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The effect of Hurricane Katrina on nekton communities in the tidal freshwater marshes of Breton Sound, Louisiana, USA

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A B S T R A C T

Hurricanes are climatically-induced resource pulses that affect community structure through the combination of physical and chemical habitat change. Estuaries are susceptible to hurricane pulses and are thought to be resilient to habitat change, because biotic communities often return quickly to pre-hurricane conditions. Although several examples provide evidence of quick recovery of estuarine nekton communities following a hurricane, few studies take place in tidal freshwater habitat where physical habitat effects can be extensive and may not be readily mitigated. We examined nekton communities (density, biomass, α and β diversity, % occurrence by residence status) in tidal freshwater marshes in Breton Sound, Louisiana, before and after a direct hit by Hurricane Katrina (2005). Vegetative marsh loss in the study area was extensive, and elevated salinity persisted for almost 6 months. Post-Katrina nekton density and biomass increased significantly, and the nekton community shifted from one of tidal freshwater/resident species to one containing brackish/migrant species, many of which are characterized by pelagic and benthic life history strategies. By spring 2007, the nekton community had shifted back to tidal freshwater/resident species, despite the enduring loss of vegetated marsh habitat.

1. Introduction

Resource pulses are defined as rare, brief, and intense phenomena that cause significant ecosystem perturbation, including change in biotic community structure (Yang et al., 2008). Many resource pulses are driven by climatic events, and the corresponding change in community structure can be direct or indirect, result either from the pulsed delivery of resources, physical disturbance, or both, and persist for varying lengths of time (Yang et al., 2008). Understanding the effects of this pulse-induced change on community structure, including its persistence through time, will provide information on ecosystem resiliency (Switzer et al., 2006).

Hurricanes are examples of climatically-induced pulses that result in periodic and often intense ecosystem disturbance. Landfalling hurricanes affect biotic community structure in both terrestrial and aquatic ecosystems through the import of chemical and biological resources and direct physical habitat change (Cahoon, 2006; Yang et al., 2008). For example, hurricanes have direct and indirect effects on tropical forest communities both from the input of nutrients from leaf fall as well as the physical change in forest structure from tree falls (Yang et al., 2008). Because of their position in the landscape, estuaries are especially vulnerable to hurricane-induced pulse events. When a hurricane makes landfall, it not only brings an intense pulse of wind and precipitation from the storm system but also a large storm surge that inundates the estuary with sea water, resuspended sediments, and nutrients (Nyman et al., 1995; Cahoon, 2006). This combination of factors causes physical and chemical changes to the estuary that affect nekton communities (Greenwood et al., 2006; Stevens et al., 2006; Paperno et al., 2006; Switzer et al., 2006). Aquatic habitats have shown resilience to hurricane effects, with nekton communities returning to pre-hurricane conditions in a matter of weeks to months (Paperno et al., 2006). However, many of these studies in estuarine habitats take place in brackish and saline zones or in lagoonal estuaries, where hurricane effects are largely chemical (e.g. hypoxia, salinity effects) and quickly mitigated (Switzer et al., 2006). In contrast, relatively little is known about the influence of hurricanes on nekton communities in tidal freshwater areas where the physical habitat disturbance to vegetated marsh habitat can be extensive and may not be readily mitigated.

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We measured the immediate and enduring effects of hurricanes on nekton community structure in tidal freshwater habitat of the upper Breton Sound estuary, Louisiana. The objective was to document effects of a direct hit from a major hurricane on nekton communities in tidal freshwater, 6-months and 18-months post-hurricane. Here, we describe the pre- and 6-month and 18-month post-hurricane community structure of estuarine nekton during annual spring riverine flooding events in upper Breton Sound estuary.

2. Study area

We studied effects of hurricane passage on nekton communities by comparing nekton assemblages before (spring 2005) and after (spring 2006 and 2007) the passage of Hurricane Katrina in upper Breton Sound estuary, Louisiana (Fig. 1). Breton Sound is a 271,000 ha estuary in the Mississippi River deltaic plain in southeast Louisiana. It is microtidal and consists of bays, lakes, bayous, canals, and fresh, intermediate, brackish, and saline marsh types. The upper estuary is separated into east and west components, geographically and hydrologically, by Bayou Terre aux Boeufs, a relic Mississippi River distributary. Dominant emergent vegetation in upper basin marshes consists of *Spartina patens* (saltmeadow cordgrass) and *Schoenoplectus americanus* (chairmaker's bulrush).

We studied the effects of the hurricane pulse on nekton communities in emergent marshes subject to flooding (inflow marshes) from the Caernarvon Freshwater Diversion structure (Caernarvon; Fig. 1). The structure is located at the head of Breton Sound and is capable of delivering substantial amounts of fresh water (227 $m^3\ s^{-1}$) and allochthonous sediments (4.5×10^8 kg $year^{-1}$) from the Mississippi River to the basin (Snedden et al., 2007a). Yearly experimental high-flow freshwater pulsing of the diversion structure began in spring 2001 to simulate seasonal flood-pulse events. Pulses release periodic large fluxes of Mississippi River water into the basin and are capable of inundating upper basin marshes (~5700 ha) for several days (Snedden et al., 2007a). Without the riverine pulse, inundation of upper basin marshes is dominated by meteorological forcing (Snedden et al., 2007b).

