

Temporal and spatial variation of waterbirds at Sayula Lagoon, Jalisco, Mexico: a five-year winter season study

M. M. Güitrón–López, F. M. Huerta–Martínez,
O. Báez–Montes, Y. F. Estrada–Sillas, L. Chapa–Vargas

Güitrón–López, M. M., Huerta–Martínez, F. M., Báez–Montes, O., Estrada–Sillas, Y. F., Chapa–Vargas, L., 2018. Temporal and spatial variation of waterbirds at Sayula Lagoon, Jalisco, Mexico: a five-year winter season study. *Arxius de Miscel·lània Zoològica*, 16: 135–150, Doi: <https://doi.org/10.32800/amz.2018.16.0135>

Abstract

Temporal and spatial variation of waterbirds at Sayula Lagoon, Jalisco, Mexico: a five-year winter season study. Wetlands in central Mexico are important habitats for assemblages of migratory and resident birds. To study variation in richness and abundance of waterbirds, we conducted monthly observations in 30 permanent plots throughout the Sayula Lagoon, Jalisco, Mexico, during the winter season (from October to March) from 2004–2007 and from 2009–2011. Seventy-three species were recorded; 39 species were winter visitors, and eight species are included in some risk category. The best represented families were: Anatidae, Scolopacidae and Ardeidae. *Spatula clypeata* and *Anser caerulescens* were the most abundant species. We found variation in richness between zones (only two were similar), but not between the seasons (only WS4 was different) or months (only November was different). Sayula lagoon is a highly dynamic ecosystem influenced by migration and the water inputs occurring during the rainy season.

Data published in GBIF ([Doi: 10.15470/cuwgqi](https://doi.org/10.15470/cuwgqi))

Key words: Avifauna, Richness, Ramsar site, Waterbirds, Wetlands

Resumen

Variación temporal y espacial de las aves acuáticas de la laguna de Sayula, Jalisco, México: estudio de cinco temporadas invernales. Los humedales del centro de México son hábitats importantes para ensambles de aves tanto migratorias como residentes. A fin de estudiar la variación en cuanto a riqueza y abundancia de las aves acuáticas, se realizaron observaciones mensuales en 30 parcelas permanentes de toda la laguna de Sayula, Jalisco, México, durante las temporadas invernales (de octubre a marzo) de los años 2004 a 2007 y 2009 a 2011. Se registraron 73 especies. Un total de 39 especies son visitantes invernales y ocho están incluidas en alguna categoría de riesgo. Las familias mejor representadas fueron: Anatidae, Scolopacidae y Ardeidae. *Spatula clypeata* y *Anser caerulescens* fueron las especies más abundantes. Se observó variación de la riqueza entre zonas (sólo dos fueron similares), pero no entre estaciones (solo WS4 fue diferente) ni entre meses (solo el mes de noviembre fue diferente). La laguna de Sayula es un ecosistema muy dinámico influido por la migración y el aporte de agua durante la temporada de lluvias.

Datos publicados en GBIF ([Doi: 10.15470/cuwqgi](https://doi.org/10.15470/cuwqgi))

Palabras clave: Avifauna, Riqueza, Sitio Ramsar, Aves acuáticas, Humedal

Resum

Variació temporal i espacial dels ocells aquàtics de la llacuna de Sayula, Jalisco, Mèxic: estudi de cinc temporades hivernals. Els aiguamolls del centre de Mèxic són hàbitats importants tant per a ensambles d'ocells migratoris com residents. Per tal d'estudiar la variació quant a riquesa i abundància dels ocells aquàtics es van portar a terme observacions mensuals en 30 parcel·les permanents de tota la llacuna de Sayula, Jalisco, Mèxic, durant les temporades hivernals (d'octubre a març) dels anys 2004 a 2007 i 2009 a 2011. S'hi van registrar 73 espècies. Un total de 39 espècies són visitants hivernals i vuit estan incloses en alguna categoria de risc. Les famílies més ben representades van ser: Anatidae, Scolopacidae i Ardeidae. *Spatula clypeata* i *Anser caerulescens* van ser les espècies més abundants. Es va observar una variació de la riquesa entre zones (només dues van ser similars), però no entre estacions (només WS4 va ser diferent) ni entre mesos (només el mes de novembre va ser diferent). La llacuna de Sayula és un ecosistema molt dinàmic influït per la migració i l'aportació d'aigua durant la temporada de pluges.

Dades publicades a GBIF ([Doi: 10.15470/cuwqgi](https://doi.org/10.15470/cuwqgi))

Paraules clau: Avifauna, Riquesa, Lloc Ramsar, Ocells aquàtics, Aiguamoll

Received: 21/06/2017; Conditional acceptance: 20/11/2017; Final acceptance: 10/07/2018

María Marcela Güitrón–López, Francisco Martín Huerta–Martínez, Oscar Báez–Montes and Yadira Fabiola Estrada–Sillas, Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara. Camino Ramón Padilla Sánchez #2100 Nextipac, Las Agujas, Zapopan, Jalisco, C. P. 45110, México.– Leonardo Chapa–Vargas–División de Ciencias Ambientales, Instituto Potosino de Investigación Científica y Tecnológica. Camino a la Presa San José #2055, Col. Lomas 4 sección, San Luis Potosí, C. P. 78216, México.

Corresponding author: F. M. Huerta–Martínez. E–mail: martin.huerta@academicos.udg.mx

Introduction

Wetlands are one of the most valuable and threatened types of ecosystems at a global level, and they are among the most endangered ecosystems as a consequence of human activity (Sebastián–González et al., 2013). In the Mediterranean area, for example, the surface area of wetlands has decreased by 80–90% in the last decades (Finlayson et al., 1992). This decrease has led to wetland protection at an international level, and waterbirds are used as indicator species (Ramsar Regional Center–East Asia, 2017).

