

Juvenile fish assemblage recruitment dynamics in a mid-Atlantic estuary: before and after Hurricane Sandy

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ABSTRACT: Hurricanes can have long-term effects on estuarine fauna. Understanding these effects is important as climate change may influence the severity and frequency of these storms. On 29 October 2012, Hurricane Sandy, a large storm spanning roughly 1850 km in diameter, made landfall in Brigantine, New Jersey (USA), approximately 20 km south of Barnegat Bay, during an ongoing study of the bay's ichthyofauna, providing an opportunity to observe fish recruitment dynamics coincident with hurricane passage. The objective of this study was to measure variance in the Barnegat Bay pre-Sandy fish assemblage relative to that of 1 and 2 yr after the storm. Barnegat Bay fishes were surveyed with an extensive otter trawl study in April, June, August, and October of 2012 (pre-Sandy), 2013 (1 yr post-Sandy), and 2014 (2 yr post-Sandy). Species composition of the fish assemblage was similar across years. Analyzed structural characteristics (abundance, diversity, richness) of the fish assemblage were occasionally more likely to occur or were larger pre-Sandy and 2 yr post-Sandy relative to 1 yr post-Sandy, but this trend was inconsistent across seasons and between structural characteristics. Furthermore, odds of occurrence and length frequency distributions for many resident species and sentinel fall/winter spawners did not indicate that variance could be definitively explained as a hurricane effect. The capability of fish to relocate from areas of temporarily unsuitable habitat and annual new recruitment of larvae and juveniles to the bay likely contributed to the observed stability in the fish assemblage.

KEY WORDS: Fish assemblage dynamics · Superstorm Sandy · Barnegat Bay · New Jersey · Episodic disturbance event · Lagoonal estuary

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1. INTRODUCTION

On 29 October 2012, Hurricane Sandy, also known as Post-tropical Cyclone Sandy and Superstorm Sandy, made landfall in Brigantine, New Jersey (USA). Prior to landfall, Hurricane Sandy transitioned to post-tropical cyclone status and drastically increased in size by merging with an early winter storm system—hence the 'Superstorm' designation (Halverson & Rabenhorst 2013, National Oceanic and Atmospheric Administration 2013). The immense diameter of the storm (1850 km) and eastward approach to the coastline, combined with a spring high tide, produced record breaking maximum water lev-

els (Hall & Sobel 2013, Forbes et al. 2014) which surpassed 2.5 m in some New Jersey coastal bays (U.S. Geological Survey 2019) and resulted in multiple temporary breaches of the barrier islands (Blake et al. 2013, Parrish et al. 2016). The magnitude of this storm surge caused severe dune erosion (Coastal Research Center 2012, Miselis et al. 2016), extensive damage to coastal property (Blake et al. 2013), and large quantities of natural and manmade debris to wash into coastal waters (Bilinski et al. 2015).

Episodic events, such as hurricanes, can have short-term and long-term effects on marine (Kaufman 1983, Fenner 1991, Heupel et al. 2003, Udyawer et al. 2013, Meléndez-Vazquez et al. 2019) and estuarine

fauna (Boesch et al. 1976, Roman et al. 2005, Paperno et al. 2006, Stevens et al. 2006, Biggs et al. 2018, Massie et al. 2019). In the short-term aftermath of Hurricanes Agnes and Isabel, juvenile freshwater and estuarine fishes within the Chesapeake Bay and tributaries shifted downstream due to a large volume of freshwater inflow and subsequent reductions in salinity (Hoagman & Wilson 1977, Ritchie 1977, Houde et al. 2005). Following the passage of Hurricane Hugo, hypoxic conditions in the Ashley River and nearby marsh creeks (South Carolina) resulted in massive fish kills (Knott & Martore 1991). However, in Barnegat Bay (New Jersey), low salinity and dissolved oxygen (DO) conditions during and after the short duration of Hurricane Sandy were absent (Taghon et al. 2017), and qualitative observations immediately after the storm failed to identify population-level impacts or instances of mass fish mortality (Bilinski et al. 2015). Delayed-onset, long-term hurricane effects on the fish assemblage dynamics in this estuarine system, emerging from the modification or destruction of essential habitat, alteration of estuarine larval supply, or a combination of these or other processes that have the potential to influence fish distributions over extended time scales, are unknown.

While previous observations of fish response to hurricane passage have been on the scale of days to weeks, interannual trends associated with these events are rarely documented. Investigation of this time scale for estuaries is critical given that they serve as nursery habitat for ecologically and economically relevant fishes and invertebrates (McHugh 1976, Potter et al. 1990, Able & Fahay 1998, 2010, Beck et al. 2001, Wasserman & Strydom 2011, Tournois et al. 2017). Shallow lagoonal estuaries (e.g. Barnegat Bay) are particularly vulnerable to perturbations from episodic storm events, which often produce extensive storm surge, sediment deposition, and shoreline erosion (Kennish & Paerl 2010) and in turn may influence the recruitment of larval and juvenile fishes to these estuaries and resulting fish assemblages. Understanding the ecological impact of episodic tropical cyclones within lagoonal estuaries is becoming increasingly important as climate change may influence the severity, frequency, and path of these storms (Mann & Emanuel 2006, Knutson et al. 2010, Grossmann & Morgan 2011, Colbert et al. 2013, Walsh et al. 2016).

Given that controlled experiments on the effects of such large spatial scale disturbance events are nearly impossible to arrange, we capitalized on a unique opportunity to track structural characteristics (abundance, diversity, richness, composition) of the estuar-

ine fish assemblage inhabiting Barnegat Bay through and beyond such an event as a baseline measure of assemblage variance and trajectory. In this we followed recommendations for an increased application of observational approaches to marine ecology by using generalized linear regression models to partition variance rather than testing significance (Bolker et al. 2009, Beninger et al. 2012, Boldina & Beninger 2016).

2. MATERIALS AND METHODS

2.1. Study area

Barnegat Bay is a shallow (mean water depth <2 m) lagoon-type (Kennish & Paerl 2010, Whitfield & Elliott 2011) estuary that extends nearly 70 km along the coast of New Jersey (Fig. 1). The bay is directly connected to the Atlantic Ocean via the Little Egg and Barnegat inlets and indirectly connected to the ocean via the Point Pleasant Canal. The canal joins the northern bay and the Manasquan River, which ultimately drains into the ocean. Freshwater input to the system is dominated by tributaries located along the western shore of the bay (Kennish 2001). Throughout most of Barnegat Bay, the water column is well mixed, but in deeper waters (e.g. the Intra-coastal Waterway), 2-layered flow is apparent (Chizmadia et al. 1984). The modeled estuarine residence time ranges from 0–50 d and is sensitive to wind speed, tides, time of year, and location within the bay (Defne & Ganju 2015).

