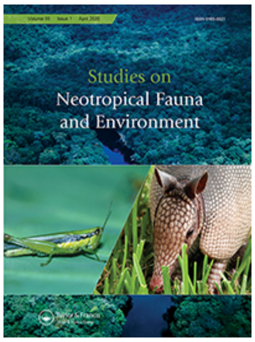

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ORIGINAL ARTICLE

Feeding ecology of the waterbirds in a tropical mangrove in the southeast Gulf of Mexico

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ABSTRACT

Species that exploit the same type of environmental resources are defined as a guild, which have similar needs in the use of food or habitat. It was analyzed the diet of five waterbirds' offsprings species (Neotropic Cormorant (*Nannopterum brasilianus)*, Reddish Egret (*Egretta rufescens*), Boat-billed Heron (*Cochlearius cochlearius*), Snowy Egret (*Egretta thula*) and Great Egret (*Ardea alba*)), by prey identification and calculated the relative importance, overlap and breadth diet. The general diet of the piscivorous guild consisted of 17 fish species from 13 genera and eight families. The highest overlap was between the Reddish Egret and Boat-billed Heron. Fish species dominated the diets of all studied waterbirds, *Poecilia velifera* was the most abundant prey species in each of the birds, suggesting that they are abundant in the wetlands system of northern Yucatan. Diet overlap in waterbirds species depends on the use of resources and feeding habitat. Since reproductive success largely depends on the availability of food resources, mainly of resident or estuarine fishes. The information about diet is important for the conservation of waterbirds.

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Introduction

Species that share morphological, physiological or behavioral attributes and perform similar ecosystem functions are recognized as guilds (McGill et al. 2006; Kraft et al. 2015). Within these groups, members of ecological guilds use the same resources in similar ways, i.e. diving birds and large wading birds (Fauth et al. 1996; Smith & Smith 2007; Tavares et al. 2015). Niche requirements of these species usually overlap regardless of the taxonomic position of the members of the guild (Root 1967). The classical point of view in ecology (Gause 1934; MacArthur 1958; Smith & Smith 2007) establishes that in order to coexist, the niches of two or more species ought to be different, especially when they use limiting resources. Pianka (1974) states that trophic overlap occurs when the competition is negligent as a result of abundant resources. Accordingly, separated niches may indicate that species are in need of avoiding competition. However, other studies have proposed that other processes can be used to predict resource utilization patterns instead of competition alone, as suggested by neutral theory (Perez-Crespo et al. 2013).

In coastal wetlands of the tropics, the high biological productivity allows many species of waterbirds to find suitable sites for feeding, resting, and nesting (Weller 1999; Flores-Verdugo et al. 2007; Holderby et al. 2014) especially when food availability can satisfy the requirements of both parents and offspring (Frederick et al. 2009). The reproductive success of birds requires a continuous supply of prey to fulfill the energy requirements of the offspring for growth and feathers production (Weller 1999).

Mangroves of the Yucatan Peninsula are an important ecosystem for the nesting of several aquatic migratory birds and they are part of a wide extension of wetlands such as Ciénegas and Petenes (springs of freshwater sourced by an underground river and which are bordered by tropical forest vegetation and mangroves of large height) (Lopez Ornat & Ramo 1992; Erwin 1996; Smardon 2006). In addition, they are habitat for threatened species (NOM 059 and IUCN), out of which we find Reddish Egret (*Egretta rufescens*). Reddish Egret is one of the rarest herons of North America because of the specificity of its habitats and its high vulnerability (Paul 1991); and in Mexico, it has a risk status under the category 'Subject to Special Protection' (SEMARNAT 2010). In addition to waterbirds, there are several endemic fish species such as *Floridichthys*

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polyommus or *Fundulus grandissimus*, which have a special protection status (NOM-059-SEMARNAT 2010). Therefore, the objective of this study is to know the diet of five waterbirds species that nest in mangroves on the Yucatan coast, this is important to establish coastal management measures, such as low ecotourism activities or conservation areas.

Methods

Study area

A waterbirds guild nests on a mangrove islet (~300 m^2) known as 'Homochen', within the wetlands and mangroves on the northern coast of the Yucatan State Reserve (21° 11′20.65″N and 89°57′1.59″W, Figure 1). This Reserve has swamps, mangroves (mainly *Rhizophora mangle* and *Avicennia germinans*), freshwater seeps, flooded grasslands and seagrass (Diario Oficial del Gobierno del Estado de Yucatan 2010). This Reserve is an important area for the conservation of bird species. Mean water levels range from 0.17 to 0.42 m at sea level in rainy season and drops to 0.12 m at sea level in dry season. In general, the hydrological flux in the Yucatan Peninsula is underground as a result of the karstic terrain.

