REPORT

Social–ecological system responses to Hurricane Sandy in the Hudson-Raritan Estuary

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Received: 10 March 2017 / Revised: 5 July 2017 / Accepted: 20 September 2017 / Published online: 13 October 2017

Abstract The impact of Hurricane Sandy on the Hudson-Raritan estuary (HRE) provided a valuable case study for exploring interactions between long-term environmental degradation, new climatic disturbance stressors, and human behavioral responses. We extend previous research on the ecological effects of major storms to compare water quality and biological parameters three years before and three years after Hurricane Sandy and consider how ecosystem shifts relate to anglers' perceptions. Results indicate that water clarity and nutrients returned to pre-storm conditions in about one year, while shifts in the biological community, including a significant increase in harmful algal species and declines in zooplankton and Atlantic menhaden, persisted for multiple years, and anglers continued to fish amidst ecosystem decline. Biotic recovery time in the HRE was longer than reports for other shallow estuaries frequently disturbed by hurricanes. Ecological and social responses suggest that the post-storm regime shifts and continued fishing pressure could further environmental degradation.

Keywords Estuaries · Environmental degradation · Hurricane Sandy · Fisheries · Plankton · Water quality

INTRODUCTION

Because of their setting within the coastal landscape, estuaries and coastal populations are susceptible to specific natural disturbances, which can be defined as external forces that cause a deviation in the structure of the system

relative to a reference condition (Pickett et al. 1989). Hurricanes and tropical storms are examples of natural disturbances to which coastal communities are adapted, yet coastal disturbances related to extreme weather events are likely to become more pervasive threats due to human-induced climate change and sea level rise (Intergovernmental Panel on Climate Change [IPCC] 2012). In addition, the level of existing habitat degradation and biodiversity loss is a major factor influencing the direction, severity, and persistence of ecosystem alterations following a major storm (Mallin and Corbett 2006). Therefore, coastal ecosystems may be especially vulnerable to more frequent disturbance given that centuries of concentrated human activities in coastal areas have led to massive biodiversity loss, altered ecosystem structure and function, and diminished recovery potential (Jackson et al. 2001; Norse and Crowder 2005; Lotze et al. 2006).

A number of studies have provided evidence that water quality degradation by hurricanes and associated impacts to biota is generally more severe in highly developed watersheds (Mallin et al. 1999; Wetz and Yoskowitz 2013), yet much of the available evidence is derived from studies of hurricanes that have affected southeastern coastal areas where hurricane impacts are more frequent (Mallin and Corbett 2006). Similar analyses in other locations that rely on multiyear monitoring data would allow for comparisons of ecosystem impacts across a greater variety of estuaries. This is especially important since existing data indicate that the relationship between hurricanes and a host of human-induced stressors in estuaries are complex and highly site specific (Mallin and Corbett 2006; Anthony et al. 2009). Scientists and resource managers have also recommended that future studies be aimed toward an improved understanding of how impacts of more frequent hurricanes will be superimposed upon existing degradation (Mallin and

Electronic supplementary material The online version of this article (doi:10.1007/s13280-017-0949-z) contains supplementary material, which is available to authorized users.

Corbett 2006; Wetz and Yoskowitz 2013), as well as responses of ecosystem users following large disturbance events (Anthony et al. 2009).

Ecological and social systems are interconnected, especially in coastal areas where human communities are culturally and economically interconnected with the environment and face the most immediate effects of climate change (Hughes et al. 2005; Anthony et al. 2009). In recognition of the importance of a multidisciplinary approach to coastal conservation and management, the overall objective of this study was to consider ecological responses of an urban estuary with a long history of environmental degradation following a major storm event, and to consider deviations in the structure of the system in relation to the perspectives and behavior of anglers who are active users of the ecosystem. The impact of Hurricane Sandy on coastal New York and New Jersey provided an ideal case study for this investigation.

The Hudson-Raritan Estuary (HRE), located between the states of New York and New Jersey, is both ecologically and economically significant. The estuary supports numerous recreational and commercial fisheries (Seara et al. 2016) and provides habitat for waterfowl, shellfish, and marine, estuarine, and anadromous fish. However, the health of this system has been undermined by a long history of overexploitation and environmental degradation. For example, the eastern oyster was declared ecologically extinct by the turn of the twentieth century, and the system continues to exhibit numerous symptoms of eutrophication, including high algal biomass, high turbidity, seasonal hypoxia, violations of the dissolved oxygen standard to protect the health of bottom-dwelling fishes, and blooms of potentially harmful phytoplankton species (United States Environmental Protection Agency [EPA] 2007; Rothenberger et al. 2014). Despite the environmental degradation that has occurred in this system, the commercial and recreational fishing industries of New York and New Jersey still play important socioeconomic roles in the region.

The biophysical and social systems of the already degraded HRE were challenged when Hurricane Sandy made landfall on October 29, 2012 at Brigantine, NJ. When the storm arrived close to spring high tide, it created a record storm surge > 3.0 m that pushed water into the HRE. Massive flooding and power outages took several wastewater treatment plants offline in New Jersey, and raw sewage carrying high levels of fecal coliform bacteria, nutrients, and other pollutants emptied into New Jersey's rivers and estuaries (New Jersey Department of Environmental Protection [NJ DEP] 2013). Over a period of 3 months, 10.3 billion gallons of untreated sewage spilled into Raritan River and Bay (Kenward et al. 2013). The commercial fishing industry in the HRE was also highly disrupted by the storm, and the U.S. Secretary of

Commerce issued both a fishery resource disaster and a catastrophic regional fishery disaster for both New York and New Jersey on November 16, 2012 (National Oceanic and Atmospheric Administration [NOAA] 2012). Damage to docks and marinas and seafood processing plants resulted in massive loss of activity and cost as much as \$105 million for recreational and \$14 million for commercial anglers (United States Department of Commerce 2013).

