Wetlands Ecol Manage (2010) 18:651–663
DOI 10.1007/s11273-010-9185-z

ORIGINAL PAPER

Hurricane storm surge and amphibian communities in coastal wetlands of northwestern Florida

Margaret S. Gunzburger · William B. Hughes · William J. Barichivich · Jennifer S. Staiger

Received: 2 July 2009 / Accepted: 30 April 2010 / Published online: 15 May 2010
© Springer Science+Business Media B.V. 2010

Abstract Isolated wetlands in the Southeastern United States are dynamic habitats subject to fluctuating environmental conditions. Wetlands located near marine environments are subject to alterations in water chemistry due to storm surge during hurricanes. The objective of our study was to evaluate the effect of storm surge overwash on wetland amphibian communities. Thirty-two wetlands in northwestern Florida were sampled over a 45-month period to assess amphibian species richness and water chemistry. During this study, seven wetlands were overwashed by storm surge from Hurricane Dennis which made landfall 10 July 2005 in the Florida panhandle. This event allowed us to evaluate the effect of storm surge overwash on water chemistry and amphibian communities of the wetlands. Specific conductance across all wetlands was low pre-storm (<100 μS/cm), but increased post-storm at the overwashed wetlands ($\bar{x} = 7{,}613$ μS/cm). Increased specific conductance was strongly correlated with increases in chloride concentrations. Amphibian species richness showed no correlation with specific conductance. One month post-storm we observed slightly fewer species in overwashed compared with non-overwashed wetlands, but this trend did not continue in 2006. More species were detected across all wetlands pre-storm, but there was no difference between overwashed and non-overwashed wetlands when considering all amphibian species or adult anurans and larval anurans separately. Amphibian species richness did not appear to be correlated with pH or presence of fish although the amphibian community composition differed between wetlands with and without fish. Our results suggest that amphibian communities in wetlands in the southeastern United States adjacent to marine habitats are resistant to the effects of storm surge overwash.

Keywords Conductivity · Salinity · Amphibian · Anuran · Caudate

M. S. Gunzburger · W. J. Barichivich · J. S. Staiger
United States Geological Survey, Southeast Ecological Science Center, 7920 NW 71st Street, Gainesville, FL 32653, USA

W. B. Hughes
United States Geological Survey, 3039 Amwiler Road, Ste 130, Atlanta, GA 30360, USA

M. S. Gunzburger (✉)
Nokuse Plantation, 13292 Co Hwy 3280, Bruce, FL 32455, USA
e-mail: phaeognathus@gmail.com

Introduction

Hurricanes are large-scale disturbances which may have strong effects on terrestrial and freshwater aquatic ecosystems through winds, rainfall, and storm surge flooding (Roman et al. 1994; Walker et al.

1991). High winds associated with Hurricane Hugo caused significant damage to tree canopy and increased the amount of woody debris on the forest floor in Puerto Rico, providing increased refugia and leading to a temporary population increase of *Eleutherodactylus coqui* following the storm (Woolbright 1991, 1996). Hurricane winds may also alter vegetation structure within freshwater wetlands which influences species composition and abundance of fishes and invertebrates (Roman et al. 1994). In some cases species in the same habitat may be affected differently by hurricanes, with population size of some species declining after a storm and others remaining the same or increasing (Loope et al. 1994; Schriever et al. 2009; Vilella and Fogarty 2005). Many ecosystems adjacent to coastal areas prone to hurricanes appear resilient to the effects of wind, rain, and flooding (Roman et al. 1994).

Freshwater wetlands in the southeastern United States support a diverse assemblage of amphibians, fish, and invertebrates (Semlitsch and Bodie 1998; Whitney et al. 2004). Community composition in isolated wetlands is influenced by hydroperiod, water chemistry, adjacent land use and management, and relative proximity to other wetlands (Eason and Fauth 2001; Snodgrass et al. 2000; Wellborn et al. 1996). Freshwater wetlands adjacent to marine environments may occasionally be flooded by storm surge from hurricanes and tropical storms. Salinity in coastal freshwater systems varies depending on rainfall, connectivity to tidal marshes, freshwater flow, and tidal cycles (Jones and West 2005). Freshwater habitats connected to tidal habitats are characterized by a salinity gradient across which species distributions are segregated based on salinity tolerance (Odum 1988; Piscart et al. 2005). Isolated wetlands in coastal areas do not experience daily variations in salinity due to tides, but may be exposed to high salinity during brief intervals of flooding from storm surges during hurricanes.

The vast majority of amphibian species occur in freshwater habitats, but many species are at least occasionally found in brackish habitats (Gomez-Mestre and Tejedo 2003; Milto 2008; Neill 1958; Ruibal 1959; Taylor 1943), and several are regularly found in brackish habitats, including *Rana cancrivora* (Dunson 1977) and *Bufo viridis* (Katz 1973). The physiological adaptations that allow these amphibian species to occur in brackish or salt-water, primarily the accumulation of urea in body tissues to facilitate water retention, are similar to the adaptations of amphibians to resist desiccation in desert environments and during aestivation (Dunson 1977; Gordon et al. 1961; Katz 1973; Konno et al. 2006; Wright et al. 2004).

In general, species not typically found in brackish habitats have poor performance with even low levels of salinity. Mortality and sub-lethal effects may be lower when organisms are exposed to gradual increases in salinity than when exposed to a sudden salinity increase (Christy and Dickman 2002; Gomez-Mestre and Tejedo 2003). Amphibians which occur in wetlands in the northeastern United States would not be expected to be adapted to high levels of salinity, but studies of the effects of the runoff of road de-icing salts into these wetlands provides an interesting example of the variation in tolerance to salinity among species (Karraker 2007; Karraker et al. 2008; Sanzo and Hecnar 2006). The elevated salinity levels observed in wetlands subjected to road salt runoff resulted in reduced egg and larval survival, reduced larval growth rates, and increased abnormalities for *R. sylvatica* and *Ambystoma maculatum* (Karraker et al. 2008; Sanzo and Hecnar 2006), but *R. clamitans* seemed more tolerant of increased salinity (Karraker 2007). In the southeastern United States, *Acris gryllus*, *Hyla cinerea*, and *Rana sphenocephala* have geographic ranges that include coastal areas and are known to occur in brackish habitats (Christman 1974; Neill 1958). However, many of these observations are of adult anurans and the extent to which amphibians use brackish habitats for the aquatic portion of their life cycle is unknown.

Despite the extensive literature on the environmental factors influencing the distribution of amphibians and the fact that many wetlands in the southeastern United States are potentially exposed to saltwater overwash during hurricanes, no previous field studies have evaluated the effect of storm surge on aquatic amphibian communities. A study of herpetofauna in terrestrial habitats adjacent to wetlands overwashed by hurricane storm surge in Louisiana found that amphibian abundance decreased and community evenness increased following storm surge overwash (Schriever et al. 2009). Our long-term amphibian monitoring program provided a unique opportunity to evaluate the effect of storm surge overwash on aquatic amphibians when some of the wetlands in our study were overwashed during a hurricane. To evaluate the effect of overwash we compared amphibian species richness and water chemistry pre- and post-storm. We also evaluated the relative importance of other factors known to influence amphibian communities, including rainfall, pH, and the presence of fish.