Sampling

We performed morning samplings (to find the food content as fresh as possible) along nine occasions from November 2012 to February 2013, during the breeding season of the waterbirds guild. In each sampling, the species of waterbirds were recorded by direct observation. Seven species of waterbirds (Neotropic Cormorant (*Nannopterum brasilianus)*,

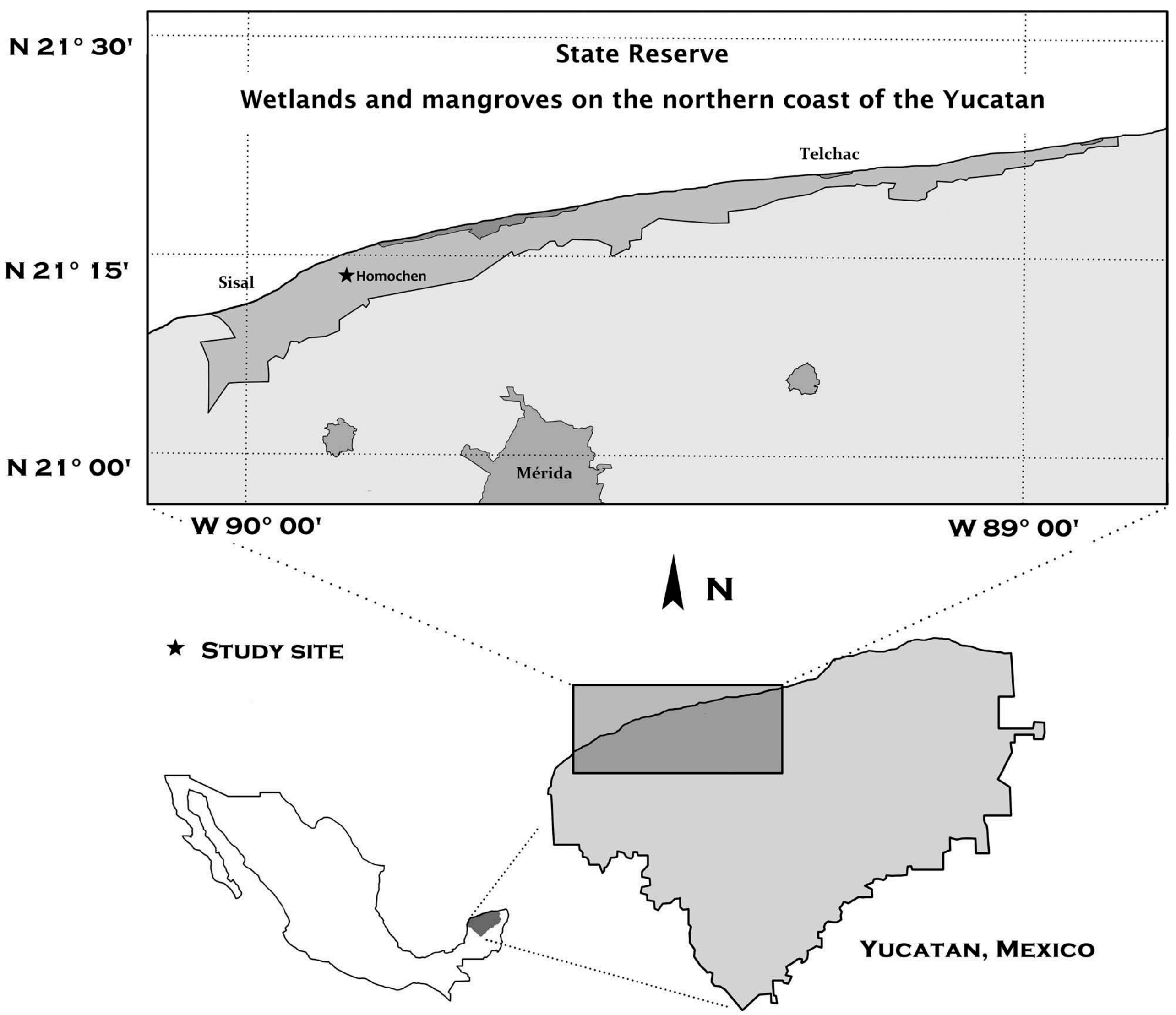

Figure 1. Map location of Homochen Peten in Yucatan, Mexico.