While acute, short-term hurricane effects on water quality (e.g., Mallin et al. 1999; Wetz and Paerl 2008; Zhang et al. 2009) and fisheries communities (Ingles and McIlvaine-Newsad 2007; Seara et al. 2016) have been examined by others, fewer studies have reported on the longer-term trends on water quality, biota, and resource users' perceptions of ecosystem change. We have maintained a monthly monitoring program of water quality and plankton assemblages in Raritan Bay since April 2010. This program allowed us to collect regular water quality data at 6 stations throughout the system for three years before and 3 years after Hurricane Sandy, establishing a seasonal background, or reference condition, against which post-storm data could be compared. Comparisons of commercial landings of two economically important fish (i.e., Atlantic menhaden and blue crab) before and after the hurricane were included, and we also interviewed anglers of the HRE on their perceptions of ecosystem change and their behavioral responses following Hurricane Sandy. The interviews supplement the findings of the biological analyses, as to provide insights on how anglers may identify and respond to both acute and longer-term ecosystem changes. In conducting semi-structured interviews that drew on participants' experiences of Hurricane Sandy in the HRE, we temporally coupled user perceptions with ecological information. Social and ecological information that are spatially co-located facilitate the understanding of social-ecological system interactions (Leslie et al. 2015), and allow managers to anticipate possible responses to and recovery strategies in future storm events (Abbott-Jamieson and Clay 2010).

MATERIALS AND METHODS

Environmental monitoring

Six sites in Raritan Bay (Fig. 1) were sampled on a monthly basis from April 2010 through November 2016. It was not possible to sample in November 2012 due to damage caused by Hurricane Sandy on the Atlantic Highlands marina. Water temperature, salinity, pH, and dissolved oxygen (DO) were determined using a YSI 6820 V2 multiparameter meter, which was calibrated prior to each

Fig. 1 The Raritan River Basin and Bay, showing the six sampling stations for temperature, salinity, pH, dissolved oxygen, Secchi depth, nutrient concentrations, and phytoplankton and zooplankton assemblages. Samples were collected from 2010 to 2016 on a monthly basis (April–November)

sample period. Water transparency was assessed using Secchi depth data (Wetzel and Likens 2001). A vertical polycarbonate Van Dorn water sampler (2.2 L) was used to collect water samples near surface (~ 0.5 m), at mid-depth (~ 1.5 m), and at low depth (~ 3.0 m; average depth at the six sampling sites is ~ 4.8 m) between 10:00 h and 12:00 h local time for biological and chemical analyses. Samples for nutrient analyses were poured into acid-cleaned bottles, maintained in darkness on ice for transport to the laboratory, and refrigerated or frozen as appropriate until analysis (EPA 1993). Phytoplankton samples were poured into amber bottles and preserved with acidic Lugol's solution on site. Zooplankton samples were collected at a depth of 1.5 m using a 12-L Schindler–Patalas trap and preserved with 4% buffered formalin. All plankton samples were held at 4 °C until analysis.

Nutrient analyses were performed using standard methods (American Public Health Association [APHA] 2012). Concentrations of all nutrients were determined colorimetrically with a HACH (Loveland, CO, USA) DR/2500 spectrophotometer. Accuracy checks, including the use of reagent blanks and standard solution adjusts, followed HACH procedures (Hach Manual for DR/2500 spectrophotometer). Nitrate (NO_3^-) was determined within 12 h of collection using the method of cadmium reduction, and the Nessler method was used within 24 h for determination of ammonium (NH_4^+). Samples for analysis of soluble reactive phosphorus (SRP) were first filtered in the field with a Whatman Puradisc 0.45 micron syringe filter and analyzed within 48 h using the ascorbic acid–molybdate blue method. Silicon (Si) was determined using the silicomolybdate method. Dissolved N:P and Si:N ratios,

precipitation data, and Raritan River discharge rates were also included in the analyses because previous studies have indicated that they are important factors governing phytoplankton species composition and bloom development (e.g., Anderson et al. 2002; Rothenberger et al. 2014; Rothenberger and Calomeni 2016).

Phytoplankton counts were conducted using a Palmer Maloney cell ($\times 400$) under a Leica DM 1000 phase contrast microscope, and cells were identified and counted until at least 100 specimens of the most common species were counted (LeGresley and McDermott 2010). Taxa abundances, including colonial and filamentous forms, were quantified by enumerating single cells, and identifications were taken to the lowest taxonomic level. For enumeration of zooplankton, a subsample of $\sim 10\%$ of the total sample was examined. Counts were conducted using a Sedgewick Rafter counting cell ($100\times$), also under a Leica DM 1000 phase contrast microscope. Identifications were taken to genus or species level.

