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AVIAN RESPONSE TO NUTRIENT ENRICHMENT IN AN OLIGOTROPHIC WETLAND, THE FLORIDA EVERGLADES

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Abstract. We studied the effects of nutrient enrichment on the bird community in an oligotrophic wetland, the Florida Everglades. Among the non-wading birds surveyed in 1996 and 1997, Boat-tailed Grackles (*Quiscalus major*) and Common Moorhens (*Gallinula chloropus*) were consistently more abundant in enriched sites, whereas Common Yellowthroats (*Geothlypis trichas*) were consistently more abundant in unenriched sites. The abundance of Red-winged Blackbird (*Agelaius phoeniceus*) was not significantly different between enriched and unenriched sites. Among wading birds, Wood Storks (*Mycteria americana*) and Great Egrets (*Ardea alba*) were significantly more abundant in enriched than unenriched areas in a dry year, 1991. Great Egrets and all wading species combined were significantly more abundant in enriched than unenriched areas in the wet year, 1995. Great Blue Herons (*Ardea herodias*) and White Ibises (*Eudocimus albus*) did not differ in abundance between enriched and unenriched areas in the dry or wet year. A significant interaction between water depth and nutrient status in the wet year indicated that wading bird abundance increased with water depth only in nutrient-enriched areas presumably because the enriched areas had greater food availability than unenriched areas at the same water depth. Bird abundance appeared to increase in nutrient-enriched areas; however, this increase was accompanied by a shift in species composition typically found in the unenriched Everglades and was a fundamental change in the Everglades' distinctive structure.

Key words: *birds, eutrophication, Everglades, nutrients, phosphorus, wading birds, wetlands.*

Respuestas de las Aves al Enriquecimiento con Nutrientes en un Humedal Oligotrófico, en los Pantanos de los Everglades en Florida

Resumen. Estudiamos los efectos del enriquecimiento con nutrientes sobre la comunidad de aves en un humedal oligotrófico, los pantanos de los Everglades en Florida. Entre las aves no vadeadoras censadas en 1996 y 1997, *Quiscalus major* y *Gallinula chloropus* fueron consistentemente más abundantes en sitios enriquecidos, mientras que *Geothlypis trichas* fue consistentemente más abundante en sitios no enriquecidos. La abundancia de *Agelaius phoeniceus* no difirió significativamente entre los sitios enriquecidos y no enriquecidos. Entre las aves vadeadoras, *Mycteria americana* y *Ardea alba* fueron significativamente más abundantes en áreas enriquecidas que en las no enriquecidas durante 1991, un año seco. En 1995, un año húmedo, *Ardea alba* y todas las demás aves vadeadoras fueron significativamente más abundantes en áreas enriquecidas que en las no enriquecidas. *Ardea herodias* y *Eudocimus albus* no difirieron en abundancia entre áreas enriquecidas y no enriquecidas en el año húmedo ni en el año seco. En el año húmedo, encontramos una interacción significativa entre la profundidad del agua y el estado de los nutrientes, lo que indicó que la abundancia de aves vadeadoras aumentó sólo en las áreas enriquecidas con nutrientes, presumiblemente debido a que las áreas enriquecidas presentaron mayor disponibilidad de alimento que las áreas no enriquecidas de una profundidad de agua equivalente. La abundancia de aves pareció aumentar en las áreas enriquecidas con nutrientes; sin embargo, este incremento estuvo acompañado con un cambio en la composición de las especies encontradas normalmente en los pantanos de los Everglades de Florida que no han sido enriquecidos, y representó un cambio fundamental en la estructura característica de los Everglades.

INTRODUCTION

The Everglades was originally an oligotrophic, phosphorus-limited wetland with nutrient inputs restricted primarily to rainfall (Davis 1994). Currently, phosphorus additions to the northern Everglades, primarily from agricultural runoff through canal discharges, are about 10–20-fold higher than historical levels (McCormick and O'Dell 1996, McCormick et al. 1999). The gradual eutrophication of the Everglades over the past 50 years has altered the biotic communities

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within these high-nutrient areas. The most obvious change is the encroachment of dense cattail (*Typha* spp.) into sawgrass (*Cladium jamaicense*) marshes and sloughs (Urban et al. 1993, Wu et al. 1997, Rutchey and Vilchek 1999). Coinciding with this shift in vegetation is an increase in the abundance of nutrient-tolerant species in the periphyton, invertebrate, and fish communities (Rader and Richardson 1992, 1994, McCormick et al. 1996, Turner et al. 1999).

Little is known about the effects of nutrient enrichment on birds in the Everglades. There is already concern about population declines in some bird species, particularly wading birds, which are thought to be the result of changes in food availability caused by altered hydrology and loss of high-quality habitat (Ogden 1994, Gawlik 2002). We have no information as to how or if nutrient enrichment has played a role in altering patterns of wading-bird habitat use. There is also no information on the effects of nutrient enrichment in the Everglades on passerines and other non-wading bird species in the bird community. Of the few studies that have examined the effects of nutrient enrichment on birds in other systems, the majority have looked at nutrient-enriched lakes and found bird abundance was positively correlated with lake nutrient level (Nilsson and Nilsson 1978, Hoyer and Canfield 1990, 1994, McCarty 1997). The lack of information on the effects of nutrient enrichment on the bird community makes this an important issue, particularly in the face of the current Everglades restoration efforts.