Methods

Study area

The study was conducted at St. Marks National Wildlife Refuge (SMNWR), a 27,500 ha refuge on the northern Gulf Coast of Florida bounded on the east by the Aucilla River and on the west by the Ochlockonee River and Bay (Fig. 1). Established in 1931, the refuge has been managed for migrating waterfowl and other native species. The predominant upland habitat is longleaf pine flatwoods interspersed with isolated wetlands, creeks, rivers, impoundments, and coastal marshes. The refuge has an active prescribed burning program and supports a diverse herpetofauna including 20 anuran and eight caudate species (Dodd et al. 2007).

As part of the United States Geological Survey's Amphibian Research and Monitoring Initiative (ARMI), 32 lentic wetlands were sampled at SMNWR, including ephemeral ponds, sinkholes, lakes, and large marshes (Table 1). Of these wetlands, 23 were sampled for both amphibians and detailed water chemistry analysis, four were sampled only for detailed water chemistry, and five were sampled only for amphibians and basic water chemistry measurements (Table 1). Wetlands ranged from 0.01 to 56 ha ($\bar{x} = 3.48$ ha), all but two were less than 7 ha in size. Wetlands were selected to encompass a range of variation of factors known to influence amphibian communities, including hydroperiod, pH, substrate type, canopy cover, aquatic vegetation, proximity to other wetlands, and the presence or absence of fish. Amphibian sampling was conducted over a 45-month period from December 2002 through August 2006; not all wetlands were visited on each trip. Prior to Hurricane Dennis, water samples for detailed chemical analyses were collected approximately annually during 2002–2005 to support ARMI program objectives unrelated to this study (Gunzburger et al. 2005). Water samples for chemical analyses were collected four times post hurricane specifically for this study during August 2005, May 2006, August 2006, and April 2008.

Most of the wetlands sampled were typically isolated from other wetlands, but the low relief of this area results in connectivity of many wetlands during periods of heavy rain and high water levels. During Hurricane Dennis, a major hurricane that made landfall in early July 2005 approximately 275 km west of SMNWR (Fig. 1), SMNWR experienced a storm surge of approximately 3 m above normal high tide (Morey et al. 2006). Seven of the wetlands in our study were flooded by the storm surge, including five

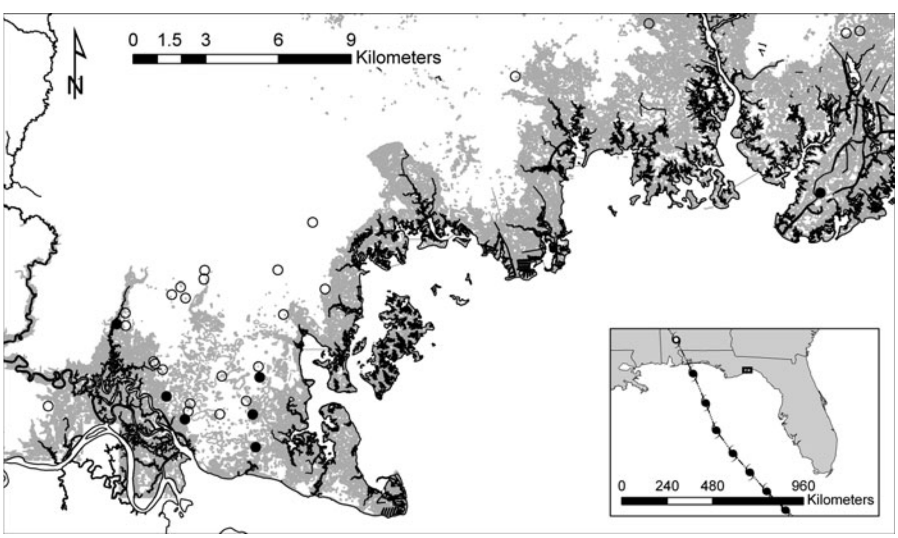

Fig. 1 Location of 32 wetlands at St. Marks National Wildlife Refuge in northwestern Florida sampled for amphibians and water chemistry over a 45-month period. *Open circles* are non-overwashed wetlands, *closed circles* are overwashed wetlands. Elevation less than 1.8 m is *shaded darker*. *Inset* map shows location of SMNWR in Florida and the approximate track of Hurricane Dennis which caused storm surge flooding at SMNWR

Table 1 Wetlands sampled from 2002 to 2008 at St. Marks National Wildlife Refuge in northwestern Florida

Wetland name	Overwashed	Number of sampling visits		Total amphibian Samples collected	Total amphibian Species detected
		Water chemistry	Amphibian		
Biggins Pond	Y	5	11	48	11
Chicky Pond		2	5	21	10
Cingulatum Pond		3	8	25	9
Corner Pond		8	10	46	10
Fat Nerodia Pond		2	6	22	8
Florida Trail Pond			3	11	5
Goose Pond		2	3	18	4
Headquarters Pond	Y	2			
Jennifer's Sink		7	7	30	6
Kingfisher Pond	Y	5	10	44	12
Otter Lake		7	7	32	8
Perkinsus Pond			5	15	5
Plum Orchard Pond		2	4	15	10
Printiss 2 Pond		1			
Printiss Pond	Y		4	14	9
Ring Pond		5	7	31	8
Small Prairie Pond		3	6	27	8
SPC Prairie Pond	Y	2	6	24	7
Spike Buck Pond		2	3	9	7
Streetlight Pond			3	10	7
Talpoideum Pond		7	10	45	10
Wakulla Field Pond			2	10	10
WBF Pond		1	6	20	7
Waypoint 103 Pond		2	5	20	7
Waypoint 150 Pond		2	7	31	8
Waypoint 19 Pond	Y	5	11	51	13
Waypoint 192 Pond		4	9	41	12
Waypoint 221 Pond		2			
Waypoint 316 Pond		1			
Waypoint 68 Pond	Y	3	7	30	11
Waypoint 69 Pond		5	10	46	12
Waypoint 79 Pond		2	13	54	9

Total amphibian samples collected is the total number of amphibian sampling methods used during each visit summed for all visits to the wetland

wetlands sampled for both amphibians and water chemistry, one wetland sampled only for detailed water chemistry, and one wetland sampled only for amphibians and basic water chemistry (Table 1). Overwashed wetlands were identified by evaluating the specific conductance level in the sampling visits post-storm compared to pre-storm levels; overwashed wetlands had higher specific conductance than non-overwashed wetlands by several orders of magnitude. In addition, qualitative observations of high-water marks on trees and the amount of dead vegetation in wetlands contributed to the identification of overwashed wetlands. Overwashed wetlands were also significantly lower in elevation ($\bar{x} = 1.52$ m) than non-overwashed wetlands ($\bar{x} = 2.19$ m; t-test t = 3.37, df = 30, $P = 0.002$) (Florida Division of Emergency Managmement 2002). The distance from overwashed wetlands to the nearest possible source of storm surge overwash ranged from 148 to 1,633 m ($\bar{x} = 743$ m). The overwashed status of the sampling sites was later confirmed using water chemistry data.