Phytoplankton and zooplankton species richness, Simpson's Diversity Index, and number of harmful algal bloom (HAB) taxa were determined for each sample. HAB taxa are those that have been identified as capable of causing harmful algal blooms (i.e., they cause harm through either toxin production, cell physical structure, or accumulated biomass; Anderson et al. 2002). Water quality parameters, plankton species richness, plankton biodiversity, and number of HAB taxa were compared among three time periods (i.e., 3 years prior to Hurricane Sandy, 1 year after Hurricane Sandy [acute], and 3 years after Hurricane Sandy [long-term]) with one-way analysis of variance (ANOVA) and Tukey's multiple comparison test. A statistical significance α level of 0.05 was used for all analyses.

In order to investigate relationships among environmental parameters, secondary consumers, and phytoplankton composition over time, ordination techniques were used. Non-Metric Multidimensional Scaling (NMDS), considered the most effective ordination method for ecological data (McCune and Grace 2002), was used to establish temporal changes in plankton assemblage structure and to interpret those differences in terms of environmental conditions. All NMDS ordinations were carried out using PC-ORD version 5.0 software (MjM software 2010). To prepare the monitoring dataset for ordination, phytoplankton and zooplankton data were compiled into separate matrices of cell number by site and sample date. To reduce the "noise" (variability) in the plankton datasets and enhance detection of assemblage patterns in relation to environmental parameters, rare taxa (defined as present in $< 5\%$ of samples) were removed prior to analysis (McCune and Grace 2002), and abundances of the remaining 81 phytoplankton species and 60 zooplankton species were log transformed after 1 was added as a constant.

Every plankton sample used in the analysis had a corresponding suite of physical and chemical measurements (described above) that could be related to ordinations by species composition.

Fisheries abundance and trends

Commercial landings of Atlantic menhaden (*Brevoortia tyrannus*) and blue crab (*Callinectes sapidus*) were assessed before and after the hurricane using fishery-dependent data of the New Jersey Division of Environmental Protection (NJ DEP). Because the majority of landings information collected by the National Marine Fisheries Service and DEP is not specifically assigned to Raritan Bay and data are considered confidential by New Jersey statute and federal fisheries law when information comes from fewer than three individuals, the NJ DEP was only able to provide data exclusive to smaller, Raritan Bay fishing ports for these two economically valuable fish (Matthew J. Coefer, Chief Records Custodian of the NJ DEP, pers. comm.). Atlantic menhaden, which supports the largest fishery by volume on the Atlantic coast, are an important prey item for bluefish (*Pomatomus saltatrix*) and striped bass (*Morone saxatilis*) and are targeted by commercial fisheries for use in fishmeal or as bait (Buchheister et al. 2015). The blue crab supports both lucrative commercial anglers and recreational anglers in Raritan Bay (Stehlik et al. 1998).

Angler interviews

Semi-structured interviews of HRE anglers were conducted to identify their perceptions of HRE ecosystem change and to illuminate their adaptive responses to the storm event that could have feedbacks on the fishery and ecosystem recovery (Appendix S1). At the outset, interviews were designed to supplement our long-term ecological monitoring with species population changes observed by HRE users. Participants were identified using snowball sampling, in which participants referred us to potential interviewees (Neis et al. 1999). We initiated the snowball sampling with references provided by our marina contacts. In total, 50 commercial and recreational anglers were identified and contacted by telephone, and 12 were interviewed. Ten interviews were conducted in-person and two were conducted over the telephone. The interviews were conducted between February and May 2016, following IRB approval in January, 2016. The interviews lasted approximately 30 min and were recorded. Identities and perspectives of participants were kept confidential, with only the authors having access to primary research documents (i.e., recordings, field notes, and transcripts).

Because the snowball sampling methods focused on active anglers in the Raritan Bay area, interviews did not

Table 1 Qualitative interview codes, including topics and associated meanings for three key areas of focus

Focus areas	Topics raised in response to questions ^a	Associated meanings ^b
Estuary ecosystem changes	Eelgrass	Concerns about water quality; faith in ecosystem recovery
	Benthic habitat	
	Temporal changes immediately following the storm;	
	Long-term, lasting well after the storm	
	Changes in fishable areas	
Species populations	Population changes:	Economic losses from business closures, fishing revenue Species populations are in flux, but availability will continue
	Clams	
	Blue Crab	
	Summer flounder (fluke)	
	Striped bass	
	Atlantic menhaden (bunker)	
Hurricane Sandy experiences	Property loss	Fishing as an escape from recovery problems; persistence of the fishery with time
	Return to fishing	
	Location of fishing	
	Enduring challenges	

^a Interview topics were defined as the subject of the statement

^b Meanings were defined as interpretations of and attitudes toward the topic of interest

include the perspectives of anglers who ceased to fish after Hurricane Sandy. Anglers that left the industry after Hurricane Sandy reported lower levels of perceived adaptive capacity than the anglers who remained active (Seara et al. 2016). The perspectives herein may therefore be biased to emphasize anglers' sustained ties to the HRE.

Of the five commercial anglers interviewed, two specialized in clam harvest, while the other fished a wide variety of species from fluke (*Paralichthys dentatus*), striped bass, Atlantic menhaden, and blue crabs. Two of these commercial anglers also worked at a seafood processing plant, and another two worked for a clam depuration plant. Two retired, commercial anglers were interviewed, both of whom fished recreationally at the time of the interview. Five recreational anglers with long-standing fishing experience in the HRE also participated. While all interviewees fished in various locations throughout the HRE, their residences varied throughout northern New Jersey. Our participants were therefore diverse in terms of the species they sought, and their dependence on (or independence from) the fishery for their livelihoods. Nonetheless, they shared a strong affiliation to fishing within their personal identities, as found in other work on angler groups (Pollnac 1988).