2.2. Hurricane Sandy

On 29 October 2012, Hurricane Sandy made landfall less than 20 km from the southern end of Barnegat Bay (Fig. 1) (Halverson & Rabenhorst 2013, National Oceanic and Atmospheric Administration 2013). The landfall location and the storm's perpendicular approach to the coastline placed Barnegat Bay on the right side of the storm track where winds are often strongest (Hall & Sobel 2013, Halverson & Rabenhorst 2013), causing this region to be one of the most severely impacted by the storm (Bilinski et al. 2015).

Storm surge magnitude within the bay varied regionally, with maximum recorded water levels reaching 2.1 m (relative to NAVD 88) in the northern bay, 1.7 m in the central bay, and 2.0 m in the southern bay (U.S. Geological Survey 2019). These maximum water levels observed in Barnegat Bay during Sandy were

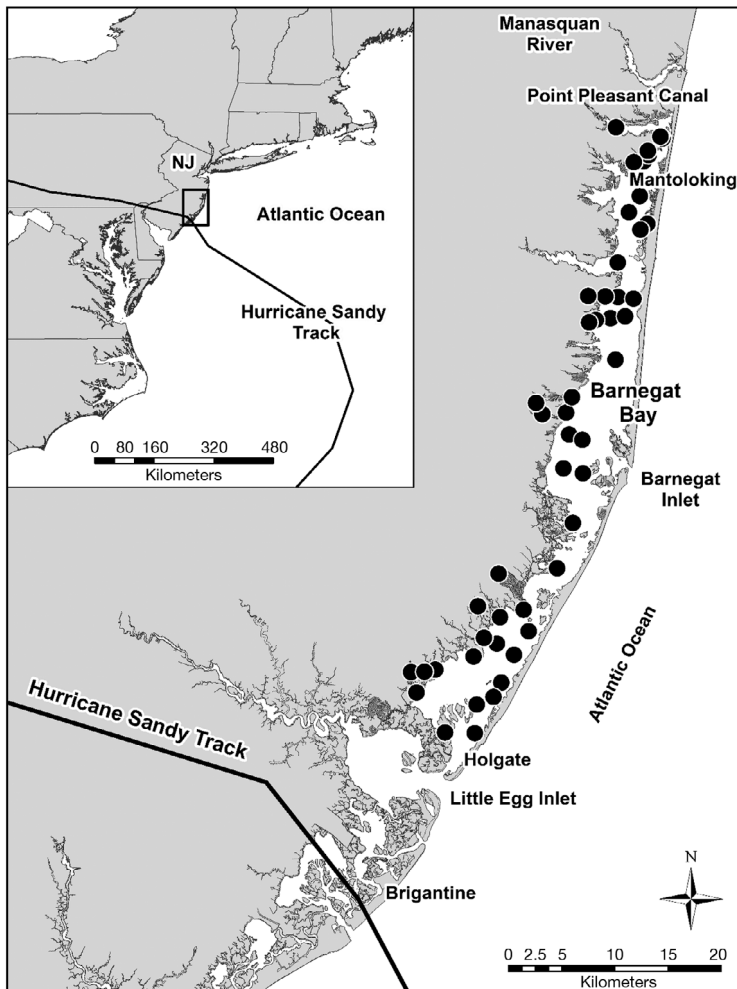


Fig. 1. Locations of sampling sites and relevant landmarks within Barnegat Bay, New Jersey (NJ), USA, where Hurricane Sandy (diameter roughly 1850 km) made landfall in Brigantine on 29 October 2012. See Table 1 for additional sampling details

comparable to observed tidal heights from previous storms that have impacted the New Jersey coastline (Psuty & Ofiara 2002, Able 2015). During the storm, a new inlet on the barrier island was temporarily formed at Mantoloking and closed by 4 November 2012 (Federal Emergency Management Agency 2013, Aretxabaleta et al. 2014). The ocean temporarily breached the barrier island at various other locations including at Holgate on the southernmost end of Long Beach Island (Bishop et al. 2016).

2.3. Sampling protocol

Otter trawl sampling occurred in April (spring), June (early summer), August (late summer), and Oc-

tober (fall) in each of 3 years (2012–2014). October 2012 sampling was completed before Hurricane Sandy made landfall in New Jersey and the next sampling event following Hurricane Sandy was 6 mo later in April of 2013. Therefore, 2012 represents pre-Sandy samples and 2013 and 2014 represent roughly 6 mo to 1 yr and 1.5 to 2 yr post-Sandy (YPS) samples, respectively. For brevity, the 2013 and 2014 samples will be referred to as '1 YPS' and '2 YPS', respectively.

Sampling consisted of three 120 s otter trawl net tows (4.9 m headrope, 19 mm mesh wings, 6.3 mm mesh codend liner) at each of 49 sites, spanning the length of the bay, during every sampling event (Fig. 1, Table 1). Trawls of this size selectively target small fishes (<200 mm) (Olin & Malinen 2003), which in Barnegat Bay mainly encompasses juvenile fishes, but also includes species with small adult stages (Able & Fahay 2010). Sampling sites were selected based on previous studies (e.g. Sugihara et al. 1979, Jivoff & Able 2001, Valenti et al. 2017) and reconnaissance sampling. From each tow, all fishes were identified and counted, and the lengths (total or fork length in mm, depending on species) of the first 20 individuals of each species were recorded. Environmental parameters (water temperature, salinity, DO, pH) were measured using a handheld Yellow Springs Instrument, and the water depth was recorded every time a site was sampled. Due to the immense

size of the hurricane (spanned from Florida to Maine) (Forbes et al. 2014), control sites (i.e. those unaffected by the hurricane) were not available for inclusion in this study.