Wetlands play a critical role in climate change, biodiversity, hydrology, and human health. In climate change, wetlands influence both global and local/regional climate by supplying water to the atmosphere through potential evapotranspiration and by taking up carbon dioxide and emitting methane. From a biodiversity aspect, although freshwater wetlands cover only 1% of the earth's surface, they are home to nearly 40% of the world's species. Hydrologically, wetlands replenish groundwater, regulate water movement, and purify water, providing these important parts of the hydrologic cycle. Regarding human health, wetlands provide the traditional medicines on which 80% of the world's population depends for primary health care (Hu et al., 2017). Wetlands inside Mexico are important habitats for a variety of aquatic and terrestrial wintering and migrating birds (Barragán et al., 2002), and

they are also reproduction sites for many resident species (Alcántara and Escalante, 2005). Despite the ecological, economic, and social importance of wetlands, studies focusing on the species inhabiting Mexico are scarce (Ramírez–Bastida et al., 2008) and mainly focused on descriptions of one–year seasonal dynamics (Enciso and Paracuellos, 1997). Some studies carried out in inland wetlands of Mexico report 36 species (Fonseca et al., 2012) and 30 species (Berumen et al., 2017), in Tlaxcala and Puebla respectively, but Cuevas and Iñiguez–Davalos (2017) report a total of 100 species for Jocotepec in Chapala, Lake Jalisco. All these studies have recognized temporal variation according to the seasonality through the year. Assessments of inter–annual changes in Mexican intercontinental wetland sites, however, are still lacking. We found only two papers about waterbirds in Sayula Lagoon. Munguía et al. (2005) documented variation in substrate composition within the Laguna de Sayula, and changes in waterfowl diversity and habitat use during the dry season, and Barba and Martínez (2008) recorded the behavior of snow geese during their winter visit. Moreover, in spite of the importance of this wetland as a waterbird refuge, the published study about temporal and spatial changes in richness, abundance, and species composition in the different habitats (Munguía et al., 2005) was performed only over one winter season and only 12 species were recorded. Studies over a longer period are therefore needed to document whether there is any variation in pattern. Avian assemblages, provide additional information on wetland function because birds use a variety of habitats and feed at a variety of trophic levels. Furthermore, many avian taxa are dependent on specific wetlands for survival or reproduction (Reeder and Wulker, 2017). Such information is important for decision–making on conservation and management. The aim of this research was to evaluate how waterbird assemblages change at the Sayula Lagoon in terms of species composition and richness–abundance. The study was performed over five winter seasons and in various zones of the lagoon.

Methods

Study area

Sayula Lagoon is located in the state of Jalisco in west central Mexico. It has been declared a Ramsar site and a priority site as it is an important migratory waterbird habitat (DUMAC, 2006). It is a non–permanent wetland that is part of a closed basin in the south of Jalisco state, Mexico (19° 54' 24", 20° 10' 32" N and –103° 27' 39", – 103° 36' 40" W) (fig. 1). The lagoon has an area of 16,800 ha and an average altitude of 1,350 m a.s.l. It has four vegetation types (Macías–Rodríguez, 2004), which in order of importance are halophytic vegetation, thorn forest, aquatic and sub–aquatic vegetation, and tropical dry forest. The weather is dry and corresponds to the semiarid subtype (García, 1973). Mean annual temperature ranges from 18 to 22°C. The rainy season takes place during the summer with an annual average precipitation of 681.5 mm (Medina and Hernández, 1993). Even though the area presents only four or five rainy months (from June to September, occasionally October), the water generally remains in the center of the basin until March, forming the Sayula Lagoon. It is an ideal landscape to study aquatic avifauna.

Field surveys

Waterbird surveys were conducted monthly over five winters, from October to March 2004–2007 and from October to March 2009–2011, as the migratory species are present in the study area in these months. Thirty (1 ha) permanent plots were randomly stratified using a numbered grid for each zone type. Each plot was located at a minimum distance of 500 m from each other in order to avoid double counts of the same individuals, following Ojasti and Dallmeier (2000). Plots were delimited with red and yellow sticks to allow their rapid location. Observations were

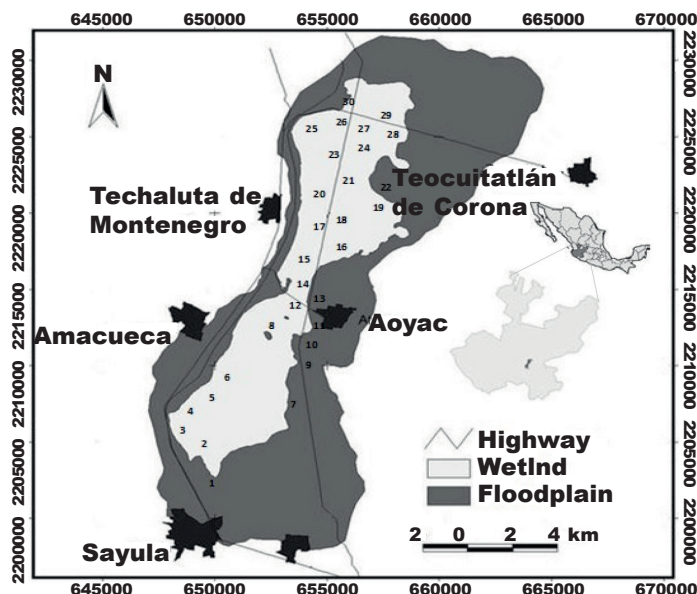


Fig. 1. Geographical location of Sayula Lagoon, Jalisco, Mexico. Numbers in the map indicate plot numbers. Coordinates are UTM, Q13N.

Fig. 1. Localización geográfica de la laguna de Sayula, Jalisco, México. Los números que figuran en el mapa corresponden a cada una de las parcelas. Las coordenadas son UTM, Q13N.

made in the eight hours after sunrise. We recorded all the bird species seen and total abundance was also recorded. The block method (Howes and Bakewell, 1989) was used to estimate numbers whenever large flocks (> 300 birds) were present. The seasonal status of species was contrasted with those published in Howell and Webb (2001). The category of species risk was assigned using the Mexican Law (NOM–059–SEMARNAT–2010) (SEMARNAT, 2010) and the IUCN Red List of Threatened Species. The on–line taxonomic Check–list of North American birds (AOU, 2015) as well as Sibley Guide to Birds (Sibley, 2001) were used.

All plots were classified as one of the five zones according to Colwell and Taft (2000), with modifications as follows: deep zone (DEEZ > 100 cm), aquatic zone (AQUZ > 20 y < 100 cm), shallow zone (SHAZ < 20 cm), muddy zone (MUDZ, zone with wet soil and some small waterlogging) and sandy zone (SANZ, zone with dry soil). This classification was possible because during the observation period (October–March) in each study year, the water level remained the same. We recorded the area or areas in which each individual bird was observed (Amparán–Salido, 2000).

Data analysis

Temporal changes were analyzed by comparing seasons and months, and spatial changes were analyzed by comparing the zones in the study area. We also studied attributes of community structure. Richness (S), was estimated through species accumulation curves using EstimateS v. 9.1.0, (Colwell, 2009). Using abundance (numbers of individuals) data and the same software, rarefaction curves were performed to compare richness between zones, months and sampled seasons. In the latter analysis, we compared the richness mean values and their 84 % confidence intervals at $p = 0.05$ (MacGregor–Fors and Payton, 2013).