Reddish Egret (*Egretta rufescens*), Boat-billed Heron (*Cochlearius cochlearius*), Snowy Egret (*Egretta thula*) and Great Egret (*Ardea alba*), Roseate spoonbill (*Platalea ajaja*) and Black-crowned Night-Heron (*Nycticorax nycticorax*)) were recorded breeding at Homochen and feeding samples were collected from chicks of five waterbirds species. During routine handling associated with weighing birds, the birds regurgitated, chicks may spontaneously regurgitate in response to disturbance, or can be easily stimulated to regurgitate. (Lewis et al. 2001; Barrett et al. 2007). Because no samples were obtained from Roseate spoonbill and Black-crowned Night-Heron, these species were not taken into the analysis.

The samples are often only partly digested material and readily identifiable. Another advantage is that this type of sampling can be repeated (using the same or different birds) through the breeding season. In total, 99 regurgitated samples were obtained. The sample size was defined by the number of regurgitations obtained from the chicks found in each nest during the collection time (Collect permit SGPA/DGVS/02210/13), Neotropic cormorant (49 samples) Reddish Egret (22), Boat-billed Heron (10), Snowy Egret (8) and Great Egret (10). The sample size were according to the accessibility of nests in the mangrove ecosystem. Samples were placed in plastic bags with 70% alcohol and transported to the Ecology Lab of the Multidisciplinary Teaching and Research Unit, Sisal. National Autonomous University of Mexico (UNAM). Fish from each regurgitated sample were identified with specialized keys and field guides, distinctive features such as coloration, fins, and teeth were used (Castro-Aguirre et al. 1999; Gallardo Torres et al. 2012a). Other present taxa (invertebrates) were also recorded and identified. All prey items were counted and weighed.

Data analysis

Diet of the waterbird species were analyzed by the Prey Specific Importance Relative Index (%PSIRI) (Brown et al. 2012) considering prey-specific abundance number and weight (%PN_i, %PW_i), and Frequency of occurrence (%FO) of taxa:

$$\%\mathrm{PSIRI}_i = \frac{\%FOi\ X\ (\%PNi + \%PWi)}{2}$$

Similarity among the diet compositions of the waterbird species was calculated with a cluster analysis based on Bray–Curtis Similarity Index, using abundance data, according to Clarke (1993). Statistical significance of clusters was evaluated by similarity profile analysis (SIMPROF). Differences in composition and abundance of prey items in waterbirds diet were compared by analysis of similarities (ANOSIM) over a Bray–Curtis similarity matrix; the null hypothesis being that there is no difference in diet composition among bird species. The contribution of each taxa to the differentiation or similarity among clusters was assessed by similarity percentages analysis (SIMPER). The graphical representation of species and their grouping was performed on MDS analysis. All analyses were run with the PRIMER 6.0 (Clarke 1993) software.

Trophic overlap was calculated from the %PSIRI data with the EcoSim Professional (Entsminger 2012) software; application of the Pianka (1974) Index takes a value between 0 and 1, with 0 listed when there is no overlap and 1 when the overlap is complete. We considered biologically significant those values higher than 0.60 (Zaret & Rand 1971; Mathur 1977).

Results

General diet consisted of 17 species and 13 genera within eight families of fish. Neotropic Cormorant, had the broadest diet, with 20 taxa of fish identified, 10 of these species inhabit fresh and brackish waters (Table 1). Their main taxa were *Floridichthys polyommus, Poecilia velifera* and *Cyprinodon artifrons* with almost 70% PSIRI (Figure 2a). Reddish Egret: feeds on 13 fish species, mainly *C. artifrons* (>50% PSIRI), and complements its diet with *F. polyommus, Fundulus persimilis, Garmanella pulchra* and *P. velifera* (~40% PSIRI). These fish inhabit marine, brackish and fresh waters (Figure 2b; Table 1). Boat-billed Heron: diet is composed of nine fish species (Figure 2c), *C. artifrons, F. polyommus*, and *P. velifera* comprise almost 70% PSIRI and these species inhabit marine, brackish and fresh waters (Table 2). Snowy Egret: feeds mainly on *Gambusia yucatana, P. velifera* and *G. pulchra* (almost 80%), complementing its diet with shrimps and insects and all found fish species inhabit brackish and fresh waters (Figure 2d; Table 2). Great Egret: feeds on 11 fish species, mainly on *Poecilidae* (55%) and *Eucinostomus* (20%) genus (Table 2).

