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Benthic infauna are resistant and resilient to hurricane disturbance

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ABSTRACT: Hurricanes disturb marine ecosystems by abrupt changes in storm-surge, erosion, freshwater inflow, material loads, or water quality. Hurricane Harvey (25 August 2017) was a Category 4 storm that entered the south Texas, USA, coast and produced a large flood in San Antonio Bay. Benthic abundance, biomass, and diversity have been measured quarterly at 4 stations beginning in 2004. From July to October 2017, macrobenthos decreased to near zero, likely because salinity and dissolved oxygen approached zero. A bivalve mollusk recruitment event began within 8 mo after the storm and continued to July 2018. These short-term responses showed that benthic communities were initially devastated but recovered in less than 1 yr, indicating resilience. However, modeling based on a 13 yr time series yielded the same trend in community metrics, suggesting that benthos would have declined in fall and increased in spring with or without the storm. The long-term results indicate that seasonal dynamics in benthos provide some resistance as well as resilience to storm disturbance. Storms occur at stochastic geological time scales and shape evolutionary history such that they likely do not cause an enduring, devastating disturbance to benthic communities.

KEY WORDS: Resistance · Resilience · Hurricane Harvey · Flood · Long-term dynamics · Infauna · Diversity · Mollusca

1. INTRODUCTION

Most post-hurricane surveys consider strong storms as natural disasters that cause severe damage to ecosystems (Tilmant et al. 1994, Paerl et al. 2001, Mallin et al. 2002, Wetz & Yoskowitz 2013, Hogan et al. 2020). These studies show that abrupt storm-surge and erosion can cause geomorphological and habitat changes; that the increase in freshwater inflow by large rain events can cause large loads of inorganic and organic material that degrade water quality; and that it is common to observe lowered concentrations of dissolved oxygen (DO) and salinity that can stress estuarine and marine organisms. Certainly, the effects on human-built infrastructure are always damaging in the areas most directly influenced by a large storm (Martínez et al. 2017). However, the natural components of coastal areas have evolved over geological time scales, and it is likely that these environments are shaped by multiple storm effects over long periods of time. In addition, estuarine biota evolved to live in wide-ranging water quality conditions. In temperate latitudes, storms that develop in the tropics are highly seasonal, usually occurring between June and November, with the highest frequency of strong storms in August through October. It is thus possible that these coastal ecosystems and organisms are adapted to the seasonal occurrence of storms, and that many ecosystem components are resistant or resilient to storm effects.

Macrobenthic organisms (small infauna) can help to resolve this question because they are relatively sessile (i.e. they cannot quickly move from the affected area), and are commonly used as bioindicators

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in studies to assess the effects of anthropogenic and natural disturbance on ecosystem health (Dauer 1984, 1993, Borja et al. 2000, Aarnio et al. 2011). Past studies have shown that storms change benthic communities. For example, in the Cape Fear estuary (North Carolina, USA), Hurricane Fran caused a decline in abundance and diversity, and this was thought to result from prolonged periods of fresh conditions and low DO (Mallin et al. 2002). The declines were greater than expected due to seasonal variation alone after Hurricanes Fran, Bertha, and Bonnie, and recovery in Cape Fear occurred by the next spring. However, declines were not as great in Cape Fear after Hurricane Floyd. After Hurricane Fran, oligohaline communities recovered in as little as 3 mo (Mallin et al. 1999). In Chesapeake Bay, benthos abundance and diversity declined after Tropical Storm Agnes, and this was also ascribed to lowered DO and salinity, but recovery did not occur for 2.5 yr (Boesch et al. 1976).

Benthic infaunal dynamics have been studied over long time scales. The eastern Bay of Seine, France, has been exposed to numerous anthropogenic disturbances, yet the benthic community diversity was stable over 28 yr of study (Bacouillard et al. 2020). Other long-term studies documented stable benthic ecological function (as indicated by biological traits of taxa) over 35 yr off the Tyne Estuary coast, UK (Frid & Caswell 2015), and 19 years in the southern North Sea shelf (Shojaei et al. 2021). In contrast, an increase in species numbers and biomass was observed over 50 yr in the Dutch Wadden Sea, likely due to climate change and de-eutrophication (Beukema & Dekker 2020). Long-term climate cycles, such as El Niño (Escobar Briones 2003, Pollack et al. 2011, Francisco & Netto 2020) and the North Atlantic Oscillation (Dippner et al. 2014), are correlated with benthic infaunal diversity and community structure. Warming of coastal waters has also caused northward shifts in benthic species distributions along the US coastline since 1990 (Hale et al. 2017). Seasonality of benthic dynamics has been observed in the Dutch Wadden Sea (Beukema & Dekker 2020), the German Bight (Shojaei et al. 2016), the North Sea (Frid et al. 2009), and Tampa Bay, USA (Santos & Simon 1980). However, the substantial spatial and temporal heterogeneity in drivers and responses indicates that any one environmental driver likely cannot explain long-term benthic dynamics (Zettler et al. 2017).

Benthic studies conducted in Texas (USA) estuaries demonstrate that long-term hydrological cycles, which affect freshwater inflow, also drive water quality (Pollack et al. 2009, Palmer et al. 2011, Paudel & Montagna 2014, Palmer & Montagna 2015, Montagna et al. 2018), can regulate benthic abundance (Pollack et al. 2011, Palmer & Montagna 2015), productivity (Montagna & Li 2010, Kim & Montagna 2012), diversity (Montagna et al. 2002, Van Diggelen & Montagna 2016), and community structure (Montagna & Kalke 1992, 1995, Ritter et al. 2005). The initial assessment after Hurricane Harvey concluded that floods caused an abrupt lowering of salinity and a decrease in DO in San Antonio Bay, leading to an 82% decrease from baseline in macrofauna abundance and a 41% decrease from baseline in macrofauna biomass, which recovered within 5 mo (Patrick et al. 2020). However, does a short-term analysis describe a true departure from baseline? Was this response similar to what might have happened during other past flood events? Archived benthic samples were analyzed to answer these questions. Samples from 13 yr prior to the storm were used to forecast benthic abundance, biomass, and diversity after the storm, and the forecast was compared with actual responses to determine if the decline after Harvey fell within expected bounds of seasonal change or represented a long-term change.

2. MATERIALS AND METHODS

2.1. Field sampling and laboratory analyses

San Antonio Bay, Texas, USA, receives inflow from the Guadalupe River and is thus part of the Guadalupe Estuary. Tidal exchange is mediated by the Matagorda Ship Channel to the north and Aransas Pass to the south. Long-term sampling began in January 1987 with the intent of determining the effects of freshwater inflow on the maintenance of productivity and the sustainability of biodiversity in Texas estuaries (Montagna & Kalke 1992, 1995, Kim & Montagna 2012, Van Diggelen & Montagna 2016). These stations were positioned to capture the signature of major flood events, and Harvey presented a flood that landed in the center of the study design (Fig. 1). Four stations aligned along a salinity gradient were repeatedly sampled: Stn A (28.39352° N, 96.77240° W) is in the upper reach and closest to the Guadalupe River; Stn B (28.34777° N, 96.74573° W) is in mid-bay; Stn C (28.24618° N, 96.76488° W) has more marine influence from Aransas Pass and Cedar Bayou that connect to the Gulf of Mexico; and Stn D (28.30210° N, 96.68435° W) is closest to the marine connection from the Matagorda Ship Channel inlet. Stns C and D are located along the Intracoastal Waterway (Fig. 1).