2.4. Data analysis

2.4.1. Abundance

Overall catch per unit effort. Prior to analysis, the abundance data from the 3 replicate trawl tows at each site were combined, regardless of species, and standardized to overall catch per unit effort (CPUE; number fish s^{-1}). Only data on fish that could be identified to species were used in this and all other analy-

Table 1. Effort (tows and sampling events) and environmental parameters for the months and years sampled (2012: pre-Sandy; 2013: 1 yr post-Sandy; 2014: 2 yr post-Sandy). Environmental parameters are the means and ranges, respectively. See Fig. 1 for sampling site locations

Month/year sampled	Tows (n)	Sampling events (n)	Temperature (°C)	Salinity	Dissolved oxygen (mg l ⁻¹)	pH	Water depth (m)
April							
2012	136	45	15.2 11.4–21.6	25.85 19.55–30.60	7.47 4.31–10.19	7.78 6.10–8.22	1.7 0.6–5.5
2013	144	48	12.7 8.8–17.7	24.95 16.25–30.65	8.97 1.12–12.48	7.81 7.17–8.41	1.9 0.7–5.0
2014	144	48	14.8 10.8–19.4	22.61 12.09–30.13	8.10 4.14–10.86	7.71 6.87–8.20	1.8 0.8–5.2
June							
2012	142	47	23.1 17.4–30.0	24.41 14.86–30.49	6.13 0.30–14.89	7.70 6.66–8.39	1.8 0.6–6.2
2013	146	49	22.7 17.4–27.4	21.99 9.45–28.53	5.30 0.13–7.65	7.62 6.58–8.13	1.7 0.8–5.5
2014	143	48	25.3 17.8–28.8	23.61 13.24–29.85	6.28 0.34–8.99	7.61 6.78–8.17	1.7 0.6–5.4
August							
2012	147	49	25.2 22.7–29.3	25.72 15.38–31.48	5.49 0.06–11.18	7.68 6.67–8.35	1.9 0.6–5.5
2013	147	49	24.0 21.9–30.6	24.97 14.42–31.07	5.76 0.16–8.42	7.75 6.95–8.17	1.9 0.8–5.0
2014	142	48	24.7 21.6–30.6	22.15 11.88–28.98	5.49 0.02–8.70	7.64 6.75–8.18	1.7 0.8–4.7
October							
2012	147	49	15.9 14.6–20.6	25.65 18.24–31.36	7.31 0.13–10.25	7.84 7.17–8.15	1.8 0.9–5.5
2013	147	49	16.6 14.5–22.4	26.84 22.15–30.21	7.06 1.15–9.54	7.76 5.67–8.20	1.9 0.9–5.2
2014	146	49	18.6 16.6–20.9	25.55 16.67–30.48	6.93 3.29–8.84	7.76 7.13–8.09	1.9 0.9–5.7
Annual totals and means							
2012	572	190	19.9 11.4–30.0	25.41 14.86–31.48	6.58 0.06–14.89	7.75 6.10–8.39	1.8 0.6–6.2
2013	584	195	19.0 8.8–30.6	24.69 9.45–31.07	6.76 0.13–12.48	7.73 5.67–8.41	1.9 0.7–5.5
2014	575	193	20.8 10.8–30.6	23.49 11.88–30.48	6.70 0.02–10.86	7.68 6.75–8.20	1.8 0.6–5.7
Seasonal totals and means							
April	424	141	14.2 8.8–21.6	24.44 12.09–30.65	8.19 1.12–12.48	7.77 6.10–8.41	1.8 0.6–5.5
June	431	144	23.7 17.4–30.0	23.32 9.45–30.49	5.90 0.13–14.89	7.64 6.58–8.39	1.7 0.6–6.2
August	436	146	24.7 21.6–30.6	24.29 11.88–31.48	5.58 0.02–11.18	7.69 6.67–8.35	1.8 0.6–5.5
October	440	147	17.1 14.5–22.4	26.01 16.67–31.36	7.10 0.13–10.25	7.79 5.67–8.20	1.9 0.9–5.7

ses in this study. Due to the large number of zero-catch sampling events in the data set (97 out of 578 events, i.e. 17%), a Bernoulli and gamma hurdle model, commonly referred to as the zero-altered

gamma (ZAG) model, was fit to the overall CPUE data. This model assumes that 2 processes govern the data; one determines if fish will be present or absent (i.e. CPUE > 0 or CPUE = 0; Bernoulli part of the

model) and the second influences the CPUE magnitude, given that fish are present (i.e. $CPUE > 0$; gamma part of the model) (Zuur & Ieno 2016). For the Bernoulli part of the model, the overall CPUE data were converted to presence or absence data and used as the response variable. For the gamma part of the model, only sampling observations with non-zero overall CPUE values were used for the response variable and all regression parameters had at least 20 observations (Zuur & Ieno 2016). Year and month were categorical covariates in both the Bernoulli and gamma models, but the interaction term was only included in the gamma model based on model selection using Akaike's information criterion (AIC) (Burnham & Anderson 2004). A site random effect was included in both the Bernoulli and gamma models. The overall CPUE ZAG generalized linear mixed model (GLMM), and all other GLMMs in this study, were run using the 'lme4' package (version 1.1-21) (Bates et al. 2015) in RStudio (version 1.2.1335) (RStudio Team 2018). All other analyses in this study were also performed in RStudio.

Species-specific CPUE. In addition to overall CPUE, the species-specific CPUEs of the 12 most abundant species collected were analyzed. These 12 species were characterized based on their estuarine usage, year classes represented in the samples, and spawning duration. Since responses to hurricanes are variable, a consistent response from species with similar characteristics would assist in discerning hurricane effects from typical interannual variability. The species-specific CPUE data were converted to presence or absence data and used as the response variable in species-specific Bernoulli GLMMs. For all models, year and month were categorical covariates, site was included as a random effect, and the interaction term was not included based on model selection using AIC. Yearly length frequency plots, coded by month, were also created for these 12 species using 'ggplot2' (version 3.1.1) (Wickham 2016), 'gridExtra' (version 2.3) (Auguie 2017), and 'gtable' (version 0.3.0) (Wickham & Pedersen 2019).

Post hoc analyses compared variables of interest in the overall CPUE hurdle model and species-specific CPUE models using the 'emmeans' package (version 1.3.5) (Lenth 2019). Reported ratios and confidence limits from the Bernoulli and gamma GLMMs were back-transformed from the logit and log scales, respectively; however, Z-tests were performed on the logit and log scales (Bolker et al. 2009). Confidence intervals and p-values were adjusted for multiple comparisons using Tukey's honest significant difference method.