Species relative abundance was estimated according to the following categories: abundant (90–100%), common (65–89%), moderately common (31–64%), uncommon (10–30%), and rare (1–9%). These percentages were obtained for each species as the number of individuals of a species divided by the total number of individuals considering all species and multiplying by 100 (Pettingill, 1969). Relative frequency was estimated to determine species representativeness over time and the following categories were assigned: very frequent (0.76–1), frequent (0.51–0.75), moderately frequent (0.26–0.50), and sporadic (0–0.25). This estimate refers only to the number of plots containing a given species divided by the total number of plots, which is not redundant with abundance because it does not refer to individuals (Krebs, 1985). In order to ensure non-redundant data, a fixed time period was assigned (10 minutes) for observation and the distance between plots was longer than 500 m.

An abundance data matrix –estimated with the Bray–Curtis' index using the 4th root data transformation to reduce the contribution of abundant species– was implemented to perform the following analyses using PRIMER 6 (Clarke and Gorley, 2005). A nonmetric multidimensional scaling (NMDS) complemented with hierarchical cluster analysis (Bray–Curtis' index using average group linkage methods, Clarke and Warwick, 2001) was implemented to compare species composition between zones, months, and seasons. To assess significant differences between groups of samples, a one-way non-parametric similarity analysis was performed (ANOSIM) using 10,000 permutations (Clarke and Gorley, 2005). We also used a one-way similarity percentage method (SIMPER) to identify the most representative species in each zone and to determine the percentage of similarity between zones. Species were selected considering those contributing with 90% of the observed similarity in this study.

Functional groups for species in the lagoon were determined according to Escofet et al. (1988) and Terres (1991) on the basis of their foraging strategy (shorebirds, ducks, small grebes, jacanas and large wading birds) and dietary strategy (herbivore, piscivore). Our categories are coarse, but match the generality of the ecological questions we addressed.

Results

Sayula Lagoon is an important part of the migratory corridor for waterfowl. It also harbors resident populations of some species with risk categories, such as the Mexican Duck (*A. platyrhynchos diazi*), which is an endangered and an endemic species. Wintering and migratory species significantly increased abundance and richness at the Sayula Lagoon from October to March. At this time of the year, these organisms represented 66% of richness and 81% of abundance with respect to resident species. Migrants and wintering species were mainly composed of waterfowl (76%) and shorebirds (24%).

General abundance and richness patterns

According to ACE, the estimated richness was 87.43 in comparison with 72 observed species, representing a sampling efficiency of 82.35%. We estimated that 15 species are yet to be recorded (fig. 2).

We identified seventy-three species over the five winter seasons (WS1, WS2, WS3, WS4 and WS5), belonging to seven orders and 13 families. Waterbird richness and diversity varied in time and space (fig. 3). WS1 was the richest and had the highest abundance value.

According to the zones, SHAZ (< 20 cm) was the richest but AQUZ (> 20 y < 100 cm), had the highest abundance value (fig. 4); this finding is supported by rarefaction analysis (fig. 5A).

Rarefaction analysis showed significant differences in richness between seasons; WS4 (37 species) and WS1 (46 species), WS2 (49 species); WS3 (42 species) and WS5 (43 species) significantly differed from WS2 (fig. 5B). The rarefaction analysis suggested that October (43 species), November (54), and March (48) differed significantly from each other. December (45), January (47), February (45) and March (48) did not differ significantly in either richness (fig. 5C) or diversity.

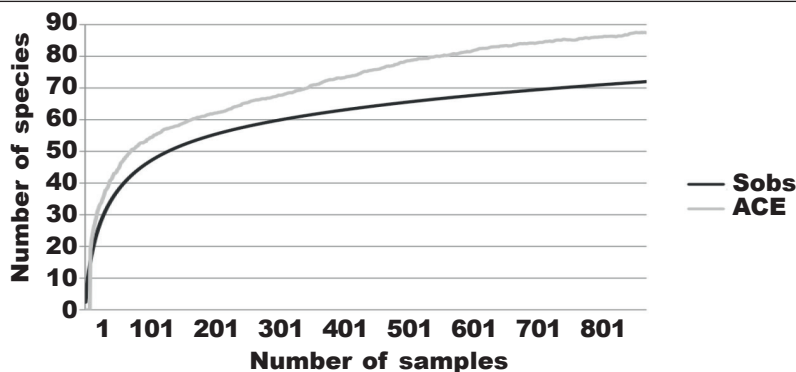


Fig. 2. Observed species accumulation curves (Sobs) and expected curves using ACE estimator.

Fig. 2. Curvas de acumulación de especies observadas (Sobs) y previstas según el estimador ACE.

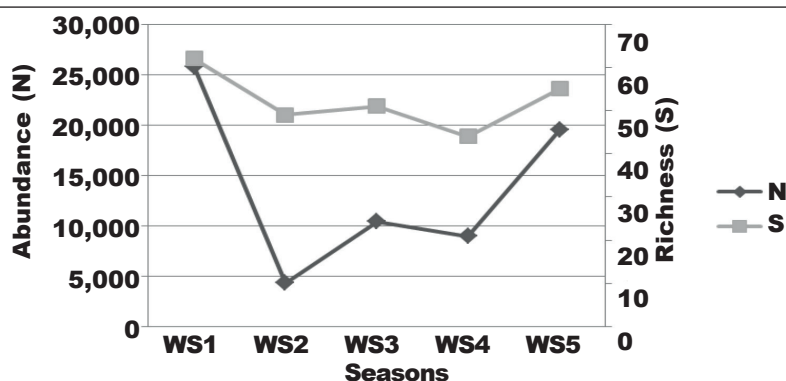


Fig. 3 Variation in abundance and richness of waterbirds over five winter seasons at Sayula Lagoon, Mexico.

Fig. 3 Variación de abundancia y riqueza de aves acuáticas en la laguna de Sayula, México.