We hypothesized that bird communities may be affected by nutrient enrichment through two major pathways, food abundance and habitat structure. Nutrient additions have altered the food web in the Everglades by increasing the biomass or changing the species composition of the periphyton, macrophyte, invertebrate, and fish communities (Rader and Richardson 1992, 1994, McCormick and O'Dell 1996, Miao and Sklar 1998, Turner et al. 1999). The increase in food resources in enriched areas may increase the abundance and change the species composition of the avian community. Nutrient additions may also affect the bird community by significantly altering the habitat types available to birds. Nutrient enrichment converts sawgrass marshes and open-water sloughs typical of unenriched areas in the Everglades to marshes covered by dense stands of cattail with few open-water areas (Davis 1994, Doren et al. 1997, Wu et al. 1997, Rutchey and Vilcheck 1999). The increase in vegetation biomass associated with cattail may help some bird species by increasing the amount of substrate available for nesting and foraging. However, it may have a negative effect on species, such as wading birds, that use the open-water sloughs for foraging or nesting.

In the first part of our study, we examined the bird community along a nutrient gradient in Water Conservation Area 2A (WCA 2A) in the northern Everglades to compare the total bird abundance, species composition and richness, and abundance of the four most common species in enriched, transitional, and unenriched areas. We hypothesized that abundance of non-wading birds would be higher in nutrient-enriched areas as the result of increased productivity leading to increased food resources. In the second part of the study, we examined wading-bird abundance in enriched and unenriched areas in WCA 2A. We hypothesized that the abundance of wading birds would be lower in nutrient-enriched areas as a result of minimal slough habitat available for foraging due to cattail encroachment. Although fish density and biomass appear to increase with nutrient additions (Rader and Richardson 1994, Turner et al. 1999), fish should be less vulnerable amid the dense vegetation of nutrient-enriched areas.

METHODS

STUDY AREA

All surveys were conducted in WCA 2A in the northern Everglades (Fig. 1). WCA 2A is a 42 206-ha wetland composed primarily of open-water sloughs, sawgrass marsh, and cattail marsh. WCA 2A receives the majority of nutrient inputs from agricultural runoff at inflow structures along the northern levee. The flow of water from north to south in WCA 2A has created a nutrient gradient across WCA 2A extending approximately 8 km into the interior of the marsh (Payne et al. 2001). This nutrient gradient is reflected by the expansion of cattail in WCA 2A. The northern, enriched portion of WCA 2A is composed of dense monotypic stands of cattail with few areas of open water. This gradually gives way to a transitional area of mixed cattail and sawgrass marsh. The unenriched central and southern areas of WCA 2A are dominated by sawgrass marsh and sloughs.

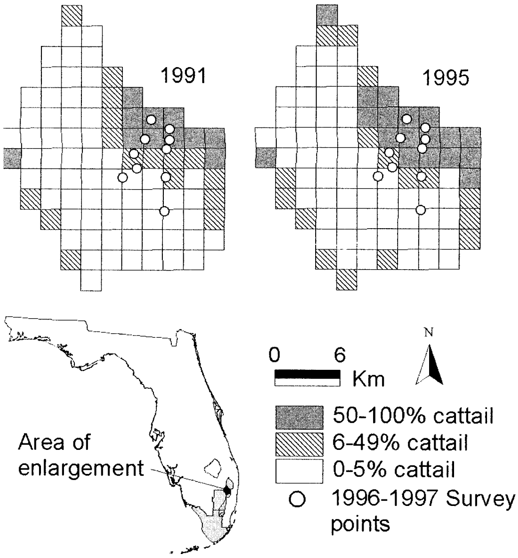

FIGURE 1. Cattail coverage designations for each of the 4-km² grid cells surveyed for wading birds in Water Conservation Area 2A, Florida Everglades, in 1991 and 1995. Cattail coverage was simplified from data in digitized maps (Rutchey and Vilchek 1999). In 1996–1997, point counts for non-wading birds were conducted at 10 locations (open circles). The northernmost four sites were designated as nutrient enriched, the southernmost two were unenriched, and the middle four were transitional.

BIRD SURVEYS

To gather information on the non-wading-bird communities across this nutrient gradient, we used two permanent north-south transects (each with five sampling sites) established by the South Florida Water Management District for phosphorus enrichment studies (Fig. 1). Sampling sites were between 940 and 3330 m apart. The sites had previously been characterized as enriched, transitional, and unenriched according to the amount of phosphorus and the periphyton, macrophyte, and macroinvertebrate communities at each site from data collected from 1994–1997 (McCormick et al. 1996, McCormick and O'Dell 1996, van der Valk and Rosburg 1997, Miao and Sklar 1998). A preliminary principal components analysis indicated that these nutrient class designations were appropriate for our bird data, so we used these designations for our analyses.