2.4.2. Diversity

The species-specific CPUE data were used to calculate Shannon diversity, with the 'vegan' package (version 2.5-4) (Oksanen et al. 2019), for each sampling event that collected at least 1 individual (diversity values are only statistically defined for samples with 1 or more individuals; Stevens 2009). This resulted in 481 observations that were used in the diversity analysis (97 out of 578 events collected no fish). Given the large number of zero diversity sampling events (i.e. those where only 1 species was collected) in the data set (96 out of 481 events, i.e. 20%), a ZAG model was fit to the diversity data. Like the CPUE model, this model assumes that 2 processes govern the data; one determines if diversity will be present or absent (i.e. $diversity > 0$ or $diversity = 0$; Bernoulli part of the model) and the second influences the magnitude of diversity, given that diversity is present (i.e. $diversity > 0$; gamma part of the model). For the Bernoulli part of the model, the diversity data were converted to presence or absence data and used as the response variable. For the gamma part of the model, only sampling observations with non-zero diversity values were used for the response variable and all regression parameters had at least 13 observations. For both parts of the model, year, month, and the interaction term were categorical covariates and site was included as a random effect.

2.4.3. Richness

Richness, the number of species collected, was also assessed as an indicator of assemblage biodiversity. Richness was standardized by totaling the number of different species collected in the replicate trawl tows at each site and dividing by the number of tows performed ($\text{number of species collected tow}^{-1}$). Due to the large number of zero-catch sampling events in the data set (17%), a ZAG model was fit to the standardized richness data in the same manner as for CPUE and diversity. For the gamma part of the model, all regression parameters had at least 20 observations. Year and month were categorical covariates in both the Bernoulli and gamma models, but the interaction term was only included in the gamma model based on model selection using AIC. A site random effect was included in both the Bernoulli and gamma models. Post hoc analyses compared variables of interest in the diversity and richness models following the protocol previously described for the CPUE models.

2.4.4. Assemblage composition

Non-metric multidimensional scaling (NMDS), a robust, unconstrained ordination technique (Minchin 1987), was used to visualize latent dissimilarities in assemblage composition across the years and months sampled. The abundance data from sites with the same habitat characteristics sampled within the same year and month were combined and standardized to CPUE, resulting in 48 sampling observations. These CPUE values were then root-root transformed and dissimilarities were calculated on the Bray-Curtis index and projected as NMDS with the 'vegan' package. An interpretable, convergent NMDS solution was reached using 3 dimensions (i.e. $k = 3$) (Clarke 1993), and the results of the first 2 dimensions were displayed as sample and species plots. The axes in the sample plot were centered, rotated so the variance of the observations was maximized along the first axis, and scaled so that 1 unit change indicates a halving of assemblage similarity between sampling observations. Species locations in the species plot are weighted averages based on the CPUE data.

3. RESULTS

3.1. Environmental parameters

The measured environmental parameters were fairly consistent across years and seasons, with the exception of seasonal shifts in water temperature and DO (Table 1). Water temperature increased from April to August and began to decrease in October. DO followed the opposite trend, decreasing from April to August and increasing slightly in October.

3.2. Abundance

3.2.1. Overall CPUE

Nearly 34 000 fish were collected during the 3 yr of sampling. Over 50% of those individuals were caught during 2014 and nearly 85% were captured during the late summer and fall months of all years (Table 2). The odds of collecting fish in any given trawl tow (CPUE occurrence odds) ranged from

Table 2. Total number of fish collected, observed species richness, and the mean \pm SE for catch per unit effort (CPUE), Shannon diversity, and standardized richness over the months and years sampled (2012: pre-Sandy; 2013: 1 yr post-Sandy; 2014: 2 yr post-Sandy)

Month/year sampled	Fish (n)	Richness (n)	CPUE (n fish s^{-1})	Diversity	Standardized richness (n species tow^{-1})
April					
2012	593	21	0.037 \pm 0.013	0.438 \pm 0.072	0.524 \pm 0.082
2013	97	21	0.006 \pm 0.002	0.598 \pm 0.124	0.319 \pm 0.071
2014	158	23	0.009 \pm 0.002	0.729 \pm 0.077	0.576 \pm 0.076
June					
2012	2041	26	0.119 \pm 0.040	0.735 \pm 0.082	0.959 \pm 0.105
2013	536	25	0.030 \pm 0.005	0.748 \pm 0.087	0.966 \pm 0.105
2014	1908	25	0.111 \pm 0.027	0.882 \pm 0.076	1.257 \pm 0.119
August					
2012	4692	34	0.266 \pm 0.067	0.775 \pm 0.073	1.544 \pm 0.133
2013	2945	33	0.167 \pm 0.028	0.392 \pm 0.067	0.939 \pm 0.099
2014	8676	41	0.591 \pm 0.264	0.818 \pm 0.083	2.066 \pm 0.199
October					
2012	2862	25	0.162 \pm 0.065	0.635 \pm 0.069	0.864 \pm 0.079
2013	1896	20	0.108 \pm 0.060	0.349 \pm 0.072	0.537 \pm 0.072
2014	7589	41	0.463 \pm 0.123	0.827 \pm 0.071	1.840 \pm 0.144
Annual totals and means					
2012	10188	50	0.148 \pm 0.027	0.664 \pm 0.035	0.983 \pm 0.058
2013	5474	47	0.078 \pm 0.017	0.514 \pm 0.038	0.692 \pm 0.048
2014	18331	58	0.294 \pm 0.074	0.819 \pm 0.036	1.437 \pm 0.082
Seasonal totals and means					
April	848	35	0.017 \pm 0.005	0.592 \pm 0.039	0.472 \pm 0.045
June	4485	34	0.086 \pm 0.016	0.788 \pm 0.045	1.061 \pm 0.064
August	16313	53	0.340 \pm 0.091	0.664 \pm 0.045	1.513 \pm 0.093
October	12347	49	0.244 \pm 0.052	0.620 \pm 0.042	1.081 \pm 0.075

roughly equal to slightly higher pre-Sandy (2012) than 1 YPS (2013) (odds ratio [OR] = 1.881, 95% confidence interval [CI]: 0.946–3.740, $p = 0.079$) and were consistently lower 1 YPS relative to 2 YPS (2014) (OR = 0.342, CI: 0.164–0.714, $p = 0.002$; see Table S1 in the Supplement at www.int-res.com/articles/suppl/m641p177_supp.pdf). CPUE occurrence odds pre-Sandy compared to 2 YPS were variable and showed no consistent trend (OR = 0.643, CI: 0.296–1.396, $p = 0.376$).

