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Relationships among fish assemblages, hydroperiods, drought, and American alligators within
palustrine wetlands of the Blackjack Peninsula, Aransas National Wildlife Refuge, Texas

Darrin M. Welchert

Thesis submitted to the
Davis College of Agriculture, Natural Resources, and Design
at West Virginia University
in partial fulfillment of the requirements
for the degree of

Master of Science
in
Wildlife and Fisheries Resources

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American alligator

Abstract

Relationships among fish assemblages, hydroperiods, drought, and American alligators within palustrine wetlands of the Blackjack Peninsula, Aransas National Wildlife Refuge, Texas

Darrin M. Welchert

The following thesis contains two chapters. In Chapter 1, I have reviewed and summarized literature pertaining to fishes and habitats of palustrine wetlands, the influence of hydroperiods on wetland fishes, the impacts of drought on wetland fishes, the importance of American alligators as ecological engineers of fish habitats within wetlands, and fish sampling within wetland habitats. Chapter 2 is a manuscript representing my thesis research. In this study, primary focus is placed on how fish diversity and how fish abundances of palustrine wetlands are influenced by drought conditions within the Blackjack Peninsula of the Aransas National Wildlife Refuge in southwestern Texas.

Seasonal hydroperiods and drought are natural disturbances that influence fish assemblages within subtropical palustrine wetlands. Few studies, however, have focused on the impacts of drought on fishes of freshwater wetlands, in part, because of the unpredictability and infrequent occurrences of drought conditions within wetland habitats. We analyzed the distribution, diversity, and abundances of fishes in relation to habitat characteristics during two wet/dry hydroperiod cycles within 77 palustrine wetland sites. During our study, below-average rainfall within two seasonal periods provided an opportunity to examine the effects of drought on the diversity and abundances of fishes and fish-habitat relationships. We captured 3,590 fishes representing 19 species and 10 families. The responses of fish diversity and total fish abundance

to drought conditions were largely driven by six common species; western mosquitofish, warmouth, black bullhead, green sunfish, bluegill, and golden topminnow. Wetland volume, maximum water depth, salinity, and dissolved oxygen changed seasonally and across pre-drought, drought, and post-drought conditions, thereby influencing species diversity and species abundances. During the drought, fishes were restricted to reduced habitats which consisted primarily of deeper areas within constructed wetlands, and holes or dens of American alligators. Our data demonstrated that drought conditions greatly reduce species diversity and species abundance on the Blackjack Peninsula of southwestern Texas. Long-term studies, however, are needed to examine recovery of habitat and fish assemblage structure.

Dedication

To my father, David J. Welchert who instilled a fondness for the outdoors at an early age by introducing me to both woods and water. He is my inspiration for getting into the wildlife field. Respect what you have and work is only what you make of it. You will never be forgotten.

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Chapter 1: Literature Review

Freshwater is one of our most important natural resources. Approximately 97.5% of the planet's 1.4 billion cubic kilometers of water is ocean, and a mere 2.5% of the global total is freshwater (Stiassny 1996). Approximately 113,000 km³ of water is deposited on the world's land masses each year, and of this some 72,000 km³ evaporates, leaving close to 41,000 km³ to replenish all the rivers and lakes, and to recharge aquifers and wetlands (Stiassny 1996). Freshwater wetlands are important for many reasons including filtration, drinking water, recreation, recharging aquifers, and habitat for fishes and wildlife.

Freshwater habitat supports a large diversity of aquatic life, and habitat losses are a major conservation concern for freshwater fishes (Stiassny 1996). Extinct, endangered, threatened, or vulnerable status are recognized for 28% (187 taxa) of freshwater and diadromous fishes within the southern United States (Warren et al. 2000). Texas is one of 11 states with 20 or more imperiled fish species (Warren and Burr 1994). Warren and Burr (1994) listed major causes of decline as: (1) physical habitat loss, degradation, or alteration; (2) chemical pollution; (3) overexploitation; and (4) introduction of nonindigenous species. Along the Texas Gulf Coast, losses of freshwater wetland habitats are attributed, in part, to agriculture and land development.

Freshwater or palustrine wetlands include all nontidal wetlands dominated by trees, shrubs, persistent emergents, emergent mosses or lichens, and all such wetlands of tidal areas with salinity from ocean-derived salts below 0.5 ppt (Cowardin et al. 1979). Palustrine wetlands can also lack vegetation, but contain all of the following four characteristics: (1) area less than 8-ha; (2) active wave-formed or bedrock shoreline features lacking; (3) water depth in the deepest part of basin less than 2 m at low water; and (4) salinity due to ocean-derived salts less than 0.5 ppt

(Cowardin et al. 1979). Jordan et al. (1998) further described wetland landscapes as being comprised of mosaics of aquatic habitats that differ with respect to plant species compositions, structural complexity, water depth, and other physical conditions. Jordan et al. (1998) described sloughs as relatively deep, structurally-simple habitats dominated by submersed and floating vegetation; and wet prairies as relatively shallow, structurally-complex habitats dominated by emergent plants.

From the mid 1950s to 1990s, palustrine (freshwater) wetlands in the state of Texas showed a net decline of 61,107.5-ha (4.3%) (Moulton et al. 1997). However, palustrine unconsolidated bottom, mostly man-made ponds, increased by 8,801.5-ha (a 137% increase) and consisted primarily of agriculture, uplands, palustrine farmed, and palustrine forested (Moulton et al. 1997). This slight increase in unconsolidated bottom wetlands was inconsequential compared to the net loss of other types of freshwater wetlands. During the same time frame, Texas palustrine emergent wetlands (freshwater marsh, wet prairie, etc.) declined 29%, with an estimated net loss of 95,142-ha, making the average annual net loss of 2,590-ha (Moulton et al. 1997). With current high rates of habitat losses, it is as important as ever to study fishes in freshwater marshes of Texas.

Freshwater wetlands are important fish habitats (Chick et al. 1999). The dynamics of fish populations in shallow marshes, however, are less well understood than those in rivers, lakes, streams, or ponds; even though marshes account for a large proportion of freshwater habitats (Kushlan 1981). In the last 40 years, several studies in Florida have furthered our understanding of fishes that inhabit freshwater marshes (Chick et al. 1999, 2004, Davis et al. 2005, Jordan et al. 1997, 1998, Kushlan 1974a, 1976, 1980, 1981, and Ruetz et al. 2005). The most important factors outlined in these studies were hydroperiod and habitat type. Although these studies were

centered on the topic of water or lack thereof, hydroperiod and habitat type each has its own effect on fish diversity and fish abundance.

Hydroperiod is the seasonal pattern of water in a wetland. Wetland habitat shrinks during a dry hydroperiod and increases during a wet hydroperiod. As expected, fish diversity and fish abundances change in response to habitat changes associated with hydroperiods (Kushlan 1974a, 1976, 1980, Jordan et al. 1998, Chick et al. 2004, Davis et al. 2005, DeAngelis et al. 2005, Ruetz et al. 2005). Jordan et al. (1998) emphasized that inundated marshes during wet hydroperiods provided opportunities for marsh fish dispersal, reproduction, and growth.

The scientific literature provides several examples of hydroperiod impacts on fish diversity and fish abundances within wetlands. The dry hydroperiod of marl prairies limited small fish densities to less than 10 fish/m², compared to 60 fish/m² in areas of Shark River Slough with multi-year hydroperiods (Davis et al. 2005). In the Everglades, Kushlan (1980) found that populations were relatively small at the beginning of the wet season (June), because of dry season mortality, and increased to a peak at the beginning of the drying period in December-January. Kushlan (1976) reported an increase in species diversity during stable water levels which was associated with an increased diversity of carnivorous species despite a drop in the diversity of omnivorous fishes. In some cases, declines in marsh water levels increase fish densities, likely reflecting a concentration effect (Jordan et al. 1998). Six of 22 species of fish and only 0.6% of the previous fish populations survived a drought-induced fish kill in Big Cypress Swamp, Florida (Kushlan 1974a). In general, negative correlations observed between fish densities and water depth likely reflect the movement of fishes into sloughs during drying events and subsequent dispersal of fishes into re-inundated marsh habitats (Jordan et al. 1998). Chick et al. (2004) found significant variation in community structure through time that

correlated with the number of day's post-dry-down suggesting that hydroperiod influences large fish communities of Everglades' marshes. Ruetz et al. (2005) noticed fish density tended to be highest and recovery slowest at sites that infrequently experienced dry downs. Ruetz et al. (2005) also found that eastern mosquitofish showed no distinct response to marsh drying (i.e. they recovered quickly). They also found that *Fundulus chrysotus* (golden topminnow) were usually at lowest abundances after a dry down period and recovered slowly. Site re-colonizations by eastern mosquitofish, golden topminnow, and two killifish species were primarily caused from *in situ* reproduction of individuals that survived the dry down period via deep water refuge habitats (Ruetz et al. 2005).