The cluster analysis and NMDS revealed two groups of zones, supporting rarefaction results: AQUZ and SHAZ (with the highest abundance) were the most similar and formed a group with MUDZ. The other zones (SANZ and DEEZ) formed another group with the lowest similarity; they were also the zones with the lowest abundance (fig. 6A). According to seasons, the analysis formed two groups: 1) WS2 and WS4 with the highest similarity, and the lowest richness and abundance values; and 2) all the remaining seasons. Among these, WS1 and WS5 had the highest richness and abundance values (fig. 6B). With respect to months, this analysis showed that January and December, the months with the highest abundance values, were the most similar, whereas March was the most different month with the lowest abundance (fig. 6C). The ANOSIM estimated a global $R = 0.016$ ($P = 0.001$) for

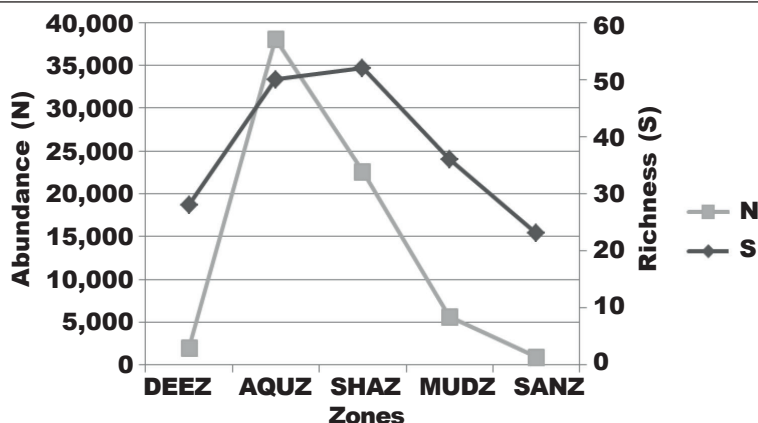


Fig. 4. Variation in abundance and richness of waterbirds in five zones (Deep DEEZ, Aquatic Zone AQUZ, Shallow SHAZ, Muddy MUDZ, Sandy SANZ) at Sayula Lagoon, Mexico.
 Fig. 4. Variación de abundancia y riqueza de especies en las cinco zonas (Deep DEEZ, Aquatic Zone AQUZ, Shallow SHAZ, Muddy MUDZ, Sandy SANZ) de la laguna de Sayula, México.

the monthly scale; in spite of the low value of the separation between groups, differences between October–February and November–March were recorded. This result is consistent with those from the NMDS, and the cluster analysis. For winter seasons, the global R-value was also low (0.041, $P = 0.001$), but significant differences among WS1–WS2, WS1–WS4, WS2–WS3 and WS3–WS4 were distinguished.

A total of 39 species were winter visitors, 24 were resident, six were occasional migrants, three were transitory migrants, and one was a summer resident. The most highly represented family was Anatidae with 18 species, followed by Scolopacidae with 15 species, and Ardeidae with 10 species. Eight species under some risk category according to NOM-059–SEMARNAT–2010 (SEMARNAT, 2010) were recorded; three of these are classified as endangered (Mexican duck *Anas platyrhynchos diazi*, American bittern *Botaurus lentiginosus*, and snowy plover *Charadrius nivosus*). Five were classified as under special protection (least bittern *Ixobrychus exilis*, least grebe *Tachybaptus dominicus*, wood stork *Mycteria americana*, king rail *Rallus elegans* and virginia rail *R. limicola*). The Mexican duck (*Anas platyrhynchos diazi*) is the only endemic species of waterbirds at Sayula Lagoon. The snowy plover (*Charadrius nivosus*) and king rail (*Rallus elegans*) are included at the IUCN Red List as Near Threatened and the remaining species are in the Least Concern category (see the [dataset published at GBIF](#)).

In terms of relative frequency, 13 species were very frequent, 15 were frequent, 13 were moderately frequent, and 32 consisted of sporadic records. Most species were sporadic (43%); this class included rails, gulls, waterfowl, and grebes. Frequent species (21%) mainly included herons, grebes, terns, and shorebirds. Moderately frequent species (18%) included some herons and other resident water birds and medium-sized shorebirds, mainly migrant. Finally, highly frequent species (18%) were mainly migrant and resident waterfowl and some medium sized shorebirds. From the recorded species, two were categorized as abundant, 10 were common, 12 were moderately common, 13 were non-common, and 36 were rare (see appendix 1).

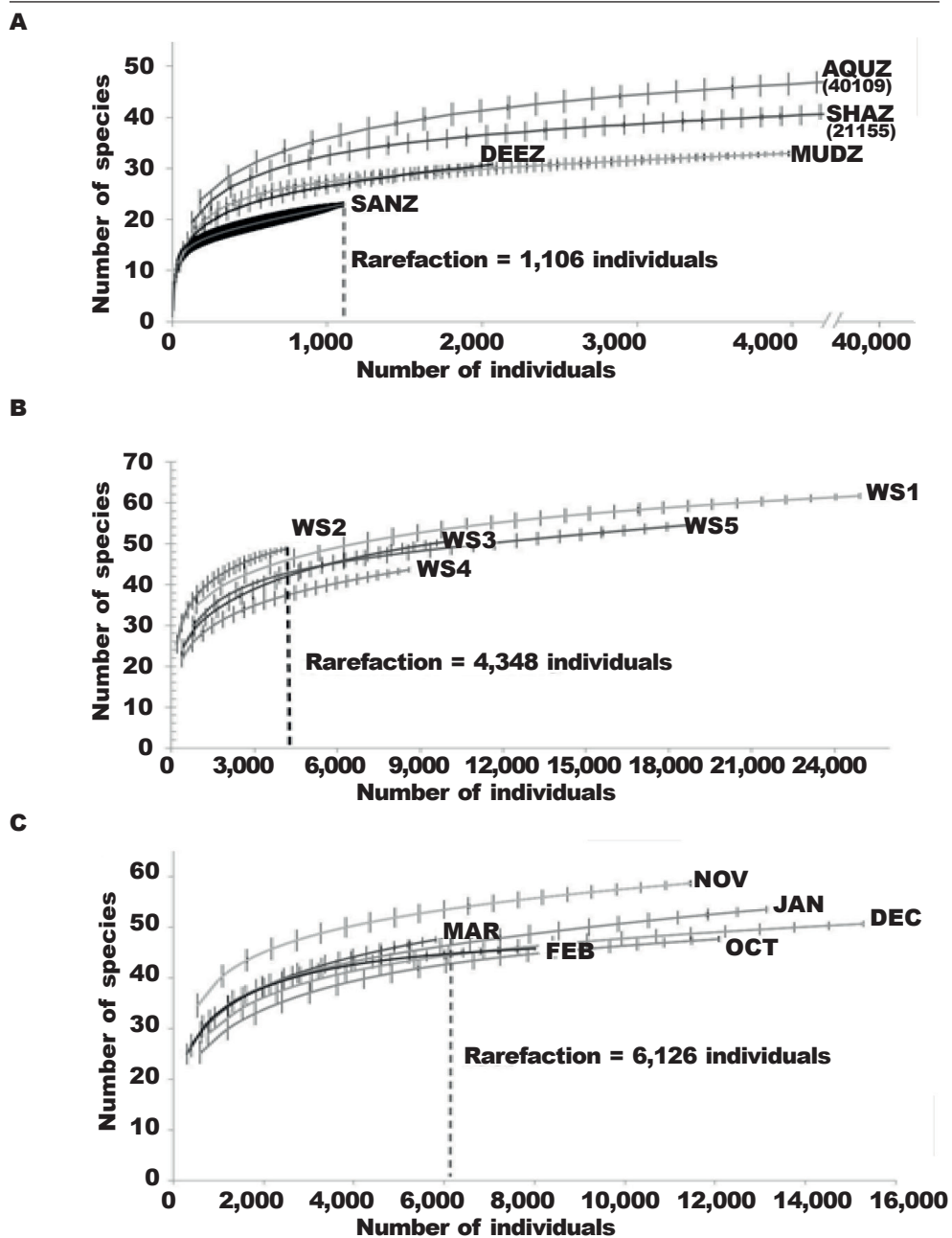


Fig. 5. Comparison of total richness by zones (A), seasons (B) and months (C) through rarefaction curves based on individual numbers.