Water chemistry

Basic water chemistry measurements (dissolved oxygen, pH, specific conductance, and temperature) were taken using a HydroLab Quanta water quality meter during each visit to each wetland according to standard USGS protocols (U.S. Geological Survey 1997 to present). Monthly rainfall accumulations were obtained from a U.S. Fish and Wildlife Service automated weather recording station at SMNWR (30.1333°N, 84.1333°W). More detailed water-quality samples were collected annually from 2002 to 2008; 27 wetlands were sampled during this period, and one to eight samples were collected from each wetland (Table 1). Water samples were collected using clean 1-l glass bottles. The bottles were opened underneath the wetland surface and allowed to slowly fill while traversing the wetland to integrate the sample. Where wetlands were too large to completely traverse, a representative portion of the wetland was selected for sampling. The glass sample-collection bottles were then placed on ice and transported to a mobile field laboratory for processing according to standard USGS protocols (U.S. Geological Survey 1997 to present). Samples were analyzed for dissolved major ions, total and dissolved nutrients, and organic carbon at the USGS National Water-Quality Laboratory in Denver, Colorado, using methods described by Fishman and Friedman (1989).

Water chemistry was analyzed using post-storm water samples to determine the effect of overwash on the chemical composition of wetlands and time-related trends in water chemistry as the wetlands recovered from the overwash. Water samples were analyzed for major ions, nutrients, and trace metals. Stiff plots were constructed to illustrate changes in major ion chemistries (potassium, sodium, magnesium, calcium, sulfate, and chloride) from 2002 to 2008. In order to confirm that changes in specific conductance were the result of saltwater overwash, and not changes in concentration of other ions, linear regression was used to determine the relation between specific conductance and chloride concentration.

Amphibian species richness and community structure

Amphibian sampling was conducted at 28 wetlands from December 2002 to August 2006 (Table 1). All wetlands were visited at least once before and after the storm, but sampling effort varied across wetlands. Before the storm, an effort was made to visit 5–10 wetlands a minimum of three times each year. After the storm, a more intensive effort was made to visit more wetlands (15–20) every six weeks between January and August 2006. The number of visits to a wetland averaged seven and ranged from 2 to 13.

Each wetland was sampled using multiple methods to detect larval and adult amphibians: dip-nets, crayfish traps, automated audio recording devices, and opportunistic visual and aural encounter surveys (Gunzburger 2007; Smith et al. 2006). Sampling effort varied across wetlands and over time, and not all methods were employed at all wetlands during each visit. Dip-netting was conducted by multiple observers for either a specified length of time or a set number of sweeps, on average 40 min or 40 sweeps combined among all observers. Dip-nets were constructed of a metal frame with mouth area 52 × 41.5 cm and 3 mm mesh size (Memphis Net and Twine). Dip-net sampling was conducted throughout all areas of each wetland in water ranging from 5 to 50 cm deep; each dipnet sweep was separated by at least 50 cm. Crayfish traps are large pyramidal traps constructed of coated wire lined with 5 mm mesh and three funnel openings that sit flush with the bottom substrate (Lee Fisher International; Johnson and Barichivich 2004). Crayfish traps were set in water 30–50 cm deep, approximately 1–2 m from the edge of each wetland, and separated by at least 2 m; traps were set a minimum of one night prior to checking, and in some instances were left in place for several days and checked daily. Automated audio recording devices were constructed of a tape recorder, timer with voice-time stamp, and 12 V battery housed within a waterproof canister and connected to an external microphone (Barichivich 2003). One automated recorder was placed at the edge of each wetland and allowed to run overnight, recording one minute every hour between 18:00 and 06:00 h. Tapes were collected and later evaluated for identification of all vocalizing anuran species. The final two sampling methods consisted of visual and aural (auditory) observations of amphibians detected during sampling. These opportunistic observations were not conducted along transects or for specified periods of time, but any amphibian seen or heard in the wetland while conducting the other methods of sampling was recorded. The species identity and life stage of all amphibians collected by all sampling methods was recorded and individuals were then released at the point of capture. Occasionally a few larvae were retained for rearing in the laboratory to confirm species identification. In addition to amphibian data, we recorded species identity of any fish captured at each wetland.

The relationship between sampling effort (the number of sampling methods used during each visit summed for all visits to each wetland) and the total number of species detected during all visits to each wetland were evaluated using linear regression. Because sampling effort was positively correlated with total species richness, the following analyses were performed using total species richness at each wetland divided by the total number of sampling methods during each visit summed for all visits to the wetland (hereafter denoted species richness/samples). This value was then square-root transformed to better meet the assumptions of normality. A series of two-way ANOVAs were performed with the factors time interval (pre- and post-storm) and overwashed (yes or no). The response variables were specific conductance, amphibian species richness/samples, adult amphibian species richness/samples, and larval amphibian species richness/samples, and number of samples.

Amphibian species richness for each wetland over the entire study was compared to several additional environmental factors to examine which influences, other than specific conductance, might be correlated with amphibian species richness. First, linear regression was used to evaluate the correlation between rainfall and amphibian species detected. The total number of amphibian species collected during each sampling interval (month) was divided by the total sampling methods used during that month across all wetlands and then subjected to square-root transformation. Linear regression analysis examined the correlation between this measure of species richness and three rainfall measures: rainfall during that month, rainfall during the previous month, and rainfall during the current and previous months combined. Second, linear regression was used to evaluate the relationship between median pH at each wetland and amphibian species richness/samples. Third, a two-way analysis of variance (ANOVA) was used to determine if amphibian species richness in wetlands that dried at least once during the course of this study or in which fish were detected at least once differed from wetlands which did not dry or in which fish were never detected. The response variable was amphibian species richness/samples and the factors were fish presence or absence and whether the wetland dried or not. We reduced our data to simply detection or non-detection of fish for two reasons. First, although fish species differ in their predatory effects on amphibians, even relatively small species such as *Gambusia holbrooki* can significantly reduce survival and alter behavior of amphibians, particularly for those species adapted to fishless wetlands (Goodsell and Kats 1999; Gregoire and Gunzburger 2008; Gunzburger and Travis 2004). Second, because our sampling was targeted toward amphibians, it is unlikely that our sampling methods collected all species of fish present in each wetland, therefore our data are not robust for a species-specific analysis of fish.

We analyzed our data based on amphibian species richness rather than occupancy estimation incorporating detection probabilities because our study design did not meet the assumptions of occupancy analysis. Specifically our localities were not randomly selected nor was our sample size of localities or number of visits to those localities sufficient to make a robust use of occupancy analysis (MacKenzie and Royle 2005).