We surveyed each of the 10 sampling sites (Fig. 1) with point counts once per week for four weeks in the summer of 1996 (July–August), winter of 1997 (February–March), and summer of 1997 (June). Bird surveys started within 30 min of sunrise and were completed by late morning. Sites were surveyed in reverse order each week to reduce time-of-day bias on bird detection. An airboat was used to get to each site, and observers waited 2 min before starting each survey, allowing birds to adjust to the disturbance (Gawlik and Rocque 1998). All sites were surveyed by one of two trained observers using a modified variable circular-plot method (Reynolds et al. 1980). All individuals seen or heard within 6 min were identified to species when possible and estimated as <50, 50–100, or >100 m from the site. Individuals observed >100 m from the site or flying over the habitat were excluded from the analyses. Late in the summer of 1996, Tree Swallows (*Tachycineta bicolor*) were recorded on surveys. These birds are not known to nest in south Florida and were probably early migrants. They were excluded from the summer 1996 data to avoid confounding patterns of resident birds. The percentage of each habitat type (sawgrass, cattail, woody vegetation, and slough) within 100 m of each study site was visually estimated in 1996.

Point counts do not adequately capture wading bird use of habitat because wading birds are quickly flushed by approaching airboats. To gather information on wading bird use of enriched and unenriched areas in WCA 2A, we obtained data from systematic reconnaissance flights (Bancroft and Sawicki 1995). For these aerial surveys, transects were established 2 km apart and oriented east to west across the Everglades. Transect lines were then divided longitudinally into 4-km² cells. These transects were usually flown monthly from January to June using a fixed-wing aircraft flying at an altitude of 60 m. All wading birds observed in strips 150 m wide along both sides of the transect were identified to species. Data for 1991 (April, May) and 1995 (January–June) for WCA 2A were used in the analysis. These years were chosen because they coincided with years in which cattail maps were available. There is a close relationship between nutrient enrichment and cattail coverage (Urban et al. 1993, Davis 1994); thus we used the amount of cattail cover in the 4-km² cells as a surrogate for nutrient enrichment.

CATTAIL AND WATER DEPTH MAPS

Rutchey and Vilchek (1999) created cattail maps for 1991 and 1995 by photointerpretation of

1:24 000 color-infrared photographs using a minimum mapping unit of 1 ha. We converted these maps to the aerial survey's 4-km² grid cell system using ArcView® (ESRI Inc. 1992). The aerial survey grid was overlain onto each cattail map. Any cell that fell outside of the WCA 2A boundary by 7% or greater was dropped from the map. The proportion of cattail coverage was calculated for each grid cell (n = 91) in each map. Cells that were dominated by cattail (cells with ≥50% cattail cover) were classified as enriched (n = 11 in 1991, n = 18 in 1995). Cells with ≤5% cattail cover were classified as unenriched (n = 64 in 1991, n = 57 in 1995). These new cattail maps for 1991 and 1995 reflect only the aerial extent of cattail in each cell and ignore the density of cattail.

Water depth is an extremely important factor in determining where wading birds will be found in the Everglades (Kushlan 1976, Hoffman et al. 1994, Bancroft et al. 2002). Simulated water depths were obtained from the South Florida Water Management Model (SFWMM; Brion 1999) for each 4-km² grid cell for each aerial survey date. The SFWMM is a spatially explicit model that simulates daily water depths in South Florida using 10.37-km² grid cells. This model has undergone extensive uncertainty analyses (Brion 1999). In WCA 2A, 90% of the observed values in the validation data set were within 5 cm of the simulated values from the SFWMM model output. The output from the SFWMM for each aerial survey date was imported into ArcView®, and the aerial survey grid was overlaid on it. A weighted average, based on the proportion of area of each water depth, was used to calculate the water depth for each aerial survey grid cell for each aerial survey date.

STATISTICAL ANALYSES

All statistical analyses were performed using SAS (SAS Institute Inc. 1999). The nutrient gradient data were examined for differences in the total number of individuals, number of species, and the number of individuals of the four most common species between the enriched, transitional, and unenriched areas. A repeated measures ANOVA was run for each of these comparisons (significance level of $P \leq 0.05$) using PROC GLM for an unbalanced design (von Ende 1993). Week and season were the within-subjects factors in the analysis (10 sites × 4 weeks × 3 seasons; n = 120). The dependent

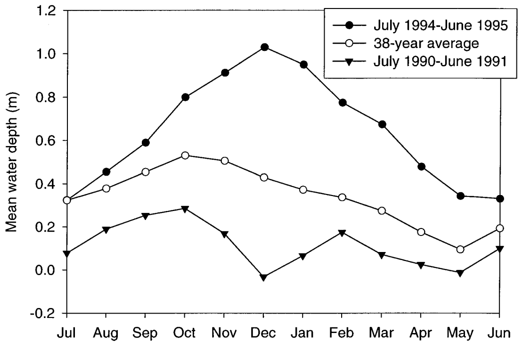

FIGURE 2. A hydrograph comparing the hydrology of the wet year (1995) and dry year (1991) with a 38-year average (1963–2000). Data are average monthly water depths from the average of three gages (1–7 in WCA 1, 2A–17 in WCA 2, 3A–4 in WCA 3) used to show the general hydrologic state of the Everglades system each month of each year.