Fig. 5. Comparación de la riqueza total por zonas (A), estaciones (B) y meses (C) mediante las curvas de rarefacción según el número de especímenes.

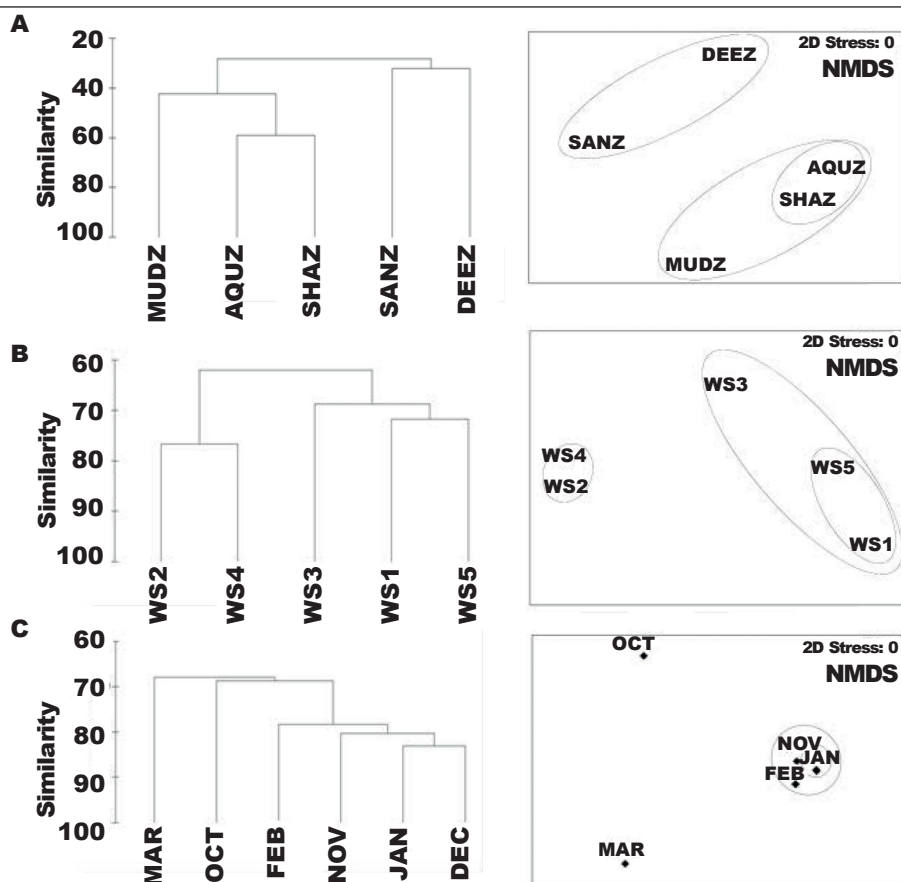


Fig. 6. Results of cluster analysis (left) and NMDS (right), for zones (A), seasons (B) and months (C).

Fig. 6. Resultados del análisis de conglomerados (izquierda) y NMD (derecha) por zonas (A), estaciones (B) y meses (C).

Five functional groups were established. Those that were best represented were shorebirds (foraging strategy) (35%). This group also had the highest richness. The second group included ducks, small grebes, and jacanas (foraging strategy) (25%). The third group consisted of large wading birds (19.5%) (foraging strategy), while piscivores (dietary strategy) (11%), and herbivores (dietary strategy) (9.5%) made up the fourth and fifth groups, respectively.

Discussion

Movement in animal populations can take place over shorter time scales than seasons but most often occurs between seasons over the year. Understanding these movement patterns is therefore essential if we are to understand the connection between local and regional dynamics (Wells et al., 2013).

This study investigated the variation in space and time of water bird assemblages over five winter seasons at Sayula Lagoon, an important site for various functional groups of aquatic birds, both migratory and resident, even when it is an intermittent wetland. Despite evident disturbance activities in the area, especially changes in land use, retention and deviation of natural water runoff, and pollution by discharges from municipal wastes (Atoyac City Council, 2010), this site is an important wetland for waterbirds, as shown by the many migratory and resident species recorded there (73), comparable to the 74 species in La Vega Baja del Segura (Alicante's web of natural and artificial wetlands) reported by Sebastián–González et al. (2013) and the 79 species reported by Cintra et al. (2007). In contrast with the latter authors, however, we found most of the species were winter visitors and only 34 were exclusively waterbirds. Some studies in inland wetlands of Mexico report half the number of species we recorded (36 species in Fonseca et al., 2012, and 30 species in Berumen et al., 2017, in Tlaxcala and Puebla respectively), however, in both studies, the sampling effort was less than ours, so this result could be related to it rather than the intrinsic richness of the area). Cuevas & Iñiguez–Davalos (2017), in contrast, report 100 species for Jocotepec, in Chapala Lake Jalisco, but only 35 were waterbirds. All these studies have reported temporal variation according to the season of the year.