Hurricane Katrina made its first Louisiana landfall on August 29, 2005 in Plaquemines Parish just south of Buras, Louisiana as a strong Category 3 (Saffir–Simpson scale, maximum = Category 5) storm, with sustained wind speeds of approximately 205 km h^{-1} (57 m s^{-1}) and a central pressure of 920 mb (92,000 Pa). The northerly storm track of Katrina took it directly across Breton Sound estuary on its way to a second northern Gulf coast landfall near the Louisiana–Mississippi border (Fig. 1). Sustained wind speed when the storm crossed Breton Sound estuary was estimated at 122–194 km h^{-1} (34–54 m s^{-1}). Storm surges from 5 to 6 m were recorded at the mouth of the Mississippi River, across Breton Sound, and into New Orleans, LA (Graumann et al., 2005; Hsu et al., 2006; Fritz et al., 2007). Hurricane Rita, which made landfall approximately 1 month later (September 24, 2005) along the Louisiana/Texas border as a Category 3 (Saffir–Simpson scale) hurricane, did not directly impact Breton Sound like Hurricane Katrina. However, the westerly track of this storm across the Gulf of Mexico brought an additional storm surge (>1 m) to Breton Sound (Day et al., 2007). The physical effects of Hurricane Katrina on Breton Sound were stark, with massive loss of emergent marsh habitat, especially in the upper basin (~106 km^2; Barras, 2007), and the storm converted large areas of vegetated marsh into shallow open lakes with mud bottoms and large balls of rolled detrital wrack (Fig. 2).

3. Methods

Storm surge effects in upper Breton Sound were determined from data obtained from the United States Geological Survey (USGS) National Water Information System (http://waterdata.usgs.gov/usa/nwis/). Specifically, we obtained salinity (practical salinity units; psu) and water level (m NAVD 88) data for upper Breton Sound from 2005 to 2007 from the station at Reggio Canal, near Wills Point, Louisiana (USGS 073745253; Fig. 1B).

We collected nekton samples in vegetated marsh habitat through winter–spring pulsed freshwater releases in 2005–2007. Sampling occurred in flooded marshes directly downstream from the Caernarvon Freshwater Diversion (inflow marshes). In 2005, nekton sampling occurred from February 14 to 28 and March 12 to 28. Sampling in 2006 occurred from March 22 to 28 and April 18 to 23. Due to equipment and logistical problems nekton were sampled in 2007 only on March 24–25. Discharge from Caernarvon was similar during each sampling period (~184 $m^3\ s^{-1}$).

Sites were sampled with a 1.14 m cylindrical (1 m^2) drop sampler. At each site, nekton were collected and environmental data were recorded. A complete description of the sampling methodology, including laboratory processing of samples is reported in Piazza and La Peyre (2007).

4. Data analysis

Nekton and environmental data were tested for normality with the Shapiro–Wilks test. Nekton density and biomass were log transformed to achieve normality. Data are reported as mean ± SE, and significance level is reported at $\alpha = 0.05$, unless indicated differently.

4.1. Environmental conditions

Differences in discrete environmental variables (salinity, dissolved oxygen, temperature, stem density, turbidity, water depth) were compared by year using multivariate analysis of variance (MANOVA). Significant MANOVA models were investigated further with univariate ANOVA.

4.2. Nekton density, biomass, diversity

ANOVA (PROC MIXED) was used to test for statistical differences in density, biomass, and diversity among years. Difference in least squared means was used to compare density and diversity among years. Alpha (α) diversity was calculated with both Shannon–Wiener diversity (H') and evenness (E), and Sorenson's Similarity Index (C_s) was used to compare beta (β) diversity among years (Magurran, 1988).

4.3. Nekton communities

To determine the effect of the hurricane pulse on estuarine nekton communities, each species was assigned a residence status based on natural history characteristics obtained from the literature and fishbase (Froese and Pauly, 2008; http://www.fishbase.org). Tidal freshwater/resident (T/R) species were defined as those that spend their entire life cycle within the estuary and are abundant in the tidal freshwater portion of the estuary. This group include species that are both stenohaline (e.g. *Lepomis macrochirus*) and euryhaline (*Poecilia latipinna*), however, most species are closely tied to the flooded marsh surface and exhibit small home ranges (Kneib, 2000; Piazza and La Peyre, 2007). Brackish/migrant (B/M) species were defined as those that spend at least a portion or