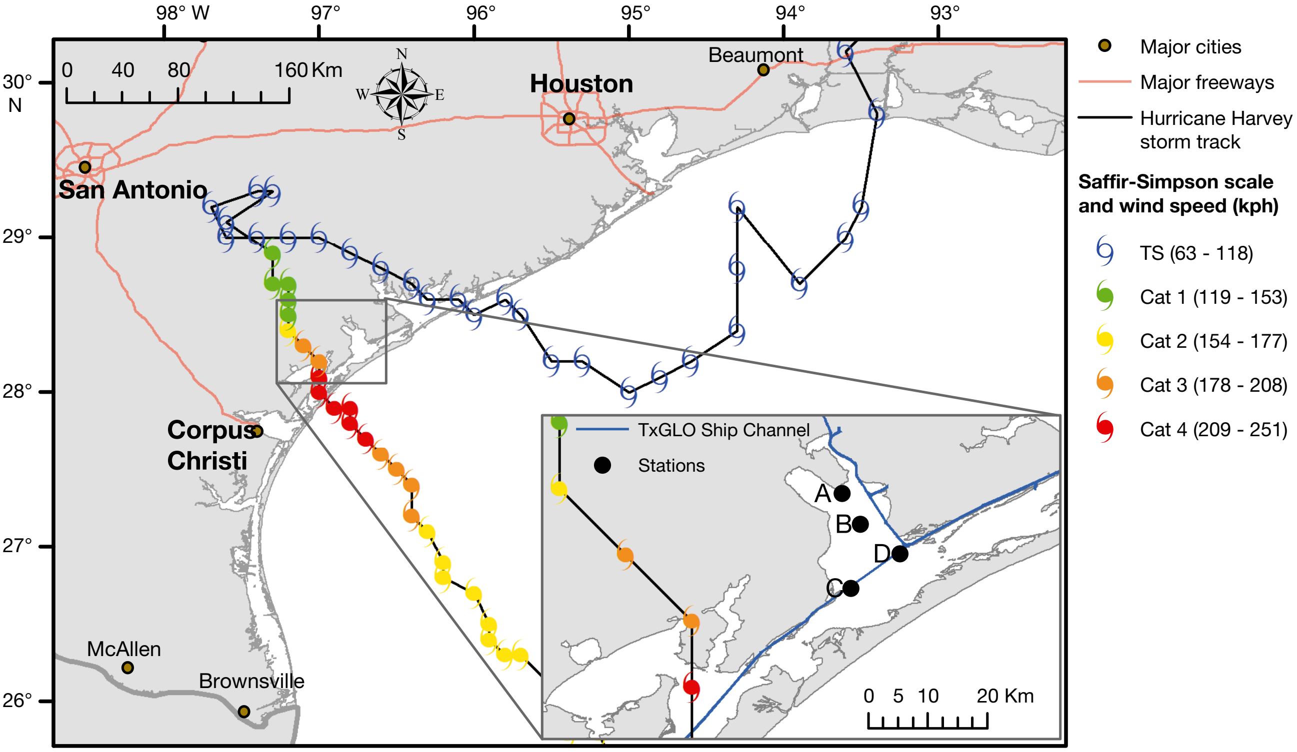

Fig. 1. Hurricane Harvey storm track along the Texas, USA, coast with windspeed. Inset: Station locations in San Antonio Bay; blue line indicates ship channels and Intracoastal Waterway. TS: tropical storm

Macrofauna were sampled with a 6.7 cm diameter core tube (35.4 cm^2 area) to a sediment depth of 10 cm. Three replicates were collected at each station and date within an area of about 2 m^2 considered representative of that station. Organisms were extracted on a 0.5 mm sieve and enumerated to the lowest taxonomic level possible. Bivalvia shells were measured along the longest axis of each shell. Biomass was determined by drying at 55°C for 24 h. Mollusca bodies were removed from shells prior to biomass measurements. A YSI 6600 multiparameter sonde was used to measure salinity, temperature, and DO during each sampling event. The measurements were read from a digital display unit (accuracy and units): temperature (±0.15°C), pH (±0.1 units), DO (±0.2 mg l^{-1}), depth (±0.1 m), and salinity (psu). Salinity was automatically corrected to 25°C. All biological and physical data are publicly available for download (Montagna 2023).

2.2. Climate and hydrology

Climate data were downloaded from the National Oceanic and Atmospheric Administration National Centers for Environmental Information (NOAA NCEI) website on 23 June 2020. Many streamflow stations malfunctioned during the storm, but data did exist for Stn USC00411880 at the Nearby Coleto Creek Reservoir, Texas, USA (28.7156° N, 97.1742° W) and were downloaded for the period 2004 to 2019.

Hydrology data were downloaded from the United States Geological Survey National Water Information System (USGS NWIS) website on 22 June 2020 for Stn 08188810 at the Guadalupe River at SH 35 near Tivoli, Texas, USA (28.47833° N, 96.8628° W).

2.3. Short-term and post-hurricane data analyses

Samples were collected 3 times prior to the storm (February, April, and July 2017) and 3 times after the storm (October 2017, and January and April 2018). This is a 2-way ANOVA design with 4 stations and 6 dates as the main effects. Abundance and biomass were natural-logarithm transformed to meet assumptions of normality of the residuals. Richness did not require transformation. Storm-related changes were assessed using a linear contrast to compare the means before and after the storm. The ANOVA and linear contrast were calculated using SAS software (SAS Institute 2020). An alpha value of 0.05 was used as the significance level.

Community structure of macrofauna species was analyzed by non-metric multidimensional scaling (nMDS) and cluster analysis using a Bray-Curtis similarity matrix (Clarke 1993) with Primer-e software (Clarke & Warwick 2001). Prior to analysis, the data were square-root transformed. Cluster analysis determines how much the station–date combinations resemble each other based on species abundances. The percent resemblance (i.e. either similarity or dissimilarity) can then be displayed on the nMDS plot to elucidate grouping of station–date combinations.

2.4. Long-term and forecasting data analysis

An exponential smoothing model (ESM) was used to create a forecast of benthic data after Hurricane Harvey. ESM is especially useful for fitting non-stationary time series. The ESM is based on the premise that weighted averages of past values can produce good forecasts of the future, the weights should emphasize the most recent data, and the forecast should require only a few parameters. The software package PROC ESM was used in SAS Institute (2017) software (SAS Institute 2017). Previous sampling demonstrates that the river-influenced upper bay (Stns A and B) differs from the marine-influenced lower bay (Stns C and D) (Montagna & Kalke 1992, 1995, Van Diggelen & Montagna 2016). The upper and lower bay were analyzed separately by averaging the 6 replicates for each quarter to create 1 value each for the upper bay with river influence and lower bay with marine influence. The data set was transformed with optimized smoothing weights for seasonal adjustments, i.e. seasonal exponential smoothing. Parameters associated with the forecasting model were optimized by PROC ESM based on the data. Although sampling began in 1987, there was a 4 yr gap with no sampling between 2000 and 2004, so continuous data for 13 yr, from January 2004 to July 2017, were used to create the forecast model, and then responses for October 2017 to October 2018 were extrapolated as forecasted responses. The actual data were plotted against the forecast values to compare the observed versus predicted response.

3. RESULTS

3.1. Short-term response

The immediate effects of the storm in San Antonio Bay were striking (Table 1). Comparing one sampling period before the storm in July to one sampling period after the storm in October, there was a 71% decline in benthos abundance, 82% decline in biomass, and 54% decline in species richness (Table 1A). Stations behaved differently over time for abundance and biomass but not diversity based on the probability level of the interaction test (Table 1B). The responses in the upper bay were distinct from the lower bay for all metrics.