For multivariate analysis of amphibian community structure, the number of visits each species was observed at each wetland during two periods, pre- and post-storm, was standardized by the number of sampling visits to each wetland. This analysis considered only capture data from crayfish trap, dip-net, and visual methods; aural and automated audio recording data were not included because these methods only detect anurans and thus might bias the results toward increased importance of anurans in community structure. The resulting proportions were then converted to a triangular matrix of Bray-Curtis coefficients (Clarke and Gorley 2006). These similarity measures were then analyzed with multidimensional scaling (MDS). Two factors were examined separately, the continuous variable specific conductance and the discrete variable presence of fish. The relationship between amphibian occurrence and specific conductance was further explored using a bubble plot. Increasing levels of conductance were represented by correspondingly larger sized circles in multidimensional space. For fish presence, a similarity percentage breakdown (SIMPER) was run to discriminate between the species responsible for the similarity within groups and the dissimilarity between groups (Clarke 1993). Data analyses were conducted using SYSTAT 11 (SYSTAT Software, Inc 2005) and Primer 6 (Clarke and Gorley 2006) software.

Results

Water chemistry

The water chemistry at six of the 27 wetlands sampled for detailed water chemistry analysis showed clear evidence of storm surge overwash (Fig. 2a). Several other wetlands showed a delayed and much smaller increase in salinity after the hurricane than the overwashed wetlands (Fig. 2b). Ponds receiving overwash directly from the hurricane storm surge showed an increase in major-ion concentrations of two to three orders of magnitude, including calcium, magnesium, sodium, potassium, chloride, and sulfate (e. g. Biggins Pond, Fig. 3a). Otter Lake (Fig. 3b) showed a much smaller increase in major ions, and the increase was not observed until almost a year following the hurricane. Many ponds showed no increase in major ions after the storm (Fig. 3c).

Chloride is a primary indicator of saltwater contamination, showing increases from less than 10 mg/l prior to overwash to 4,900 mg/l about one month after the overwash. Chloride concentrations may have been higher immediately after the overwash, but samples were not collected until one month later. Specific conductance showed a strong positive linear correlation with chloride concentration [chloride = 0.3038 (specific conductance)—13.183, $R^2 = 0.998$, df = 89, $P = 0.001$], indicating conductance can be used to predict chloride concentration where water samples were not collected. Specific conductance was low and fairly constant across wetlands prior to the storm surge (generally <100 µS/cm), but increased post-storm at the overwashed wetlands and remained much higher for the following 12 months (Fig. 4). Specific conductance values in overwashed wetlands immediately post-storm ranged from 932 to 15,900 µS/cm with a mean value of 7,613 µS/cm, well above the range considered to be brackish (1,600–4,800 µS/cm). Specific conductance was significantly higher in overwashed than in non-overwashed wetlands post-storm (ANOVA, F = 21.9, $P < 0.001$, df = 1).

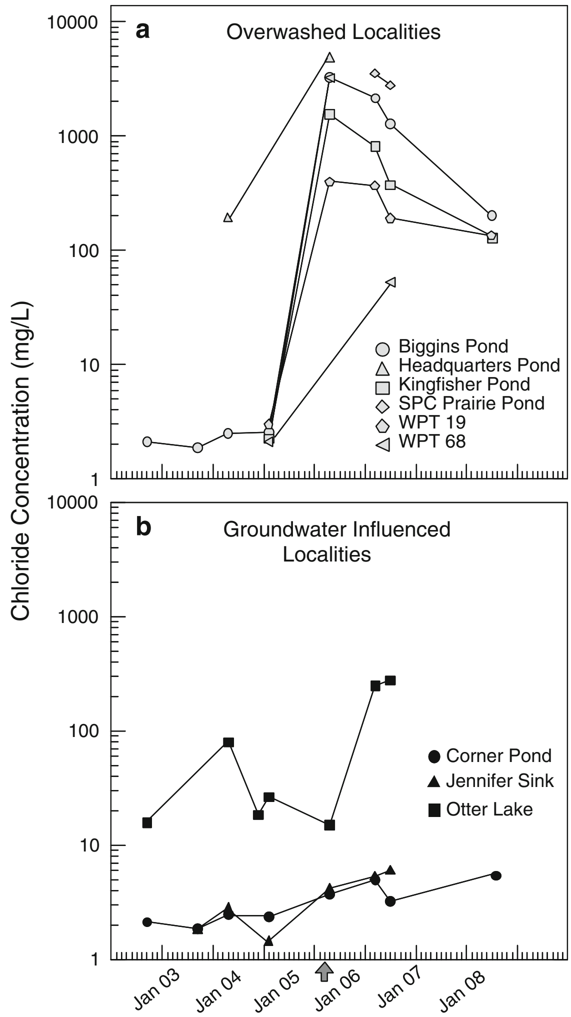

Fig. 2 Chloride concentration from 2002 to 2008 at **a** six wetlands overwashed by storm surge from Hurricane Dennis and **b** 3 wetlands potentially influenced by high-salinity groundwater at St. Marks National Wildlife Refuge, Florida. *Gray arrow* on X-axis at July 2005 indicates landfall of Hurricane Dennis

Amphibian species richness and community structure

A total of 19 anuran and seven caudate species were detected at the 28 wetlands sampled for amphibians (Table 2). Amphibian species richness did not differ

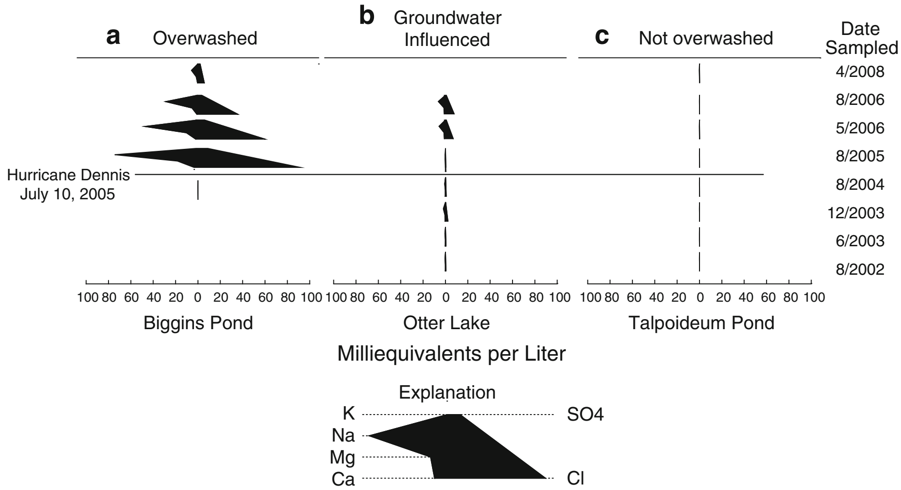

Fig. 3 Representative examples of water chemistry (concentration of potassium, sodium, magnesium, calcium, sulfate and chloride) at **a** a representative overwashed wetland, **b** a groundwater influenced wetland, and **c** a not overwashed wetland from 2002 to 2008 at St. Marks National Wildlife Refuge, Florida

between overwashed and non-overwashed wetlands ($F = 1.68$, $P = 0.201$, df = 1), but was greater across all wetlands prior to the storm surge than after ($F = 7.58$, $P = 0.008$, df = 1), there was no significant interaction effect ($F = 0.11$, $P = 0.743$, df = 1; Fig. 5). This pattern was similar for larval amphibians when analyzed separately; species richness was higher pre-storm ($F = 4.52$, $P = 0.038$, df = 1) but species richness did not differ between overwashed and non-overwashed wetlands ($F = 2.44$, $P = 0.124$, df = 1) and there was no significant interaction effect ($F = 1.83$, $P = 0.182$, df = 1; Fig. 5). No significant differences were found for adult anuran species richness (overwash: $F = 0.95$, $P = 0.335$, df = 1; time interval: $F = 2.94$, $P = 0.092$, df = 1, interaction: $F = 3.4$, $P = 0.7$, df = 1; Fig. 5). On the first post-storm visit in August 2005, there were slightly fewer species in overwashed than non-overwashed wetlands. This trend did not continue with further sampling in 2006, although specific conductance levels remained elevated at overwashed wetlands (Fig. 4).