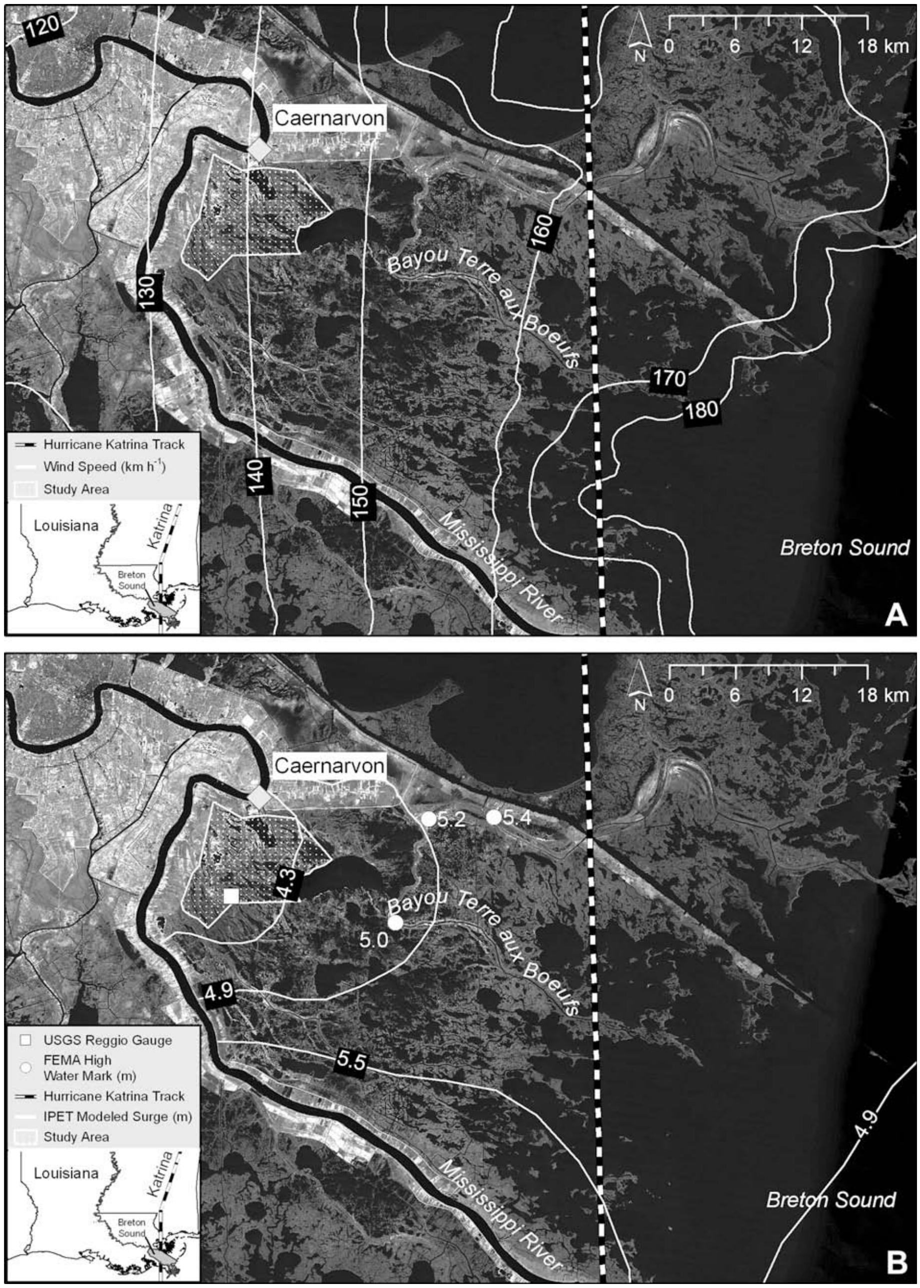

Fig. 1. Maps showing Breton Sound estuary, Louisiana and (A) wind speed (km h^{-1}) and (B) storm surge height (m) during Hurricane Katrina. The white stippled area in both maps delineates the boundary of the tidal freshwater marshes where nekton were sampled during this study. The storm track of Hurricane Katrina is shown as a dashed black and white line on both the maps and inset. The square on panel B indicates the position of the United States Geological Survey (USGS) National Water Information System station at Reggio Canal, near Wills Point, Louisiana (USGS 073745253). Wind speed data are from NOAA, Atlantic Oceanographic and Meteorological Laboratory (http://www.aoml.noaa.gov/hrd/Storm_pages/katrina2005/wind.html). Water level contours are based on an ADCIRC coastal storm surge model and are modified from (US Army Corps of Engineers, 2006; https://ipet.wes.army.mil) and Keim and Muller (in press). Water level points (white dots) are observed high water marks from the Federal Emergency Management Agency (FEMA, 2006, map B-12). Background image (Landsat Thematic Mapper 5) is from October 28, 2006.

all of their life cycle in the estuary, but typically in more saline water than tidal freshwater species (Kneib, 2000). Migrating members of this group spawn on the continental shelf and migrate into the estuary to spend the juvenile portion of their life cycle. Members of this group that spend their entire life cycle in the estuary spawn in polyhaline waters but may move into fresher portions of the estuary. Members of this group were generally either pelagic (e.g. *Anchoa mitchilli*) or bottom-oriented (e.g. *Gobiosoma bosc*) and less associated with the marsh surface than T/R species.