Along with hydroperiod, habitat type and structure are important to fish density and assemblage. Jordan et al. (1997) noticed that small-sized species dominated the wet prairie fish assemblages sampled in Florida. Jordan et al. (1998) found that eastern mosquitofish and golden topminnows were more abundant in sloughs than in wet prairies. The relative abundance of numerically dominant fishes (and hence assemblage structure) varied with habitat type and month (Jordan et al. 1998). Fish densities were positively correlated with plant biomass (i.e. habitat complexity) and negatively with water depth (i.e. hydrology) in sloughs and wet prairies in Florida (Jordan et al. 1998).

Previous studies have broadened our knowledge of the ecology of fish assemblages within freshwater marshes of Florida, however, less is known of fishes from shallow freshwater wetlands of Texas. While studying fish assemblages in Brazos River oxbow lakes in Texas, Winemiller et al. (2000) found that harsh conditions of periodic desiccation in shallow vegetated oxbows favored small fishes that are efficient colonizers. *Gambusia affinis* (western mosquitofish), a small fish in Brazos River oxbow lakes, tolerated critical dissolved oxygen

(DO) concentrations between 0.49 and 0.73 mg/L. Further analysis of body length distributions of the fishes in Brazos River oxbow lakes reinforced this pattern; shallow lakes were strongly dominated by small fishes (Winemiller et al. 2000). Gelwick et al. (2001) sampled freshwater sloughs, diked wetlands, and salt marshes on the Texas Gulf Coast. They found that physiological tolerance to salinity, other physiochemical parameters, and life-history strategies determine how animals respond to temporal habitat heterogeneity. Capone and Kushlan (1991), while studying fish assemblages in dry-season stream pools, reported that pools with western mosquitofish were shallow, ephemeral, in small channels, and farthest from permanent pools. Pools dominated by *Ameiurus melas* (black bullhead) were deeper, more persistent, in large channels, less habitat diverse and close to permanent water (Capone and Kushlan 1991). In the Sulfur River, *Lepomis cyanellus* (green sunfish) and western mosquitofish were pioneer species, survived harsh conditions, and invaded areas with low populations of other species (Capone and Kushlan 1991). All three studies documented the resilience of fishes in shallow water wetlands of Texas.

Although most wetland fish species persist during seasonal dry hydroperiods, many are temporarily extirpated from wetlands during extended periods of drought. Drought, defined as a lack of precipitation that leads to drying of aquatic habitats, is a natural process in wetland ecosystems (Magoulick and Kobza 2003). Droughts maintain community structure by resetting succession, a process determined by disturbance history (frequency, temporal sequence, and intensity) (Trexler et al. 2005). Drought disturbance can be described by changes in habitat or organisms, and can be compared among systems (Lake 2000).

Droughts alter fish communities by changing habitat condition. Droughts cause a decrease in surface area and volume, and an increase in extremes of physical and chemical water quality

parameters (Magoulick and Kobza 2003). Water depth is known to strongly influence the dynamics and structure of fish populations (Robinson and Tonn 1989, Capone and Kushlan 1991, Gelwick et al. 1997, Magoulick and Wilzbach 1997, Magoulick 2000). During drought, lower elevation areas within wetlands typically hold water for longer periods of time, and provide refuge areas for fishes. Droughts can destroy habitat patches and create new ones that are colonized and inhabited by different types of biota (Lake 2000). Several water chemistry parameters influence fish survival during drought including dissolved oxygen, water temperature, pH, and nutrient content. Surface water temperature associated with most shallow refuges follows ambient air temperatures closely, although during peak dry conditions, temperatures may closely match daily minima because of evaporative cooling (Magoulick and Kobza 2003).

Within wetlands, drought often fragments habitat and fish distributions. Refugia exist at a range of spatial and temporal scales: from the smallest (e.g. microhabitat) to the largest (e.g. drainage basin) (Magoulick and Kobza 2003). Depending on the spatial scale of the refuge and barriers to fish movement, local populations of species may interact to form isolated communities. Barriers could be physical obstructions to movement (e.g. dams, waterfalls, or isolated pools), biotic factors (e.g. competition or predation) or physiochemical factors (e.g. low concentrations of dissolved oxygen) (Magoulick and Kobza 2003).

Habitat conditions linked with biotic interactions can structure fish communities in dry season refugia by influencing mortality rates, birth rates, or migration rates (Magoulick and Kobza 2003). Droughts force fish to retreat into small ponds or other areas that remain inundated (Gaff et al. 2004). The geographic extent of aquatic habitat defines the amount of available habitat for fishes, where fluctuations in available habitat act to either cause fishes to move or

concentrate fishes (Canton et al. 1984, Matthews 1998, Matthews and Marsh-Matthews 2003). Population dynamics of fishes using refugia during drought are best modeled by modified source-sink dynamics, but dynamics are likely to change with spatial scale (Magoulick and Kobza 2003).

Not all fishes are successful in finding refugia during droughts, and some die from desiccation (Gaff et al. 2004). Some species have a relatively high tolerance to drought conditions, whereas others are intolerant. Morphological, physiological and behavioral characteristics of individual fishes influence resistance or resilience to drought conditions (Matthews 1998). Greater fish densities in refugia make them more susceptible to predation as well as starvation (Gaff et al. 2004). During extended drought conditions, fish species diversity is reduced, where sensitive species do not survive and tolerant taxa persist (Matthews 1998). While most species can tolerate short-term exposure to hypoxia, only a few are adapted to persist under such conditions (Matthews 1987, 1998). Some fishes within tropical dry season pools can aestivate, or obtain air at the water surface via superior mouth orientation (Kramer 1983, Kramer 1987). Unique behavioral and physiological attributes of fish species are critically important for survival, especially in regards to species resistant to physicochemical extremes (e.g. low oxygen concentrations, fluctuating pH, and heat shock) (Magoulick and Kobza 2003).

Limited movement and reduced choice of cover increase predation risk in refuge habitats (Magoulick and Kobza 2003). Larger fish could potentially influence any population of small fish in water deep enough for large fish to survive (Gaff et al. 2004), especially if these fish are confined to isolated drought refugia. While stranded within dry season pools, fishes are vulnerable to both aquatic and terrestrial predators, such as fishes, alligators, amphibians, and birds (Kushlan 1976).

Drought impacts can be measured in terms of impact on fish assemblages. Matthews (1998) described fish assemblages in several ways including number of species, number of families, species richness within families, numbers of prey species versus piscivorous species, proportional composition of the assemblage by trophic groups, distribution of abundance of species at a locality, and body-size patterns. The number of species in a given area or habitat type depends on a number of factors, including climate (temperate or tropical), altitude, and habitat (stream, river, lake, or marine) (Matthews 1998). In general, fish diversity within a given area increases with habitat diversity. In palustrine wetlands, habitat can range from vegetated to non-vegetated, temporary to permanent, man-made to natural, and large to small. Furthermore, local habitat size factors that influence fish assemblages include width, depth, pool area, volume, and discharge (Matthews 1998). Species richness in many aquatic systems is positively related to area (Matthews 1998). According to Scheffer et al. (2006) fish communities tend to be poor or even absent in small isolated lakes. Scheffer et al. (2006) stated that fish species richness is typically low (1-3 species) with lake or pond size under 1-ha and increases gradually with lake size.