Table 1. Short-term response of benthic metrics. (A) Change from 1 sample period before and after the storm, and 3 sample periods before and after the storm, averaged across all stations. (B) Probability values for the result of the 2-way ANOVA and linear contrasts. Abundance and biomass tests based on natural logarithm (ln)-transformed values. Days are given as prior to (−) or after (+) Hurricane Harvey; Δ: change; Δ%: percent change

(A) Period	Days	Abundance (n m^{-2})	Biomass (g m^{-2})	Richness (n sample^{-1})
05 Jul 2017	−51	15766	12.44	6.17
09 Oct 2017	+45	4633	2.21	2.83
	Δ	−11133	−10.23	−3.34
	Δ%	−71	−82	−54
22 Feb 2017	−184	13386	6.00	5.33
18 Apr 2018	+236	23920	7.35	7.53
	Δ	10534	1.35	2.20
	Δ%	79	23	41

(B) Test	Treatment	df	Abundance (ln n+1 m^{-2})	Biomass (ln g+1 m^{-2})	Richness (n sample^{-1})
ANOVA	Period	5	<0.0001	<0.0001	<0.0001
ANOVA	Station	3	<0.0001	<0.0001	0.0040
ANOVA	Period×Station	15	<0.0001	0.0043	0.0696
Contrast	Before vs After	1	<0.0001	0.0039	<0.0001
Contrast	Upper vs Lower	1	<0.0001	<0.0001	0.0045

The proportional declines decrease when examining these relationships 3 sampling periods before and after the storm (Table 1), but there was still a decline in benthos abundance (Fig. 2A), biomass (Fig. 2B), and diversity (richness) (Fig. 2C) after the storm. Four months prior to the storm in April 2017, abundance was as high as 53 900 ind. m^{-2} and dropped to a high of 9800 ind. m^{-2} in October 2017 and a high of 9400 ind. m^{-2} in January 2018 (linear contrast, $F_{1,48}$ = 68.5, $p < 0.0001$). Biomass decline was not as great, but it did decline from a maximum of 38.6 g m^{-2} in July 2017 to a maximum of 6.1 g m^{-2} in October 2017 and 1.7 g m^{-2} in January 2018 (linear contrast, $F_{1,48}$ = 40.4, $p < 0.0001$). Diversity declined from a maximum of 10 species core^{-1} prior to the storm to 3 species core^{-1} in October 2017 and 7 species core^{-1} in January 2018 (linear contrast, $F_{1,48}$ = 18.5, $p < 0.0001$).

Community structure changed after the storm (Fig. 3), resulting in a gradient across the bay where Stns C and D (with the most marine influence) cluster together and Stns A and B (with the most freshwater influence) cluster together. However, the storm resulted in 2 changes: (1) most of the C and D replicates clustered near the A and B replicates, indicating flood-water influence; and (2) there was greater dispersion among the samples, because there was 69% similarity in community structure prior to the storm, which decreased to 46% similarity after the storm. On average, all species declined about 61%, but 2 species increased after the storm. The polychaete *Spiochaetopterus costarum* increased 750%, and the bivalve mollusk *Mulinia lateralis* increased 276% (Table 2).

Noting clear seasonality, 3 bivalve species (*Macoma mitchelli*, *Mulinia lateralis*, and *Rangia cuneata*) were otherwise generally consistent in composition, abundance, and size distribution prior to the storm (Table 3). There was nearly nothing (i.e. only 1 mollusk found in all samples) in the sediment for the first 5 mo after the storm. By April 2018, there was a recruitment event of small *Mulinia lateralis*. These newly recruited mollusks grew by July 2018 (Fig. 4). Thus, recovery by the benthos was led by a shift from a community dominated by polychaetes to one dominated by mollusks.

3.2. Comparison to long-term forecast

In contrast to the short-term view (Fig. 2), the long-term view (Fig. 5) is quite different. The 13 yr of quarterly benthic data from January 2004 to July 2017 were used to forecast benthic response for the 5 quarters after the storm, i.e. October 2018 to July 2019 and then compared to actual values. If the hurricane had an unusual effect, then the actual values should fall outside the 90% confidence bands.

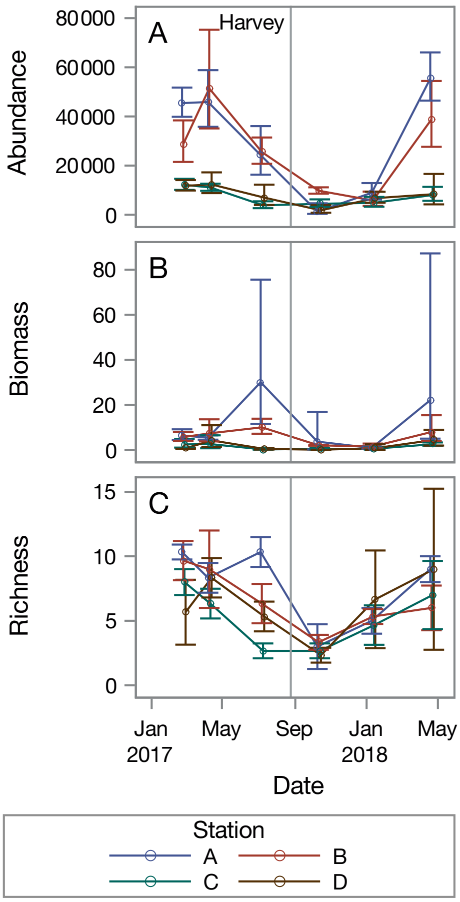

Fig. 2. Benthic infauna metrics at 4 stations (Stns A–D) in San Antonio Bay based on a short-term study (data from Patrick et al. 2020) before and after Hurricane Harvey (vertical line). Data are presented as average of 3 replicates and standard deviation for (A) abundance, (B) biomass, and (C) richness

The exponential smoothing forecast model predicted that benthic abundance, biomass, and diversity after the storm would approach actual values; thus, the long-term view suggests few long-term effects of the storm. The forecast model predicted that benthic abundance would have declined as it does every fall, and then recovered as it does every spring (Fig. 5A,B). The abundance recovery after the storm was greater than expected, but within bounds of error. The forecast model predicted that benthic biomass would have also declined after that time period, with or without the storm (Fig. 5C,D). The spring recruitment was also higher than expected for both abundance and biomass and almost reached beyond the expected bounds. The forecast model predicted that benthic diversity (i.e. richness) would also decline after the storm (Fig. 5E,F). The recovery was as expected, with values that were nearly exactly as predicted. However, even though the number of species were as predicted, the community structure was very different.

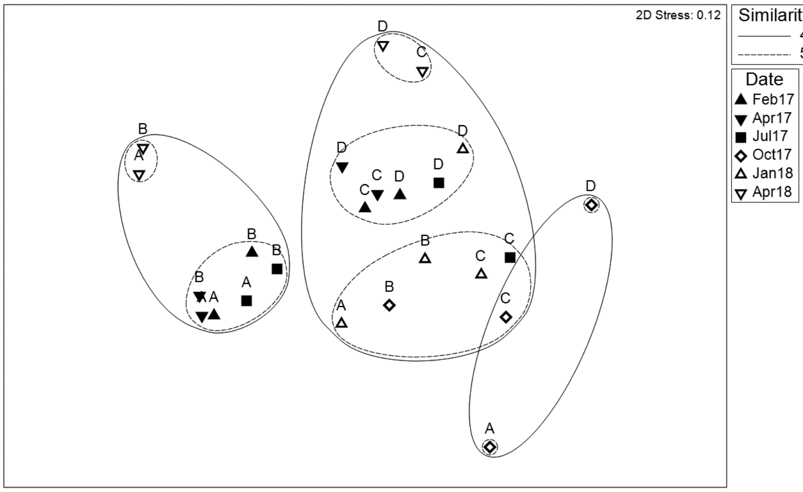

Fig. 3. Benthic community structure using non-metric multidimensional scaling (nMDS) at 4 stations (Stns A–D) in San Antonio Bay based on a short-term study (data from Patrick et al. 2020) before (closed symbols) and after (open symbols) Hurricane Harvey. Three replicates per station–date; data were square-root transformed

There were 4 periods over the 13 yr when the abundance forecast was off, and this was from July 2007, January 2008, July 2009, and July 2015. The actual values were lower than the forecast every time if they exceeded the confidence band. The periods in 2007 and 2015 were also flood periods with high precipitation (Fig. 6A) and river discharge (Fig. 6B), and very low average salinities of 0.6 and 1.8, respectively (Fig. 6C). However, the middle period in July 2009 was a drought when salinities were high, average 29.6. Biomass and richness were also low during the floods prior to Harvey. It therefore appears that extreme events (both floods and droughts) can also strongly disturb benthic communities.