5. Results

5.1. Environmental characteristics

A strong pulse of marine water was propagated into upper Breton Sound estuary, during and immediately following passage of Hurricane Katrina (Fig. 3). During this time, the water level and salinity were approximately 3 m and 15 psu, respectively, at the Reggio gauge. After Katrina, storm surge estimates > 5 m were documented in Breton Sound by the US Federal Emergency

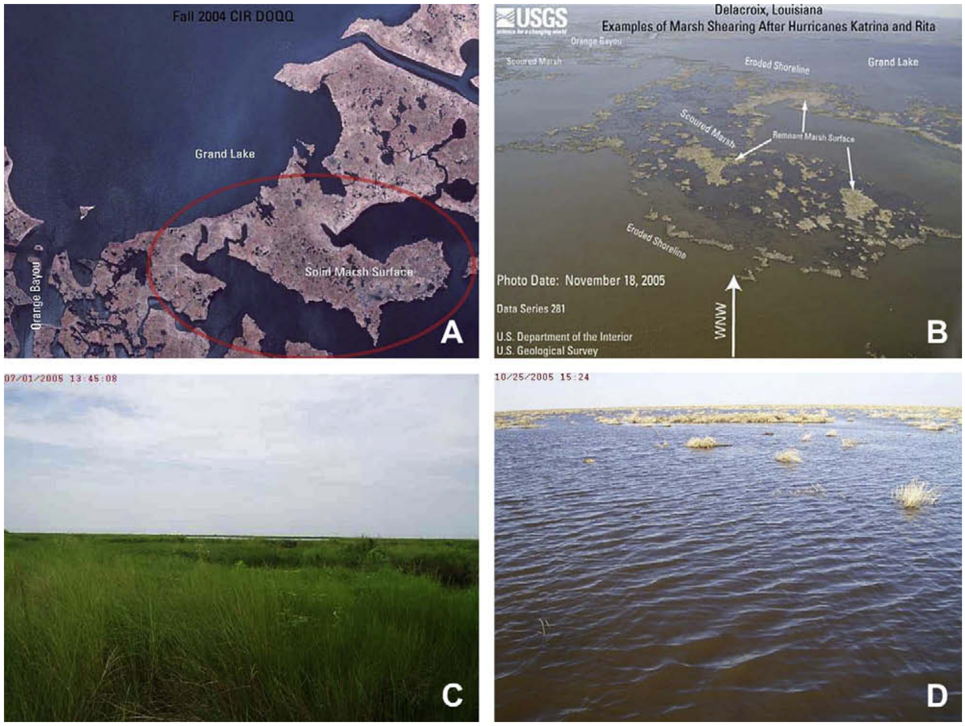

Fig. 2. Photographs showing the physical habitat change due to Hurricane Katrina. The first set of photographs (A,B) illustrates the large-scale vegetated marsh loss that occurred in Breton Sound estuary as a result of Hurricane Katrina. The area inside the red oval in Fig. 2A is the area in Fig. 2B. Also shown is a small-scale illustration of the pre- (C) and post-hurricane (D) condition of the marshes sampled during this study. Photos A and B are taken from Barras (2007), and photos C and D are courtesy of S. Piazza, US Geological Survey, National Wetlands Research Center, Coastal Restoration Field Station, Baton Rouge, LA.

Management Agency (FEMA, 2006; Fig. 1). Water levels returned to pre-hurricane conditions relatively quickly; however salinity in the upper estuary remained elevated above 3 psu into January 2006, due to the additive effects of Hurricane Rita and a period of moderate to severe drought that began in early 2005 and persisted through the end of the year (US Drought Monitor, 2005; http://www.drought.unl.edu/).

By the time we sampled nekton in late March 2006, environmental conditions had returned to levels typical of early spring in upper Breton Sound (Lane et al., 2007; Table 1). However, three trends deserve particular attention. Mean turbidity doubled between 2005 and 2006. Additionally, mean water depth increased and mean vegetative cover decreased between 2005 and 2007 (Table 1).

5.2. *Nekton density, biomass, diversity, and communities*

A total of 20,057 individuals were collected over the 3 year study period. Nekton density was significantly different by year ($F_{2,274} = 8027$, $p < 0.0003$), with a pronounced increase in 2006 (Fig. 4a). Mean nekton biomass (g m^{-2}; 19.76 ± 1.83 SE, $N = 290$) was also significantly different by year ($F_{2,274} = 7.03$, $p < 0.001$), and followed the same pattern as nekton density. The increase in density during the 2006 sampling year was largely driven by high densities of riverine grass shrimp (*Palaemonetes paludosus*) and opposum shrimp (*Taphromysis bowmani*) in the spring following Hurricane Katrina (Table 2). Although previously not collected from drop samples, *T. bowmani* was caught in most (62%) samples in 2006, and its presence was still significant in spring 2007 (33%; Table 2).

Species richness in upper Breton Sound increased after Hurricane Katrina from 16 taxa spring 2005 to 26 taxa in 2006 and decreased again in 2007 to only 12 taxa (Table 2). This increase in species richness in 2006 was driven by an increase in B/M species in spring 2006 samples. Mean Shannon diversity ($H' = 0.79 \pm 0.02$ SE) and evenness ($E = 0.63 \pm 0.02$ SE) were significantly different by year (H': $F_{2,274} = 12.00$, $p < 0.0001$. E: $F_{2,256} = 15.06$, $p < 0.0001$; Fig. 4b).