Interview transcripts underwent a content analysis that focused on anglers' perceptions of estuary ecosystem changes, species populations, and the participants' adaptations after Hurricane Sandy. While recall bias may occur in retrospective accounts, interviews pertaining to natural

disaster experiences, including hurricanes, tend to remain vibrant and reliable after the event (Norris and Kaniasty 1992). Relevant passages of all interviews were transcribed and coded for topics and associated meanings surrounding the interview topics noted above (Table 1). Coded interview passages were then compared across interviews to identify themes. Information was also recorded about the participants, the forms of fishing that they conducted, and background on their fishing businesses, where applicable. We wrote intermediary findings memos in which interview data were compared, and patterns in responses were identified (Emerson et al. 2011). The interviews were analyzed with our HRE ecosystem findings in mind, and in doing so, the qualitative findings emphasize the temporal connections between anglers' perceptions and ecosystem disturbances associated with Hurricane Sandy.

RESULTS

Water quality and plankton trends

Water quality and plankton data indicate that there were significant environmental differences among the three time periods compared. Surface salinities, which ranged from 11 to 40 (grand mean for surface waters 26 ± 0.2), were dependent upon precipitation patterns and Raritan river discharge rates (Fig. 2). During the pre-hurricane period from 2010 to 2012 and the year following Hurricane

Fig. 2 Monthly mean Raritan River discharge rates (solid line) measured by United States Geological Survey at Bound Brook (about 20 km upstream from the study area at site 1), and monthly precipitation totals (dashed line) for New Brunswick (i.e., the nearest municipal area) acquired from the New Jersey Weather & Climate Network from April 2010 through June 2016

Table 2 Water quality parameters before (i.e., 2010–2012), 1 year after (i.e., 2013), and 2–3 years after (i.e., 2014–2015) Hurricane Sandy, which made landfall on October 29, 2012. Parameters were measured on a monthly (i.e., from April through November) basis from April 2010 to April 2016 at 6 sites and 3 depths within Raritan Bay ($N = 24$ per site per year). Values are means (SEs). For each comparison, ANOVA F-statistics and P values are shown ($df = 2$). Different letters indicate significant differences among station types for each parameter (Tukey's multiple comparison test: $P < 0.05$). 9.59 (0.13)^a

Parameter	2010–2012	2013	2014–2016	F	P
DO (mg L^{-1})	9.59 (0.13) ^a	9.59 (0.21) ^a	8.83 (0.14) ^b	8.59	<0.001
Salinity	25.1 (0.23) ^a	25.3 (0.31) ^a	28.2 (0.30) ^b	41.9	<0.0001
Secchi depth	1.53 (0.04) ^a	1.29 (0.03) ^b	2.1 (0.08) ^c	52.3	<0.0001
Nitrate ($\mu\text{g L}^{-1}$)	795 (31.2) ^a	1350 (128) ^b	866 (32.1) ^a	24.8	<0.0001
Ammonium ($\mu\text{g L}^{-1}$)	96.5 (5.2)	117 (11.4)	109 (5.39)	2.42	0.09
SRP ($\mu\text{g L}^{-1}$)	47.2 (1.25) ^a	61.3 (3.13) ^b	44.8 (2.54) ^a	10.9	<0.0001
Silicon ($\mu\text{g L}^{-1}$)	3330 (147) ^a	3280 (292) ^a	4140 (219) ^b	5.80	<0.01
N:P	24.2 (1.6) ^a	29.2 (3.4) ^b	38.5 (4.3) ^c	6.74	<0.01
Si:N	5.6 (0.34)	4.36 (0.54)	6.4 (0.67)	2.37	0.09

Sandy, surface salinities throughout the bay were near average (Table 2). Surface salinities were significantly higher from 2014 to 2016 in association with reduced precipitation and river discharge in those years (Fig. 2, Table 2). Dissolved oxygen ranged from 4.0 to 20.2 mg L^{-1} (grand mean for surface waters 9.7 ± 0.16 and bottom waters 8.8 ± 0.15) with the lowest concentrations occurring in summer months, especially during low precipitation periods (Fig. 3). DO concentrations throughout the bay were significantly higher before and directly

after Hurricane Sandy than from 2014 to 2016 (Table 2). Water clarity ranged from 0.5 to 5.3 m (grand mean 1.8 ± 0.03) with significantly lower water clarity in the year following Hurricane Sandy (Table 2). Nitrate and soluble phosphorus concentrations ($907 \pm 29 \mu\text{g NO}_3^{-1} \text{ L}^{-1}$, range of 20–9000 $\mu\text{g NO}_3^{-1} \text{ L}^{-1}$; $47 \pm 1.2 \mu\text{g SRP L}^{-1}$, range of 1.0–450 $\mu\text{g SRP L}^{-1}$) continue to indicate eutrophic conditions (Table 1; Wetzel 2001). Concentrations of both nutrients were significantly higher in the period directly following Hurricane Sandy (Table 2).