While abundance and biomass varied seasonally over time, but stayed within a narrow range, temporal patterns of diversity (as richness) were more irregular. For example, diversity remained low from 2004 to 2011, then stepped up between 2011 and 2015, and stepped down again after 2015 (Fig. 5E,F). An extended drought between 2011 and 2015 resulted in generally higher salinity levels averaging 25.6. In contrast, between 2004 and 2011, salinity averaged 14.5 and decreased to 12.9 in the period after 2015.

Location within San Antonio Bay and the relative salinity values strongly influenced community structure (Fig. 7). The nMDS plot clustered upper bay

Table 2. Community structure changes over the short term (i.e. 3 quarters before and 3 quarters after the storm). Species abundance and contribution as percent of the entire community listed in order of dominance. Δ%: percent change from 9 mo prior to 9 mo after storm; Biv: Bivalvia; Gas: Gastropoda; Mol: mollusks; Nem: Nemertea; Oli: Oligochaeta; Pol: Polychaeta. Full list available in Table S1 in the Supplement at www.int-res.com/articles/suppl/m707p001_supp.xlsx

Taxa	Species	Abundance (n m^{-2})			Δ%	Contribution (%)	
		Before	After	Average		Species	Cumulative
Pol	*Mediomastus ambiseta*	14143	6492	10317	–54	55.30	55.30
Pol	*Streblospio benedicti*	5744	1261	3502	–78	18.77	74.07
Biv	*Mulinia lateralis*	843	3167	2005	276	10.75	84.82
Gas	*Texadina sphinctostoma*	441	819	630	86	3.38	88.20
Pol	*Capitella capitata*	630	158	394	–75	2.11	90.31
Biv	*Rangia cuneata*	473	24	248	–95	1.33	91.64
Pol	*Hermundura ocularis*	236	181	209	–23	1.12	92.76
Pol	*Glycinde solitaria*	181	189	185	4	0.99	93.75
Oli	Oligochaeta (unidentified)	284	55	169	–81	0.91	94.66
Nem	Nemertea (unidentified)	213	118	165	–44	0.89	95.54
Pol	*Spiochaetopterus costarum*	32	268	150	750	0.80	96.35
Mol	*Macoma mitchelli*	236	24	130	–90	0.70	97.04
	Subtotal 12 dominants	23455	12756	18106	–46	2.96	100.00
	Rare species	20	25	35			
	Subtotal rare species	473	630	552	33		
	Total all species	23928	13386	18657	–44		

Table 3. Mean (SD) bivalve mollusk shell lengths (mm) and number present for 3 species over the short term

Year–mo	*Macoma mitchelli*			*Mulinia lateralis*			*Rangia cuneata*		
	Mean	SD	n	Mean	SD	n	Mean	SD	n
2017–02	6.87	(3.04)	20	2.14	(1.74)	50	1.52	(0.76)	9
2017–04	12.11	(4.49)	7	4.22	(2.98)	29	3.10	(1.01)	31
2017–07	11.14	(8.21)	3	5.36	(2.67)	28	14.85	(4.78)	18
2017–10			0		0	20.75	(2.76)	2	
2018–01	3.54	(1.83)	2	3.67	(3.97)	3			
2018–04	8.50		1	3.84	(1.56)	399	32.10		1
2018–07			0	5.72	(1.43)	459	35.20		1
2018–10			0	6.17	(1.39)	220	23.90		1

stations (A and B) together and the lower bay stations (C and D) together. A total of 176 species were found over the 13 yr period, but 16 species made up 90% of all species found (Table 4; Table S2 in the Supplement at www.int-res.com/articles/suppl/m707p001_supp.xlsx). The 5 most dominant species over the long term (*Mediomastus ambiseta*, *Streblospio benedicti*, *Mulinia lateralis*, *Texadina sphinctostoma*, and *Capitella capitata*) made up 80% of all individuals found and were identical to those found over the short term. All 5 species had higher abundances in the upper bay than in the lower bay, but twice as many species were found in the lower bay (163) compared to the upper bay (82).

The long-term sampling periods were classified based on salinity quartile ranges, whereby the lower 25% were wet, the upper 25% were dry, and the middle 50% were average. Dry periods were found to the left of Fig. 7 and wet periods were found to the right. Where there is overlap in samples in the center of the chart, there are predominantly average periods for upper and lower bay stations. During dry periods, the upper bay structure is in the center and overlaps with lower bay periods when it is average or wet. Nine species increased during wet periods relative to dry periods, and 7 increased at least 19%: Chironomidae larvae (94%), *Hobsonia florida* (86%), *Rangia cuneata* (73%), *Texadina sphinctostoma* (55%), *Capitella capitata* (44%), *Hermundura ocularis* (27%), and *Macoma mitchelli* (19%). However, 17 species increased at least 31% in dry periods relative to wet periods, and the top 10 were *Molgula*

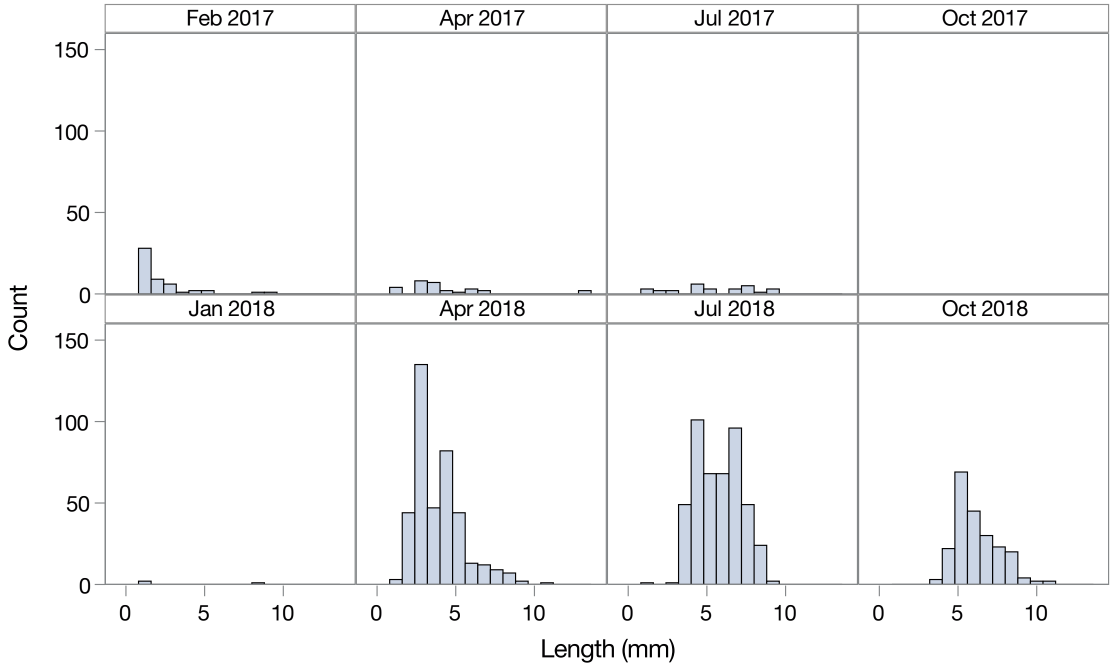

Fig. 4. Size (length in mm) distribution of *Mulina lateralis* for all samples on each sampling date over the short term, with number of individuals per bin