Higher numbers of B/M species were caught in the project area after Hurricane Katrina (Fig. 4c). The number of B/M species dropped to pre-storm levels in spring 2007. Resident species persisted through the study period, but the following trends were apparent: (1) densities of *Gambusia affinis* and *Heterandria formosa* decreased post-Katrina; and (2) densities of *Lucania parva* increased post-Katrina. Nekton communities in the first spring (2006) following Hurricane Katrina were less similar ($C_s = 0.57$) to pre-hurricane communities (2005) than those of spring 2007, 18 months post-hurricane ($C_s = 0.71$). Interestingly, nekton communities were least similar between spring 2006 and 2007 ($C_s = 0.53$).

6. Discussion

This study documented higher nekton densities and a shift from a nekton community consisting almost exclusively of tidal freshwater/resident (T/R) species toward one that included a number of brackish/migrant (B/M) species after a direct hit by Hurricane Katrina in August 2005. Differences in nekton density were largely attributed to large catches of *Palaemonetes paludosus* and *Taphromysis bowmani*. *T. bowmani* is a mysid shrimp that was not captured in samples in the spring prior to the storm. The emergence of this species in drop samples, as well as the community shift toward B/M, especially those with pelagic and benthic life history strategies, was likely due to the combination of elevated salinity and the stark loss of vegetated marsh habitat that resulted from the hurricane winds and storm surge. Effects were short lived,

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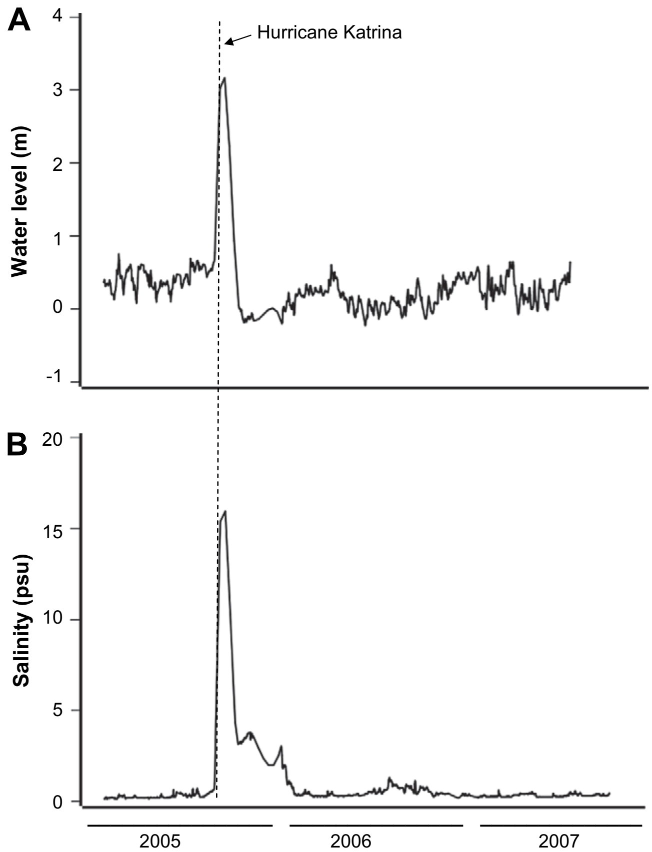

Fig. 3. Hydrographs of continuous (A) water level and (B) salinity from January 1, 2005–December 31, 2007, taken at United States Geological Survey (USGS) National Water Information System station at Reggio Canal, near Wills Point, Louisiana (USGS 073745253). The vertical dashed line marks the passage of Hurricane Katrina.