Similarity and trophic overlap

Groupings revealed by cluster analysis (Figure 3) were supported by SIMPROF analysis ($p < 0.05$): a first group formed by Reddish Egret, Boat-billed Heron and Neotropic Cormorant with 57.3% similarity, and a second group formed by Snowy Egret and Great Egret with 40.0% similarity. Dissimilarity between these two groups was 75.8%. Taxa that contributed the most to differentiation of the groups were *C. artifrons* (31.9%), *P. velifera* (19.0%), *G. yucatana* (15.0%) and *F. polyommus* (12.0%).

Table 1. Diet composition of Neotropic cormorant (*N. brasilianus*) and Reddish Egret (*E. rufescens*) by percent frequency of occurrence (%FO), Percent of number (%N), prey specific abundance by number (%PN), percent of weight (W%), prey specific abundance by weight (%PW) and Prey Specific Importance Relative Index (%PSIRI).

	%FO	%N	%PN	%W	%PW	%PSIRI
N. brasilianus						
Astyanax sp.	0,5882	0,1318	22,3979	0,0563	9,5750	0,0947
M. colei	0,5882	0,1318	22,3979	0,0080	1,3545	0,0704
Strongylura spp.	0,5882	0,1318	22,3979	0,0604	10,2757	0,0968
S. notata	1,7647	0,3953	22,3979	0,8091	45,8512	0,6066
C. artifrons	12,3529	23,3202	188,7822	2,8714	23,2448	13,1918
F. polyommus	23,5294	31,3570	133,2675	47,4870	201,8197	39,7110
Fundulus sp.	0,5882	0,1318	22,3979	0,4748	80,7106	0,3055
F. grandissimus	9,4118	4,0843	43,3959	11,2683	119,7260	7,7326
F. persimilis	0,5882	0,1318	22,3979	0,3684	62,6348	0,2519
G. pulchra	0,5882	0,1318	22,3979	0,0124	2,1018	0,0726
B. belizanus	5,2941	1,5810	29,8639	2,0969	39,6080	1,8524
G. yucatana	4,7059	1,1858	25,1976	0,1275	2,7090	0,6614
Poecilia spp.	1,1765	0,6588	55,9947	0,1124	9,5517	0,3884
P. velifera	20,5882	29,7760	144,6264	17,0227	82,6817	23,5709
P. mexicana	0,5882	0,1318	22,3979	0,0506	8,5942	0,0918
Eucinostomus spp.	2,9412	0,9223	31,3570	0,6075	20,6541	0,7705
E. argenteus	0,5882	0,1318	22,3979	0,4316	73,3775	0,2838
E. harengulus	1,7647	1,1858	67,1937	0,7811	44,2632	0,9907
Mayaheros spp.	1,1765	0,2635	22,3979	1,0883	92,5043	0,6809
M. urophthalmus	10,5882	4,2161	39,8185	12,8097	120,9803	8,5753
E. rufescens						
Mugil spp.	4,6154	1,3889	30,0926	0,2303	4,9908	0,8100
M. colei	3,0769	0,3968	12,8968	0,4634	15,0616	0,4303
S. timucu	1,5385	0,1984	12,8968	0,6664	43,3131	0,4326
C. artifrons	24,6154	75,0000	304,6875	27,4166	111,3798	51,2343
F. polyommus	16,9231	5,9524	35,1732	23,7146	140,1317	14,8410
F. grandissimus	6,1538	1,3889	22,5694	15,3591	249,5852	8,3782
F. persimilis	10,7692	3,1746	29,4785	18,5483	172,2340	10,8670
G. pulchra	9,2308	4,9603	53,7368	1,4205	15,3883	3,1920
G. yucatana	4,6154	1,5873	34,3915	0,2523	5,4661	0,9203
Poecilia sp.	3,0769	0,5952	19,3452	0,6636	21,5674	0,6297
P. velifera	12,3077	4,9603	40,3026	8,5804	69,7154	6,7738
E. harengulus	1,5385	0,1984	12,8968	1,3985	90,9041	0,7989
E. gula	1,5385	0,1984	12,8968	1,1846	77,0011	0,6919

The values supported the SIMPROF results. The most important taxa were *C. artifrons, F. polyommus* and *P. velifera* for Neotropic Cormorant and Boat-billed Heron; *C. artifrons* and *F. polyommus* for Reddish Egret; *G. pulchra, G. yucatana* and *P. velifera* for Snowy Egret; and the *Poecilia* sp. and *Eucinostomus* sp. for Great Egret.