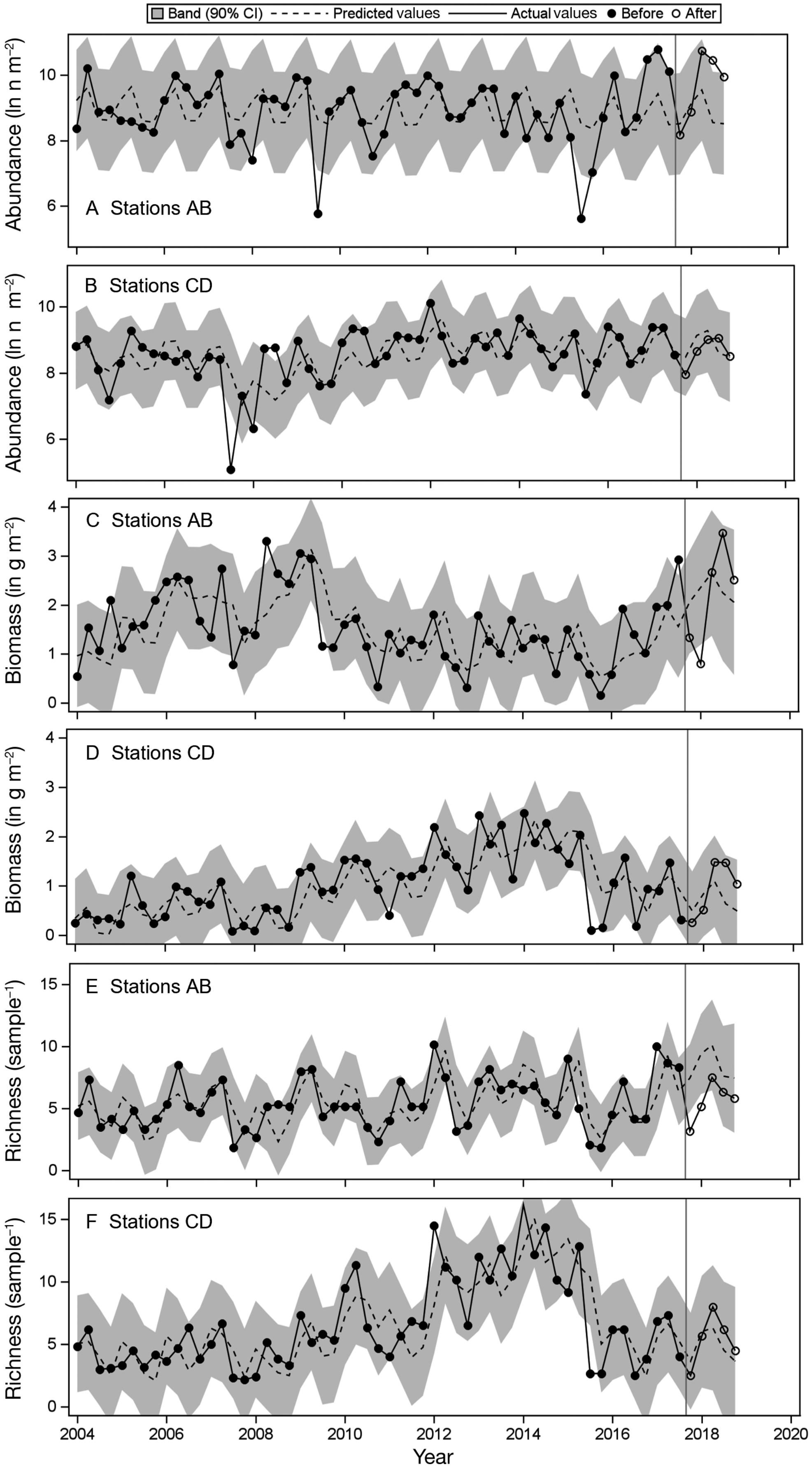

Fig. 5. Long-term benthic dynamics with actual values prior to Hurricane Harvey (black filled circles), actual values after the hurricane (open circles), time of hurricane (vertical line), and predicted values (dashed lines) and 90 % confidence bands (shaded areas). (A) Abundance for upper Stns A and B, R^2 = 40 %. (B) Abundance for lower Stns C and D, R^2 = 46 %. (C) Biomass for upper Stns A and B, R^2 = 34 %. (D) Biomass for lower Stns C and D, R^2 = 49 %. (E) Richness for upper Stns A and B, R^2 = 54 %. (F) Richness for lower Stns C and D, R^2 = 43 %

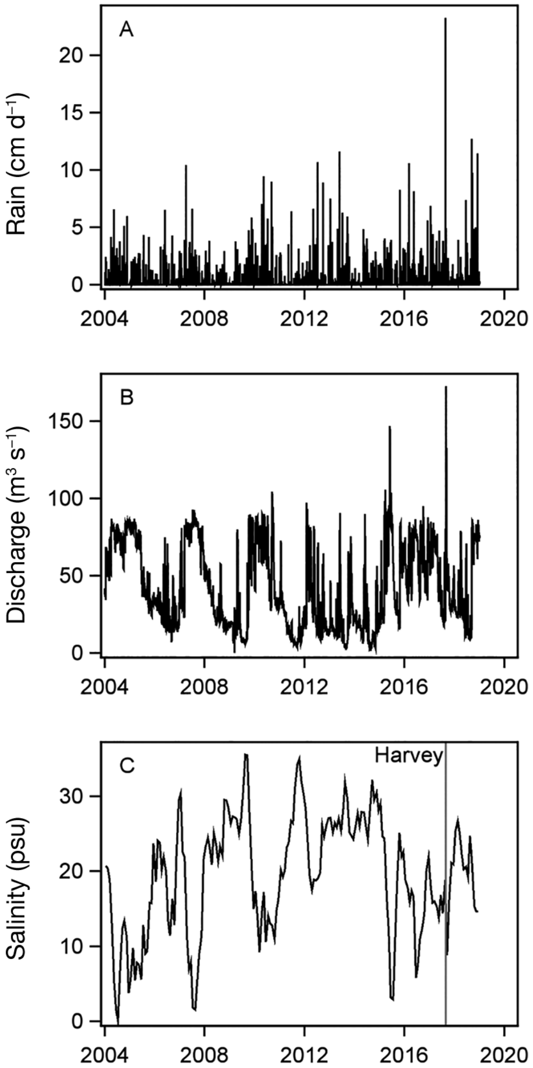

Fig. 6. Long-term climatic metrics. (A) Daily precipitation totals at Coleto Creek Reservoir. (B) Daily river flow rate at United States Geological Survey gage 08188810 on the Guadalupe River. (C) Average bay-wide monthly salinity from Texas Parks and Wildlife Department sampling

manhattensis (100%), *Nuculana acuta* (100%), *Polydora cornuta* (94%), *Axiothella* sp. (89%), *Microprotopus* sp. (87%), *Oxyurostylis* sp. (83%), *Paraprionospio pinnata* (81%), *Cossura delta* (77%), *Gyptis brevipalpa* (74%), and *Dipolydora caulleryi* (72%).