Water levels within zones vary throughout the year. At the Sayula Lagoon, while the area covered by water averages 9,000 ha in the rainy season (July to October), the lagoon is almost completely dry during the rest of the year (Red Mocaf, 2005). This dryness promotes the formation of wide sandy zones with salty soils and some water portions at the center and southern portions of the lagoon. In these areas, halophytic, aquatic, and sub aquatic vegetation types are mixed; these findings are supported by Munguia et al. (2005), who documented variation in substrate composition within the Laguna de Sayula, and changes in waterfowl diversity and habitat use during the dry season. Wetlands with thorn scrub are also present in smaller proportions. Therefore, due to this environmental heterogeneity, which is originated by complex water level dynamics, the water bird community has a high species richness value (73), representing 53% of the recorded water bird species in Jalisco (Palomera–García et al., 2007), excluding pelagic species. The highest S in this study was recorded in November 2004 in AQUZ, and the highest abundance corresponded to October of the same year in SHAZ; according to the information provided by CONAGUA–Jalisco (unpublished data), 2004 was the wettest in the study period. The most abundant species in the entire study were Northern shoveler (*Spatula clypeata*) (32% of the total abundance), snow goose (*Anser caerulescens*) (14.5%) and long-billed dowitcher (*Limnodromus scolopaceus*) (6%). In contrast, in other wetlands in Jalisco State, Laguna de Zapotlán has 47 species (Michel–Parra et al., 2005), Estero La Manzanilla has 45 species (Hernández, 2000), Chamela region has 83 species (Arizmendi et al., 2002), Lago de Chapala has 39 species (López–Velázquez, 2011), and Estero El Salado has 60 species (Molina et al., 2012). In another state wetland, Valsequillo Reservoir in Puebla, which is a Ramsar site, 30 species were observed (Berumen et al., 2017). Sayula contains the highest reported species richness to date but this could be due to the sampling effort (five winter seasons in the current study vs. one-year sampling period in the other areas). If we consider a one-year sampling, richness seems to be similar to that in other wetlands. The species richness recorded throughout the current study contrasts with that reported by Delgadillo (1995), who found a richness of 62 species at the same study site. In comparison with the list of species reported by Delgadillo, 55 species are the same, and we did not record seven species: *Aythya valisineria*, winter migrant; *Nomonyx dominicus*, resident at west Pacific and Gulf Coast; *Calidris melanotos*, transient; *Leucophaeus pipixcan*, transient; *Larus californicus*, winter migrant; *Larus argentatus*, winter migrant; and *Sternula antillarum*, summer migrant Northern coast of Mexico. Also in the declaratory document as a Ramsar site, 58 species are listed, three of which were not recorded in the current study (*Aythya valisineria*, *Calidris melanotos* and *Rissa tridactyla*, winter migrant only at North Baja Ca-

lifornia) (Ramsar, 2003). These missing species could be resident species or species that are present at some times of the year but not in winter, meaning that the period with the highest richness of water birds at the study site is winter.

In comparison with distribution maps published by Howell and Webb (2001), seven of the 73 species we recorded are not expected to occur in the Sayula Lagoon. Moreover, there are also differences in the seasonal status (see appendix 1). According to our results, the sampling effort was sufficient to record most species in the study area. Therefore, ours is a representative sampling effort according to the ACE estimator, which allowed us to make inferences regarding bird responses to the zoning in the study site, and to temporal variations, which demonstrates the importance of recording for more than a year, in opposition to the consideration by Berumen et al. (2017), who recognized that a one-year sampling might not be sufficient to determine species' number and abundance because species' number varies year to year, especially in some families.

Species records according to zone provides information related to their habitat preferences. Waterbirds have morphological adaptations for feeding (Cody, 1985). These are limited according to the water depth, and each species has its own foraging depth preference (Elphick and Oring, 2003). There are discrepancies about the optimal foraging depth; whereas some authors state that 25 cm is optimal (Paillisson and Marion, 2002), others suggest that between 13 and 35 cm is best, depending on the species. Colwell and Taft (2000), stated that numbers of waterbirds, ducks and shorebirds increase in shallow wetlands, while numbers of swimming species increase in deep wetlands. This relationship between foraging and water depth is consistent with results obtained in our study, where we recorded that the richness and abundance of species was inversely related to water depth, supporting findings by Robertson and Massenbauer (2005) and Holm and Clausen (2006). In our study, the highest richness was recorded at MUDZ, SHAZ and in part of the AQUZ. These zones contained all kinds of species groups, such as swimming birds (waterfowl, grebes, cormorants), wading birds (herons, storks, rails) and shorebirds, in concordance with observations of Hamza et al. (2015). In waters deeper than 100 cm (DEEZ), richness decreased drastically, and only some swimming bird species (waterfowl, grebes, gulls, terns and pelicans) were recorded.

The high values of richness and diversity between the shallow and water zones are probably due to their spatial proximity and similar environmental characteristics. Most species in this zone belong to the functional group of ducks, but shorebirds and large wading birds are represented in smaller proportions. Ducks used muddy zones as resting sites, but not for feeding. This zone provides resources mainly for shorebirds, herbivores and large wading birds, which use the site for feeding. Plots dominated with halophytic vegetation provide habitat for snow geese and shorebirds when the cover is less. Furthermore, in the deep zone, waterfowl and other species such as swimming and diving birds (grebes, gulls, terns and pelicans) are the dominant species and in the sandy zone waders, shorebirds and herbivores such as geese were recorded. Our results show that the maintenance of a high environmental diversity is important when the management aim is to promote high species diversity and to provide resources for all species groups simultaneously.

In the Sayula Lagoon, November was the richest month due to the arrival of migrant species and because some sites remained flooded, thus promoting the presence of water bird species. In contrast, December was the month with the highest abundance due to the arrival of more migrant individuals. Among seasons, we also detected important fluctuations, which is consistent with reports by Blake and Loiselle (2016), who stated that long-term estimations with waterfowl over 49 and 14 years respectively, have demonstrated temporal variations with cycles of periods of decreases in numbers followed by periods of recovery in abundance. These cycles may be related to changes in reproductive habitat and to continental climatic patterns, among other factors. In our study, the first season was the richest and the one with the highest abundance. This coincides with the highest precipitation recorded

throughout the study (CONAGUA–Jalisco, unpublished data). Our results suggest that the complex water dynamics in the Sayula Lagoon have allowed the existence of a variety of habitats, promoting the co–existence of many different water bird species in the lagoon. Not only the abundant species, but also rare species contribute to the water bird community structure within the lagoon. Future trends for these assemblages may vary in response to climate change. On the other hand, water control through either flooding of wetlands such as the Sayula Lagoon or channelization could provide a strategy to manage bird assemblages in years of moderate or excessive rain. Therefore, future research should elucidate more specific data about the controlling effect that water impinges on aquatic bird assemblages.

Our results show that the environmental heterogeneity at the Sayula Lagoon provides feeding and resting sites for many water bird species, mainly migrants, which is consistent with Hamza et al. (2015). Future studies must evaluate the effects of other variables, such as vegetation and nutrients and determine to what extent changes in bird populations are related to limnological changes (Green and Figuerola, 2003) or with the intensity of human presence at the site. To ensure sustainability and to promote the existence of a greater diversity, it is necessary to define sites for conservation and maintenance of habitats through the analysis of the richest sites, and identify habitats in which it is necessary to establish ecological restoration activities in order to provide a variety of environments and depths for all species that use the wetland.