variable was the total number of individuals (i.e., number of individuals per site per survey), number of species, number of Boat-tailed Grackles, number of Common Moorhens, number of Common Yellowthroats, or number of Red-winged Blackbirds (see Appendix for scientific names). After running the repeated measures ANOVA, the sphericity test for orthogonal components was examined to determine if the assumption of sphericity for a within-subjects effect was violated ($P \leq 0.05$). If the assumption of sphericity was violated, the Greenhouse-Geisser adjusted P-value was reported for that within-subjects effect to adjust for the violation, which typically causes an inflated F-value (von Ende 1993).

The two years used in the wading-bird analysis, 1991 (a dry year) and 1995 (a wet year; hereafter we refer to these as the dry or wet year; Fig. 2), were analyzed separately because previous work (Bancroft et al. 2002) found that wading bird response to vegetation may depend on hydrologic conditions. They found that in a dry year, foraging wading birds congregated primarily in shallow water while in a wet year, birds responded to vegetation composition as well.

An ANCOVA with water depth as a covariate was performed using PROC MIXED and a Poisson distribution (Littell et al. 1996) to compare wading-bird abundance in enriched and unenriched cells (75 cells × 2 months, n = 150 in 1991; 75 cells × 6 months, n = 450 in 1995).

TABLE 1. Repeated measures ANOVA comparing the effects of nutrient status (i.e., enriched, transitional, and unenriched) on bird abundance and species richness for birds surveyed at 10 point count sites during four weekly visits in each of three seasons, summer 1996, winter 1997, and summer 1997 ($n = 120$).

		Bird abundance		Species richness	
Source of variation	df	MS	*P*	MS	*P*
Nutrient status	2	758.8	0.05	6.7	0.20
Season	2	294.5	0.09	22.9	<0.01
Week	3	163.3	0.39	1.9	0.57
Season × Nutrient status	4	115.9	0.38	1.8	0.42
Week × Nutrient status	6	108.2	0.61	1.0	0.89
Season × Week	6	178.6	0.43	6.6	<0.01
Season × Week × Nutrient status	12	64.0	0.84	1.5	0.60

The number of White Ibises (*Eudocimus albus*), Wood Storks (*Mycteria americana*), Great Egrets (*Ardea alba*), Great Blue Herons (*Ardea herodias*), or all species (all wading bird species recorded), per cell per survey, was used as the dependent variable in the analysis. A significant interaction term ($P \leq 0.05$) between nutrient status and water depth indicated that the regression coefficients were not constant between nutrient status groups (SAS Institute Inc. 1991). Therefore, in cases where the interaction was not significant, we reran the model without the interaction term; otherwise, we retained the interaction term and interpreted significant effects within the context of this interaction. Type III sums of squares (the adjusted sums of squares) were used to compute the *F*-tests.

RESULTS

NUTRIENT GRADIENT ANALYSIS

Water quality data gathered during a previous study along the nutrient gradient showed that the enriched and unenriched sites had an average total phosphorus concentration of 116 $\mu g\ L^{-1}$ and 8 $\mu g\ L^{-1}$, respectively, in 1994–1995 (see McCormick et al. 1996 for more water quality information). The habitat types at the study sites reflected this phosphorus gradient. Enriched sites averaged 82% cattail, 3% sawgrass, 14% slough, and 1% woody vegetation. The transitional sites averaged 40% cattail, 41% sawgrass, 17% slough, and 2% woody vegetation. The unenriched sites averaged 2% cattail, 60% sawgrass, and 38% slough.

When all seasons were pooled, we observed 1790 birds representing 32 species (excluding wading birds) at study sites along the gradient. Sites were dominated by Red-winged Blackbirds, Common Moorhens, Boat-tailed Grackles, and Common Yellowthroats. The unenriched sites had on average fewer of these species than the enriched sites, except for Common Yellowthroats, which were more abundant in the unenriched sites. There was a difference in species composition between enriched and unenriched sites (Appendix). Shorebirds, such as Killdeer, Black-necked Stilts, Greater Yellowlegs, Lesser Yellowlegs, and Common Snipes, that prefer sparsely vegetated areas were present at unenriched sites but not enriched sites. The enriched sites generally had more rails and bitterns (Least Bittern, King Rail, Sora), which prefer heavily vegetated areas. The enriched sites also tended to have more American Coots, Tree Swallows, and Marsh Wrens, whereas the unenriched sites had more Pied-billed Grebes, Ospreys, Red-shouldered Hawks, and Limpkins.

The repeated measures ANOVA indicated that there was a marginally significant effect of nutrient status ($P = 0.05$) on the total number of individuals found at a site (Table 1, Fig. 3). There were consistently more individuals in the enriched sites than transitional and unenriched sites (Fig. 3). This difference was more pronounced in the summers than in the winter, although this interaction was not significant. There was a significant effect of season on species richness (Table 1). There was no significant effect of nutrient status on species richness, although there was a tendency for there to be more species in the enriched sites compared to the transitional and unenriched sites (Fig. 3).