Palustrine wetland habitats in the southeastern United States are often influenced by American alligator *Alligator mississippiensis*. This species resides in rivers, lakes, bayous, marshes, and other bodies of water within Florida, the Gulf, and other areas of the Lower Atlantic Coastal Plains (Conant and Collins 1998). Alligators are ecological engineers that alter landscapes through creation and maintenance of small ponds, called alligator holes. Alligator holes play a key ecological role by providing both drier and wetter habitats for other organisms (Jones et al. 1994, Campbell and Mazzotti 2004). During drought, alligator holes hold water, and provide a refuge for aquatic organisms. Most research studies on alligator holes are from within

the Florida Everglades. In Texas, alligators alter habitat by creating holes in natural and constructed wetlands. Alligator holes are typically circular in shape with vegetation on the periphery, and are often extended to form underground dens (Kushlan 1974b, Campbell and Mazzotti 2004). Alligators tunnel dens as far as 6.1 m in length, ending with an enlarged chamber with a ceiling above water level to permit breathing (U.S. Fish and Wildlife Service 2008). Features of alligator dens are poorly understood, in part, because of difficulties in observing the internal den (Gaff et al. 2004).

Alligators dig and maintain holes and dens that provide refuge for fishes, frogs, and snakes during dry periods (Craighead 1968, Kushlan 1974b, Rice and Mazzotti 2004, U.S. Fish and Wildlife Service 2008). Digging of dens and further excavation of pond bottoms enlarge a wetland's capacity during critical low water periods (Kushlan 1974b). Alligator holes are present during wet periods, however, they are possibly most important to other aquatic species during dry hydroperiods and drought conditions. Numbers of fish increase in alligator holes during periods when adjacent marshes are drying, demonstrating that ponds serve as refugia for aquatic organisms (Kushlan 1974b).

Survival rates are unknown for fishes within alligator holes (Palmer and Mazzotti 2004). Fishes in alligator holes are vulnerable to predation and fish make up a large portion of the diet of alligators (Delany and Abercrombie 1986, Bondavalli and Ulanowicz 1999) and some wading birds (Bondavalli and Ulanowicz 1999, Gaff et al. 2004, Mazzotti and Campbell 1997, Trexler et al. 2003). Fish predation in alligator holes likely regulates the carrying capacity of these relatively small areas. Fish may be reduced to levels that are compatible with survival of remnant populations due to limited space and reduced oxygen levels of dry-season alligator holes

(Mazzotti and Campbell 1997). Fishes that survive the dry season in alligator holes are one source of future fish populations (Rice and Mazzotti 2004).

Past fish research and monitoring on Blackjack Peninsula, ANWR, has been primarily focused on brackish and salt marsh habitats. These habitats are important to waterbirds, including the federally endangered *Grus americana* Linnaeus (whooping crane) which spends much of its time in brackish and salt marsh habitats, with only occasional trips to freshwater (Gunter 1950, Allen 1971). From February to July 1946, Gunter (1950) sampled nine stations with six salt/brackish sites and three freshwater sites. A single pond, fed by a windmill known as McHugh's Well, was selected as the only freshwater station regularly sampled. Two other freshwater sites, Hog Lake and Salada Well, were examined once in May 1946. Allen (1971) sampled six stations in brackish and salt waters on ANWR. Of the 10 bodies of water sampled by the Corpus Christi Fisheries Resource Office in 1994 and 1996, only two were freshwater sites which included Burgentine and Jones Lakes (Dilworth et al. 1999). McAlister and McAlister (1995) stated that strictly freshwater fishes and several tolerant brackish-water species inhabit the ponds and sloughs that dot the inland parts of the Blackjack Peninsula. A total of five freshwater sites combined were monitored from all previous studies. Since few freshwater sites have been sampled and no comparisons have been made between different habitat types, much can be learned about palustrine wetlands of ANWR. In fact, little is known about the distribution, diversity, and abundances of fishes within palustrine wetlands of ANWR.

Several fish sampling methods exist for palustrine wetlands. Freshwater wetland habitats in Florida, similar to those of ANWR, have been sampled with electrofishing and throw traps. These gears differ in sampling biases. Understanding gear selectivity is important for fisheries assessments, because some species are not vulnerable to specific gear types (Breen et al. 2006).

Electrofishing accounted for higher catch per unit effort, almost all taxa, and a broad range of fish sizes compared to gill nets and traps nets in floodplain wetlands (Knight and Bain 1996). However, gill nets and trap nets accounted for several species not captured with electrofishing (Knight and Bain 1996). Jordan et al. (1997) stated that throw traps provided relatively accurate and precise estimates of fish density, size, and community structure across a range of environmental conditions. They recovered an average of 83% of fishes present in 1 m² throw traps. Kushlan (1974c) found that both large and small fishes were caught in four drop traps which sampled a surface area of 1 m². Kushlan (1981) observed that the 1 m² throw trap showed no bias against particular fish species, but were biased against fish larger than 20 mm. Furthermore, Chick et al. (1999) demonstrated the effectiveness of airboat electrofishing for sampling large fishes (≥ 8 cm SL) in shallow vegetated habitats. Miranda and Lucas (2004) excluded fishes smaller than 7 cm from analyses, because electrofishing was not efficient at capturing small fishes. Chick et al. (1999) and Ruetz et al. (2007) suggested the use of a combination of methods (i.e. electrofishing, throw trapping, and block netting) to accurately describe fish assemblages of shallow vegetated habitats. The use of several sampling techniques will reduce gear bias and gear selectivity. Some sampling approaches have multiple applications, such as electrofishing with backpack, barge, or boat units. One advantage of a backpack unit is that operators are closer to the water and thus can readily see and capture smaller fishes (Vaux et al. 2000). Meador et al. (2003) found relatively similar interannual estimates of variability in fish species richness among sampling gears for wadeable streams. They suggest that combining data across years from backpack or towed-barge electrofishers adds relatively little variability. Several different temporal transects lengths have been used for electrofishing in wetland and/or shallow water habitats. Fish sampling in vegetated or non-vegetated shallow water habitats has

included four minute transects (Vaux et al. 2000), five minute transects (Killgore et al. 1989, Chick et al. 1999, 2004), or 10 minute transects (Schulz et al. 1999, Ruetz et al. 2007). Transect sampling requires standardization and consistency during the research project.

In Chapter 1, I have reviewed and summarized literature pertaining to fishes and habitats of palustrine wetlands, the influence of hydroperiods on wetland fishes, the impacts of drought on wetland fishes, the importance of American alligators as ecological engineers of fish habitats within wetlands, and fish sampling within wetland habitats. Chapter 2 is a manuscript representing my thesis research. In this study, primary focus is placed on how fish diversity and fish abundances of palustrine wetlands are influenced by hydroperiod and drought conditions within the Blackjack Peninsula of the Aransas National Wildlife Refuge in southwestern Texas.

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**Effects of drought on freshwater fishes within palustrine wetlands of the Blackjack
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Chapter 2: Effects of drought on freshwater fishes within Palustrine Wetlands of the Blackjack Peninsula, southwestern Texas

Abstract – Seasonal hydroperiods and drought are natural disturbances that influence fish assemblages within subtropical palustrine wetlands. Few studies, however, have focused on the impacts of drought on fishes of freshwater wetlands, in part, because of the unpredictability and infrequent occurrences of drought conditions within wetland habitats. We analyzed the distribution, diversity, and abundances of fishes in relation to habitat characteristics during two wet/dry hydroperiod cycles within 77 palustrine wetlands of the Blackjack Peninsula, Aransas National Wildlife Refuge, Texas. During our study, below-average rainfall within two seasonal periods provided an opportunity to examine the effects of drought on the diversity and abundances of fishes and fish-habitat relationships. We captured 3,590 fishes representing 19 species and 10 families. The responses of fish diversity and total fish abundance to drought conditions were largely driven by six common species; western mosquitofish, warmouth, black bullhead, green sunfish, bluegill, and golden topminnow. Wetland volume, maximum water depth, salinity, and dissolved oxygen changed seasonally and across pre-drought, drought, and post-drought conditions, thereby influencing species diversity and species abundances. During the drought, fishes were restricted to reduced habitats which consisted primarily of deeper areas within constructed wetlands, and holes or dens of American alligators. Our data demonstrated that drought conditions greatly reduce species diversity and species abundance on the Blackjack Peninsula of southwestern Texas. Long-term studies, however, are needed to examine recovery of habitat and fish assemblage structure.