Acknowledgements

The first two years of this work were part of the Integral Project: *Restauración Ecológica Participativa de la Laguna de Sayula*, funded by the "Red Mexicana de Organizaciones Campesinas Forestales, A.C. (Red Mocaf)" with funds from the North American Wetland Conservation Act (NAWCA), and from the "Laboratorio Laguna de Sayula" at the "Centro Universitario de Ciencias Biológicas y Agropecuarias (Universidad de Guadalajara)". We thank the municipal authorities from Amacueca, Jalisco for their hospitality and help. José L. Castañeda, Raúl Robles, Juan P. Tenorio, Guillermo Barba and Carlos Vázquez provided valuable help during fieldwork. We thank the anonymous reviewers for their thoughtful comments that helped to substantially improve the manuscript.

References

- Alcántara, J. L., Escalante, P., 2005. Current threats to the Lake Texcoco globally important bird area. In: *Bird Conservation Implementation and Integration in the Americas*: 1143–1150 (C. Ralph, J. Rich, D. Terrell, Eds.) Proceedings of the Third International Partners in Flight Conference. 2002 March 20–24; Asilomar, California, Volume 2 General Technical Report PSW–GTR–191. Albany, CA: U.S. Dept. of Agriculture, Forest Service, Pacific Southwest Research Station.
- Amparán–Salido, R. T., 2000. Diversidad de la comunidad de aves acuáticas y caracterización de sus hábitats en la Laguna de Zapotlán, Jalisco, México. Tesis Maestría. Universidad Autónoma de Nuevo León, Nuevo León, México.
- AOU (American Ornithologists' Union), 2015. *Check–list of North American birds*. www.aou.org/index.php [Accessed on 12 April 2018].
- Arizmendi, M. C., Márquez–Valdelamar, L., Ornelas, J. F., 2002. Avifauna de la región de Chamela, Jalisco. In: *Historia Natural de Chamela*: 297–329 (F. A. Noguera, J. H. Vega–Rivera, A. N. García–Aldrete, M. Quesada–Avendaño, Eds.). Instituto de Biología, UNAM. México.
- Atoyac City Council, 2010. Plan de Desarrollo Municipal de Atoyac, Jalisco 2010–2020. <http://www.atoyac.jalisco.gob.mx/pdf/PDM2010–2010.pdf> [Accessed on 24 March 2017].

- Barba, C. G., Martínez, S. H., 2008. Conducta Invernal del Ganso nevado (*Chen caerulescens*, Linnaeus 1758) en la subcuenca Sayula, Jalisco, México. *Scientia CUCBA*, 10(1–2): 65–80.
- Barragán, S. J., López–López, E., Babb, K. A., 2002. Spatial and temporal patterns of a waterfowl community in a reservoir system of the Central Plateau, México. *Hydrobiologia*, 467: 123–131.
- Berumen, S. A., Maimone, C. M., Villordo, G. J., Olivera, A. C., González, O. J., 2017. Cambios temporales de la avifauna acuática en el sitio Ramsar "Presa de Valsequillo", Puebla, México. *Huitzil, Revista Mexicana de Ornitología*, 18(2): 202–211.
- Blake, J. G., Loiselle, B. A., 2016. Long-term changes in composition of bird communities at an "undisturbed" site in eastern Ecuador. *The Wilson Journal of Ornithology*, 128(2): 255–267.
- Cintra, R., Ribeiro Simões Dos Santos, P. M., Banks, L. C., 2007. Composition and Structure of the Lacustrine Bird Communities of Seasonally Flooded Wetlands of Western Brazilian Amazonia at High Water. *Waterbirds*, 30(4): 521–540.
- Clarke, K. R., Gorley, R. N., 2005. PRIMER (Plymouth Routines In Multivariate Ecological Research). PRIMER: Getting started with v6. PRIMER–E Ltd.
- Clarke, K. R., Warwick, R. M., 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. PRIMER–E, Plymouth, U.K.
- Cody, M. L., 1985. *Habitat Selection in Birds*. Academic Press, USA.
- Colwell, M. A., Taft, O. W., 2000. Waterbird communities in managed wetlands of varying water depth. *Waterbirds*, 23: 45–55.
- Colwell, R. K., 2009. EstimateS: statistical estimation of species richness and shared species from samples. Version 6.0. <http://viceroy.eeb.uconn.edu/estimates> [Accessed 3 March 2017].
- Cuevas, J. C., Iñiguez–Dávalos, L. I., 2017. Aves del Puerto Interior Turístico Jocotepec, en el Lago de Chapala, Jalisco, México. *Huitzil*, 18(2): 261–271.
- Delgadillo, V. A., 1995. *Identificación y censo de la avifauna migratoria y residente de la Laguna de Sayula, Jalisco*. Tesis de licenciatura, Universidad de Guadalajara.
- DUMAC (Ducks Unlimited de México, A. C.), 2006. *28 Humedales Prioritarios*. URL: <http://www.dumac.org/dumac/habitat/esp/proyectos01.htm> [Accessed on 28 May 2017].
- Elphick, C. S., Oring, L.W., 2003. Conservation implications of flooding rice fields on winter waterbird communities. *Agriculture, Ecosystems and Environment*, 94: 17–29.
- Enciso, J. P., Paracuellos, M., 1997. Dinámica estacional de la comunidad de aves acuáticas en los humedales del levante almeriense (SE ibérico). Caracterización e importancia ornítica provincial. *Oxyura*, 9: 29–43.
- Escofet, A., Loya–Salinas, D., Arredondo, J., 1988. El estero de Punta Banda (Baja California, México) como hábitat de avifauna. *Ciencias Marinas*, 14(4): 73–100.
- Finlayson, C. M., Hollis, G. E., Davis, T. J., 1992. Managing Mediterranean wetlands and their birds. *Slimbridge: International Waterfowl and Wetlands Research Bureau*, Special Publication No 20: 1–285.
- Fonseca, J., Pérez–Crespo, M. J., Cruz, M., Porras, B., Hernández–Rodríguez, E., Martínez, J. L., Lara, C., 2012. Aves acuáticas de la Laguna de Acuitlapico, Tlaxcala, México. *Huitzil*, 13(2): 104–109.
- García, E., 1973. *Modificaciones al sistema de clasificación climática Köppen*. 2ª. Edición. Instituto de Geografía, Universidad Nacional Autónoma de México, México, D.F.
- Green, A. J., Figuerola, J., 2003. *Aves acuáticas como bioindicadores en los humedales. Ecología, manejo y conservación de los humedales*. Instituto de Estudios Almerienses. España.
- Hamza, F., Hammouda, A., Selmi, S., 2015. Species richness patterns of waterbirds wintering in the gulf of Gabe s in relation to habitat and anthropogenic features. *Estuarine, Coastal and Shelf Science*, 165: 254–260.