Fig. 3 Dissolved oxygen concentrations across all sites and sampling periods in Raritan Bay from April 2010 to April 2016 compared with the New Jersey state standard for fish health (≥ 5 mg DO L⁻¹). Timing of Hurricane Sandy is indicated by a dashed line

Table 3 Plankton species richness and diversity before (i.e., 2010–2012), 1 year after (i.e., 2013), and 2–3 years after (i.e., 2014–2015) Hurricane Sandy, which made landfall on October 29, 2012. Parameters were measured on a monthly (i.e., from April through November) basis from April 2010 to April 2016 at 6 sites within Raritan Bay ($N = 8$ per site per year). Values are means (SEs). Zooplankton abundance is reported as the number of organisms L⁻¹. For each comparison, ANOVA F-statistics and P values are shown ($df = 2$). Different letters indicate significant differences among station types for each parameter (Tukey's multiple comparison test: $P < 0.05$)

Parameter	2010–2012	2013	2014–2016	F	P
Phytoplankton species richness	9.24 (0.44) ^a	10.7 (0.72) ^a	8.60 (0.29) ^b	3.02	0.05
Phytoplankton biodiversity	0.61 (0.02)	0.66 (0.02)	0.58 (0.01)	2.30	0.10
Proportion HAB taxa	11.3 (1.19) ^a	25.2 (3.49) ^b	17.7 (3.01) ^c	10.4	<0.0001
Zooplankton Abundance	2.3×10^3 (33.0) ^a	6.3×10^2 (8.30) ^b	3.6×10^2 (6.77) ^b	15.4	<0.0001
Zooplankton species richness	6.25 (0.25) ^a	3.60 (0.33) ^b	3.10 (0.20) ^b	59.0	<0.0001
Zooplankton biodiversity	0.59 (0.03) ^a	0.48 (0.02) ^b	0.42 (0.02) ^b	17.3	<0.0001

Overall, both nitrate and SRP concentrations were ~ 1.5 times higher directly after Hurricane Sandy. Ammonium concentrations ranged from 1.0 to 580 $\mu\text{g NH}_4 \text{ L}^{-1}$ (grand mean $102.4 \pm 3.7 \mu\text{g NH}_4 \text{ L}^{-1}$). N:P ratios (grand mean 33.6) were significantly higher from 2014 to 2016, and Si:N ratios (grand mean 5.9) were not significantly different among the three time periods (Table 2).

A total of 75 phytoplankton taxa were found in samples, and 14 of those have been identified as capable of causing HABs. Although phytoplankton species diversity did not change significantly before and after Hurricane Sandy (Table 3), there was a significant increase in HAB species directly after the storm (Figs. 4, 5, Table 3). NMDS of phytoplankton species abundance clearly demonstrates changes in plankton species composition

Fig. 4 Ordination of all samples by phytoplankton species composition showing temporal change in environmental conditions and plankton composition. Each point represents a single sample from one of the six sites in a particular season and year (April 2010–June 2016). All samples retrieved before Hurricane Sandy are indicated by white symbols and those retrieved after Hurricane Sandy are indicated by symbols in shades of gray with darker shades indicating greater time post-disturbance. The relative distance between points reflects relative similarity in phytoplankton species composition. **a** Vectors indicate strength and direction of environmental gradients (r^2 cutoff value = 0.10; Si:N = dissolved Si:N ratio, DO = dissolved oxygen, SRP = soluble reactive phosphorus). **b** Vectors indicate strength and direction of phytoplankton species gradients (r^2 cutoff value = 0.40) **c** Vectors indicate strength and direction of zooplankton species gradients (r^2 cutoff value = 0.20). Abbreviated taxa are *Skeletonema costatum*, harmful algal bloom (HAB) species, and *Heterocapsa triquetra*

Fig. 5 Mean abundance of harmful algal bloom taxa (a) and zooplankton (b), and annual commercial landings for Atlantic menhaden (c) and blue crab (d) in Raritan Bay. Timing of Hurricane Sandy is indicated by a dashed line. Landings data were collected by the New Jersey Department of Environmental Protection

that occurred following Hurricane Sandy (Fig. 4). As evidenced by the clear separation of samples collected directly after Hurricane Sandy in spring 2013 and those collected from summer 2013 through fall 2015 in the ordination diagram (Fig. 4), phytoplankton assemblages were distinctly different in the three years following the disturbance. HAB taxa, such as *Oscillatoria* spp., *Heterocapsa triquetra*, and *Heterosigma akashiwo*, were most abundant in the months following the storm (Fig. 4b). In June 2013, *H. akashiwo*, a potentially toxic raphidophyte, reached densities of 1×10^4 cells ml^{-1} , and *Oscillatoria* spp. reached densities of 7.4×10^4 cells ml^{-1} and accounted for over 70% of the algal cells counted in August 2013. Increases in HAB taxa were associated with elevated SRP and ammonium concentrations and lower salinity, DO, and zooplankton densities (Fig. 4). Zooplankton abundance, species richness, and biodiversity were significantly lower in both periods after Hurricane Sandy (Figs. 4 and 5, Table 3). Samples collected in 2016 were more similar in phytoplankton species composition to those collected in the years before Hurricane Sandy (Fig. 4).