Fourteen amphibian species were collected at both overwashed and non-overwashed wetlands both before and after the storm surge (Table 2). Species not detected post-storm from overwashed wetlands but present in non-overwashed wetlands were *Hyla squirella*, *Pseudacris ornata*, *Rana catesbeiana*, *Rana clamitans*, and *Pseudobranchus striatus* (Table 2). Two of these species, *R. clamitans* and *R. catesbeiana*, were also not detected at the overwashed wetlands prior to the storm. One species (*Pseudacris nigrita*) was found post-storm at overwashed wetlands and not at non-overwashed wetlands (Table 2). The five rarely detected species (detected at two or fewer wetlands) were only found prior to the storm (Table 2). Although there were more total visits post-storm (107) than pre-storm (83), the pre-storm visits occurred over a 31-month period, whereas post-storm sampling was conducted over a 12-month period. The assemblage of amphibian species detected during this study represents most of the amphibian species found on SMNWR; a 2002–2005 drift fence study found only two additional species, *Eleutherodactylus planirostris* and *Plethodon grobmani*, both of which are entirely terrestrial and therefore are unlikely to be encountered during wetland sampling (Dodd et al. 2007).

Sampling effort varied across wetlands; number of visits ranged from 2 to 13 and the total number of sampling methods used across all visits ranged from 9 to 54. The total number of sampling methods used at a wetland was positively correlated with total number of amphibian species detected at that wetland ($R^2 = 0.41$, $F = 17.8$, $P < 0.001$, df = 1). Significantly more samples were made after the storm than before (ANOVA, $F = 3.94$, $P = 0.05$, df = 1), but there was no difference in the number of samples between overwashed and non-overwashed wetlands ($F = 3.63$, $P = 0.06$, df = 1).

Amphibian species richness fluctuated seasonally over the 45-month study period at the 28 wetlands; species richness tended to be higher in the summer and lower in the winter (Fig. 4). There was no relationship between amphibian species richness/sample and rainfall during the current month ($F = 0.89$, $P = 0.36$, df = 1), the previous month

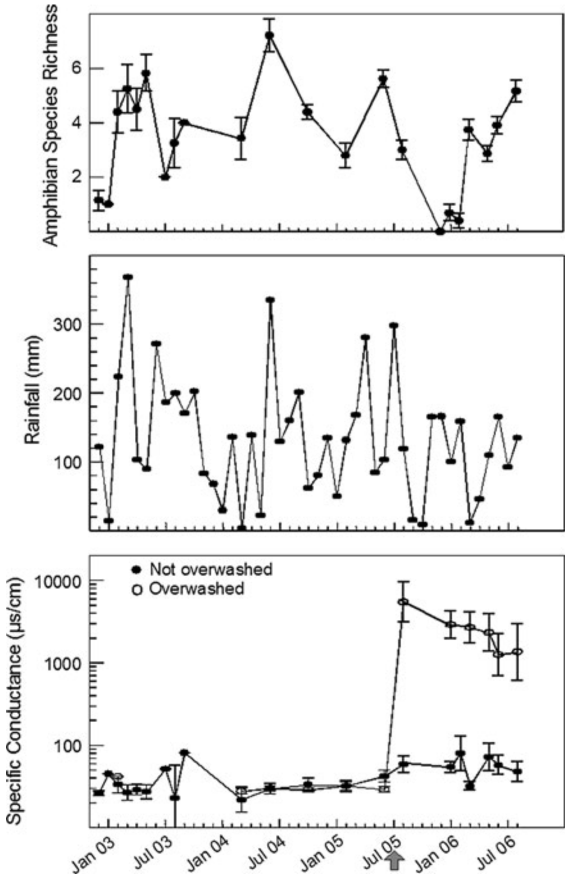

Fig. 4 Amphibian species richness (mean for all wetlands visited each month with standard error), monthly precipitation accumulation from St. Marks National Wildlife Refuge, Florida weather station, and conductance (µs/cm) (mean with standard error for overwashed and not overwashed wetlands separately) for 28 wetland wetlands over the 45 month sampling interval. *Gray arrow* on X-axis at July 2005 indicates landfall of Hurricane Dennis

(F = 1.3, $P = 0.28$, df = 1) or total rainfall during the current and previous month combined (F = 3.06, $P = 0.096$, df = 1). Total rainfall during the year post-storm (January–December 2006) was the lowest for any of the 4 years of the study (2003: 1,982 mm, 2004: 1,434 mm, 2005: 1,593 mm, 2006: 1,217 mm) (Fig. 4). All wetlands were acidic (overall median pH 4.29, SD = 0.66), and there was no correlation of amphibian species richness/sample with median pH ($R^2 = 0.11$, F = 3.08, $P = 0.09$, df = 1).

Fish were collected in 20 wetlands during at least one sampling visit; the most commonly encountered species were *G. holbrooki*, *Elassoma* sp., *Enneacanthus* sp., *Fundulus* sp., *Lepomis gulosus*, and *Centrarchus macropterus*. *G. holbrooki* was the most widely distributed fish species, it was found in all but one of the 20 wetlands in which fish were detected. Eleven wetlands dried completely at least once during the 45-month sampling interval. Over the course of this study, two previously fishless wetlands were colonized by fish (*G. holbrooki*, *Fundulus chrysotus*, *Elassoma* sp., *Enneacanthus* sp., *Leptolucania ommata*, *Dormitator maculatus*) during the storm surge, and four wetlands with fish dried completely and fish were not detected during visits after the wetlands refilled. There were no significant differences in amphibian species/

Table 2 Amphibian species composition before and after storm surge at overwashed ($N = 6$) and non-overwashed ($N = 22$) wetlands at St. Marks National Wildlife Refuge