Introduction

Documenting the diversity and abundance of species and understanding species-habitat relationships are critical components for the conservation and management of wetland ecosystems. Freshwater (palustrine) wetlands within subtropical coastal areas are commonly comprised of small and large ponds which may be connected during wet seasons and isolated during dry seasons (Kushlan 1976, Chick et al. 2004). Within these freshwater wetland complexes, species diversity and species abundance are controlled, in part, by changes in habitat size and habitat connectivity in relation to the timing and duration of wet and dry hydroperiods (Davis et al. 2005). Some fishes move long distances, colonize new habitats, and expand distributions during wet hydroperiods when wetland habitats are inundated and connected (Kushlan 1974a, Jordan et al. 1998, Ruetz et al. 2005). During dry hydroperiods or drought conditions, fish populations may be reduced within shallow habitats, or extirpated if ponds are dewatered completely.

Seasonal dry hydroperiods and droughts are often critical periods for fishes within freshwater wetlands. During dry periods, physical habitat changes toward shallower water depths, smaller pond volumes, and less connectivity among ponds (Ostrand and Wilde 2001, Magoulick and Kobza 2003). Also, changes in water quality often include higher salinity and lower levels of dissolved oxygen (Magoulick and Kobza 2003). Biotic interactions, such as predation and competition, reduce fish diversity and fish abundance during extended dry periods (Matthews 1998). The abiotic and biotic impacts on wetland ecosystems during seasonal dry hydroperiods are heightened during extreme drought conditions (Matthews 1998). Unlike cyclical hydroperiods, droughts are not predictable, nor can be planned *a priori* in most scientific study designs. In freshwater wetlands, both hydroperiod and drought cause changes to fish diversity

and fish abundance, and further understanding of these environmental impacts will aid conservation and management of wetland ecosystems.

In the last 40 years, several studies have furthered our understanding of fishes in palustrine wetlands in subtropical climates of the southern United States, particularly in Florida (Chick et al. 1999, 2004, Davis et al. 2005, Jordan et al. 1997, 1998, Kushlan 1974a, 1976, 1980, 1981, Ruetz et al. 2005). These studies have emphasized the importance of wet and dry hydroperiods in shaping both fish diversity and fish abundance within wetland ecosystems (Chick et al. 2004, Davis et al. 2005, Kushlan 1974a, 1976, 1980, Jordan et al. 1998, Ruetz et al. 2005). During wet hydroperiods, Kushlan (1974a) and Jordan et al. (1998) found that inundated wetlands increased opportunities for dispersal, reproduction, and growth of fishes. During a study on fish dispersal, Ruetz et al. (2005) found that distances among sites were important for synchronizing fish population dynamics among long-hydroperiod and short-hydroperiod sites. Kushlan (1976) and Chick et al. (2004) reported temporal changes in fish community structure during wet and dry hydroperiods. Kushlan (1980) found that fish population sizes were small within wetlands at the beginning of the wet season because of dry season mortality, but increased to a peak at the beginning of the drying period. Interestingly, Kushlan (1974b) reported increased numbers of fishes in alligator holes within a Florida wetland during the dry hydroperiod, indicating that alligators may play a role in creating refugia for aquatic organisms.

Although several studies have examined the ecology of freshwater wetlands in Florida, few studies have focused on shallow freshwater wetlands of Texas. Gelwick et al. (2001) sampled freshwater slough and diked wetlands, and salt marshes on the Texas Gulf Coast. They found that physiological tolerance to salinity and other physiochemical parameters along with life-history strategies determine how animals respond to habitat heterogeneity and habitat change.

Fishes with small size and colonizing abilities survived periodic desiccation in shallow vegetated oxbows of the Brazos River, Texas (Winemiller et al. 2000). Dry-season stream pools of the Sulfur River, Texas, contained fish assemblages of tolerant species (Capone and Kushlan 1991). All three studies documented a relatively high population resilience of tolerant fishes in shallow freshwater habitats of Texas.

The Aransas National Wildlife Refuge (ANWR), located in southwestern Texas, includes palustrine wetlands, but few studies have examined the diversity and abundance of fishes within these habitats. Many studies within ANWR have focused on brackish and salt marshes associated with the federally endangered whooping crane *Grus americana* (Gunter 1950, Allen 1971). Only five freshwater sites within ANWR were examined previously (Gunter 1950, Dilworth et al. 1999). Information on fish assemblages and fish-habitat relationships are needed for management of palustrine wetlands within ANWR. Our research objectives were to document the distribution, diversity, and abundances of fishes in relation to habitat characteristics and wet/dry hydroperiods within palustrine wetlands of the Blackjack Peninsula, ANWR, Texas. During our study, below-average rainfall within two seasonal periods provided an opportunity to examine the affects of drought on the diversity and abundances of fishes and fish-habitat relationships.

Study site

This study was conducted on the Blackjack Peninsula, a unit of the ANWR, Texas (28° 13' 51" N 96° 52' 14" W, approximate center, Figure 1). The Blackjack Peninsula is 19,126-ha and bordered by private land to the north, St. Charles Bay on the west, San Antonio and Mesquite Bays on the east, and Aransas Bay to the south. The peninsula is approximately 25.7 kilometers long and 3.2 to 11.3 kilometers wide (Gunter, 1950). Palustrine wetlands comprise

approximately 5,641-ha of the Blackjack Peninsula. The climate of the area is subtropical with an average temperature of 21 °C (McAlister and McAlister, 1995). The coldest month (January) averages 12 °C; the warmest months (July to August) average 28 °C. The 49 year average for precipitation is 96.06 cm (McAlister and McAlister, 1995). Typically, a wet hydroperiod occurs during summer; June and September contain the most precipitation. Lower rainfall amounts are typical for the dry hydroperiod of winter.

Two ecological communities exist within freshwater habitats of the Blackjack Peninsula: freshwater and ridge-and-swale communities (McAlister and McAlister 1995). The freshwater community, supported by temporary ponds and sloughs, contains the following common plants: duckweed *Lemna* spp., arrowhead *Sagittaria* spp., cattails *Typha* spp., and bulrush *Schoenoplectus* spp. The ridge-and-swale topography, supporting the most widespread community on the Blackjack Peninsula, was formed as a late Pleistocene sea withdrew and coastal breezes piled up parallel bands of sand creating the current ridges (McAlister and McAlister 1995). The sandy ridges provide the elevation (sometimes only a meter) necessary for woody perennials and frequently flooded swales (McAlister and McAlister 1995). Vegetation in freshwater swales is similar to that found in other freshwater communities, including saw grass *Cladium* spp., cattails, and bulrush. These sites may be depopulated of fishes during droughts and revitalized during washovers (McAlister and McAlister 1995).

Palustrine wetlands are defined within the National Wetland Inventory (NWI) as all nontidal wetlands dominated by trees, shrubs, persistent emergents, emergent mosses or lichens, and all such wetlands in tidal areas with salinity from ocean-derived salts below 0.5 ppt (Cowardin et al. 1979). It also includes wetlands lacking such vegetation, but with all four of the following characteristics: (1) area less than 8 ha; (2) active wave-formed or bedrock shoreline features

lacking; (3) water depth in the deepest part of basin less than 2 m at low water; and (4) salinity due to ocean-derived salts less than 0.5 ppt. Water chemistry is normally fresh, but may range to brackish and saline in semiarid and arid climates (Schot 1999). Most palustrine wetlands on ANWR are of two primary categories: palustrine emergent and nonvegetated. The palustrine emergent category includes all freshwater wetlands dominated (greater than 75%) by rooted herbaceous (nonwoody) vegetation (Moulton et al. 1997). Palustrine systems that are classified as nonvegetated (less than 30 % aerial coverage by vegetation) are called palustrine unconsolidated bottom (Moulton et al. 1997).

Materials and Methods

A total of 77 wetland sites were sampled during four seasonal periods; two summer periods and two winter periods. We expected summer sampling periods to occur within wet hydroperiods, and winter sampling periods within dry hydroperiods. A total of 28 sites were sampled during two summer periods (25 July 2008 – 6 Oct 2008, and 15 July 2009 – 25 Aug 2009), and a total of 49 sites were sampled during two winter periods (22 Dec 2008 – 26 Mar 2009, and 3 Feb 2010 – 25 Mar 2010). A total of 40 sites were classified as emergent and 37 were unconsolidated bottom (Moulton et al. 1997). Also, 27 sites were natural, and 50 sites were constructed or altered wetlands.