Fisheries landings

Although causal relationships cannot be confirmed by this study, there are notable correlations between plankton and fisheries landings data (Fig. 5). From 2010 to 2015, average weight of annual commercial landings for the planktivorous Atlantic menhaden in Raritan Bay was approximately 2.1×10^6 kilograms. From 2011 to 2012, there was a sharp, 88% decline in Atlantic menhaden landings (Fig. 5c) that coincided with a sharp increase in HAB taxa abundance (Fig. 5a) and a decrease in mean zooplankton abundance (Fig. 5b). Although Atlantic menhaden landings increase in 2013, they decline in 2014 and 2015 (Fig. 5c). The average weight of the blue crab harvest in Raritan Bay from 2010 to 2014 was 1.5×10^5 kilograms. Unlike Atlantic menhaden, there is a consistent decline in blue crab harvest during this period (Fig. 5d). The weight of the blue crab harvest in 2015 is approximately 98% less than the weight of the harvest in 2010, and the rate of the decline increases from an $\sim 8\%$ annual decline before 2012 to a $\sim 45\%$ average annual decline after 2012.

Angler Interviews

Many anglers were aware of coastal ecosystem degradation prior to Hurricane Sandy, for example:

“We’ve been dealing with a loss of eelgrass in the back bays and I think that’s something that was exacerbated by Sandy. I don’t think it was the sole

reason why eelgrass populations are down. But without the eelgrass in those back bays it impacts the entire ecosystem.”

Other anglers recognized the effects of climate change on the HRE:

“Well I think that over the years even before Sandy, the fishing areas have been depleted...the big thing that is happening [ecosystem degradation] is even before Sandy—it’s ongoing. Sandy may have had some effect on that but the temperature rise in the areas...that’s why you see species of fish moving north.”

Many anglers recognized long-term ecosystem degradation that unfolded prior to the storm event, but signaled that their abilities to operate under the slowly deteriorating conditions were not as threatening to their interests as Hurricane Sandy.

Participants described Hurricane Sandy and the aftermath as a devastating experience. Despite the overwhelming land damage experienced—lost buildings, fishing equipment, and even homes—anglers responded with a near-immediate return to the water. Many of the interviewees returned to fishing in the Bay well before recovery efforts had taken hold on land. In the minds of many participants, there was no other option but to fish: “You just get right back in [the water], there are a lot of guys who took their home equity loans to put their boats back together.”

Most, if not all, anglers interviewed readily spoke of their observations surrounding shifts in species populations after Hurricane Sandy. One angler identified an absence of fluke in the typical locations. Clammers also noted shifts in the benthic habitat where their catches were harvested, and agreed that their species of catch was still recovering from Hurricane Sandy:

“We were doing about 22–25 million clams per year before the storm. Right now we are at about 16 million. The clams are still there but we figure we lost two years of spawn, we’re just starting to see the thumbnail seeds coming up.” Most anglers who sought striped bass observed that their catch populations suffered after the storm, and that only 3 years later, “They’re [striped bass] gradually coming back and getting back to their natural migration patterns.” One angler attributed the population declines that immediately followed the storm to widespread pollution within estuary tributaries, noting that, “There’s a lot of striped bass that move up rivers and spend the winter there. After Sandy, all these estuaries were loaded with crap—pesticides, paint, whatever was in people’s garages. A lot of those fish that would winter over didn’t winter over in 2012, 2013.” In the eyes of the

anglers, Hurricane Sandy reshaped Raritan's fishery productivity in both the months immediately after the storm, and in the years to follow. In response to these near-term shifts in species populations, our participants made two adaptations to their operations so that their return to the estuary was productive. Changes in fishing locations occurred both immediately after the storm, and into the seasons after. For example, "I didn't fish my area [in the weeks after Sandy]—it was quarantined...I was down South Jersey by Ocean City." Many anglers indicated that they traveled farther distances or out of their home waters, particularly to find fluke. The anglers who continued to fish after the hurricane also changed the species that they harvested. For example, a common, pre-hurricane catch for one fishing co-op was fluke. When there was an absence of fluke after Hurricane Sandy, they harvested what was available: "We have a few boats that go bunker [Atlantic menhaden] fishing in the summer that kept us alive...."

The anglers of our study had a mindset of perseverance that enabled their adaptations. The anglers' similarly believed that the productivity of the HRE would endure, even while recognizing that the ecosystem's integrity was compromised. Many anglers did not view the hurricane as something that permanently lessened their ability to harvest fish, nor as something that lessened the long-term availability of fish to catch. Rather, most of our participants approached the short- and long-term impacts of the hurricane as another change in the ecosystem, akin to the species population fluxes that they had observed in the past: "The old saying is people come in and ask, 'Why don't you have this [type of] fish?' We don't have it because we aren't catching that fish right now. It's called fishing, not catching." The sentiment expressed in this statement, repeated by many of our participants, is indicative of the ecosystem degradation and uncertain fish stocks that anglers have responded to in the past and that they intend to respond to in the future. On the trend of steady ecosystem decline, these anglers will do what they can to keep fishing.

DISCUSSION

The degree to which an estuary is impacted by climatic disturbance depends upon factors other than storm severity. These factors include existing biodiversity and habitat heterogeneity and the amount and type of watershed development. Decreased species and habitat diversity can result in diminished recovery potential when the loss of species functional groups causes drastic alterations in ecosystem functioning (Folke et al. 2004). The presence of high-density urban land cover, wastewater treatment plants, and landfills greatly exacerbate the amount of water quality degradation following major storms (Mallin et al.