4. DISCUSSION

4.1. Benthos response to disturbances

A persistent question in marine ecology has been: How do benthic communities respond to disturbances? The research results on benthic response and change in community structure has been used to develop indicators of ecosystem health and environmental assessment tools (Pearson & Rosenberg 1978, Rhoads et al. 1978, Dauer 1993, Borja et al. 2000). Recently, focus has been on distinguishing between characteristics of resilience and resistance to change in response to disturbances (Dauer 1984, Dippner et al. 2014, Hogan et al. 2020, Patrick et al. 2022b). In simple colloquial terms, resistance can be thought of as ‘bending without breaking,’ and resilience can be thought of as ‘recovering from a setback.’ Many infaunal benthos are small in size; have short generation times; can produce many eggs, larvae, or offspring; and have rapid growth rates. These characteristics are often associated with *r*-selected species, so it is reasonable to hypothesize that infaunal benthos have intrinsic resilience and are evolutionarily advantaged to return to a previous condition or state after a disturbance. In contrast, these resilience traits would not necessarily confer traits of resistance.

Hurricanes are stochastic in terms of year-to-year dynamics, but not stochastic in seasonal terms because they occur primarily in the fall in the northern hemisphere. Thus, organisms that have life cycles with seasonal dynamics will be advantaged in that their populations might have a cycle of recruitment in spring. Seasonal cycles can lead to species succession, thus controlling community dynamics (Blasius et al. 2020). Seasonal changes dominate long-term population dynamics in the benthos of the Seine Estuary (Fromentin et al. 1997), the Wadden Sea (Beukema & Dekker 2020), the North Sea (Frid et al. 2009), the Gulf of Mexico (Escobar Briones 2003), and Texas estuaries (Montagna et al. 1993, Montagna & Kalke 1995, Montagna & Li 2010). Because of seasonality, it is reasonable to hypothesize that a population which will ‘recover’ by recruitment each spring can be thought of as having resistance to seasonal disturbance events.

The idea that there are trade-offs between resistance and resilience in response to disturbance events caused by storms has recently been proposed (Patrick et al. 2022b). The pattern was observed in a diverse array of 4138 ecosystems ranging from aquatic to terrestrial that were subject to repeated disturbances by storms. It was found that communities subjected to regularly occurring disturbances will exhibit either resistance or resilience, but not both, as evidenced by inverse covariance of resistance and resilience among ecosystem community responses. The strength of a disturbance could increase recovery times if taxa are extirpated from an ecosystem and replaced by opportunistic taxa, thus leading to low resilience. In contrast, increased resistance is conferred if mobile species can escape effects of disturbances. However, the relatively immobile infaunal benthos do not possess this capability. The resistance–resilience trade-off hypothesis predicts that benthos will be primarily characterized as a resilient community. This prediction does not take into account seasonal dynamics common in many benthic populations.

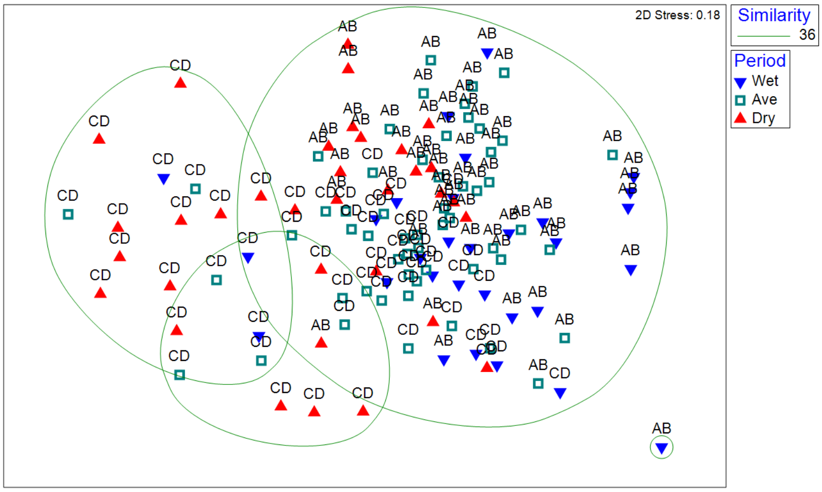

Fig. 7. Benthic community structure using non-metric multidimensional scaling (nMDS) in the upper bay (Stns A and B) and lower bay (Stns C and D) from 2004 to 2019. Symbols are for wet, average (ave), and dry periods based on quartiles of salinity ranges

4.2. Hurricane as a disturbance

Hurricane Harvey made landfall on Friday, 25 August 2017 at 22:00 h local time about 48 km (30 miles) northeast of Corpus Christi, Texas, as a Category 4 hurricane with winds up to 209 km h^{-1} (130 miles h^{-1}). This is the strongest hurricane to hit the middle Texas coast since Carla in 1961. After the windstorm and storm surge, coastal flooding occurred due to the storm lingering over Texas for 4 more days (Thyng et al. 2020). Total precipitation in the watershed of the San Antonio and Guadalupe Rivers ranged from 28 to 40 mm (Patrick et al. 2020), which produced a large flood peaking 7 to 8 d after the storm (Fig. 6). Both the rainfall amount and river discharge were much higher than experienced since 2004. Increased inflows to the estuaries can cause increased loads of inorganic and organic matter, which in turn drive primary production of coastal ‘blue carbon’ (Arismendez et al. 2009). The biological responses are immediate because the enhanced nutrient and carbon loads can significantly enhance respiration (Russell et al. 2006, Russell & Montagna 2007). The storm also caused a large decrease in salinity and DO concentrations that could kill or stress many estuarine and marine organisms (Patrick et al. 2020).

The climatic conditions in the Guadalupe Estuary (i.e. San Antonio Bay) prior to the storm were relatively typical, with salinity around 10 psu prior to the storm compared to a long-term average salinity of 17 ± 5 psu (Montagna et al. 2011). As the hurricane approached, storm surge pushed salinities over 30 psu with in-rushing sea water (Walker et al. 2021). Salinities dropped as the storm passed and the rain-swollen rivers began to flow. Salinity dropped to zero within 7 d of the storm. Salinity increased to 6 psu by 6 October 2017, and to 10 psu by 9 October 2017. Once the rivers started to flow, nutrients and organic matter

Table 4. Community structure in the upper (Stns A,B) and lower (Stns C,D) bay over the long term (i.e. 2004–2019). Species abundance and contribution of the entire community listed in order of dominance. Biv: Bivalvia; Cru: Crustacea; Gas: Gastropoda; Nem: Nemertea; Oli: Oligochaeta; Pol: Polychaeta; Uro: Urochordata. Full list available in Table S2

Taxa	Species	Abundance (n m^{-2})			Contribution (%)	
		A,B	C,D	Mean	Species	Cumulative
Pol	*Mediomastus ambiseta*	7530	4178	5854	54.0	54
Pol	*Streblospio benedicti*	2702	594	1648	15.2	69
Biv	*Mulinia lateralis*	1126	448	787	7.3	76
Gas	*Texadina sphinctostoma*	570	18	294	2.7	79
Pol	*Capitella capitata*	252	17	134	1.2	80
Pol	Oligochaeta (unidentified)	228	3	115	1.1	81
Pol	*Glycinde solitaria*	67	162	114	1.1	83
Nem	Nemertea (unidentified)	112	115	114	1.0	84
Pol	*Axiothella* sp.	19	186	102	0.9	85
Uro	*Molgula manhattensis*	31	173	102	0.9	85
Biv	*Rangia cuneata*	200	0	100	0.9	86
Pol	*Hermundura ocularis*	76	124	100	0.9	87
Pol	*Dipolydora caulleryi*	2	184	93	0.9	88
Pol	*Cossura delta*	102	69	86	0.8	89
Cru	*Hemicyclops* sp.	24	95	60	0.6	89
Pol	*Clymenella torquata*	0	117	59	0.5	90
	160 other species	728	1454	1080	10.0	100
	Total	13 769	7937	10 842		

loading enhanced respiration of organic matter, and DO started to decline, reaching zero about 9 d after the storm. The DO did not recover until 15 d after the storm (Walker et al. 2021).