A suite of habitat variables was collected at each site including water temperature (°C), DO (mg/L), conductivity (µS), salinity (ppt), and pH (YSI 85 and YSI pH10, Yellow Springs Instrument, Yellow Springs, Ohio). Also, turbidity was measured with a La Motte TC-3000e turbidity meter (LaMotte Company, Chestertown, Maryland). Water depth was sampled from a cross section of the widest portion of each wetland to the nearest 0.01 m. A Tripod Data

System's Recon (Trimble Navigation Limited, Sunnyvale, California) unit loaded with ArcPad 7.0 (Environmental Science Research Institute, Redlands, California) was used to map the area of each wetland site. ArcGIS 9.2 (ESRI 2007) was used to measure area in m^2 and define wetland types using NWI data. Water volume (m^3) for each site was calculated as average water depth multiplied by wetland area.

Chick et al. (1999) and Ruetz et al. (2007) suggested the use of a combination of methods to accurately describe fish assemblages of shallow habitats. To limit sampling bias from a single gear type, we used boat and backpack electrofishing, throw traps, and minnow traps. The boat (3.6 m long aluminum hull, 9.9-hp outboard, and single Wisconsin anode array) and backpack (Smith-Root LR-20) methods of electrofishing followed Vaux et al. (2000) and Shoenebeck et al. (2005). Because most sites were less than 5-ha, we typically sampled two transects separated by 50 m buffers, unless restricted by the site size (Burkhardt and Gutreuter 1995, Schulz et al. 1999). Transects consisted of 10 minutes of pedal time (Schulz et al. 1999, Ruetz et al. 2007). The initial transect location was chosen randomly using a random number table or generated in ArcGIS 9.2 (ESRI 2007).

Sampling with throw traps (1 m^2) followed methods of Kushlan (1981) and Jordan et al. (1997, 1998). The throw trap, a box-like frame of copper pipe with 3 mm netting material on four sides, was 1 m wide by 1 m long and 0.75 m tall. The trap was deployed by one person and pressed into the substrate. Herbaceous plants were uprooted and removed, then dipnets were passed through the trap until at least five consecutive passes were made without fish. Five throw traps were used per site. A total of six round minnow traps were used at each site. Both minnow and throw traps were randomly placed using a random number table or ArcGIS 9.2 (ESRI 2007). However, sampling with throw and minnow traps was discontinued during the drought of winter

2008/2009 because both gears were difficult to deploy in shallow water and in areas with American alligators *Alligator mississippiensis*. Alligator and alligator dens were counted during each sampling event at each site.

Fishes were identified, counted, and released at the site of capture, except taxa with questionable identification were preserved and later examined in the laboratory. Also, representative samples of each species were preserved and deposited into the Texas Natural Science Center in Austin, Texas. Species diversity, total species abundance, and abundances for each species were recorded for each site.

For analysis, generalized linear models with negative binomial distributions and log link functions were fit to count data of species diversity and species abundance (SAS 1990). A candidate model set, representing 27 alternative hypotheses, was developed using single or combinations of 10 explanatory variables (four categorical variables and 6 environmental covariates). Categorical variables were wetland class (emergent vs. unconsolidated bottom), wetland origin (natural vs. constructed), hydroperiod (summer wet season vs. winter dry season), and season (summer 2008, winter 2008/2009, summer 2009, and winter 2009/2010). Environmental covariates were DO, salinity, turbidity, pH, maximum water depth, and water volume. Conductivity was not used as an explanatory variable, given a strong correlation ($r = 0.92$) between conductivity and salinity. A variance inflation factor ($\hat{c}$ = residual deviance/degrees of freedom) estimated from the global model was used to adjust for over dispersion (Burnham and Anderson 2002). The dispersion-corrected, second order Akaike information criterion ($QAIC_c$) was used for model selection and inference (Burnham and Anderson 2002).

Results

Physical habitat and water quality changed by seasons and to a larger extent by drought conditions during the first winter and second summer sampling seasons. The expected hydroperiod cycle (wet summer and dry winter) was reversed during the last half of our study because of summer drought and unusually high rainfall amounts during winter (Figure 3). The driest conditions occurred during the sampling period of summer 2009, followed by the wettest conditions during winter 2009/2010. Wetland volume (m^3) was widely variable among the four seasonal sampling periods because of the unusual dry and wet periods, and was lowest during summer 2009 (mean= 34.1 m^3 , Table 1). Maximum water depth decreased during the summer 2009 drought (mean= 0.65 m), but increased (212%) in winter 2009/2010 (mean= 2.0 m , Table 1). Conductivity (mean= $6126.8 \text{ }\mu\text{S}$), salinity (mean= 3.5 ppt), and turbidity (mean= 347.8 NTU) were highest during drought conditions (winter 2008/2009 - summer 2009; Table 1). Dissolved oxygen (DO mg/L) exceeded a mean value of 5.0 mg/L during all seasonal periods (Table 1), although variation increased during drought conditions with 36% of sites below 5.0 mg/L . With an overall decrease in water (maximum depth and volume), the sampling proportion of natural to constructed wetlands shifted toward a higher number of constructed wetlands (Figure 2) because these sites with lower elevations typically held water longer through the drought period (Figure 3). Most of the natural wetland sites were completely dewatered during the drought, and fish populations were restricted to deeper habitats, such as those provided by constructed wetlands or by alligator dens. American alligator abundance and den sites were observed more frequently as water levels decreased during the drought period (Figure 4). Alligator and den sites were most abundant during winter 2008/2009 and summer 2009.

A total of 3,590 fishes from 19 species and 10 families were captured with electrofishers, minnow traps, and 1 m² throw traps (Table 2, see species distribution maps in *Supplemental material*, Figures S1–S19). Centrarchidae and Fundulidae were the most common families with 5 and 3 species, respectively. Western mosquitofish *Gambusia affinis*, the most abundant species, was captured at 66% of sites. Warmouth *Lepomis gulosus*, black bullhead *Ameiurus melas*, green sunfish *Lepomis cyanellus*, bluegill *Lepomis macrochirus* and golden topminnow *Fundulus chrysotus* were collected at 31, 29, 27, 25, and 22% of sites, respectively. All 19 species were captured by electrofishing, and 8 species were captured only by electrofishing (Table 2). Four species were captured at only one site; alligator gar *Atractosteus spatula*, bayou killifish *Fundulus pulvereus*, sheepshead minnow *Cyprinodon variegatus*, and largemouth bass *Micropterus salmoides*. We captured three species that were not previously reported from ANWR; American eel *Anguilla rostrata*, blackstripe topminnow *Fundulus notatus*, and green sunfish (Table 2).

Mean values of species diversity and total species abundance declined across the four seasonal sampling periods. One exception, however, was a relatively high mean value for total species abundance during the third sampling season (summer 2009), which was influenced by a high number of western mosquitofish at a single site (Table 3). For species diversity, data supported the seasonal period model as the best approximating model ($\Delta\text{QAIC}_c = 0.0$, QAIC_c weight = 0.36, Table 4). The four seasonal period models with covariates were also weighted (QAIC_c weights = 0.11–0.23), but these models were close to the seasonal period model only because of the addition of one model parameter, providing support for the seasonal period model but not support for the covariates (Table 4, Burnham and Anderson 2002). In addition to no support for environmental covariates, the data did not support wetland class, wetland origin, or

hydroperiod as variables explaining variation in species diversity (Table 4). For total species abundance, the seasonal period + wetland volume model was the only one supported by the data. Our estimates of total species abundances differed across seasonal sampling periods, and were highest before the drought, lower during the drought periods of winter 2008/2009 and summer 2009, and lowest during the wet hydroperiod of winter 2009/2010.

