on fish densities in that area as compared to other areas, we hypothesize that they were greater because of the high nutrient (especially phosphorus; P) content of the water. Since that time, water quality in the canal near the S6 pump has improved with P levels decreasing from a median of 64 ppb in water year 2005 to 20 ppb by water year 2013 (Surratt Unpublished data) and there may no longer be greater abundances of fish in that area. In addition, Stormwater Treatment Area 1West (STA 1 W), an artificial marsh approximately 12 km north of the start of the L-39 route, has provided additional alligator habitat. Since its establishment in 1994, STA 1 W has become increasingly populated with alligators despite no evidence of nesting within its borders. It is possible that alligators from the western part of the L-39 Canal route have migrated to STA1W where food is plentiful.

Our estimates of average detection probability (0.113 in marsh and 0.133 in canals) are low, but are comparable to similar studies. Rates of detection outside of the Everglades range from 0.09 (spotlight survey mark-resighting estimates) at Lake Woodruff in North-central Florida (Woodward et al. 1996) and South Carolina (Rhodes and Wilkinson 1994) to over 0.30 (mark-recapture estimates, spotlight, and aerial surveys) in a man-made lake in South Carolina (Murphy 1977; Brandt 1989). Other estimates of alligator detection probability in the Everglades range from 0.03 to 0.09 (spotlight surveys using a two stage hierarchical model) depending on the time of year, water depth, and size class (Fujisaki et al. 2011) and 0.15 to 0.21 (mock spotlight surveys analyzed with program MARK) depending on habitat (Carter 2010). The variability in detection rates across routes and years reinforces the need for using analytical methods that account for imperfect detection in the analysis of counts whenever alligator abundance is compared across space or time.

This study and that of Fujisaki et al. (2011) found strong evidence of an effect of water depth on detection of alligators, and our study found somewhat weaker support for an effect of temperature on alligator detection probability (Fig. 2). This is consistent with results from a study by Bugbee (2008) where alligator emergence rates were lower when both water depths and temperature were higher. Lower emergence rates mean that animals, though present in the study area, are not available for counting. Our study also found strong evidence that detection of alligators is different in canals and marshes, and illustrates that caution should be used when interpreting differences in raw counts from different habitats. Awareness of these factors is important in the design and analysis of spotlight count data of alligators.

The results of this study clearly indicate that dry downs can cause a declining trend in alligator abundance and that there are greater effects with more intense or frequent dry downs. This has important implications for determining hydrologic targets for restoration and year to year water management, which must balance water needs for municipal and agricultural uses as well as for the Everglades. Extreme dry downs and consecutive year dry downs could have a very negative impact on alligators, particularly if there are no suitable refugia available to dispersing alligators. We had no consecutive dry years during our ten-year study period. It is therefore difficult to know how multi-year dry events would impact the population, but it is likely that the declines seen during single dry years in this study would continue. We had only one period where there were two consecutive years where water depths were not low. The highest rate of population increase was observed during that time period which supports our hypothesis that multi-year hydroperiods (i.e., consecutive years without a dry-down) are desirable for alligators and that on average dry downs once every 3 to 5 years may support alligator populations at levels targeted as performance measures for Everglades restoration (Hart et al. 2012).

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