Within the month of April, CPUE was larger pre-Sandy compared to 1 YPS (ratio [R] = 3.526, CI: 1.507–8.250, $p = 0.002$) or 2 YPS (R = 2.837, CI: 1.340–6.008, $p = 0.003$; Table S1). Comparison of April CPUE values between 1 and 2 YPS yielded no definitive trend between years (R = 0.805, CI: 0.361–1.793, $p = 0.800$). The June CPUE values for pre-Sandy ($p < 0.001$) and 2 YPS ($p < 0.001$) were consistently larger than 1 YPS CPUE values. In August, 1 YPS CPUE was smaller than the 2 YPS CPUE (R = 0.502, CI: 0.271–0.931, $p = 0.024$). Two YPS October CPUE was notably larger relative to pre-Sandy ($p < 0.001$) or 1 YPS CPUE ($p < 0.001$). No trend was observed in the October pre-Sandy and 1 YPS CPUE comparison (R = 1.572, CI: 0.804–3.073, $p = 0.253$; Table S1).

3.2.2. Species-specific CPUE

The 12 most abundant species collected accounted for 97% of the total catch. Bay anchovy *Anchoa mitchilli* was the most abundant species collected overall, accounting for approximately 57% of the total catch and dominating catches in every year, regardless of month, with the exception of April 2013 and April 2014 when Atlantic herring *Clupea harengus* and naked goby *Gobiosoma bosc* were the most abundant species collected, respectively. After *A. mitchilli*, Atlantic silverside *Menidia menidia* (17%), fourspine stickleback *Apeltes quadracus* (6%), and northern pipefish *Syngnathus fuscus* (4%) were the next most abundant species collected (Table 3).

No consistent trends in annual CPUE occurrence odds were observed for species with similar estuarine usage, year classes represented, or spawning durations (Table 4). Young of the year (YOY) were collected for all of the 12 most abundant species, and most of these species had odds of occurrence that were influenced by year, although the odds of occurrence for *Anchoa mitchilli* and Atlantic menhaden *Brevoortia tyrannus* were fairly uniform across years. *G. bosc*, *M. menidia*, Atlantic croaker *Micropogonias undulatus*, oyster toadfish *Opsanus*

tau, summer flounder *Paralichthys dentatus*, and winter flounder *Pseudopleuronectes americanus* had higher CPUE occurrence odds 2 YPS relative to pre-Sandy or 1 YPS and inconsistent CPUE occurrence odds pre-Sandy relative to 1 YPS. The odds of occurrence for *Apeltes quadracus* and silver perch *Bairdiella chrysoura* were higher pre-Sandy and 2 YPS compared to 1 YPS, with no consistent trend between pre-Sandy and 2 YPS odds. Spot *Leiostomus xanthurus* and *S. fuscus* CPUE occurrence odds varied for all years, with the exception of *L. xanthurus* odds 1 YPS compared to 2 YPS (Table 4). Trends in seasonal CPUE occurrence odds were observed for many species, but these trends varied for species with similar estuarine usage, year classes represented, and spawning durations (Table S2).

No consistent patterns in annual length frequency distributions were observed for species characterized as estuarine residents or transients or species with similar year classes represented or spawning duration (Figs. 2, 3, & 4). For *G. bosc*, *A. mitchilli*, *Paralichthys dentatus*, and *S. fuscus*, length frequency distribution patterns were similar among years (Figs. 2B, 3A,D, & 4D, respectively). One YPS *Apeltes quadracus* CPUE was low relative to pre-Sandy and 2 YPS abundances, especially in August and October when no individuals were collected (Table 3); this absence of individuals is reflected in the punctuated length frequency distribution 1 YPS (Fig. 2A). *O. tau* and *Pseudopleuronectes americanus* <50 mm were absent or less abundant pre-Sandy and 1 YPS compared to 2 YPS (Fig. 2C,D, respectively). Individuals of *B. chrysoura* >90 mm were rare in 1 YPS samples (Fig. 3B). Although *M. undulatus* was most abundant 2 YPS (Table 3), individuals >60 mm, which were collected pre-Sandy and 1 YPS in August and October, were absent (Fig. 3C). *Brevoortia tyrannus* length frequency distributions were fairly similar across years, but individuals <35 mm were absent pre-Sandy while individuals >130 mm were absent 2 YPS (Fig. 4A). *L. xanthurus* had highly variable length frequency distributions among years (Fig. 4B). Length frequency distributions for *Menidia menidia* 1 and 2 YPS were similar; however, in pre-Sandy samples, individuals <30 mm were absent (Fig. 4C).

3.3. Diversity

The odds of observing diversity (diversity occurrence odds) did not vary annually within April or June, but did vary annually in August and October (Table S3). In August and October, the odds of diver-

Table 3. Mean catch per unit effort (number of fish per 360 s) for all species collected over the months and years sampled (2012: pre-Sandy; 2013: 1 yr post-Sandy; 2014: 2 yr post-Sandy). Superscripts on scientific names indicate that the species is unique to a particular year (2: 2012; 3: 2013; 4: 2014). Estuarine usage based on Kennish & Lutz (1984) and Able & Fahay (2010). Species in the non-metric multidimensional scaling (NMDS) plot were coded by number for clarity (see Fig. 5); pairings are listed here