Analysis of similarities (ANOSIM) suggested a trophic spectrum that differed among bird species ($R = 0.358$; $p < 0.001$): between Neotropic Cormorant and Snowy Egret ($R = 0.550$; $p = 0.001$); between Reddish Egret and Snowy Egret ($R = 0.457$; $p = 0.001$); between Reddish Egret and Great Egret ($R = 0.379$; $p = 0.002$); and between Boat-billed Heron and Snowy Egret ($R = 0.360$; $p = 0.009$).

Trophic overlap is shown in Table 3, ranged from 0.18 to 0.94. Values of >0.60 are considered biologically significant. Neotropic cormorant shows a trophic overlap with the piscivores species Reddish Egret, Boat-billed Heron, and Great Egret. Boat-billed Heron with Reddish Egret for the consumption of endemic fish species *C. artifrons* and *F. polyommus* and Great Egret with Snowy Egret mainly for feeding on invertebrates (Figure 3).

Discussion

Fish-dominated diets of the birds in this study, despite the abundance of other potential prey in the wetlands of Yucatan, such as crustaceans, insects, amphibians and reptiles (Kushlan 2005; Nelson 2005); only Snowy Egret and Great Egret consumed non-fish preys, and in low quantities, in contrast to other studies of North America and Caribbean, where an important part of the diet corresponds to crustaceans and insects (Willard 1977; Denis & Jimenez 2009; Lorenzon et al. 2013).

In the coastal wetland known as 'cienega' 17 species of fishes have been reported (Gallardo-Torres et al. 2012b). The most abundant fish species directly related to the feeding of the herons, are mainly resident species such as *F. polyommus, P. velífera*, and *C. artifrons*. These species are not of commercial importance but are a key link on the functioning of the ecosystem as a food source for birds, fish, mammals, and reptiles (Denis & Jimenez 2009).