The four dominant species in the study sites also showed significant differences in abundance across the gradient. Boat-tailed Grackles and Common Moorhens showed a significant effect of nutrient status ($P \leq 0.02$) and season ($P \leq 0.02$) on abundance (Table 2, Fig. 3). These spe-

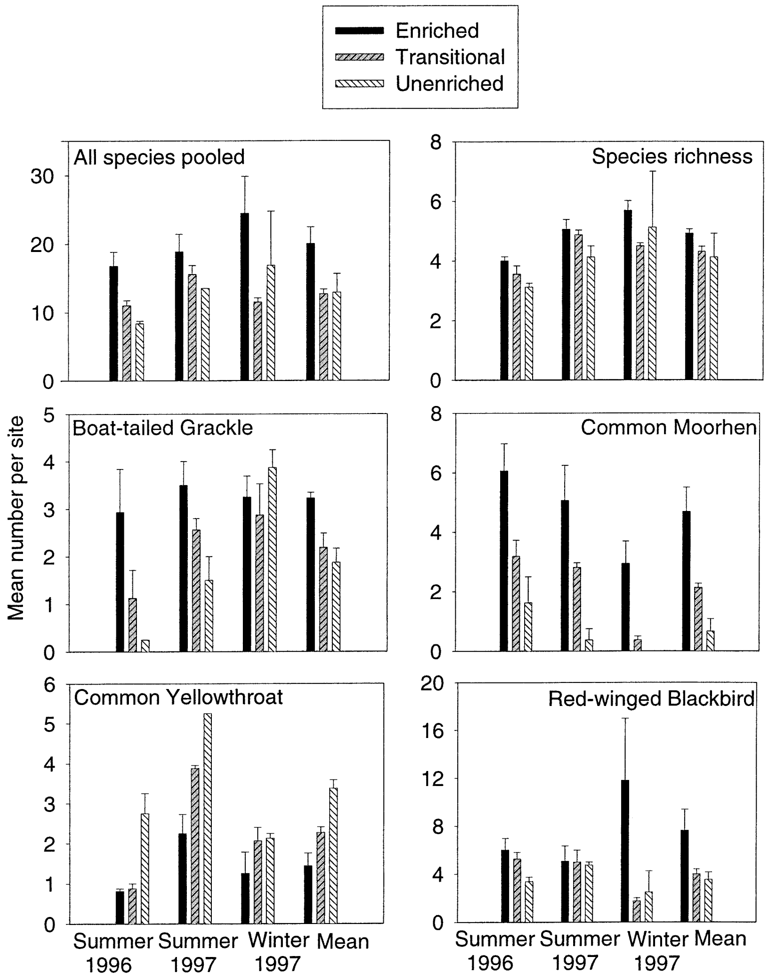

FIGURE 3. The mean ± SE total number of individuals of all species, species richness, and the number of the four most common non-wading-bird species per site in enriched (n = 4), transitional (n = 4), and unenriched (n = 2) sites in WCA 2A, Florida Everglades, 1996–1997. Means were calculated on the mean number of individuals (or species) from four visits per site per season. Lack of error bars indicates identical values at each site.

cies had more individuals in the enriched sites than the transitional and unenriched sites, except for Boat-tailed Grackles in winter, which did not show a clear pattern (Fig. 3). Common Yellowthroats also showed a significant effect of nutrient status ($P < 0.01$) and season ($P < 0.01$) on abundance. This was the only species of the four analyzed that had more individuals in the unenriched sites than the transitional and enriched sites, although this pattern was not as clear in winter (Fig. 3). There were no significant effects on the abundance of Red-winged Blackbirds; however, there tended to be more individuals in enriched sites than transitional and unenriched sites (Table 2, Fig. 3).

To assess the potential for sampling bias from differences in detection probabilities among the nutrient classes, we compared frequency distributions of bird abundance versus sampling distances. Three response variables (total bird abundance, species richness, number of Common Moorhen) had significant differences in detection probabilities between enriched and unenriched areas. This was driven by a significant difference in detection probability in one season, summer 1996, for all three response variables

TABLE 2. Repeated measures ANOVA comparing the effects of nutrient status (i.e., enriched, transitional, and unenriched) on the abundance of the four most common bird species found along the nutrient gradient. Point counts were conducted at 10 stations during four weekly visits in each of three seasons, summer 1996, winter 1997, and summer 1997 ($n = 120$).