Analyses of species abundances were conducted separately for six common species; western mosquitofish, warmouth, black bullhead, green sunfish, bluegill, and golden topminnow. For western mosquitofish abundance, data supported the seasonal period + water volume model ($\Delta\text{QAIC}_c = 0.0$, QAIC_c weight = 0.47) and also supported models of hydroperiod + maximum water depth ($\Delta\text{QAIC}_c = 1.8$, QAIC_c weight = 0.19), hydroperiod + water volume ($\Delta\text{QAIC}_c = 2.6$, QAIC_c weight = 0.13) and seasonal period + maximum water depth ($\Delta\text{QAIC}_c = 3.2$, QAIC_c weight = 0.10, Table 5). Western mosquitofish were collected at different abundances among seasons, and higher numbers were collected from wetland ponds with smaller water volumes, including an influential observation of 435 individuals in an estimated 19.3 m³ wetland volume during summer 2009. For warmouth, seasonal period + salinity was the best approximating model and the only model supported by the data ($\Delta\text{QAIC}_c = 0.0$, QAIC_c weight = 0.85, Table 5). Warmouth were not captured at sites with salinity values > 2.5 ppt. A single model (maximum water depth, $\Delta\text{QAIC}_c = 0.0$, QAIC_c weight = 0.69) was supported for black bullhead (Table 5). Abundance data of black bullhead, however, supported the maximum water depth model, where higher numbers of black bullhead were collected in shallow habitats of < 1 m depth. Two models were weighted substantially for green sunfish abundance; seasonal period + dissolved oxygen ($\Delta\text{QAIC}_c = 0.0$, QAIC_c weight = 0.55), and seasonal period + salinity ($\Delta\text{QAIC}_c = 1.2$, QAIC_c weight = 0.30, Table 5). Green sunfish were rarely captured at sites with DO < 6.0 mg/L, and

were not captured at sites with salinity values > 2.5 ppt. For bluegill, data supported models with seasonal period + maximum water depth ($\Delta\text{QAIC}_c = 0.0$, QAIC_c weight = 0.39), seasonal period + salinity ($\Delta\text{QAIC}_c = 1.2$, QAIC_c weight = 0.21), and seasonal period ($\Delta\text{QAIC}_c = 1.3$, QAIC_c weight = 0.20, Table 5). Bluegill were captured at higher abundances in shallow water during the drought periods of winter 2008/2009 and summer 2009, and were rarely collected during the wet period of winter 2009/2010. Lastly, a single model (seasonal period + salinity, $\Delta\text{QAIC}_c = 0.0$, QAIC_c weight = 0.99) was supported for abundance data of golden topminnow (Table 5). Golden topminnows were not found at sites with salinity > 1.3 ppt.

Discussion

Our study was designed to examine the diversity and abundances of fishes on the Blackjack Peninsula during two dry seasons (winters of 2008/2009 and 2009/2010) and two wet seasons (summers of 2008 and 2009). The dry/wet hydroperiod cycle of the Blackjack Peninsula, however, was altered by drought conditions during winter 2008/2009 and summer 2009. Following the first sampling season, drought conditions coincided with lower estimates of fish diversity and fish abundance during the second and third seasonal sampling periods. The lowest estimates of fish diversity and fish abundances were found during winter 2009/2010, after drought-impacted wetlands were inundated from unusually high rainfall amounts. Our results are similar to Kushlan (1980), who found that fish population sizes were small within wetlands at the beginning of the wet season because of dry season mortality. The drought conditions during our study were more severe than that expected from a normal seasonal dry hydroperiod, and over half of the natural wetlands of the Blackjack Peninsula were completely dewatered. Lower estimates of fish diversity and fish abundance resulted from habitat reduction during the drought.

The low estimates of fish diversity and fish abundance following drought resulted from a lag effect of drought-induced mortality and a lower sampling efficiency associated with small population sizes within large wetland areas.

An important finding from our study is an increased understanding of drought affects on fish diversity and fish abundance within freshwater wetlands of ANWR. Influences of seasonal hydroperiod fluctuations of water levels on fish diversity and abundance are not new information, but were previously described by others (Kushlan 1976, Capone and Kushlan 1991, Winemiller et al. 2000, Chick et al. 2004, Gaff et al. 2004, Ruetz et al. 2005). In our study, however, drought conditions represented an extreme case of habitat conditions expected during dry hydroperiods, and drought conditions persisted during the expected dry and wet hydroperiods. Further, an unusually wet period occurred in Winter 2009/2010 when a dry hydroperiod was expected within ANWR. Our results are not representative of typical climate patterns in southwestern Texas, but provide insights into how fish diversity and fish abundances within shallow freshwater wetlands respond to climate change.

In addition to documenting drought-induced changes in diversity and abundance of fishes, our data also provided baseline information on the distributions of fishes of the Blackjack Peninsula. A list of species (Table 2) and maps of species distributions (*Supplemental Materials*, Figures S1–S19) were important components of this research because this information was previously unavailable, and an understanding of the presence and distribution of fishes were critical needs for management plans of ANWR. In addition to documenting a total of 19 species of freshwater fishes, this study added three fishes to the list of species known to occur within ANWR.

Wetland origin (natural vs. constructed) was expected to be an important factor associated with the diversity and abundance of fish species, but models with wetland origin were not supported. Constructed wetlands on ANWR (locally called dugouts) were constructed primarily to provide freshwater sources for cattle grazing, resident wildlife, and the endangered whooping crane. Within shallow freshwater wetland complexes, constructed wetlands often have deeper habitats than natural wetland areas. Maximum water depths of constructed wetlands from our study (mean = 1.1 m, SE = 0.09) were similar to those of natural habitats (mean = 0.94, SE = 0.14); however, a higher proportion of constructed wetlands were sampled at low water levels during drought periods. The selection of constructed and natural wetlands was not random during drought conditions, which represents a bias and a weakness of our study. During drought, most of the shallower natural wetland habitats were dewatered completely, and were not available to sample. Removal of dewatered sites from the sampling design was a weakness of this study, given that an analysis may have supported an effect of wetland origin if the zero values of diversity and abundance were included for dewatered habitats.

Support for environmental covariates in models associated with observational field studies can be misleading, because of correlations between covariates (McCullagh and Nelder 1989). In our study, sampling efficiency is likely correlated with variables associated with sampling area, such as maximum water depth and wetland volume. In several cases, we documented that higher fish abundances were associated with lower maximum water depths or smaller wetland volumes, but this effect may be explained by an increase in sampling efficiency associated with smaller sampling areas. Conversely, low abundance estimates during the final sampling period were influenced possibly by low sampling efficiencies given small numbers of fishes within recently-inundated larger sampling areas.

For our study, we could not foresee the drought prior to data collection, and did not fit a model representing a drought effect, such as a time trend model that parameterized a decline in species diversity or species abundance across the two year time period. Although we could have fit a time trend model after data collection, it is generally not appropriate to add and fit a post-hoc model (Anderson et al. 2001). However, data often supported models that parameterized among-season variation for species diversity or species abundance, and data typically followed a trend corresponding with seasonal drought conditions. Although long-term studies are needed to address the impacts of drought (Matthews and Marsh-Matthews 2003), our two year study demonstrated that drought can greatly reduce the diversity and abundances of fishes within shallow freshwater wetlands. Our study also emphasized the importance of maintaining some deep habitats within wetland complexes, which are useful as refuge habitat during periods of drought, and may be created artificially by constructing wetlands, or naturally by alligators.

Future research on the Blackjack Peninsula should address the influence of American alligator dens on fish survival during drought conditions. This became more evident as American alligator and den counts were much higher during periods of drought. Surveys of American alligators (sightings and den counts) were not an initial research objective, but these data were recorded at each study site, and are discussed because of their potential importance in creating and maintaining fish habitats during drought conditions. Alligators create holes and associated dens by digging downward within wetland habitats, thus creating areas of lower elevation which hold water and provide a refuge area for aquatic species during drought conditions (Palmer and Mazzotti 2004). Campbell and Mazzotti (2001) found that alligator holes were typically 1 m deeper than the surrounding marsh depths. Kushlan (1974b) found an increase in fish abundances within alligator holes during a dry hydroperiod in a Florida wetland,

suggesting that these ponds serve as refugia for aquatic organisms. Craighead (1968) found that alligator activities lead to structural similarities between constructed and natural wetland ponds.

Further research should also examine the function of artificially constructed wetlands on the Blackjack Peninsula. Based on our data, constructed wetlands provide refuge areas on the Blackjack Peninsula through lower elevation habitats that maintain water for longer periods during drought conditions. However, it is possible that alligators move to the deeper habitats of constructed wetlands during droughts, instead of digging dens and creating refuge habitat within natural wetlands. Further research on the relationships among natural wetlands, constructed wetlands, locations and abundances of alligator dens, and fish refuge areas would benefit conservation and management planning for drought conditions.