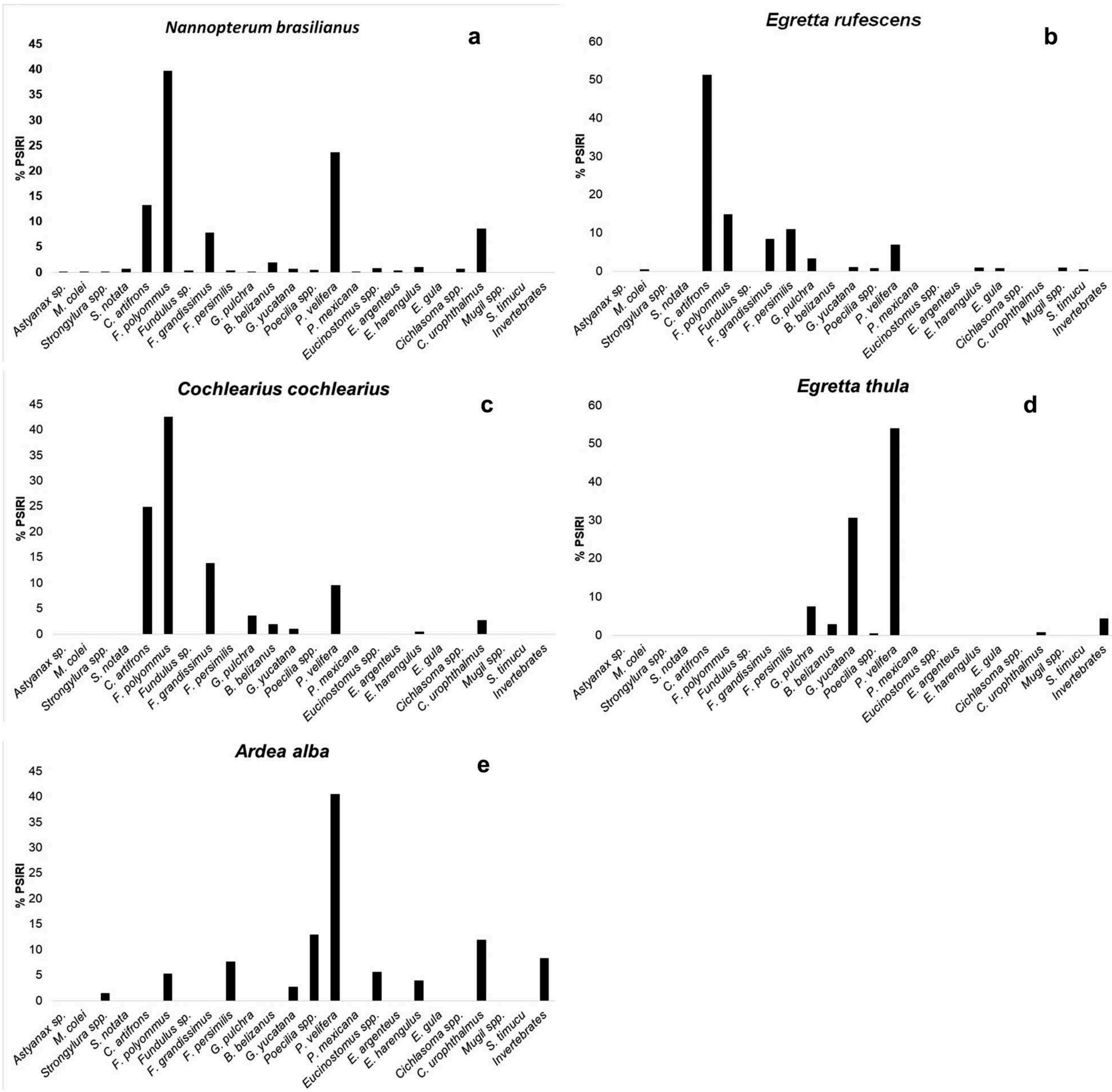

Figure 2. Waterbirds diet in the Northern coast of Yucatan. (a) *Nannopterum brasilianus*; (b) *Egretta rufescens*; (c) *Cochlearius cochlearius*; (d) *Egretta thula*; (e) *Ardea alba.*

The Neotropic Cormorant is considered a generalist consumer that can feed on fish, mollusks, amphibians, insect larvae, and crustaceans (Nelson 2005), although its main food source are fishes. In the Lagoa dos Patos, Brazil, the diet of this waterbird consisted of 10 Families of fish representing 99.9% of biomass and 99.7% of consumed individuals (Barquete et al. 2008). In Bocaripo-Chacopata Lagoon, Venezuela, the diet of this waterbird consisted of four fish families, two of gastropods and one of crustaceans. Even though the invertebrate catch is considered to be accidental (Muñoz-Gil et al. 2012), it is evident that the Neotropic Cormorant has trophic plasticity or opportunistic behavior and consumes a variety of prey types according to their abundance and availability (Barquete et al. 2008; Muñoz-Gil et al. 2012). As the diet of the Neotropic Cormorant was entirely fish, this may indicate high abundance and availability of these resources in the wetlands of Yucatan.

The diet of Reddish Egret and Boat-billed Heron were similar. They mostly consumed the same prey, *Cyprinodon artifrons*, and *Floridichthys polyommus*, endemic species which have a low relative abundance of 4.8% and 27.0%, respectively, in the wetlands system of northern Yucatan (Gallardo Torres et al. 2012a).