		Boat-tailed Grackle		Common Moorhen		Common Yellowthroat		Red-winged Blackbird	
Source of variation	df	MS	P	MS	P	MS	P	MS	P
Nutrient status	2	19.7	0.02	150.8	<0.01	30.5	<0.01	207.2	0.11
Season	2	32.6	0.02	59.0	<0.01	56.3	<0.01	2.4	0.87
Week	3	11.6	0.08	3.9	0.34	1.7	0.47	47.5	0.58
Season × Nutrient status	4	8.7	0.29	3.5	0.46	5.2	0.01	137.6	0.22
Week × Nutrient status	6	7.0	0.20	1.8	0.77	1.1	0.75	40.4	0.76
Season × Week	6	12.7	0.20	3.7	0.10	3.2	0.22	52.7	0.58
Season × Week × Nutrient status	12	9.1	0.40	2.4	0.26	2.3	0.35	67.8	0.63

suggesting that these were the data with the greatest potential for bias. To determine whether these observations affected the results, we reran the analyses for the three variables excluding summer 1996 data. Only total bird abundance had a different result: the effect of nutrient status changed from marginally significant ($P = 0.05$) to nonsignificant ($P = 0.09$).

WADING BIRD ANALYSIS

White Ibis and Great Egret were the most abundant wading bird species recorded in both the dry and wet year. In the dry year, the mean water depth in WCA 2A in each cell was 12 cm, and the average number of wading birds observed each survey (all cells combined) was 804. In the wet year, the mean water depth in each cell was 26 cm, and the average number of wading birds observed each survey was 323. The entire Everglades system was quite wet, even during the dry season, in the wet year compared to the dry year (Fig. 2).

The ANCOVA results for the dry year showed no significant interaction between nutrient status and water depth. All models were rerun without the interaction term (Table 3). Wood Storks and Great Egrets were significantly more abundant ($P < 0.01$) in the enriched compared to the unenriched cells (Fig. 4). White Ibises, Wood Storks, Great Egrets, Great Blue Herons, and all species combined showed a significant effect of water depth on bird abundance ($P \leq 0.04$, Table 3).

The ANCOVA results for the wet year indicated that Great Egrets and all species combined had significantly more individuals ($P < 0.01$) in

TABLE 3. Analysis of covariance examining the effects of nutrient status (i.e., enriched and unenriched) and water depth as a covariate on the abundance of wading birds in the dry year, 1991 ($n = 150$), and the wet year, 1995 ($n = 450$).

	Nutrient status		Water depth		Nutrient status × Water depth[a]	
Species	F	P	F	P	F	P
1991						
Great Blue Heron	0.1	0.79	4.4	0.04		
Great Egret	10.6	<0.01	7.6	<0.01		
White Ibis	0.7	0.39	6.6	0.01		
Wood Stork	15.7	<0.01	4.9	0.03		
All species	3.1	0.08	9.8	<0.01		
1995						
Great Blue Heron	<0.1	0.91	1.3	0.26		
Great Egret	7.5	<0.01	0.7	0.41	10.7	<0.01
All species	46.0	<0.01	1.8	0.18	8.8	<0.01

[a] When the Nutrient status × Water depth interaction was not significant, the model was rerun without the interaction term, and the F and P values are not applicable.

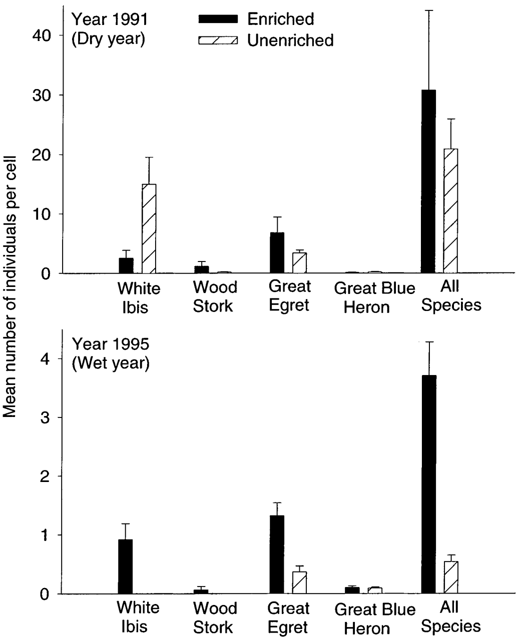

FIGURE 4. The mean ± SE number of four common wading bird species, and all species combined, per enriched (n = 22 in 1991, n = 108 in 1995) and unenriched (n = 128 in 1991, n = 342 in 1995) 4-km^2 cells in 1991, a dry year, and 1995, a wet year, in WCA 2A, Florida Everglades.

the enriched cells compared to the unenriched cells (Table 3, Fig. 4). For White Ibises and Wood Storks, the ANCOVA models did not converge, so no models were developed for these two species. However, White Ibises, Wood Storks, and Great Blue Herons tended to have more individuals in enriched compared to unenriched cells (Fig. 4). No species in the wet year showed a significant effect of water depth on bird abundance. However, the interaction between nutrient status and water depth was significant for Great Egrets and all species combined ($P < 0.01$, Table 3), so this interaction term was included in these two models. The interaction term was significant in these cases because the enriched cells had an increase in bird abundance with increased water depth while the unenriched cells had a decrease in abundance with increased water depth. White Ibises, Wood Storks, and Great Blue Herons tended to show a similar pattern. In contrast, this interaction term was never significant for the models in the dry year because both the enriched and unenriched cells had a decrease in bird abundance with increased water depth.