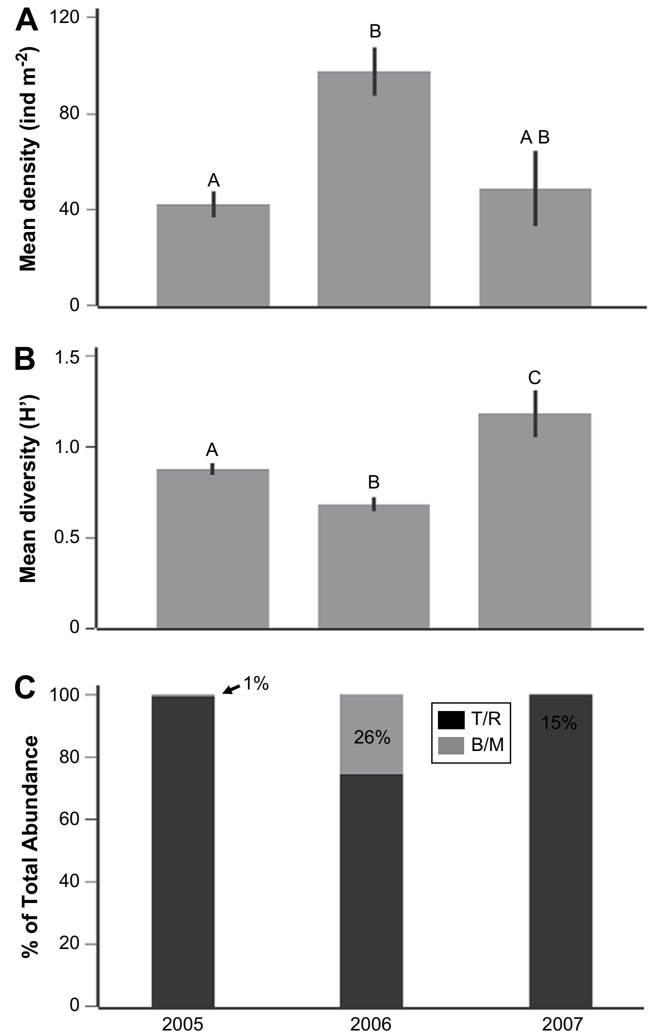

Fig. 4. Mean (±SE) (A) nekton density (ind. m^{-2}), and (B) Shannon–Weiner Diversity (H'), of nekton caught at flooded marsh sampling sites pre- (spring 2005) and post-Hurricane Katrina (spring 2006, 2007). Capital letters denote significant statistical differences ($\alpha = 0.05$) between years. Graph C shows the percentage of total nekton abundance that belonged to either the tidal freshwater/resident group (T/R; black) or the brackish/migrant group (B/M; gray) for the same years. Species were grouped according to salinity tolerance and life history characteristics, and definitions are provided in the text.

as by spring 2007, the nekton community had shifted back to T/R species, and communities were more similar between 2005 and 2007 than between post-hurricane sample dates, despite the lasting loss of vegetated marsh habitat.

6.1. Nekton community change

Increased nekton density post-hurricane was driven by two shrimp species, *Palaemonetes paludosus* and *Taphromysis bowmani*. Although mysid shrimp are not often considered in studies of estuarine nekton, *T. bowmani* was included in the nekton assemblage in this study because it was an important indicator of the habitat change. As with many mysids, *T. bowmani* is an estuarine animal known to occur in large schools (shoals) in a range of shallow open water habitats across a full range of salinities including almost freshwater (Price, 1982). Mysid shrimp generally avoid densely vegetated marshes, even during high flooding (Allen, 1982). Therefore, the increased amount of open water observed

Table 1
Mean (±SE) and range of environmental characteristics (water temperature, salinity, dissolved oxygen, turbidity, vegetative cover, water depth) measured on the flooded marsh surface in upper Breton Sound estuary, Louisiana during nekton sampling in spring 2005–2007 through winter–spring riverine pulse events.

Variable	2005 $N = 141$	2006 $N = 140$	2007 $N = 9$
	Mean ± SE (range)	Mean ± SE (range)	Mean ± SE (range)
Temperature (° C)	17.88 ± 0.31 (10.5–28.1)	21.9 ± 0.44 (13.1–31.3)	17.2 ± 1.08 (13.2–22.4)
Salinity (psu)[1]	0.2 ± 0.01 (0.2–0.7)	0.2 ± 0.00 (0.1–0.3)	0.2 ± 0.01 (0.2–0.3)
Dissolved oxygen (mg l^{-1})	3.8 ± 0.18 (1.0–9.4)	3.5 ± 0.13 (0.5–8.1)	8.5 ± 0.66 (5.8–12.7)
Turbidity (NTU)[2]	15.4 ± 0.77 (0.8–50.0)	30.8 ± 1.32 (10.1–82.5)	9.2 ± 1.53 (5.8–20.0)
Vegetative cover (stems m^{-2})	123.4 ± 12.23 (0.00–618.0)	102.1 ± 15.9 (0.0–1259.0)	15.4 ± 12.45 (0.0–114.0)
Water depth (mm)	254.5 ± 10.3 (26.0–723.0)	283.2 ± 14.8 (29.6–821.8)	369.4 ± 55.64 (141.0–674.0)

[1] psu, practical salinity units.
[2] NTU, nephelometric turbidity units.

Table 2
Mean nekton density (ind m^{-2}) and percent occurrence in drop samples by species pre- (2005) and post-Hurricane Katrina (2006, 2007). Nekton were sampled on the flooded marsh surface in upper Breton Sound estuary, Louisiana during winter–spring riverine pulse events in spring 2005–2007. Residence status classification is as follows: T/R, tidal freshwater/Resident; B/M, brackish/migrant. Definitions for both categories are given in the text.