Fish assemblage in the palustrine wetlands of ANWR, Texas are linked to hydroperiod, and can be strongly influenced by drought conditions. During the drought, fishes were restricted to the only remaining habitats which consisted primarily of constructed wetlands, and American alligator holes or dens. Our data demonstrated that drought conditions can greatly reduce species diversity and species abundance on the Blackjack Peninsula. Further research is needed on the importance and interactions of constructed wetlands and alligator dens on providing fish refuge during drought. Also, long-term research is needed that addresses the recovery rates of fish populations following drought, which includes an understanding of dispersal rates of fishes between temporary and permanent wetlands during wet hydroperiods.

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Figure 1. Locations of palustrine wetland study sites on the Blackjack Peninsula, Aransas National Wildlife Refuge (ANWR), Texas.

Figure 2. Sampling frequency of natural and constructed wetlands during four seasonal sampling periods on the Blackjack Peninsula, Aransas National Wildlife Refuge, Texas.

Figure 3. Monthly precipitation amounts (cm) from February 2008 through March 2010 summarized from the Aransas National Wildlife Refuge, WxCoder III NOAA, National Weather Service, weather station.

Figure 4. Total counts of alligators (juveniles and adults) and alligator dens at 77 wetland sites during four seasonal sampling periods on the Blackjack Peninsula, Aransas National Wildlife Refuge, Texas.

Table 1. Means and standard errors (SE) of wetland habitat characteristics for four seasonal sampling periods on the Blackjack Peninsula, Aransas National Wildlife Refuge, Texas.

Habitat characteristic	Summer 2008		Winter 2008/2009		Summer 2009		Winter 2009/2010	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Maximum Depth (m)	0.50	0.06	0.88	0.08	0.65	0.05	2.0	0.10
Volume (m ³)	2692.0	1375.0	1848.7	1104.1	34.1	10.5	19788.3	6274.1
DO (mg/L)	6.30	0.00	7.3	0.54	5.0	0.72	5.9	0.67
Water Temp. (°C)	29.2	1.1	17.1	0.76	29.0	0.36	14.7	0.91
Conductivity (µS)	694.8	129.9	2149.0	340.2	6126.8	1731.5	402.9	69.1
pH	8.0	0.37	8.4	0.10	8.2	0.15	7.6	0.28
Salinity (ppt)	0.33	0.06	1.3	0.22	3.5	0.97	0.25	0.05
Turbidity (NTU)	67.5	25.1	296.3	156.1	347.8	125.9	4.7	1.3

Table 2. Total number of fish and species collected from July 2008 to March 2010 from wetland sampling sites using all three methods: electrofishing (EF), minnow traps (MT), and 1 m² throw traps (TT).

Species		Gear Type			Total Abundance
		EF	TT	MT	
Lepisosteidae					
<i>Atractosteus spatula</i> (Lacepède)	(alligator gar)	3	0	0	3
<i>Lepisosteus oculatus</i> Winchell	(spotted gar)	31	2	0	33
Anguillidae					
<i>Anguilla rostrata</i> (Lesueur)	(American eel)	5	0	0	5
Ictaluridae					
<i>Ameiurus melas</i> (Rafinesque)	(black bullhead)	245	45	4	294
<i>Ameiurus natalis</i> (Lesueur)	(yellow bullhead)	31	0	0	31
Mugilidae					
<i>Mugil cephalus</i> Linnaeus	(striped mullet)	27	0	0	27
Atherinopsidae					
<i>Menidia beryllina</i> (Cope)	(inland silverside)	78	0	0	78
Fundulidae					
<i>Fundulus chrysotus</i> (Günther)	(golden topminnow)	101	74	6	181
<i>Fundulus notatus</i> (Rafinesque)	(blackstripe topminnow)	26	113	0	139
<i>Fundulus pulvereus</i> (Evermann)	(bayou killifish)	4	0	0	4
Poeciliidae					
<i>Gambusia affinis</i> (Baird and Girard)	(western mosquitofish)	1406	516	9	1931
<i>Poecilia latipinna</i> (Lesueur)	(sailfin molly)	113	16	1	130
Cyprinodontidae					
<i>Cyprinodon variegatus</i> Lacepède	(sheepshead minnow)	28	0	0	28
Centrarchidae					
<i>Lepomis cyanellus</i> Rafinesque	(green sunfish)	151	41	16	208
<i>Lepomis gulosus</i> (Cuvier)	(warmouth)	189	32	8	229
<i>Lepomis macrochirus</i> Rafinesque	(bluegill)	132	32	19	183
<i>Lepomis symmetricus</i> Forbes	(bantam sunfish)	31	6	13	50
<i>Micropterus salmoides</i> (Lacepède)	(largemouth bass)	8	0	0	8
Eleotridae					
<i>Dormitator maculatus</i> (Bloch)	(fat sleeper)	25	3	0	28
Total Fish		2634	880	76	3590
Total Species		19	11	7	19
Total Transect/ Traps		145	56	37	238

Table 3. Mean values and standard errors (SE) of species diversity (total number of species per site), total species abundance, and species abundances of six common species for four seasonal sampling periods on the Blackjack Peninsula, Aransas National Wildlife Refuge, Texas.

Species diversity and abundance	Summer 2008		Winter 2008/2009		Summer 2009		Winter 2009/2010	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Species diversity	5.6	0.95	3.8	0.40	2.0	0.32	0.41	0.17
Species abundance								
Total species abundance	56.1	21.9	28.8	4.5	59.5	21.1	3.3	1.9
Western mosquitofish	13.6	9.9	8.1	2.5	48.4	20.5	1.3	0.7
Warmouth	7.9	3.7	4.1	1.1	0.1	0.1	0.0	0.0
Black bullhead	12.9	5.5	2.7	1.1	3.3	2.2	0.0	0.0
Green sunfish	5.9	2.7	3.2	1.1	0.4	0.3	0.0	0.0
Bluegill	4.7	2.9	3.0	0.9	0.2	0.2	0.0	0.0
Golden topminnow	2.6	1.8	2.4	0.9	0.2	0.1	0.0	0.0

Table 4. Model selection statistics from separate analyses on fish diversity and total fish abundance from 77 wetland sites on the Blackjack Peninsula, Aransas National Wildlife Refuge, Texas. K is the number of estimated model parameters. QAIC_c is Akaike's Information Criteria with corrections for overdispersion and small sample size. Explanatory variables included wetland class (emergent or unconsolidated bottom), wetland origin (natural vs. constructed wetlands), hydroperiod (summer or winter), seasonal period (summer 2008, winter 2008/2009, summer 2009, and winter 2009/2010), and six habitat covariates (dissolved oxygen, maximum water depth, pH, salinity, turbidity, and wet land volume).

Explanatory variables	K	Species diversity		Total species abundance	
		Δ QAIC _c	weight	Δ QAIC _c	weight
Dissolved oxygen (DO)	4	44.4	0.00	31.3	0.00
Max water depth (MWD)	4	32.0	0.00	9.1	0.01
pH	4	44.9	0.00	31.7	0.00
Salinity	4	46.6	0.00	30.9	0.00
Turbidity	4	46.5	0.00	31.6	0.00
Wetland volume (WV)	4	34.8	0.00	13.5	0.00
Wetland class (WC)	5	49.3	0.00	33.8	0.00
WC + DO	6	48.9	0.00	35.9	0.00
WC + MWD	6	36.7	0.00	13.7	0.00
WC + salinity	6	51.2	0.00	34.8	0.00
WC + WV	6	39.4	0.00	17.1	0.00
Wetland origin (WO)	5	48.2	0.00	33.5	0.00
WO + DO	6	47.2	0.00	35.4	0.00
WO + MWD	6	35.7	0.00	13.6	0.00
WO + salinity	6	50.3	0.00	35.3	0.00
WO + WV	6	36.7	0.00	17.8	0.00
Hydroperiod	5	49.1	0.00	24.6	0.00
Hydroperiod + DO	6	48.2	0.00	26.7	0.00
Hydroperiod + MWD	6	34.7	0.00	11.3	0.00
Hydroperiod + salinity	6	50.8	0.00	26.9	0.00
Hydroperiod + WV	6	44.4	0.00	10.2	0.01
Seasonal period	7	0.0	0.36	10.4	0.01
Seasonal period + DO	8	1.7	0.16	12.8	0.00
Seasonal period + MWD	8	2.3	0.11	10.8	0.00
Seasonal period + salinity	8	1.9	0.14	12.9	0.00
Seasonal period + WV	8	1.0	0.23	0.0	0.96
Global (all variables)	19	28.8	0.00	25.7	0.00

Table 5. Model selection statistics from separate analyses on abundance data of six common fishes from 77 wetland sites on the Blackjacket Peninsula, Aransas National Wildlife Refuge, Texas.