Scientific name	Common name	NMDS	Estuarine usage	April			June			August			October		
				2012	2013	2014	2012	2013	2014	2012	2013	2014	2012	2013	2014
<i>Alosa pseudoharengus</i> ²	Alewife	1	Transient	0.000	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Anchoa hepsetus</i>	Striped anchovy	2	Transient	0.000	0.000	0.000	0.000	0.000	0.000	1.265	0.123	0.563	0.000	0.020	0.082
<i>Anchoa mitchilli</i>	Bay anchovy	3	Transient	3.713	0.104	0.083	12.974	3.612	8.896	72.253	55.405	80.838	51.760	34.431	74.276
<i>Anguilla rostrata</i>	American eel	4	Transient	0.000	0.021	0.083	0.186	0.123	0.261	0.184	0.081	0.031	0.000	0.000	0.071
<i>Apeltes quadracus</i>	Fourspine stickleback	5	Resident	0.644	0.167	0.250	10.766	0.204	6.269	0.061	0.000	18.594	0.408	0.000	19.235
<i>Archosargus probatocephalus</i> ²	Sheepshead	6	Southern stray	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000
<i>Astroscopus guttatus</i> ³	Northern stargazer	7	Shelf stray	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.000	0.000
<i>Bairdiella chrysoura</i>	Silver perch	8	Transient	0.022	0.000	0.000	0.000	0.000	0.000	9.503	0.367	4.969	2.265	0.429	3.531
<i>Brevoortia tyrannus</i>	Atlantic menhaden	9	Transient	2.844	0.083	0.000	7.697	1.020	3.792	0.123	0.367	0.625	0.618	0.286	0.143
<i>Caranx crysos</i> ⁴	Blue runner	10	Southern stray	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.042	0.000	0.000	0.000
<i>Caranx hippos</i>	Crevalle jack	11	Southern stray	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.083	0.000	0.021	0.000
<i>Centropristis striata</i>	Black seabass	12	Transient	0.067	0.000	0.104	0.213	0.102	0.166	0.327	0.061	0.385	0.020	0.000	0.204
<i>Chaetodon ocellatus</i> ⁴	Spotfin butterflyfish	13	Southern stray	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.031	0.000	0.000	0.020
<i>Chasmodes bosquianus</i>	Striped blenny	14	Resident	0.022	0.000	0.000	0.021	0.000	0.000	0.020	0.020	0.354	0.020	0.020	0.123
<i>Chilomycterus schoepfi</i>	Striped burrfish	15	Transient	0.000	0.000	0.000	0.000	0.020	0.083	0.082	0.000	0.219	0.000	0.000	0.000
<i>Clupea harengus</i>	Atlantic herring	16	Transient	0.044	0.500	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Conger oceanicus</i> ²	Conger eel	17	Transient	0.022	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Cynoscion regalis</i>	Weakfish	18	Transient	0.000	0.000	0.000	0.000	0.000	0.000	0.408	0.102	0.188	0.020	0.000	0.082
<i>Dactylopterus volitans</i> ³	Flying gurnard	19	Southern stray	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.000	0.000
<i>Dasyatis say</i>	Bluntnose stingray	20	Southern stray	0.000	0.000	0.000	0.000	0.000	0.000	0.041	0.020	0.000	0.000	0.000	0.000
<i>Etropus microstomus</i>	Smallmouth flounder	21	Transient	0.000	0.021	0.063	0.000	0.000	0.103	0.000	0.000	0.021	0.020	0.000	0.041
<i>Eucinostomus argenteus</i> ²	Spotfin mojarra	22	Southern stray	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000
<i>Fundulus heteroclitus</i>	Mummichog	23	Resident	0.844	0.167	0.208	0.032	0.020	0.167	0.000	0.000	0.438	0.020	0.000	0.092
<i>Fundulus luciae</i> ³	Spotfin killifish	24	Resident	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Fundulus majalis</i> ⁴	Striped killifish	25	Resident	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Gadus morhua</i> ⁴	Atlantic Cod	26	Transient	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Gobiosox strumosus</i> ⁴	Skilletfish	27	Southern stray	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.063	0.000	0.000	0.082
<i>Gobiosoma bosc</i>	Naked goby	28	Resident	0.044	0.104	0.333	0.064	0.020	0.318	0.388	0.796	2.698	0.041	0.143	2.042
<i>Gobiosoma ginsburgi</i>	Seaboard goby	29	Resident	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.061	0.250	0.000	0.000	0.725
<i>Hippocampus erectus</i>	Lined seahorse	30	Transient	0.089	0.000	0.042	0.213	0.020	0.062	0.020	0.000	0.229	0.041	0.000	0.163
<i>Hypobliennius hentz</i>	Feather blenny	31	Resident	0.022	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.208	0.000	0.000	0.123
<i>Ictalurus punctatus</i> ³	Channel catfish	32	Resident	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.000	0.000
<i>Lagodon rhomboides</i>	Pinfish	33	Transient	0.000	0.000	0.000	0.234	0.041	0.000	0.306	0.082	0.021	0.000	0.000	0.000
<i>Leiostomus xanthurus</i>	Spot	34	Transient	3.467	0.000	0.021	5.654	0.388	0.524	6.751	0.204	0.000	0.735	0.061	0.000
<i>Lepomis gibbosus</i> ⁴	Pumpkinseed	35	Resident	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.125	0.000	0.000	0.062

Table continued on next page

Table 3 (continued)