Species	Common name	Residence status	2005 ($N = 141$)	%	2006 ($N = 140$)	%	2007 ($N = 9$)	%
Fishes								
Heterandria formosa	Least killifish	T/R	14.0 ± 3.74	64	0.1 ± 0.04	6	6.9 ± 4.24	44
Gambusia affinis	Mosquitofish	T/R	5.27 ± 1.05	49	1.4 ± 0.29	36	6.4 ± 3.55	44
Lucania parva	Rainwater killifish	T/R	2.7 ± 0.69	41	8.0 ± 1.15	64	10.0 ± 5.49	100
Poecilia latipinna	Sailfin molly	T/R	0.6 ± 0.13	21	0.3 ± 0.11	9	0.1 ± 0.11	11
Cyprinodon variegatus	Sheepshead minnow	T/R	0.5 ± 0.13	17	0.2 ± 0.07	7	–	0
Fundulus chrysotus	Golden topminnow	T/R	0.1 ± 0.03	8	–	0	–	0
Fundulus pulverous	Bayou killifish	T/R	0.02 ± 0.02	1	0.04 ± 0.02	3	–	0
Lepomis macrochirus	Bluegill	T/R	0.1 ± 0.03	6	0.1 ± 0.05	6	0.4 ± 0.24	33
Lepomis punctatus	Spotted sunfish	T/R	0.02 ± 0.02	2	–	0	0.1 ± 0.11	11
Lepomis microlophus	Redear sunfish	T/R	0.01 ± 0.01	1	0.04 ± 0.02	4	0.7 ± 0.55	22
Lepomis megalotis	Longear sunfish	T/R	–	0	–	0	0.1 ± 0.11	11
Anguilla rostrata	American eel	B/M	0.01 ± 0.01	1	–	0	–	0
Notropis spp.	Shiner	T/R	0.01 ± 0.01	1	–	0	–	0
Micropterus salmoides	Largemouth bass	T/R	–	0	0.01 ± 0.01	1	–	0
Anchoa mitchilli	Bay anchovy	B/M	–	0	0.2 ± 0.07	9	–	0
Citharichthys spilopterus	Bay whiff	B/M	–	0	0.01 ± 0.01	1	–	0
Elops saurus	Ladyfish	B/M	–	0	0.02 ± 0.02	1	–	0
Gobiosoma bosc	Naked goby	B/M	–	0	0.2 ± 0.11	5	–	0
Microgobius gulosus	Clown goby	B/M	–	0	0.05 ± 0.03	3	–	0
Menidia beryllina	Inland silverside	B/M	–	0	0.6 ± 0.14	19	–	0
Membras martinica	Rough silverside	B/M	–	0	0.01 ± 0.01	1	–	0
Micropogonias undulatus	Atlantic croaker	B/M	–	0	0.01 ± 0.01	1	–	0
Syngnathus scovelli	Gulf pipefish	B/M	–	0	0.01 ± 0.01	1	–	0
Brevoortia patronus	Gulf menhaden	B/M	–	0	0.01 ± 0.01	1	–	0
Arius felis	Hardhead catfish	B/M	–	0	0.01 ± 0.01	1	–	0
Crustaceans								
Palaemonetes paludosus	Riverine grass shrimp	T/R	16.8 ± 2.74	77	43.6 ± 6.3	79	19.4 ± 4.94	100
Cambarellus spp.	Crayfish	T/R	1.2 ± 0.17	43	0.13 ± 0.06	7	1.9 ± 1.10	56
Procambarus spp.	Crayfish	T/R	0.9 ± 0.12	40	0.26 ± 0.08	10	1.4 ± 0.47	67
Callinectes sapidus	Blue crab	B/M	0.02 ± 0.02	1	0.5 ± 0.07	34	–	0
Menippe adina	Gulf stone crab	B/M	–	0	0.04 ± 0.02	3	–	0
Taphromysis bowmani	Opposum shrimp	T/R	–	0	41.1 ± 6.97	62	1.4 ± 0.80	33

with the loss of vegetation likely favored assembly and habitat use by mysids, including *T. bowmani*. Assembly pulses and redistribution of shrimp have been shown in past studies to be due to hurricane-induced habitat change and detrital nutrient pulses in both estuarine and stream habitat (Stevens et al., 2006). Additionally, the conversion of habitat to a more pelagic environment with large balls of decomposing marsh wrack favors plankton production and detrital microbes, both important food sources for mysids (Vilas et al., 2008).

In addition to the change in resource availability, it is also possible that the loss of densely vegetated habitat and high turbidity following Hurricane Katrina may have increased the ability of our sampling gear to capture both *Palaemonetes paludosus* and *Taphromysis bowmani*. Gear efficiency can change in a system due to hurricane-induced change (Greenwood et al., 2006). However, results from 2007 show that densities of *P. paludosus* returned to pre-hurricane levels and the density of *T. bowmani* decreased markedly, despite the enduring absence of vegetated marsh habitat. This suggests that, while a temporary increase in trap efficiency may have been a factor, the density pulses of these two animals were more likely driven by the temporary increase in resource availability from decomposing wrack in 2006.

In addition to the emergence of *Taphromysis bowmani*, nekton community change was driven by an increase in B/M species, largely composed of pelagic (*Anchoa mitchilli*, *Elops saurus*, *Brevoortia patronus*, Atherinopsidae) and benthic (*Citharichthys spilopterus*, Gobiidae) species. Most of the pelagic and benthic species that were captured in spring 2006 were not captured in spring 2007. This suggests that the period of elevated salinity following Katrina may have temporarily made upper basin marshes more favorable to B/M species and facilitated their movement into upper estuary areas that are typically fresher. Species redistribution is common with changed physiochemical conditions (Paperno et al., 2006). The sudden influx of new species caused a decrease in species diversity due to a decrease in evenness (Magurran, 1988), a common pattern resulting from disturbance (Paperno et al., 2006; Switzer et al., 2006).