Explanatory variables	K	Western mosquitofish		Warmouth		Black bullhead		Green sunfish		Bluegill		Golden topminnow	
		Δ	QAIC _c	Δ	QAIC _c	Δ	QAIC _c	Δ	QAIC _c	Δ	QAIC _c	Δ	QAIC _c
		QAIC _c	weight	QAIC _c	weight	QAIC _c	weight	QAIC _c	weight	QAIC _c	weight	QAIC _c	weight
Dissolved oxygen (DO)	4	22.2	0.00	33.4	0.00	16.0	0.00	12.2	0.00	14.9	0.00	20.6	0.00
Max water depth (MWD)	4	7.6	0.01	24.9	0.00	0.0	0.69	12.9	0.00	5.9	0.02	19.1	0.00
pH	4	26.1	0.00	33.2	0.00	14.5	0.00	17.8	0.00	15.3	0.00	23.4	0.00
Salinity	4	26.6	0.00	26.9	0.00	17.0	0.00	13.4	0.00	12.6	0.00	10.5	0.01
Turbidity	4	26.9	0.00	34.3	0.00	17.2	0.00	17.8	0.00	15.4	0.00	14.0	0.00
Wetland volume (WV)	4	12.3	0.00	28.3	0.00	9.8	0.01	14.8	0.00	12.9	0.00	20.5	0.00
Wetland class (WC)	5	27.7	0.00	36.2	0.00	19.5	0.00	19.9	0.00	17.7	0.00	22.0	0.00
WC + DO	6	26.9	0.00	37.7	0.00	20.6	0.00	16.6	0.00	19.5	0.00	23.7	0.00
WC + MWD	6	11.0	0.00	29.3	0.00	3.9	0.10	17.3	0.00	10.5	0.00	21.4	0.00
WC + salinity	6	28.2	0.00	31.4	0.00	21.4	0.00	16.8	0.00	16.8	0.00	15.1	0.00
WC + WV	6	14.6	0.00	32.1	0.00	14.5	0.00	19.5	0.00	17.5	0.00	23.9	0.00
Wetland origin (WO)	5	27.5	0.00	36.6	0.00	19.3	0.00	20.1	0.00	17.7	0.00	21.9	0.00
WO + DO	6	25.6	0.00	37.9	0.00	20.4	0.00	15.7	0.00	19.5	0.00	24.1	0.00
WO + MWD	6	12.2	0.00	29.0	0.00	4.6	0.07	17.3	0.00	9.4	0.00	20.9	0.00
WO + salinity	6	29.8	0.00	31.3	0.00	21.5	0.00	17.8	0.00	16.9	0.00	15.1	0.00
WO + WV	6	16.7	0.00	32.2	0.00	13.5	0.00	14.4	0.00	17.3	0.00	23.4	0.00
Hydroperiod	5	10.8	0.00	36.5	0.00	16.9	0.00	20.0	0.00	17.5	0.00	22.4	0.00
Hydroperiod + DO	6	12.5	0.00	38.0	0.00	18.7	0.00	16.5	0.00	19.4	0.00	24.7	0.00
Hydroperiod + MWD	6	1.8	0.19	25.9	0.00	4.5	0.07	16.4	0.00	5.9	0.02	21.6	0.00
Hydroperiod + salinity	6	12.9	0.00	31.1	0.00	19.2	0.00	17.8	0.00	16.9	0.00	15.0	0.00
Hydroperiod + WV	6	2.6	0.13	32.9	0.00	11.7	0.00	19.5	0.00	17.6	0.00	24.6	0.00
Seasonal period	7	4.4	0.05	5.7	0.05	8.1	0.01	3.9	0.08	1.3	0.20	11.6	0.00
Seasonal period + DO	8	6.2	0.02	8.1	0.01	7.8	0.01	0.0	0.55	3.4	0.07	13.5	0.00
Seasonal period + MWD	8	3.2	0.10	8.0	0.02	6.9	0.02	5.5	0.04	0.0	0.39	13.9	0.00
Seasonal period + salinity	8	5.7	0.03	0.0	0.85	10.2	0.00	1.2	0.30	1.2	0.21	0.0	0.99
Seasonal period + WV	8	0.0	0.47	5.0	0.07	7.7	0.01	5.9	0.03	3.1	0.08	13.3	0.00
Global (all variables)	19	28.3	0.00	22.3	0.00	32.7	0.00	23.8	0.00	21.2	0.00	19.5	0.00

***Atractosteus spatula* (alligator gar)**

Figure S1. Collection site for alligator gar *Atractosteus spatula* on the Blackjack Peninsula, Aransas National Wildlife Refuge.

Lepisosteus oculatus (spotted gar)

Figure S2. Collection sites for spotted gar *Lepisosteus oculatus* on the Blackjack Peninsula, Aransas National Wildlife Refuge.

***Anguilla rostrata* (American eel)**

Figure S3. Collection sites for American eel *Anguilla rostrata* on the Blackjack Peninsula, Aransas National Wildlife Refuge.

Ameiurus melas (black bullhead)

Figure S4. Collection sites for black bullhead *Ameiurus melas* on the Blackjack Peninsula, Aransas National Wildlife Refuge.

***Ameiurus natalis* (yellow bullhead)**

Figure S5. Collection sites for yellow bullhead *Ameiurus natalis* on the Blackjack Peninsula, Aransas National Wildlife Refuge.

***Mugil cephalus* (striped mullet)**

Figure S6. Collection sites for striped mullet *Mugil cephalus* on the Blackjack Peninsula, Aransas National Wildlife Refuge.

***Menidia beryllina* (inland silverside)**

Figure S7. Collection sites for inland silverside *Menidia beryllina* on the Blackjack Peninsula, Aransas National Wildlife Refuge.

Fundulus chrysotus (golden topminnow)

Figure S8. Collection sites for golden topminnow *Fundulus chrysotus* on the Blackjack Peninsula, Aransas National Wildlife Refuge.

***Fundulus notatus* (blackstrip topminnow)**

Figure S9. Collection sites for blackstripe topminnow *Fundulus notatus* on the Blackjack Peninsula, Aransas National Wildlife Refuge.

***Fundulus pulvereus* (bayou killifish)**

Figure S10. Collection sites for bayou killifish *Fundulus pulvereus* on the Blackjack Peninsula, Aransas National Wildlife Refuge.

***Gambusia affinis* (western mosquitofish)**

Figure S11. Collection sites for western mosquitofish *Gambusia affinis* on the Blackjack Peninsula, Aransas National Wildlife Refuge.

***Poecilia latipinna* (sailfin molly)**

Figure S12. Collection sites for sailfin molly *Poecilia latipinna* on the Blackjack Peninsula, Aransas National Wildlife Refuge.

***Cyprinodon variegatus* (sheepshead minnow)**

Figure S13. Collection sites for sheepshead minnow *Cyprinodon variegatus* on the Blackjack Peninsula, Aransas National Wildlife Refuge.

***Lepomis cyanellus* (green sunfish)**

Figure S14. Collection sites for green sunfish *Lepomis cyanellus* on the Blackjack Peninsula, Aransas National Wildlife Refuge.

Figure S15. Collection sites for warmouth *Lepomis gulosus* on the Blackjack Peninsula, Aransas National Wildlife Refuge.

Lepomis macrochirus (bluegill)

Figure S16. Collection sites for bluegill *Lepomis macrochirus* on the Blackjack Peninsula, Aransas National Wildlife Refuge.

***Lepomis symmetricus* (bantam sunfish)**

Figure S17. Collection sites for bantam sunfish *Lepomis symmetricus* on the Blackjack Peninsula, Aransas National Wildlife Refuge.

***Micropterus salmoides* (largemouth bass)**

Figure S18. Collection sites for largemouth bass *Micropterus salmoides* on the Blackjack Peninsula, Aransas National Wildlife Refuge.

***Dormitator maculatus* (fat sleeper)**

Figure S19. Collection sites for fat sleeper *Dormitator maculatus* on the Blackjack Peninsula, Aransas National Wildlife Refuge.