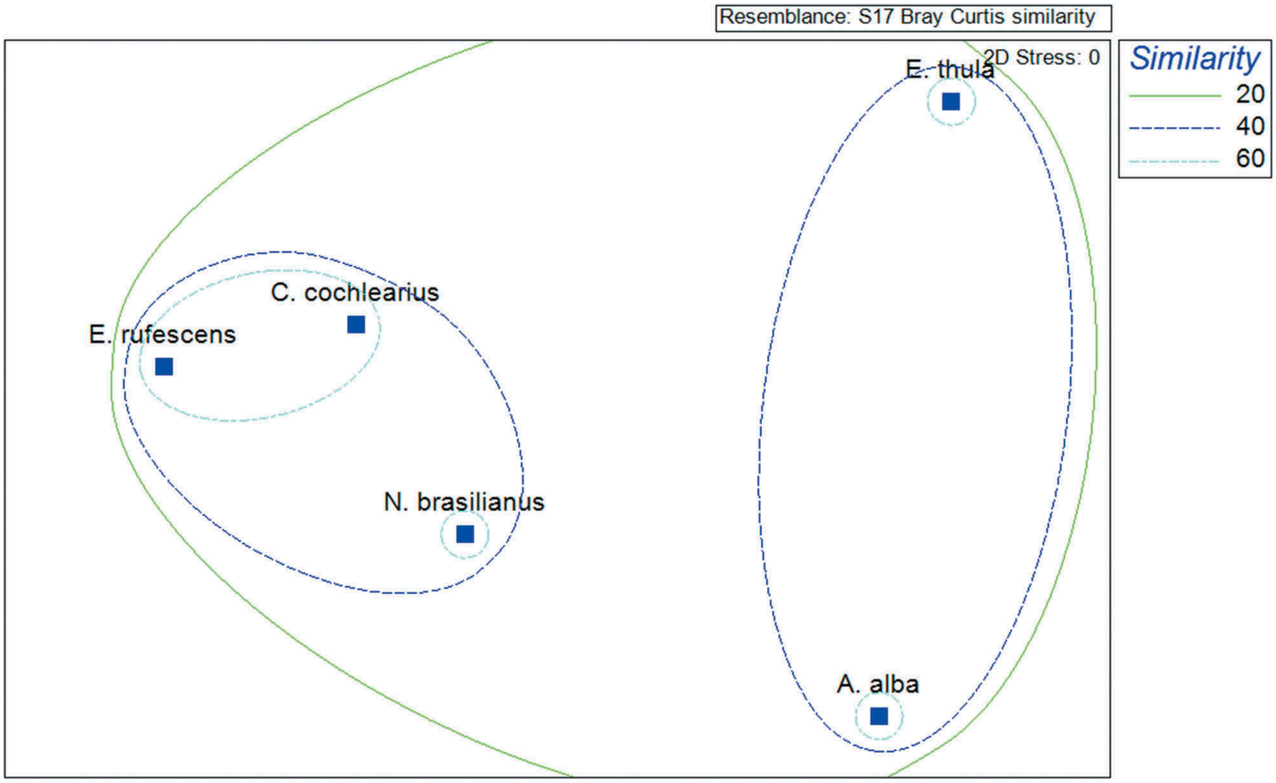

Figure 3. NMDS analysis and similarities based on taxa consumed by waterbird species that inhabit the northern coast of Yucatan.

Table 2. Diet composition of Boat-billed Heron (*C. cochlearius*), Snowy Egret (*E. thula*) and Great Egret (*A. alba*) by percent frequency of occurrence (%FO), Percent of number (%N), prey specific abundance by number (%PN), percent of weight (W%), prey specific abundance by weight (%PW) and Prey Specific Importance Relative Index (%PSIRI).

	%FO	%N	%PN	%W	%PW	%PSIRI
C. cochlearius						
C. artifrons	26,6667	46,7532	175,3247	2,8452	10,6694	24,8719
F. polyommus	10,0000	23,8095	238,0952	60,8742	608,7425	42,4660
F. grandissimus	10,0000	3,4632	34,6320	24,0249	240,2488	13,7843
G. pulchra	10,0000	6,9264	69,2641	0,2372	2,3720	3,5923
B. belizanus	3,3333	2,5974	77,9221	1,0626	31,8767	1,8353
G. yucatana	10,0000	1,7316	17,3160	0,1150	1,1497	0,9260
P. velifera	20,0000	11,6883	58,4416	7,2757	36,3786	9,5098
E. harengulus	3,3333	0,4329	12,9870	0,3086	9,2580	0,3718
M. urophthalmus	6,6667	2,5974	38,9610	2,6721	40,0818	2,6425
E. thula						
G. pulchra	16,0000	10,8280	67,6752	4,0652	25,4075	7,4466
B. belizanus	8,0000	1,2739	15,9236	4,1898	52,3730	2,7319
G. yucatana	24,0000	43,9490	183,1210	17,0949	71,2288	30,5220
Poecilia spp.	4,0000	0,6369	15,9236	0,0192	0,4794	0,3281
P. velifera	24,0000	37,5796	156,5817	70,3068	292,9450	53,9432
M. urophthalmus	4,0000	0,6369	15,9236	0,7287	18,2167	0,6828
Invertebrates	20,0000	5,0955	25,4777	3,5954	17,9770	4,3455
A. alba						
Strongylura spp.	3,8462	1,5385	40,0000	1,2272	31,9078	1,3828
F. polyommus	7,6923	4,6154	60,0000	5,9572	77,4440	5,2863
F. persimilis	3,8462	1,5385	40,0000	13,7199	356,7185	7,6292
G. yucatana	3,8462	4,6154	120,0000	0,5824	15,1427	2,5989
Poecilia spp.	11,5385	16,9231	146,6667	8,9400	77,4801	12,9315
P. velifera	26,9231	50,7692	188,5714	30,1398	111,9477	40,4545
Eucinostomus spp.	23,0769	9,2308	40,0000	2,0260	8,7792	5,6284
E. harengulus	3,8462	4,6154	120,0000	3,2449	84,3664	3,9301
M. urophthalmus	11,5385	4,6154	40,0000	19,0781	165,3438	11,8468
Invertebrates	3,8462	1,5385	40,0000	15,0844	392,1957	8,3115

Table 3. Trophic overlap index of waterbirds. Significant are in bold.