	Overwashed		Non-overwashed	
	Before	After	Before	After
Anura				
Acris gryllus	x	x	x	x
Bufo quercicus	x	x	x	x
Bufo terrestris	x	x	x	x
Gastrophryne carolinensis		x	x	x
Hyla chrysoscelis			*	
Hyla cinerea	x	x	x	x
Hyla femoralis	x	x	x	x
Hyla gratiosa	x	x	x	x
Hyla squirella	x		x	x
Pseudacris crucifer			*	
Pseudacris nigrita	x	x	x	
Pseudacris ocularis	x	x	x	x
Pseudacris ornata	x		x	x
Rana catesbeiana			x	x
Rana clamitans			x	x
Rana grylio	x	x	x	x
Rana heckscheri			*	
Rana sphenocephala	x	x	x	x
Scaphiopus holbrookii			*	
Caudata				
Ambystoma cingulatum			*	
Ambystoma talpoideum	x	x	x	x
Amphiuma means	x	x	x	x
Eurycea quadridigitata	x	x	x	x
Notophthalmus viridescens	x	x	x	x
Siren spp.	x	x	x	x
Pseudobranchus striatus	x		x	x

* Species detected at 2 or fewer wetlands

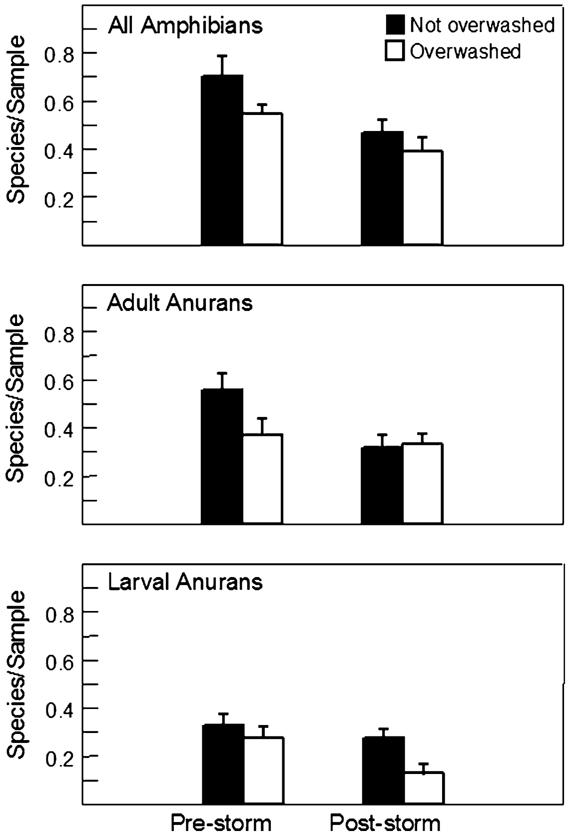

Fig. 5 Species richness/total number of samples across all visits for all amphibians, adult anurans, and larval anurans at 28 wetlands at St. Marks National Wildlife Refuge, Florida pre- and post-storm at overwashed and non-overwashed wetlands

sample in wetlands with and without fish (F = 0.13, $P = 0.72$, df = 1), in wetlands that did or did not dry (F = 2.01, $P = 0.17$, df = 1), and no significant interaction effect (F = 0.67, $P = 0.42$, df = 1).

We found no clear pattern between amphibian community structure and specific conductance. Wetlands with the greatest conductance (denoted by larger circles) grouped prominently in the center of the MDS, whereas less conductive wetlands (denoted by smaller circles) were scattered throughout (Fig. 6a). Relative to the distribution of all wetlands, the compact grouping of the most conductive sites is indicative of a homogenized amphibian community. The presence of fish was correlated with amphibian community structure as can be seen in the left to right break of wetlands containing fish and those without (Fig. 6b). Further, similarity values of amphibian communities in fishless wetlands were higher ($\bar{x}$ similarity = 47.1,

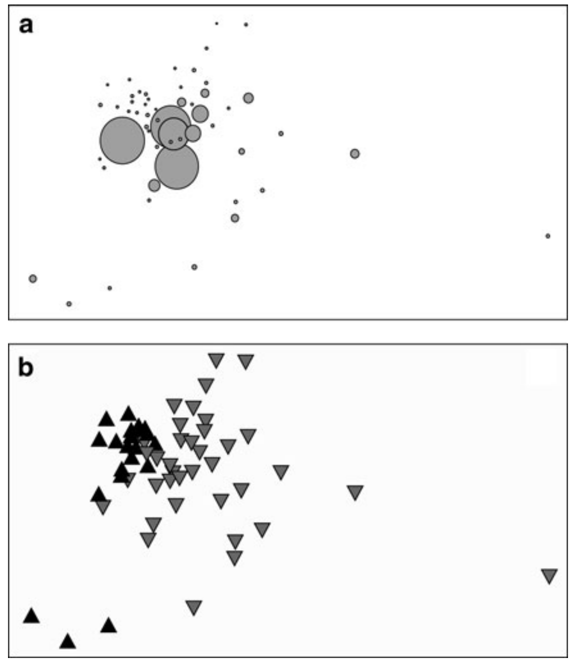

Fig. 6 Multidimensional scaling of amphibian communities observed at St. Marks National Wildlife Refuge, Florida before and after storm surge overwash from Hurricane Dennis. **a** *Superimposed circles* of increasing size with increasing specific conductance. **b** *Black triangles* represent fishless wetlands and *gray inverted triangles* wetlands with fish. Stress value 0.16

SD = 6.52) than amphibian communities in wetlands with fish ($\bar{x}$ similarity = 31.4, SD = 11.3) which is reflected in the tighter grouping of fishless sites in the MDS plot (Fig. 6b). Both wetland types were dominated by *A. gryllus* and *R. sphenocephala*, but share few other species in common (Table 3). There was a negative relationship between fish presence and detection of *Ambystoma talpoideum*, *Bufo quercicus, Hyla femoralis*, *Hyla gratiosa*, and *P. ornata*. In contrast, *Notophthalmus viridescens* and *Rana grylio* were more commonly encountered with fish (Table 3).

Discussion

Wetlands at St. Marks National Wildlife Refuge flooded by storm surge overwash from Hurricane Dennis showed substantial changes in water chemistry from the pre-storm condition. Overwashed wetlands experienced a dramatic initial increase in chloride concentrations which decreased markedly over time

Table 3 Species level contribution to the similarity of amphibian communities in wetlands with and without fish and the dissimilarity between those communities

Species	Percent occurrence		Similarity				Dissimilarity	
			With fish		Without fish			
	With fish	Without fish	$\bar{x}$ (SD)	% Contribution	$\bar{x}$ (SD)	% Contribution	$\bar{x}$ (SD)	% Contribution
Acris gryllus	0.43	0.61	9.44 (0.8)	30	13.8 (1.2)	31	10.5 (1.2)	15
Rana sphenocephala	0.50	0.61	14.08 (1.0)	44	14.9 (1.3)	34	9.9 (1.1)	14
Hyla femoralis	0.08	0.37			6.93 (1.1)	16	7.9 (1.1)	11
Rana grylio	0.33	0.04					6.7 (1.0)	10
Pseudacris ocularis	0.05	0.18	5.7 (0.7)	18	1.97 (0.3)	4	5.8 (0.5)	8
Hyla gratiosa	0.01	0.25			3.73 (0.8)	8	5.1 (1.1)	7
Ambystoma talpoideum	0.01	0.20					4.2 (0.7)	6
Bufo terrestris	0.08	0.07					3.1 (0.5)	5
Notophthalmus viridescens	0.12	0.00					2.4 (0.5)	3
Siren spp.	0.04	0.10					2.3 (0.5)	3
Rana catesbeiana	0.08	0.03					2.0 (0.5)	3
Bufo quercicus	0.02	0.08					1.7 (0.5)	3
Hyla cinerea	0.06	0.01					1.5 (0.3)	2