Scientific name	Common name	NMDS	Estuarine usage	April		June		August		October					
				2012	2013	2014	2012	2013	2014	2012	2013	2014			
<i>Lepomis macrochirus</i> ⁴	Bluegill	36	Resident	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.021	
<i>Leucoraja erinacea</i> ⁴	Little skate	37	Shelf stray	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020
<i>Lucania parva</i>	Rainwater killifish	38	Resident	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.000	0.265	0.000	0.000	0.051
<i>Lutjanus griseus</i> ⁴	Gray snapper	39	Southern stray	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.041
<i>Menidia beryllina</i>	Inland silverside	40	Resident	0.017	0.063	0.000	0.000	0.000	0.000	0.000	0.000	0.646	0.000	0.000	0.000
<i>Menidia menidia</i>	Atlantic silverside	41	Transient	0.222	0.021	0.229	0.213	0.388	4.651	0.449	0.633	84.896	0.102	2.653	49.133
<i>Menticirrhus saxatilis</i>	Northern kingfish	42	Transient	0.000	0.021	0.000	0.000	0.000	0.000	0.039	0.061	0.169	0.061	0.000	0.020
<i>Micropogonias thalassinus</i>	Green goby	43	Southern stray	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.041	0.042	0.020	0.020	0.000
<i>Micropogonias undulatus</i>	Atlantic croaker	44	Transient	0.111	0.063	0.000	0.075	0.102	0.000	0.102	0.020	0.000	0.287	0.041	3.898
<i>Morone americana</i>	White perch	45	Resident	0.000	0.083	0.000	0.000	0.000	0.042	0.041	0.000	0.000	0.000	0.000	0.166
<i>Morone saxatilis</i> ⁴	Striped bass	46	Transient	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Mugil cephalus</i> ²	Striped mullet	47	Transient	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000
<i>Mugil curema</i>	White mullet	48	Transient	0.000	0.000	0.000	0.000	0.000	0.000	0.082	0.000	0.083	0.000	0.000	0.000
<i>Mustelus canis</i>	Smooth dogfish	49	Transient	0.000	0.000	0.000	0.021	0.020	0.000	0.061	0.041	0.021	0.000	0.000	0.020
<i>Mycteroperca microlepis</i> ³	Gag	50	Southern stray	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.000	0.000
<i>Opsanus tau</i>	Oyster toadfish	51	Resident	0.000	0.104	0.021	0.149	0.143	0.323	0.224	0.286	1.386	0.163	0.000	0.469
<i>Paralichthys dentatus</i>	Summer flounder	52	Transient	0.044	0.063	0.104	0.319	0.388	1.037	0.306	0.123	0.919	0.347	0.061	0.245
<i>Peprilus triacanthus</i>	Butterfish	53	Shelf stray	0.000	0.000	0.000	0.021	0.020	0.000	0.000	0.020	0.188	0.000	0.041	0.041
<i>Perca flavescens</i> ²	Yellow perch	54	Resident	0.000	0.000	0.000	0.027	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Pogonias cromis</i>	Black drum	55	Transient	0.049	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.021	0.000	0.000	0.020
<i>Pollachius virens</i>	Pollock	56	Transient	0.000	0.042	0.167	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>Pomatomus saltatrix</i>	Bluefish	57	Transient	0.000	0.000	0.000	0.043	0.204	0.146	0.265	0.183	0.115	0.000	0.020	0.061
<i>Prionotus carolinus</i> ⁴	Northern searobin	58	Transient	0.000	0.000	0.042	0.000	0.000	0.020	0.000	0.000	0.021	0.000	0.000	0.020
<i>Pseudopleuronectes americanus</i>	Winter flounder	59	Resident	0.200	0.042	0.104	1.463	3.061	10.062	0.000	0.020	1.052	0.000	0.000	0.367
<i>Scophthalmus aquosus</i> ⁴	Windowpane	60	Transient	0.000	0.000	0.083	0.000	0.000	0.042	0.000	0.000	0.000	0.000	0.000	0.000
<i>Selene setapinnis</i>	Atlantic moonfish	61	Southern stray	0.000	0.000	0.000	0.000	0.000	0.000	0.061	0.000	0.000	0.041	0.020	0.020
<i>Selene vomer</i>	Lookdown	62	Southern stray	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.063	0.000	0.041	0.000
<i>Sphoeroides maculatus</i>	Northern puffer	63	Transient	0.000	0.000	0.000	0.106	0.184	1.125	0.243	0.102	0.803	0.000	0.000	0.082
<i>Sthenotomus chrysops</i>	Scup	64	Transient	0.000	0.000	0.000	0.000	0.000	0.042	0.041	0.020	0.000	0.000	0.000	0.000
<i>Strongylura marina</i> ⁴	Atlantic needlefish	65	Transient	0.000	0.000	0.000	0.000	0.000	0.041	0.000	0.000	0.000	0.000	0.000	0.000
<i>Symphurus plagiusa</i> ⁴	Blackcheek tonguefish	66	Southern stray	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.041
<i>Syngnathus fuscus</i>	Northern pipefish	67	Transient	0.533	0.167	0.667	2.192	0.735	1.738	1.755	0.612	10.542	0.857	0.327	10.133
<i>Synodus foetens</i> ²	Inshore lizardfish	68	Transient	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.000	0.000	0.000
<i>Tautoga onitis</i>	Tautog	69	Resident	0.000	0.042	0.021	0.021	0.041	0.021	0.102	0.061	0.365	0.000	0.020	0.429
<i>Tautoglabrus adspersus</i>	Cunner	70	Resident	0.000	0.000	0.000	0.021	0.020	0.000	0.000	0.041	0.542	0.000	0.000	0.082
<i>Trinectes maculatus</i>	Hogchoker	71	Resident	0.000	0.000	0.063	0.021	0.041	0.104	0.020	0.041	0.021	0.258	0.041	0.062
<i>Urophycis regia</i>	Spotted hake	72	Transient	0.156	0.125	0.542	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000

Table 4. Post hoc test results for annual comparisons (2012: pre-Sandy; 2013: 1 yr post-Sandy; 2014: 2 yr post-Sandy) of the species-specific Bernoulli generalized linear mixed models. Reported ratios and confidence intervals were back-transformed from the logit scale. Species were characterized by estuarine usage (T: transient; R: resident), dominant year class collected (ages 0 [young of year], 1, or 1+), and spawning duration for comparison. Characterizations are based on Kennish & Lutz (1984) and Able & Fahay (2010)

	Estuarine usage	Dominant year classes collected	Spawning duration	—2012/2013—		—2012/2014—		—2013/2014—	
				Odds ratio	p	Odds ratio	p	Odds ratio	p
<i>Anchoa mitchilli</i>	T	0, 1	Apr–Nov	1.286 0.698–2.371	0.599	1.406 0.762–2.595	0.393	1.093 0.597–2.003	0.936
<i>Apeltes quadracus</i>	R	0, 1	Apr–May	5.028 1.339–18.876	0.012	0.442 0.171–1.142	0.108	0.088 0.024–0.327	<0.001
<i>Bairdiella chrysoura</i>	T	0, 1	Jun–Aug	10.391 3.492–30.923	<0.001	1.357 0.591–3.116	0.666	0.131 0.045–0.382	<0.001
<i>Brevoortia tyrannus</i>	T	0	Aug–Nov	1.591 0.636–3.983	0.462	1.888 0.731–4.881	0.259	1.187 0.438–3.219	0.915
<i>Gobiosoma bosc</i>	R	0, 1	May–Sep	0.444 0.147–1.339	0.196	0.079 0.027–0.227	<0.001	0.178 0.075–0.420	<0.001
<i>Leiostomus xanthurus</i>	T	0	Nov–Jan	8.622 3.572–20.811	<0.001	34.794 8.927–135.609	<0.001	4.035 0.985–16.525	0.053
<i>Menidia menidia</i>	T	0, 1	Apr–Jul	0.783 0.329–1.859	0.784	0.194 0.088–0.428	<0.001	0.248 0.118–0.522	<0.001
<i>Micropogonias undulatus</i>	T	0, 1	Aug–Nov	2.249 0.651–7.772	0.276	0.363 0.137–0.964	0.040	0.161 0.050–0.523	0.001
<i>Opsanus tau</i>	R	0, 1, 1+	Jun–Aug	1.446 0.536–3.905	0.659	0.319 0.133–0.769	0.007	0.221 0.086–0.564	0.001
<i>Paralichthys dentatus</i>	T	0, 1, 1+	Sep–Mar	1.545 0.761–3.134	0.321	0.463 0.249–0.862	0.010	0.300 0.153–0.586	<0.001
<i>Pseudopleuronectes americanus</i>	R	0, 1, 1+	Jan–Mar	0.518 0.212–1.266	0.196	0.186 0.078–0.447	<0.001	0.360 0.167–0.777	0.005
<i>Syngnathus fuscus</i>	T	0, 1	Apr–Aug	2.157 1.015–4.583	0.044	0.297 0.148–0.596	<0.001	0.138 0.064–0.298	<0.001