2002; Peierls et al. 2003; Paerl et al. 2010). This combination of pressures results in ecosystems with greater vulnerability to disturbances and reduced capacity to generate ecosystem services (Folke et al. 2004). The Hudson-Raritan Estuary is an example of a coastal ecosystem where a dense human population, land use change and associated water quality degradation, and biodiversity loss have resulted in increased vulnerability to recurrent disturbance (EPA 2007; Rothenberger et al. 2014). Our multiyear monitoring dataset as a whole indicates pre-existing degradation in this coastal ecosystem that most likely reflects the numerous municipal discharges to the HRE, the sensitivity of water quality variables to alterations in land use, and reduced nutrient filtering capacity as a result of significant reductions in the Eastern oyster and the sea grass, *Zostera marina* (Campanella et al. 2010; Zu Ermgassen et al. 2013; Rothenberger et al. 2014). Interview responses indicate that anglers are highly aware of ecosystem degradation predating Hurricane Sandy.

The impact of Hurricane Sandy provided an opportunity to explore linkages among long-term coastal ecosystem decline, climatic disturbance, and anglers' perceptions of and responses to ecosystem shifts in a degraded estuary. With 6 years of available background monitoring data, it is possible to separate event-scale responses from long-term trends. Our baseline monitoring data indicate that nutrient over-enrichment, regular algal blooms, and seasonal hypoxia are the current ecosystem regime, or reference condition, in the HRE. The data also indicate that, much like other estuaries impacted by hurricanes (e.g., Peierls et al. 2003; Burkholder et al. 2004; Roman et al. 2005; Wetz and Yoskowitz 2013), the HRE experienced a number of direct alterations to water quality and biota in the aftermath of Hurricane Sandy.

Raritan Bay water clarity was significantly lower and nitrate and SRP concentrations were significantly higher in the year following Hurricane Sandy compared to background levels. These water quality parameters did not return to background levels at monitoring sites until spring 2014. This recovery time is somewhat longer than reports for shallow estuaries frequently disturbed by hurricanes, such as the Albemarle–Pamlico Estuarine System, which are often resilient and quick to recover in water quality and biota following a major storm (i.e., 4–7 weeks to return to background levels; Peierls et al. 2003; Burkholder et al. 2004). These other studies also report an inverse relationship between nutrients and salinity, as substantial rainfall washes in dissolved nutrients and particulate material from connected watersheds (Wetz and Yoskowitz 2013). In contrast, precipitation totals and river discharge associated with Hurricane Sandy were less than expected, and the massive storm surge actually increased salinity in the HRE. Therefore, post-storm changes in water clarity and

nutrients documented in this study were more likely related to high-velocity winds that mixed bottom sediments into the water column and the discharge of raw sewage. The unique characteristics of this storm and watershed may help explain the persistence of post-storm water quality changes. Sewer overflows and the discharge of untreated sewage and street debris following storms have long been considered important sources of pollutants to the HRE (EPA 2007; Reilly et al. 2016). Furthermore, the second largest WWTP in the state of New Jersey (i.e., the Middlesex County wastewater treatment plant) has its outfall located at monitoring site 2, and our dataset indicates that SRP values are significantly higher at this site than at other stations (Rothenberger et al. 2014). Elevated concentrations of phosphorus are characteristic of human and animal wastewater, and can contribute to HABs (Mallin et al., 1999).

Monitoring data indicate that HAB species increased significantly in the year following Hurricane Sandy in association with elevated N and P and reduced water clarity and zooplankton abundance. A significant increase in HAB species occurred in the year following Hurricane Sandy, especially during summer 2013. Several other studies have reported phytoplankton blooms occurring after a lag phase of weeks to months post-hurricane (Peierls et al. 2003; Wetz and Yoskowitz 2013), allowing high turbidity and flushing rates to lessen. Many of the abundant HAB species in the warm season following Hurricane Sandy are known to be mixotrophs, a nutritional strategy that is promoted by low light and during periods when nutrient availability is out of stoichiometric balance (Burkholder et al. 2008). The wind disturbance and sewer overflows associated with Hurricane Sandy resulted in low light conditions, high organic loads, and abundant bacterial and other prey whose growth is stimulated by elevated nutrients. These conditions offered the competitive advantage to small, fast-growing, mixotrophic species, such as *Heterosigma akashiwo*, able to utilize organic matter under low light conditions (Burkholder et al. 2008; Wetz and Yoskowitz 2013).

Another factor possibly contributing to increased abundance of harmful phytoplankton species is the significant post-hurricane decline in zooplankton abundance. Experimental studies in this system and others have shown that the relationship between increased nutrients and increased phytoplankton abundance is magnified in the absence of strong top-down control exerted by zooplankton grazers (Rothenberger and Calomeni 2016). It is not clear, however, whether low zooplankton abundance occurred as a result of poisoning by phycotoxins (Turner and Tester 1997) or other factors (e.g., environmental conditions, pollutants, predation). Experiments do suggest that some of the HAB species that were abundant in summer 2013, such

as *H. akashiwo* and *Oscillatoria* spp., are preferentially avoided, nutritionally inadequate, and/or toxic to zooplankton grazers (Paerl and Fulton 2006; Graham and Strom 2010; Yu et al. 2010). Regardless of the cause, mean total zooplankton abundance in 2013, 2014, 2015, and 2016 is three to six times lower than that from 2010 to 2012. This overall decline is important since zooplankton grazing can contribute to prevention or termination of blooms (Turner and Tester 1997).