DISCUSSION

NUTRIENT GRADIENT ANALYSIS

We hypothesized that non-wading birds would be more abundant in nutrient-enriched areas compared to unenriched areas. The results of this study suggest that some members of the bird community tend to increase in abundance in nutrient-enriched compared to unenriched areas, and have an intermediate response in transitional areas. Of the four dominant species in the study, Boat-tailed Grackles and Common Moorhens were more abundant in enriched compared to unenriched sites. Red-winged Blackbirds tended to show the same pattern, although not as strongly, and so did the total number of individuals of all species pooled. Changes in habitat (i.e., increased amount of substrate for nesting or foraging) or changes in the food web that increased food resources were presumably the cause of the increased bird abundance in nutrient-enriched areas. The bird community in enriched areas tended to have more species that prefer densely vegetated areas whereas unenriched areas had more species that utilize open areas.

The increase in bird abundance as a response to nutrient enrichment in the Everglades is consistent with other studies that have examined avian response to nutrient enrichment. McCarty (1997) found significantly more Tree Swallows foraging over artificially enriched ponds compared with controls in response to increased insect production due to nutrient additions. Nilsson and Nilsson (1978) found a 65% higher density of birds in artificially enriched, formerly oligotrophic lakes, but did not find a significant increase in species richness in these enriched lakes compared to unenriched lakes. Hoyer and Canfield (1994) studied a range of Florida lakes from oligotrophic to hypereutrophic and found that bird abundance and species richness increased in lakes with more nutrients.

WADING BIRD ANALYSIS

The results of this study do not support our hypothesis that the abundance of wading birds is lower in nutrient-enriched compared to unenriched areas (as categorized by cattail coverage). Wood Storks, Great Egrets, and all species combined were significantly more abundant in enriched areas, although this depended on the hydrologic year. Great Egret was the only wading bird species that was significantly more common in enriched areas in both the wet and dry years. It is possible that because the dry year was preceded by two years of drought, there was a flush of nutrients into the marsh, including unenriched areas, due to oxidation of peat soils. However, the amount of phosphorus released into the marsh would have been much greater in enriched areas due to higher amounts of phosphorus in the enriched soils, and should not have affected our comparison of enriched and unenriched sites.

We expected decreased wading bird abundance in nutrient-enriched areas because cattail invasion left few open-water sloughs for foraging. We suspect the increased abundance of wading birds in nutrient-enriched areas was because the few open-water areas available to wading birds had a higher density of fish or had fish that were more vulnerable to capture compared to sloughs in the unenriched areas. Rader and Richardson (1994) found a greater density of fish and Turner et al. (1999) found a greater biomass of fish in enriched compared to unenriched areas of the Everglades. However, for fish to be vulnerable to wading birds, open-water areas must be present. The majority of open-water sites in enriched areas in our study had been created by airboat traffic and may be unique to our study area. If there had been no artificial openings in the enriched areas, we might not have seen an increase in the abundance of wading birds.

The nonsignificant interaction between water depth and nutrient status in the dry year was consistent with our expectation that wading birds would heavily use areas with shallow water where food resources are presumably concentrated (Bancroft et al. 1994), and that this would occur in both enriched and unenriched areas. There were many wading birds within the Everglades system in the dry year (approximately 12 640 birds per survey in WCA 1–3), and abundances of all five wading bird groups analyzed were negatively correlated with water depth. In the dry year, decreasing water levels concentrated and made food resources available for wading birds.

The significant interaction between water depth and nutrient status in the wet year indicated that the relationship between wading-bird abundance and water depth differed between enriched and unenriched areas. In the wet year there were high water levels, and few wading birds used the Everglades system (approximately 2391 birds per survey in WCA 1–3). No wading-bird species' abundance was correlated with water depth. Bird abundance increased with decreasing water depth in unenriched areas, as it did in both areas in the dry year. However, the opposite was true in the enriched areas: bird abundance increased with water depth. In the wet year, the concentration of fish by shallow water was probably limited, so wading birds had fewer high-quality habitat patches to exploit.

Bancroft et al. (2002) found similar patterns in wading bird use of the Everglades in wet and dry years. Their results indicated that in a dry year, wading bird abundance was correlated primarily with water depth. However in a wet year, bird abundance was correlated with water depth as well as with vegetation types. These patterns suggest that different mechanisms drive wading bird abundance depending on hydrologic conditions. In dry years the abundance of wading birds is primarily driven by the concentration of food from decreasing water levels, but in wet years wading bird abundance is also driven by habitat characteristics that may make food available.

RESTORATION IMPLICATIONS

Although bird abundance may increase in nutrient-enriched areas of the Everglades, this is not necessarily a desirable event. Excluding wading birds, the avian community in the Everglades generally has low species richness and abundance (Gawlik and Rocque 1998). Turner et al. (1999) proposed that the Everglades is unique because the Everglades' lower trophic levels have a relatively high biomass while the higher trophic levels appear to have a relatively low biomass. Turner et al. (1999) compared the biomass per unit area of periphyton, invertebrates, and fish in the Everglades with different systems around the world. They found that the Everglades had a higher periphyton biomass and a lower biomass of invertebrates and fish. The authors suggested that an important goal for Everglades restoration is to maintain this structure of low biomass in the higher trophic levels because this feature makes the system unique. By artificially increasing the abundance of the avian community through eutrophication, the Everglades will lose an important distinctive characteristic. In recognition of the detrimental effects of nutrient enrichment, a major component of the Everglades restoration plan is the construction of water-treatment wetlands to reduce the level of phosphorus entering the system (South Florida Water Management District 1999).