Species are ordered based on their contribution to dissimilarity

after the storm, but none of the wetlands returned to their pre-storm chloride levels during the study period, even the three sampled 33 months post-storm in April 2008 (Fig. 2). Although the salinity of overwashed wetlands remained elevated above pre-storm levels for over a year, there was no detectable correlation of increased specific conductance with amphibian species richness or community structure in any of the wetlands. Apparently this suite of amphibian species can tolerate the elevated salinity levels we observed in this study. Amphibian species of the southeastern United States Coastal Plain may have an evolutionary history with, or local adaptation to, occasional exposure to brackish water and thus may be better able to cope with increases in salinity than some inland vernal pool species (Karraker et al. 2008; Sanzo and Hecnar 2006). However, we did not quantify abundance of individuals, survival, growth rates, or recruitment of metamorphosing individuals, which may have been affected by changes in salinity.

The resilience of amphibian communities in this study to hurricane storm surge is within the range of effects of hurricanes on amphibians demonstrated in previous studies. The effects of hurricanes on amphibians have primarily been studied in terrestrial species and have demonstrated varied effects including decreases in abundance (Schriever et al. 2009; Vilella and Fogarty 2005), no change in species occurrence or population abundance (Hawley 2006), and increases in abundance (Vilella and Fogarty 2005; Woolbright 1996). One previous study demonstrated that after hurricanes the change in salinity varied significantly in wetland areas adjacent to terrestrial amphibian surveys at seven localities in Louisiana, but across all localities the responses of amphibian communities appeared similar with decreased abundance, decreased species diversity, and increased evenness (Schriever et al. 2009).

The cycling of water through the wetlands is not clearly understood and probably differs among the individual wetlands (Whitney et al. 2004). For some of the wetlands rainwater is clearly the only source of recharge; these wetlands are completely dry during extended periods of low or no rainfall. Other wetlands, such as Jennifer's Sink, have a direct connection to groundwater and rarely, if ever, dry completely. Several of the wetlands sampled are intermediary between these extremes, possibly having a connection with the local water table during wet conditions and moving toward a perched water table during dryer conditions. Regardless of the hydrology of the individual wetlands, the only likely process for removal of chloride is movement of salty water through the wetland substrate and into the groundwater system with subsequent replacement by fresh rainwater.

Jennifer's Sink, Otter Lake, and Corner Pond were not directly exposed to storm surge overwash, but nonetheless showed a small increase in chloride concentration that was first detected about 1 year after Hurricane Dennis (Fig. 2). This chloride increase could result from seepage of saltwater into the ground, with subsequent movement through the shallow subsurface and into these wetlands. The relatively slow movement of groundwater would account for the observed delay in the increase in salinity at these three wetlands, which is in stark contrast with the immediate response observed in the overwashed ponds. The relatively small increase in chloride concentrations suggests that saltwater intrusion into the surficial aquifer was diluted by the large volume of fresh groundwater present.

We did not find evidence that amphibian species richness in wetlands in this study was correlated with several factors already established as important in structuring amphibian assemblages: presence of fish, pond drying, pH, and rainfall (Cortwright and Nelson 1990; Eason and Fauth 2001; Wellborn et al. 1996). Although the number of amphibian species did not differ between wetlands with and without fish, the species composition of the amphibian community did differ among these wetlands with a specific suite of species tending to occur in wetlands without fish. No significant effect of rainfall on amphibian species richness was detected within each sampling interval (month), however, our dataset was limited to less than 5 years. Previous studies have shown a longer time series may be necessary to understand the influence of weather patterns on amphibians (Daszak et al. 2005). Significantly fewer amphibian species were detected post-storm than before, both in overwashed and non-overwashed wetlands. Although this could be due to a large-scale effect of the hurricane on amphibians at SMNWR, we suggest it is more likely due to two factors unrelated to the storm: the post-storm sampling interval was shorter than the pre-storm sampling interval, resulting in less chance of detecting rare species, and rainfall post-storm (2006) was lower than in any of the 3 years prior to the storm.

Amphibian communities in wetlands at St. Marks National Wildlife Refuge appear to be resilient to the effects of hurricane storm surge overwash and the resulting increased salinity. Our results indicate that previously isolated wetlands flooded by storm surge will continue to support amphibian populations.

Acknowledgements We thank James Burnett, Joe Reinman and Michael Keys of SMNWR. For assistance with amphibian field sampling we thank Steve Johnson, Linda Casey, Julia Earl, Denise Gregoire, Clint Smith, Andy Sheldon, Linda Sheldon, David Cook, Kevin Enge, Matthew Aresco, and Pierson Hill. Sue Hartley, Dan Calhoun, Mindi Dalton, Alan Cressler, and Deedee Black assisted with water sampling. C. Kenneth Dodd, Jr., Erin Muths, Steve Lawrence, and Matthew Aresco provided comments on an earlier draft of the manuscript. This research was funded by the USGS Amphibian Research and Monitoring Initiative and a USGS Bureau Venture Capital Grant to MSG and WBH. Research was conducted under SMNWR Special Use Permit 41640-02011 and USGS IACUC Protocol # 2006-04.

References

Barichivich WJ (2003) Appendix IV: guidelines for building and operating remote field recorders. In: Dodd CK Jr (ed) Monitoring amphibians in Great Smoky Mountains National Park. USGS Circular No. 1258, pp 87–94

Christman SP (1974) Geographic variation for salt water tolerance in the frog *Rana sphenocephala*. Copeia 1974:773–778

Christy MT, Dickman CR (2002) Effects of salinity on tadpoles of the green and golden bell frog (*Litoria aurea*). Amphibia-Reptilia 23:1–11

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143

Clarke KR, Gorley RN (2006) PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth

Cortwright SA, Nelson CE (1990) An examination of multiple factors affecting community structure in an aquatic amphibian community. Oecologia 83:123–131

Daszak P, Scott DE, Kilpatrick AM, Faggioni C, Gibbons JW, Porter D (2005) Amphibian population declines at the Savannah River Site are linked to hydroperiod, not chytridiomycosis. Ecology 86:3232–3237

Dodd CK Jr, Barichivich WJ, Johnson SA, Staiger JS (2007) Changes in a Florida panhandle Gulf Coast herpetofaunal community over a 28-year period. Am Midl Nat 158:29–48

Dunson WA (1977) Tolerance to high temperature and salinity by tadpoles of the crab-eating frog, *Rana cancrivora*. Copeia 1977:375–378

Eason GW, Fauth JE (2001) Ecological correlates of anuran species richness in temporary pools: a field study in South Carolina, USA. Israel J Zool 47:346–365