4.3. Benthic response to a hurricane

Based on an initial assessment of Hurricane Harvey effects on benthos in the Guadalupe Estuary Patrick et al. (2020, our Fig. 2) concluded that the hypoxia and hyposaline conditions caused a large decline in the benthos abundance, biomass, and diversity. Community structure also changed (Fig. 3). Bivalve abundance and size distribution were average prior to the storm and showed seasonal cycles (Rener 2022). Only 1 mollusk was found in all sediment samples for the first 5 mo after the storm. Then, following a recruitment event in April 2018, *Mulinia lateralis* increased in size through July 2018 (Fig. 4). This short-term view suggests vulnerability of benthos to hurricane impacts but also a strong resilience given the recovery from a large loss within 9 mo after the storm. This short-term view also demonstrates a devastating effect of the Hurricane on benthos in San Antonio Bay. Past studies reported these same kinds of responses for benthos in other estuaries, such as the loss of species due to lowered salinity after the storm (Zink et al. 2020); a loss of polyhaline species with lowered salinity and an increase in opportunist species after the disturbance (Boesch et al. 1976); or a decline in benthos due to lowered salinities and lowered DO (Mallin et al. 1999, 2002).

However, the long-term dynamics indicate that benthos are resistant to hurricane disturbance. If the hurricane had a devastating or particularly unusual effect, then the actual values after the storm should have fallen outside the confidence bands of the forecasted values, but they did not. Thus, the long-term view suggests few long-term effects of the storm. The forecast model predicted that benthic abundance would have declined just as it does every fall and recovers again, as it does every spring. The actual abundance recovery in upper San Antonio Bay (Stns A and B) after the storm was a little greater than predicted but near the bounds of error. Overall, the recovery progressed as forecasted, with values that were nearly exactly as predicted for diversity. However, although the number of species were as predicted, the community structure was very different from a typical year because of the large dominance of juvenile bivalves. The long-term view alone would suggest a resistant rather than resilient benthos, but the short-term observations indicated low resistance. Any discussion of resilience versus resistance must place conclusions in the context of temporal and spatial scale, noting that the recovery was presumably aided by recruits from populations adapted to spawn after floods.

Although the abundance, biomass, and diversity metrics were not substantially affected by the hurricane, community structure was very different. The change was primarily due to recruitment of *Mulinia lateralis*, which is known to be a boom-and-bust species in which spawning is triggered by abrupt salinity declines (Montagna et al. 1993). This recruitment event is a good example of benthic succession theory whereby small, rapidly growing species appear immediately after a disturbance event (Pearson & Rosenberg 1978, Rhoads et al. 1978). The only other species that increased dramatically was the polychaete *Spiochaetopterus costarum*. Chaetopterid polychaetes feed using mucous bags and are known to aggregate with organic matter deposition (López-Jamar 1981, Nishi & Arai 1996). All other species declined proportionally, so the community structure shift was due primarily to these 2 species increasing and species present prior to the storm decreasing in abundance.

4.4. Conclusion

Many researchers classify hurricanes (and cyclones) as disturbances that cause extensive damage to benthic environments (Wachnicka et al. 2020). However, short-term studies can often miss important ecological relationships and dynamics (Hampton et al. 2019), and short-term studies of these environmental disturbances provide only a limited understanding of the benthic ecosystem dynamics. Potentially, natural cycles could confound those effects associated with major disturbances, leading to misinterpretations. Typical or unusual antecedent conditions could also confound post-disturbance analyses, including misinterpretation of the resistance–resilience framework when applied to short-term analyses. All 3 of these reasons were used to justify a call for a network of sentinel sites to monitor and measure ecosystem responses to catastrophic events across the globe (Hogan et al. 2020, Patrick et al. 2022a). The current work supports this idea because it has demonstrated that short-term responses must be viewed in the context of long-term dynamics.

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LITERATURE CITED

Aarnio K, Mattila J, Törnroos A, Bonsdorff E (2011) Zoobenthos as an environmental quality element: the ecological significance of sampling design and functional traits. Mar Ecol 32(Suppl 1):58–71

Arismendez SS, Kim HC, Brenner J, Montagna PA (2009) Application of watershed analyses and ecosystem modeling to investigate land–water nutrient coupling processes in the Guadalupe Estuary, Texas. Ecol Inform 4:243–253

Bacouillard L, Baux N, Dauvin JC, Desroy N, Geiger KJ, Gentil F, Thiébaut E (2020) Long-term spatio-temporal changes of the muddy fine sand benthic community of the Bay of Seine (eastern English Channel). Mar Environ Res 161:105062

Beukema JJ, Dekker R (2020) Half a century of monitoring macrobenthic animals on tidal flats in the Dutch Wadden Sea. Mar Ecol Prog Ser 656:1–18

Blasius B, Rudolf L, Weithoff G, Gaedke U, Fussmann GF (2020) Long-term cyclic persistence in an experimental predator–prey system. Nature 577:226–230

Boesch DF, Diaz RJ, Virnstein RW (1976) Effects of Tropical Storm Agnes on soft-bottom macrobenthic communities of the James and York estuaries and the lower Chesapeake Bay. Chesap Sci 17:246–259

Borja A, Franco J, Pérez V (2000) A marine biotic index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. Mar Pollut Bull 40:1100–1114

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

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edn. PRIMER-E, Plymouth

Dauer DM (1984) High resilience to disturbance of an estuarine polychaete community. Bull Mar Sci 34:170–174

Dauer DM (1993) Biological criteria, environmental health and estuarine macrobenthic community structure. Mar Pollut Bull 26:249–257

Dippner JW, Möller C, Kröncke I (2014) Loss of persistence of the North Atlantic Oscillation and its biological implication. Front Ecol Evol 2:57

Escobar Briones E (2003) The effect of the 1997–1998 ENSO on the benthic macrofaunal biomass in the southwestern Gulf of Mexico. Geofis Int 42:517–522

Francisco AS, Netto SA (2020) El Niño–Southern Oscillations and Pacific Decadal Oscillation as drivers of the decadal dynamics of benthic macrofauna in two subtropical estuaries (southern Brazil). Ecosystems 23:1380–1394

Frid CLJ, Caswell BA (2015) Is long-term ecological functioning stable: the case of the marine benthos? J Sea Res 98:15–23

Frid CLJ, Garwood PR, Robinson LA (2009) Observing change in a North Sea benthic system: a 33 year time series. J Mar Syst 77:227–236

Fromentin JM, Ibanez F, Dauvin JC, Dewarumez JM, Elkaim B (1997) Long-term changes of four macrobenthic assemblages from 1978 to 1992. J Mar Biol Assoc UK 77:287–310

Hale SS, Buffum HW, Kiddon JA, Hughes MM (2017) Subtidal benthic invertebrates shifting northward along the US Atlantic Coast. Estuar Coasts 40:1744–1756

Hampton SE, Scheuerell MD, Church MJ, Melack JM (2019) Long-term perspectives in aquatic research. Limnol Oceanogr 64:S2–S10

Hogan JA, Feagin RA, Starr G, Ross M and others (2020) A research framework to integrate cross-ecosystem responses to tropical cyclones. Bioscience 70:477–489

Kim HC, Montagna PA (2012) Effects of climate-driven freshwater inflow variability on macrobenthic secondary production in Texas lagoonal estuaries: a modeling study. Ecol Model 235-236:67–80

López-Jamar E (1981) Spatial distribution of the infaunal benthic communities of the Ria de Muros, North-West Spain. Mar Biol 63:29–37

Mallin MA, Posey MH, Shank GC, McIver MR, Ensign SH, Alphin TD (1999) Hurricane effects on water quality and benthos in the Cape Fear watershed: natural and anthropogenic impacts. Ecol Appl 9:350–362