	N. brasilianus	E. rufescens	C. cochlearius	E. thula	A. alba
N. brasilianus	-	**0.6422**	**0.8366**	0.4297	**0.6427**
E. rufescens		-	**0.9359**	0.1780	0.1903
C. cochlearius			-	0.3648	0.3758
E. thula				-	**0.6207**
A. alba					-

Even though it seems that these herons consume prey that is abundant. Ramo and Busto (1993) found that fish of the same genus in the Sian Ka'an Biosphere Reserve in the Yucatan Peninsula (*Cyprinodon variegatus* and *Floridichthys carpio*), are numerically dominant in the herons' diet, even though low abundances of *F. carpio* are recorded in the system. Nonetheless, the Reddish Egret and Boat-billed Heron show a high trophic overlap index and are grouped in Yucatan just as in Sian Ka'an. Populations of Reddish Egret in the Gulf of Mexico (Texas and Bahamas) similarly use *C. variegatus* as dominant prey (85%) (Holderby et al. 2014); these authors suggested that rather than being a specialized predator, the Reddish Egret shows a preference for sites where these fish are relatively abundant. In contrast, Boat-billed Heron colonies on the Mexican Pacific coast feed mostly on shrimps (Dickerman & Juarez 1971), supporting the idea that this heron is not a trophic specialist.

The Snowy Egret and Great Egret are generalists; they can consume annelids, aquatic and terrestrial insects, shrimps, crabs, prawns, snails, amphibians, reptiles, birds and small mammals. Although their diets are usually dominated by fish (Kushlan 1978, 2005), these herons display a broad variety of foraging techniques and can therefore obtain prey in a wide range of environments (Kushlan 1978, 2005). In our study site, fish predominated the diet of waterbirds as they did in Sian Ka'an. In both sites fish of *Poecilia* genus composed 27% of the Snowy Egret's diet, enclosing *P. velifera* in the northern coast and *P. orri* in the eastern Yucatan Peninsula (Ramo & Busto 1993). For the Great Egret, *P. velifera* accounted for 30% of the biomass consumed in the present Yucatan study site; whereas in Sian Ka'an, *Astyanax fasciatus* was the most consumed prey by this species and the *Poecilia* genus represents 6% of the consumed biomass (Ramo & Busto 1993). In the Everglades wetlands, *Poecilia* genus forms 30% of the diet of the Great Egret and 17% for the Snowy Egret (Trexler et al. 1994). In both northern Yucatan and Sian Ka'an, the Snowy Egret and Great Egret have similar diets. These species group separately from a group comprising the Neotropic Cormorant, Reddish Egret, and Boat-billed Heron.

The bird guild shows segregation in their use of resources. Reddish Egret and Boat-billed Heron seem to have a preference for freshwater species while Neotropic Cormorant, Snowy Egret, and Great Egret mostly consume marine species, this behavior indicates the feeding habitats, which can be toward the sea or to the 'cenotes' of fresh water to avoid competition for resources. In the same way, the size of the prey species was greater as the size of the chicks increased, in this sense there is a distribution of resources related to sizes (Lachlan et al. 2009). Therefore, these characteristics are related to their behavior and hunting strategies, since the studied wetland is considerably shallow (-<10 cm) and it does not have the required depth for the Neotropic Cormorant to feed, thus it has to fly to deeper surrounding areas such as the sea or nearby lagoons. According to Denis and Jimenez (2009), coexistence of several wading bird species in a colony results from the partitioning of resources such as nesting sites, nest season, and food. Because the differential selection of prey could be important for reducing interspecific competition. This study has considered the diet of the offspring of five species of waterbirds. Since reproductive success depends largely on available food resources, this information is important for the conservation of waterbirds. Management schemes must take into account not only the nesting sites but also the spatial distribution of fish, especially the ones that are most consumed such as Poeciliidae (especially *P. velifera* and *G. yucatana*) and Cyprinodontidae (particularly *C. artifrons, F. polyommus, Fundulus persimilis*, and *Fundulus grandissimus*).

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Disclosure statement

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