Changes in plankton assemblages may also have been associated with changes in higher trophic levels. Although fish and shellfish data included in this study were limited, commercial landings data do indicate a sharp decline in the weight of Atlantic menhaden landings in 2012. The exact cause of this decline is difficult to pinpoint. It is possible that a reduction in fishing effort following Hurricane Sandy resulted in a reduction in annual landings by weight in 2012. However, interview data indicate that anglers continued to fish Atlantic menhaden after the storm, and the decline is more likely the result of a combination of factors, including HABs, decreased zooplankton abundance, and increased contaminant loads. *H. akashiwo* has been known to cause massive fish kills with a not yet fully described mechanism (Dorantes-Aranda et al. 2015), and reduced grazing of HAB species also minimizes the transfer of nutrients and carbon to higher trophic levels (Mitra and Flynn 2006). The significant reduction in zooplankton abundance and increase in wastewater-related contaminants likely further degraded habitat conditions for the planktivorous Atlantic menhaden (Mitra and Flynn 2006; Phillips et al. 2016). Post-hurricane declines in Atlantic menhaden, an important prey item for a number of commercially important predatory fish in the HRE, likely contributed to the striped bass and fluke population declines noted by our angler participants. For example, predator–prey analyses of striped bass and Atlantic menhaden along the east coast have linked deteriorating health of striped bass to declining menhaden abundance (Upphoff 2003). The decline in the blue crab dredge harvest following Hurricane Sandy captured by the landings data is difficult to interpret without additional information, but was supported by the interview findings. Anglers indicated that shellfish populations, particularly blue crabs and clams, were negatively impacted following the storm. Alterations in geomorphology and scouring of sediments are often important factors impacting benthic organisms following hurricanes (e.g., Edmiston et al. 2008). Finally, previous losses of *Z. marina* in the HRE likely contributed to decreased recovery potential of biota after the storm. Survival of estuarine species, such as fluke and blue crab, is enhanced in continuous seagrass beds (Manderson et al. 2000; Hovel and Lipcius 2001). This important connection

was recognized by some of the anglers who participated in our study.

Altogether, monitoring data suggest that biological community structure is not returning to pre-hurricane levels as quickly as water quality. While light and nutrients appear to return to pre-hurricane levels in about one year, alterations to plankton assemblages are longer-lasting. Our ecological observations suggest that increased storm frequency may have profound short- and long-term effects on the plankton supporting the base of the food web. Angler interviews supported this observation, in that they experienced changes in available fish populations well after the hurricane.

Anglers responded to the ecosystem effects of Hurricane Sandy with behavioral adaptations that enabled them to keep fishing. From the angler's perspective, there would be fish to catch, but the location and type of fish available had changed. In order to access harvestable populations, anglers traveled to different locations or pursued different species. Like shrimpers responding to coastal storm damages in Louisiana, our participants faced immense infrastructure challenges with destroyed businesses, docks, and even homes (Ingles and McIlvaine-Newsad 2007). Nonetheless, the anglers who participated in our study expressed a faith in the HRE to provide fishable species. This attitude seemed to be influenced by their knowledge of the ecosystem, and strong affiliations with fishing identities—two occupational characteristics that are supported by previous studies (e.g., Pollnac 1988). Seara et al. (2016) call attention to the fact that anglers of the Raritan Bay region often acted based on their perceived adaptive capacity. Anglers may discuss their confidence in the estuary's productivity not necessarily out of knowledge about the system, but out of a hope that their livelihoods and infrastructure investments will continue vis à vis long-term decline and storm intensification. Our work supports a somewhat counterintuitive behavioral feedback unfolding after hurricane events: some resource users will return to fishing activity after major storm events, even if the ecosystem has not responded to changes induced by the disturbance (Ingles and McIlvaine-Newsad 2007). The combination of ecosystem regime shifts and post-storm fishing pressure feedbacks could lead to further environmental degradation (Folke et al. 2004).

CONCLUSION

The results of this investigation point to several important directions for future research. First, long-term monitoring (i.e., > 10 years) of ecosystem processes (e.g., climatic factors, watershed land use change, water quality) and community characteristics (plankton biomass and species

composition, food web structure, fisheries) is vital for improving our understanding of the full magnitude of human influence on coastal ecosystem functioning. Therefore, we intend to continue collection of environmental data in the HRE. Inclusion of better methods for estimating the abundance and distribution of fish (i.e., sonar technology) will enable more tightly coupled investigations of ecosystem productivity and angler response in future studies. In conclusion, our work contributes an understanding of long-term coastal ecosystem decline in the context of climate-driven changes in coastal storm events. In doing so, we may make more informed inferences of the responses that occurred shortly after the storm, and those that may unfold within long-term recovery.

Acknowledgements Funding support for this research was provided by the Lafayette College Department of Biology. We thank Wayne Leibel in Lafayette's Biology Department for providing comments on earlier versions of this manuscript, Phil Auerbach for technical field support, Penn State Analytical laboratories for total iron analysis, and Captain Mick Trzaska, captain and owner of the CRT II, for transporting us to our sampling sites. Tessa Broholm, Samantha Gleich, Erika Hernandez, Virginia Hoyt, Juliana Ventresca, and Karolina Vera assisted with water sampling and nutrient analysis. We thank two anonymous reviewers for counsel on the manuscript.

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