Mallin MA, Posey MH, McIver MR, Parsons DC, Ensign SH, Alphin TD (2002) Impacts and recovery from multiple hurricanes in a Piedmont–Coastal Plain River System: Human development of floodplains greatly compounds the impacts of hurricanes on water quality and aquatic life. Bioscience 52:999–1010

Martínez ML, Taramelli A, Silva R (2017) Resistance and resilience: facing the multidimensional challenges in coastal areas. J Coast Res 77:1–6

Montagna PA (2023) Effects of Hurricane Harvey on benthos of San Antonio Bay. Gulf of Mexico Research Initiative Information and Data Cooperative (GRIIDC), Harte Research Institute, Texas A&M University–Corpus Christi, Corpus Christi, TX

Montagna PA, Kalke RD (1992) The effect of freshwater inflow on meiofaunal and macrofaunal populations in the Guadalupe and Nueces Estuaries, Texas. Estuaries 15:307–326

Montagna PA, Kalke RD (1995) Ecology of infaunal Mollusca in south Texas estuaries. Am Malacol Bull 11:163–175. http://www.biodiversitylibrary.org/item/172621#page/489/mode/1up

Montagna PA, Li J (2010) Effect of freshwater inflow on nutrient loading and macrobenthos secondary production in Texas lagoons. In: Kennish MJ, Paerl HW (eds) Coastal lagoons: critical habitats of environmental change, CRC Press, Taylor & Francis Group, Boca Raton, FL, p 513–539

Montagna PA, Stockwell DA, Kalke RD (1993) Dwarf surfclam *Mulinia lateralis* (Say, 1822) populations and feeding during the Texas brown tide event. J Shellfish Res 12: 433–442. https://www.biodiversitylibrary.org/item/23121#page/445/mode/1up

Montagna PA, Kalke RD, Ritter C (2002) Effect of restored freshwater inflow on macrofauna and meiofauna in upper Rincon Bayou, Texas, USA. Estuaries 25:1436–1447

Montagna PA, Brenner J, Gibeaut J, Morehead S (2011) Coastal impacts. In: Schmidt J, North GR, Clarkson J (eds) The impact of global warming on Texas, 2nd edn. University of Texas Press, Austin, TX, p 96–123

Montagna PA, Hu X, Palmer TA, Wetz M (2018) Effect of hydrological variability on the biogeochemistry of estuaries across a regional climatic gradient. Limnol Oceanogr 63:2465–2478

Nishi E, Arai Y (1996) Chaetopterid polychaetes from Okinawa Island, Japan, with notes on the feeding behaviour of *Spiochaetopterus costarum costarum.* Publ Seto Mar Biol Lab 37:51–61

Paerl HW, Bales JD, Ausley LW, Buzzelli CP and others (2001) Ecosystem impacts of three sequential hurricanes (Dennis, Floyd, and Irene) on the United States' largest lagoonal estuary, Pamlico Sound, NC. Proc Natl Acad Sci 98:5655–5660

Palmer TA, Montagna PA (2015) Impacts of droughts and low flows on estuarine water quality and benthic fauna. Hydrobiologia 753:111–129

Palmer TA, Montagna PA, Pollack JB, Kalke RD, DeYoe HR (2011) The role of freshwater inflow in lagoons, rivers, and bays. Hydrobiologia 667:49–67

Patrick CJ, Yeager L, Armitage AR, Carvallo F and others (2020) A system level analysis of ecosystem responses to hurricane impacts on a coastal region. Estuar Coasts 43: 943–959

Patrick CJ, Hensel E, Kominoski JS, Stauffer BA, McDowell WH (2022a) Extreme event ecology needs proactive funding. Front Ecol Environ 20:496–497

Patrick CJ, Kominoski JS, McDowell WH, Branoff B and others (2022b) A general pattern of trade-offs between ecosystem resistance and resilience to tropical cyclones. Sci Adv 8:eabl9155

Paudel B, Montagna PA (2014) Modeling inorganic nutrient distributions among hydrologic gradients using multivariate approaches. Ecol Inform 24:35–46

Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr Mar Biol Annu Rev 16: 229–311

Pollack JB, Kinsey JW, Montagna PA (2009) Freshwater Inflow Biotic Index (FIBI) for the Lavaca-Colorado Estuary, Texas. Environ Bioindic 4:153–169

Pollack JB, Palmer TA, Montagna PA (2011) Long-term trends in the response of benthic macrofauna to climate variability in the Lavaca-Colorado Estuary, Texas. Mar Ecol Prog Ser 436:67–80

Rener LM (2022) Effect of freshwater inflow on mollusk community and population dynamics in Texas estuaries. MSc thesis, Texas A&M University–Corpus Christi, TX

Rhoads DC, McCall PL, Yingst JY (1978) Disturbance and production on the estuarine seafloor. Am Sci 66:577–586

Ritter C, Montagna PA, Applebaum S (2005) Short-term succession dynamics of macrobenthos in a salinity-stressed estuary. J Exp Mar Biol Ecol 323:57–69

Russell MJ, Montagna PA (2007) Spatial and temporal variability and drivers of net ecosystem metabolism in Western Gulf of Mexico Estuaries. Estuar Coasts 30:137–153

Russell MJ, Montagna PA, Kalke RD (2006) The effect of freshwater inflow on net ecosystem metabolism in Lavaca Bay, Texas. Estuar Coast Shelf Sci 68:231–244

Santos SL, Simon JL (1980) Response of soft-bottom benthos to annual catastrophic disturbance in a south Florida estuary. Mar Ecol Prog Ser 3:347–355

SAS Institute (2017) SAS/ETS® 14.3 User's guide. SAS Institute, Cary, NC

SAS Institute (2020) SAS/STAT® 15.2 User's guide. SAS Institute, Cary, NC

Shojaei MG, Gutow L, Dannheim J, Rachor E, Schröder A, Brey T (2016) Common trends in German Bight benthic macrofaunal communities: assessing temporal variability and the relative importance of environmental variables. J Sea Res 107:25–33

Shojaei MG, Gutow L, Dannheim J, Schröder A, Brey T (2021) Long-term changes in ecological functioning of temperate shelf sea benthic communities. Estuar Coast Shelf Sci 249:107097

Thyng K, Hetland RD, Socolofsky SA, Fernando N, Turner EL, Schoenbaechler C (2020) Hurricane Harvey caused unprecedented freshwater inflow to Galveston Bay. Estuar Coasts 43:1836–1852

Tilmant JT, Curry RW, Jones R, Szmant A and others (1994) Hurricane Andrew's effects on marine resources. BioScience 44:230–237

Van Diggelen AD, Montagna PA (2016) Is salinity variability a benthic disturbance in estuaries? Estuar Coasts 39: 967–980

Wachnicka A, Armitage AR, Zink I, Browder J, Fourqurean JW (2020) Major 2017 hurricanes and their cumulative impacts on coastal waters of the USA and the Caribbean. Estuar Coasts 43:941–942

Walker LM, Montagna PA, Hu X, Wetz MS (2021) Timescales and magnitude of water quality change in three Texas estuaries induced by passage of Hurricane Harvey. Estuar Coasts 44:960–971

Wetz MS, Yoskowitz DW (2013) An 'extreme' future for estuaries? Effects of extreme climatic events on estuarine water quality and ecology. Mar Pollut Bull 69:7–18

Zettler ML, Friedland R, Gogina M, Darr A (2017) Variation in benthic long-term data of transitional waters: Is interpretation more than speculation? PLOS ONE 12: e0175746

Zink IC, Browder JA, Kelble CR, Stabenau E, Kavanagh C, Fratto ZW (2020) Hurricane-mediated shifts in a subtropical seagrass associated fish and macroinvertebrate community. Estuar Coasts 43:1174–1193

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