Unlike the low abundance in the non-wading bird community, records indicate that wading birds historically were very abundant in the Everglades. In the 1930s, there were an estimated 50 000–100 000 wading-bird nests per year in the Everglades, the majority of which were White Ibis nests (Ogden 1994, Frederick 1995). By the 1990s, the Everglades averaged approximately 15 000 nests per year, dominated by White Ibis (Crozier et al. 2000). There has been much concern over these declines in wading bird populations over the past 70 years. Although it appears that eutrophication may create good foraging conditions for wading birds when open-water areas are present, the long-term effects of nutrient enrichment may be detrimental to wading birds and other components of the system. Nutrient additions ultimately create dense cattail marshes that eliminate all slough habitat necessary for wading birds to forage. As eutrophication of the Everglades continues, dense cattail gradually encroaches into the interior portions of the Everglades, making less and less habitat available to wading birds. Restoring the natural processes and functions of the Everglades by restoring the natural hydrology is a way to help wading bird populations recover without changing the composition and abundance of the other components of the system. Nutrient enrichment fundamentally changes the structure of the oligotrophic Everglades, and therefore is incompatible with ecosystem restoration.

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APPENDIX. Mean ± SD number of individuals per site for 32 species recorded during point counts in enriched (n = 48), transitional (n = 48), and unenriched (n = 24) areas along the nutrient gradient in Water Conservation Area 2A in 1996 and 1997. Wading birds were not sampled adequately with this survey and are not reported.

Common name	Scientific name	Enriched	Transitional	Unenriched
Pied-billed Grebe	*Podilymbus podiceps*			0.08 ± 0.28
Anhinga	*Anhinga anhinga*	0.04 ± 0.20	0.23 ± 0.69	
Least Bittern	*Ixobrychus exilis*	1.13 ± 1.72	0.46 ± 0.74	0.38 ± 0.65
Green Heron	*Butorides virescens*	0.35 ± 0.64	0.06 ± 0.24	0.04 ± 0.20
Fulvous Whistling-Duck	*Dendrocygna bicolor*		0.35 ± 2.45	
Mottled Duck	*Anas fulvigula*	0.02 ± 0.14		0.08 ± 0.41
Osprey	*Pandion haliaetus*			0.04 ± 0.20
Northern Harrier	*Circus cyaneus*	0.02 ± 0.14		
Red-shouldered Hawk	*Buteo lineatus*			0.04 ± 0.20
King Rail	*Rallus elegans*	0.08 ± 0.45	0.08 ± 0.35	
Sora	*Porzana carolina*	0.46 ± 1.34	0.04 ± 0.20	
Purple Gallinule	*Porphyrula martinica*		0.02 ± 0.14	
Common Moorhen	*Gallinula chloropus*	4.69 ± 2.88	2.13 ± 1.75	0.67 ± 1.09
American Coot	*Fulica americana*	0.23 ± 0.75		
Limpkin	*Aramus guarauna*			0.13 ± 0.45
Killdeer	*Charadrius vociferus*			0.08 ± 0.28
Black-necked Stilt	*Himantopus mexicanus*			0.13 ± 0.61
Greater Yellowlegs	*Tringa melanoleuca*		0.04 ± 0.20	0.08 ± 0.41
Lesser Yellowlegs	*Tringa flavipes*			0.04 ± 0.20
Common Snipe	*Gallinago gallinago*			0.04 ± 0.20
White-winged Dove	*Zenaida asiatica*		0.02 ± 0.14	
Yellow-billed Cuckoo	*Coccyzus americanus*		0.02 ± 0.14	
White-eyed Vireo	*Vireo griseus*	0.02 ± 0.14		
Tree Swallow	*Tachycineta bicolor*	0.29 ± 1.24	0.17 ± 1.15	0.08 ± 0.28
Marsh Wren	*Cistothorus palustris*	0.06 ± 0.24	0.02 ± 0.14	
Yellow-rumped Warbler	*Dendroica coronata*	0.02 ± 0.14		
Palm Warbler	*Dendroica palmarum*	0.08 ± 0.35		
Common Yellowthroat	*Geothlypis trichas*	1.44 ± 1.47	2.27 ± 1.63	3.38 ± 2.18
Swamp Sparrow	*Melospiza georgiana*	0.04 ± 0.29	0.06 ± 0.43	0.04 ± 0.20
Northern Cardinal	*Cardinalis cardinalis*	0.02 ± 0.14		
Red-winged Blackbird	*Agelaius phoeniceus*	7.63 ± 14.87	4.00 ± 2.95	3.54 ± 3.87
Boat-tailed Grackle	*Quiscalus major*	3.23 ± 3.00	2.19 ± 2.43	1.88 ± 2.89