- Hernández, V. S., 2000. Aves acuáticas del Estero La Manzanilla, Jalisco, México. *Acta Zoológica Mexicana* (nueva serie), Número 80. Instituto de Ecología, A. C. Xalapa, México.
- Holm, T. E., Clausen, P., 2006. Effects of water level management on autumn staging waterbirds and macrophyte diversity in three Danish coastal lagoons. *Biodiversity and Conservation*, 15: 4399–4423.
- Howell, S. N. G., Webb, S., 2001. *A Guide to the Birds of Mexico and Northern Central America*. Oxford University Press, New York, USA.
- Howes, J., Bakewell, D., 1989. *Shorebirds Studies Manual*. Asian Wetland Bureau. Publication No. 55. Kuala Lumpur, Malasia.
- Hu, S., Niu, Z., Chen, Y., C., Li, L., Zhang, H., 2017. Global wetlands: Potential distribution, wetland loss, and status. *Science of The Total Environment*, 586: 319–327.
- Krebs, C. H., 1985. *Ecología, estudio de la distribución y la abundancia*. Segunda Edición. México, D. F. Editorial Harla.
- López–Velázquez, R., H.O. Covarrubias L., R.M. González M., J. Cortés A., L.F. Aguirre N. 2011. Aves del Lago de Chapala. Gobierno de Jalisco, Comisión Estatal del Agua de Jalisco, Sociedad Mexicana de Geografía y Estadística, Grupo Bargo de México, S.A. de C.V. Jalisco, México.
- MacGregor–Fors, I., Payton, M. E., 2013. Contrasting diversity values: Statistical inferences based on overlapping confidence intervals. *PLoS ONE*, 8(2): e56794, [doi:10.1371/journal.pone.0056794](https://doi.org/10.1371/journal.pone.0056794).
- Macías–Rodríguez, M. A., 2004. Vegetación y flora de la Laguna de Sayula: Guía ilustrada. Universidad de Guadalajara, México.
- Medina, R. J., Hernández, J. E., 1993. Evaluación hidrogeológica de la subcuenca del Lago de Sayula. In: *Análisis Geográfico y Social de la Zona Zacoalco–Sayula*: 198 (Munguía, C. F., Coord.). Sociedad de Geografía y Estadística de Jalisco, México
- Michel–Parra, J. G., Guzmán–Arroyo, M., Covarrubias–Tovar, N., Rocha–Chávez, G., Espinosa–Arias, J. A., Barajas–Martínez, A., Orendaín–Verduzco, T., GonzálezGuerra, G., Magaña–Virgen, M. E., Ramírez, R., 2005. Humedales de México. Ficha Informativa de los Humedales de Ramsar Laguna de Zapotlán. Comisión Nacional de Áreas Naturales Protegidas. <http://ramsar.conanp.gob.mx/lsr.php> [Accessed on 11 March 2018].
- Molina, D., Torres–Guerrero, J., Avelarde–Gómez, M. de la L., 2012. Riqueza de aves del Área Natural Protegida Estero El Salado, Puerto Vallarta, Jalisco, México. *Huitzil*, 13(1): 22–38.
- Munguía, P., López, P., Fortes, I., 2005. Seasonal changes in waterbird habitat and occurrence in Laguna de Sayula, western Mexico. *The Southwestern Naturalist*, 50(3): 318–322.
- Ojasti, J., Dallmeier, F. (Eds.), 2000. *Neotropical Wild Fauna Management*. SI/MAB Series #5. Smithsonian Institution/MAB Biodiversity Program, Washington, D.C.
- Paillisson, J. M., Marion, L., 2002. Bird assemblages as bio–indicators of water regime management and hunting disturbance in natural wet grasslands. *Biological Conservation*, 106: 115–127
- Palomera–García, C., Santana, E., Contreras–Martínez, S., Amparán–Salido, R., 2007. Jalisco. In: *Avifaunas Estatales de México*: 1–48 (R. Ortiz–Pulido, A. Navarro–Sigüenza, H. Gómez de Silva, O. Rojas–Soto, T. A. Peterson, Eds.). CIPAMEX, Pachuca, Hidalgo, México.
- Pettingill, O. S. Jr., 1969. *Ornithology in laboratory and field*. Burgess, Minneapolis, Minnesota.
- Ramírez–Bastida, P., Navarro–Sigüenza, A. G., Peterson, A. T., 2008. Aquatic bird distributions in Mexico: designing conservation approaches quantitatively. *Biodiversity and Conservation*, 17: 2525–2558.
- Ramsar, 2003. Sitios Ramsar en México. <https://www.gob.mx/conanp/acciones-y-programas/sitios-ramsar> [Accessed on 3 March 2011].
- Ramsar Regional Center – East Asia, 2017. *The Designation and Management of Ramsar Sites – A practitioner’s guide*. Available online at www.ramsar.org and www.rrecea.org

- Red Mocaf (Red Mexicana de Organizaciones Campesinas Forestales A. C.), 2005. *Sistemas de Información Geográfica y caracterización ambiental de la cuenca de la Laguna de Sayula*. Informe técnico, <http://www.alianzamesoamericana.org/red-mexicana-de-organizaciones-campesinas-forestales-red-mocaf/>
- Reeder, B., Wulker, B., 2017. Avifauna use of reference and restored bottomland forest wetlands in Eastern Kentucky. *Ecological Engineering*, 108: 498–504, <http://dx.doi.org/10.1016/j.ecoleng.2017.06.025>
- Robertson, D., Massenbauer, T., 2005. Applying hydrological thresholds to wetland Management for waterbirds, using bathymetric surveys and GIS. In: *MODSIM International Congress on Modelling and Simulation: 2407–2413* (A. Zenger, R. M. Argent, Eds.) Modelling and Simulation Society of Australia and New Zealand Australia.
- Sebastián–González, E., Botella, F., Sánchez–Zapata, J. A., 2013. Patrones, procesos y conservación de comunidades: el caso de las aves acuáticas en humedales artificiales. *Revista Catalana d'Ornitologia*, 29: 75–92.
- SEMARNAT, 2010. Norma Oficial Mexicana NOM–059–SEMARNAT–2010. Protección ambiental–Especies nativas de México de flora y fauna silvestres–Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio–Lista de especies en riesgo. Diario Oficial de la Federación, 6 de marzo.
- Sibley, D. A., 2001. *The Sibley Guide to Birds*. National Audubon Society. Alfred A. Knopf, New York.
- Terres, J., 1991. *The Audubon Society Encyclopedia of North American Birds*. Wing Books, New York, U.S.A.
- Wells, K., Dolichb, T., Wahlc, J., O'Haraa, R. B., 2013. Spatio–temporal dynamics in waterbirds during the non–breeding season: Effects of local movements, migration and weather are monthly, not yearly. *Basic and Applied Ecology*, 14(2013): 523–531.