Our study also documented a shift in T/R fish species. Prior to Hurricane Katrina, T/R fishes were dominated by *Heterandria formosa* and *Gambusia affinis*. However, in spring 2006, there was a pronounced decrease in these two species and an increase in *Lucania parva*. This shift in dominance was likely due to the elevated salinities following the storm, because these three species are functionally similar and inhabit similar habitats (Kneib, 2000). While *H. formosa* and *G. affinis* have shown tolerance for high salinity in laboratory experiments, both species are typically found in fresher areas of the estuary (Nordlie and Mirandi, 1996; Nordlie, 2006). In contrast, *L. parva* exhibits a higher salt tolerance and is often found in higher salinity estuarine areas (Nordlie, 2006). This shift in dominance is consistent with resilience theory, which suggests that after a disturbance there will be a dominance shift between functionally similar species with different tolerances for the stressor (Peterson et al., 1998).

6.2. Nekton community recovery and ecosystem resilience

Nekton communities largely returned to pre-storm conditions (i.e. 2005) within 18 months of hurricane passage. These results agree with other studies in estuarine environments that show relatively short effects on biota and community structure and high

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ecosystem resiliency to hurricane pulses (Waide, 1991). These results are particularly interesting because the vegetation density and water level data from 2007 suggest that vegetated marsh habitat either was not recovering or was very slow to recover. Yet, despite the lack of vegetated marsh habitat, the nekton community returned to pre-storm conditions, an unexpected result because many estuarine resident and transient nekton species are critically dependent on the vegetated marsh habitat. However, the effects of marsh loss are often not reflected in abundance of nekton, and this may be due to a temporary increase in marsh-edge habitat that occurs with marsh loss (Chesney et al., 2000).

This relatively quick return to pre-storm conditions may be due to the fact that the nekton community in our study was largely composed of generalist T/R species. In terrestrial systems that receive extreme physical damage, effects on biotic communities are often long-lasting. However, generalist species often remain largely unaffected. For example, in tropical forest ecosystems, insectivorous bird and bat species are often less affected and return to pre-hurricane levels relatively quickly as compared to canopy and frugivorous species (Waide, 1991). This same effect has been shown in bird and moth communities in response to forest clear cutting and other timber management strategies (Chambers et al., 1999; Pearson and Manuwal, 2001; Summerville and Crist, 2002).

This return to pre-storm conditions may also be due to mitigating effects of the Caernarvon freshwater diversion on salinity. The combination of the storm surge and extended drought conditions following the passage of Hurricane Katrina resulted in a period of elevated salinities that persisted for approximately 6 months. This increase in salinity likely expanded the range of favorable habitat for B/M species to upper estuary marshes, while creating unfavorable conditions for T/R species with limited salt tolerance. However, once Caernarvon began discharging riverine water into the basin, prior to our sampling, salinity in upper Breton Sound quickly returned to pre-storm conditions, and salinity conditions were similar to pre-hurricane conditions through 2007. Therefore, the salinity effects from the storm did not persist, and our 2007 results show a consequential disappearance of B/M species and a return of T/R species that declined post-Katrina (*Heterandria formosa*, *Gambusia affinis*) to pre-storm levels.

It is also possible that this relatively rapid return to a pre-storm nekton community by spring 2007 may represent a sampling effect. Sample size during 2007 was very limited ($N = 9$), due to equipment and logistical issues. Additionally, due to differences in timing of the freshwater pulses the sampling dates did not cover the same range of time as 2005 and 2006 samples. Perhaps the lack of B/M species (which were relatively rare) as well as the sharp decrease in *Taphromysis bowmani* in 2007 reflected this limited sampling effort. We know that sampling intensity affects species richness because the probability of capturing rare species increases with sample size (MacArthur and Wilson, 1967; Magurran, 1988). Small sample sizes often do not allow for an adequate spatial or temporal representation of the area being studied (MacArthur and Wilson, 1967). Therefore, it is possible that our results may be biased toward common species in 2007. However, we tested this effect by randomly selecting nine samples from both 2005 and 2006 and comparing them against the 2007 samples. The resulting patterns for nekton abundance, diversity and community change were identical to those we found with the full data set. Therefore, we believe that this relatively rapid return to a pre-storm nekton community by spring 2007 was real and not a sampling effect.

7. Conclusion

This study provides important and rare data regarding the effects of hurricane-induced disturbance on estuarine nekton communities in tidal freshwater areas that experienced extensive and enduring physical habitat effects. In particular, this study documents a certain amount of resilience by the estuarine nekton community in the face of enduring physical habitat change, and short-term chemical changes. Understanding the range of community change and resiliency that is experienced by a system in response to disturbance provides insight into ecosystem function and guides management and restoration of coastal systems.

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