Fishman MJ, Friedman LC (1989) Methods for determination of inorganic substances in water and fluvial sediments, Book 5, Chap. A1. U.S. Geological Survey Techniques of Water-Resources Investigations, 545 p

Florida Division of Emergency Managmement (2002) LiDAR database. Tallahassee, FL. Available onine: http://www.floridadisaster.org/gis/LiDAR/
Gomez-Mestre I, Tejedo M (2003) Local adaptation of an anuran amphibian to osmotically stressful environments. Evolution 57:1889–1899
Goodsell JA, Kats LB (1999) Effect of introduced mosquitofish on pacific treefrogs and the role of alternative prey. Conserv Biol 13:921–924
Gordon MS, Schmidt-Nielsen K, Kelly HM (1961) Osmotic regulation in the crab-eating frog (*Rana cancrivora*). J Exp Biol 38:659–678
Gregoire DR, Gunzburger MS (2008) Effects of predatory fish on survival and behavior of larval Gopher Frogs (*Rana capito*) and Southern Leopard Frogs (*Rana sphenocephala*). J Herpetol 42:97–103
Gunzburger MS (2007) Evaluation of seven aquatic sampling methods for amphibians and other aquatic fauna. Appl Herpetol 4:47–63
Gunzburger MS, Travis J (2004) Evaluating predation pressure on green treefrog larvae across a habitat gradient. Oecologia 140:422–429
Gunzburger MS, Dodd CK Jr, Barichivich WJ, Staiger JS (2005) Southeast amphibian research and monitoring initiative 2005 annual report. United States Geological Survey, Florida Integrated Science Center, Gainesville FL, USA
Hawley TJ (2006) Alterations in frog assemblages after Hurricane Iris in Belize. Herpetol Rev 37:407–411
Johnson SA, Barichivich WJ (2004) A simple technique for trapping *Siren lacertina, Amphiuma means*, and other aquatic vertebrates. J Freshwater Ecol 19:263–269
Jones MV, West RJ (2005) Spatial and temporal variability of seagrass fishes in intermittently closed and open coastal lakes in southeastern Australia. Estuar Coast Shelf Sci 64:277–288
Karraker NE (2007) Are embryonic and larval green frogs (*Rana clamitans*) insensitive to road deicing salt? Herpetol Conserv Biol 2:35–41
Karraker NE, Gibbs JP, Vonesh JR (2008) Impacts of road deicing salt on the demography of vernal pool-breeding amphibians. Ecol Appl 18:724–734
Katz U (1973) Studies on the adaptation of the toad *Bufo viridis* to high salinities: oxygen consumption, plasma concentration, and water content of the tissues. J Exp Biol 58:785–796
Konno N, Hyodo S, Matsuda K, Uchiyama (2006) Effect of osmotic stress on expression of a putative facilitative urea transporter in the kidney and urinary bladder of the marine toad *Bufo marinus*. J Exp Biol 209:1207–1216
Loope L, Duever M, Herndon A, Snyder J, Jansen D (1994) Hurricane impacts on uplands and freshwater swamp forest. Bioscience 44:238–246
MacKenzie DI, Royle JA (2005) Designing occupancy studies: general advice and allocating survey effort. J Appl Ecol 42:1105–1114
Milto KD (2008) Amphibians breed in the Baltic Sea. Russ J Herpetol 15:8–10
Morey SL, Baig S, Bourassa MA, Dukhovskoy DS, O'Brien JJ (2006) Remote forcing contribution to storm-induced sea level rise during Hurricane Dennis. Geophys Res Lett 33:L19603
Neill WT (1958) The occurrence of amphibians and reptiles in saltwater areas, and a bibliography. Bull Mar Sci Gulf Carib 8:1–97
Odum WE (1988) Comparative ecology of tidal freshwater and salt marshes. Ann Rev Ecol Syst 19:147–176
Piscart C, Lecerf A, Usseglio-Polatera P, Moreteau J, Beisel J (2005) Biodiversity patterns along a salinity gradient: the case of net spinning caddisflies. Biodivers Conserv 14:2235–3349
Roman CT, Aumen NG, Trexler JC, Fennema RJ, Loftus WF, Soukup MA (1994) Hurricane Andrew's impact on freshwater resources. Bioscience 44:247–255
Ruibal R (1959) The ecology of a brackish water population of *Rana pipiens*. Copeia 1959:315–322
Sanzo D, Hecnar SJ (2006) Effects of road de-icing salt (NaCl) on larval wood frogs. Environ Pollut 140:247–256
Schriever TA, Ramspott J, Crother BI, Fontenot CL Jr (2009) Effects of Hurricanes Ivan, Katrina, and Rita on a southern Lousisiana herpetofauna. Wetlands 29:112–122
Semlitsch RD, Bodie JR (1998) Are small, isolated wetlands expendable? Conserv Biol 12:1129–1133
Smith LL, Barichivich WJ, Staiger JS, Smith KG, Dodd CK Jr (2006) Detection probabilities and site occupancy estimates for amphibians at Okefenokee National Wildlife Refuge. Am Midl Nat 155:149–161
Snodgrass JW, Komoroski MJ, Bryan AL Jr, Burger J (2000) Relationships among isolated wetland size, hydroperiod, and amphibian species richness: implications for wetland regulations. Conserv Biol 14:414–419
SYSTAT Software, Inc (2005) SYSTAT 11 manual. Point Richmond, CA
Taylor EH (1943) A new ambystomid salamander adapted to brackish water. Copeia 1943:151–156
U.S. Geological Survey (1997 to present) National field manual for the collection of water-quality data, Book 9, Chaps. A1–A9. U.S. Geological Survey Techniques of Water-Resource Investigations. http://pubs.water.usgs.gov/twri9A
Vilella FJ, Fogarty JH (2005) Diversity and abundance of forest frogs (Anura: Leptodactylidae) before and after Hurricane Georges in the Cordillera Central of Puerto Rico. Carib J Sci 41:157–162
Walker LR, Lodge DJ, Brokaw NV, Waide RB (1991) An introduction to hurricanes in the Caribbean. Biotropica 23:313–316
Wellborn GA, Skelly DK, Werner EE (1996) Mechanisms creating community structure across a freshwater habitat gradient. Ann Rev Ecol Syst 27:337–363
Whitney E, Means DB, Rudloe A (2004) Priceless Florida: natural ecosystems and native species. Pineapple Press, Sarasota, p 423
Woolbright LL (1991) The impact of hurricane Hugo on forest frogs in Puerto Rico. Biotropica 23:462–467
Woolbright LL (1996) Disturbance influences longterm population patterns in the Puerto Rican frog, *Eleutherodactylus coqui* (Anura: Leptodactylidae). Biotropica 28:493–501
Wright P, Anderson P, Weng L, Frick N, Wong WP, Ip YK (2004) The crab-eating frog, *Rana cancrivora*, up-regulates hepatic carbamoyl phosphate synthetase I activity and tissue osmolyte levels in response to increased salinity. J Exp Zool 301A:559–568