sity occurrence were consistently higher pre-Sandy (2012) and 2 YPS (2014) compared to 1 YPS (2013). No trend was observed when pre-Sandy and 2 YPS August diversity occurrence odds were compared (OR = 1.956, CI: 0.241–15.876, $p = 0.733$). In October, diversity occurrence odds ranged from much lower to roughly equal pre-Sandy relative to 2 YPS (OR = 0.086, CI: 0.007–1.097, $p = 0.062$). The magnitude of diversity observed did not vary annually within April, June, or October, but varied annually in August where diversity was larger pre-Sandy ($p = 0.012$) and 2 YPS ($p = 0.001$) compared to 1 YPS (Table S3).

3.4. Richness

Collections included individuals of 72 different species (Table 3) with the highest richness occurring in the months of August and October (Table 2). In each year, a number of unique species were collected (i.e. those only collected in that year). Five unique

species were collected both pre-Sandy and 1 YPS, and 14 unique species were collected 2 YPS (Table 3).

Due to the nature of presence and absence data, the odds of observing richness (richness occurrence odds) in any given trawl tow (Table S4) are identical to the CPUE occurrence odds, which were previously described in Section 3.2.1 and therefore the results are not repeated here. The magnitude of the observed richness varied annually within all months except April (Table S4). In June and October, richness was smaller pre-Sandy and 1 YPS relative to 2 YPS; however, in June there was no consistent trend in richness for the pre-Sandy and 1 YPS comparison ($R = 1.020$, CI: 0.779–1.335, $p = 0.984$), whereas in October, pre-Sandy richness was larger than 1 YPS richness ($R = 1.387$, CI: 1.052–1.827, $p = 0.015$). August richness was consistently smaller 1 YPS compared to pre-Sandy ($p < 0.001$) or 2 YPS ($p < 0.001$), with no consistent trend between pre-Sandy or 2 YPS richness ($R = 0.833$, CI: 0.645–1.075, $p = 0.213$; Table S4).

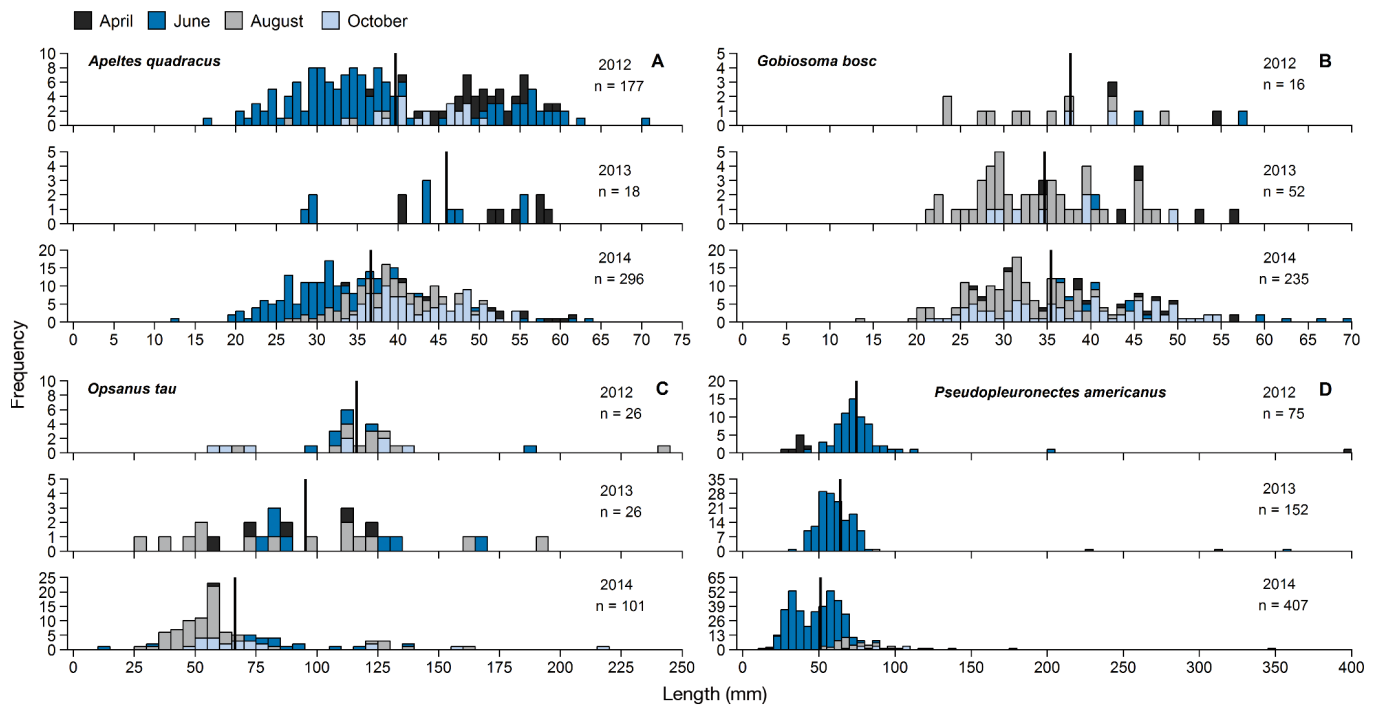


Fig. 2. Length frequency plots broken up by year (2012: pre-Sandy; 2013: 1 yr post-Sandy; 2014: 2 yr post-Sandy) for select estuarine resident species. See Table 4 for additional species characteristics. Black vertical lines indicate yearly mean length for each species

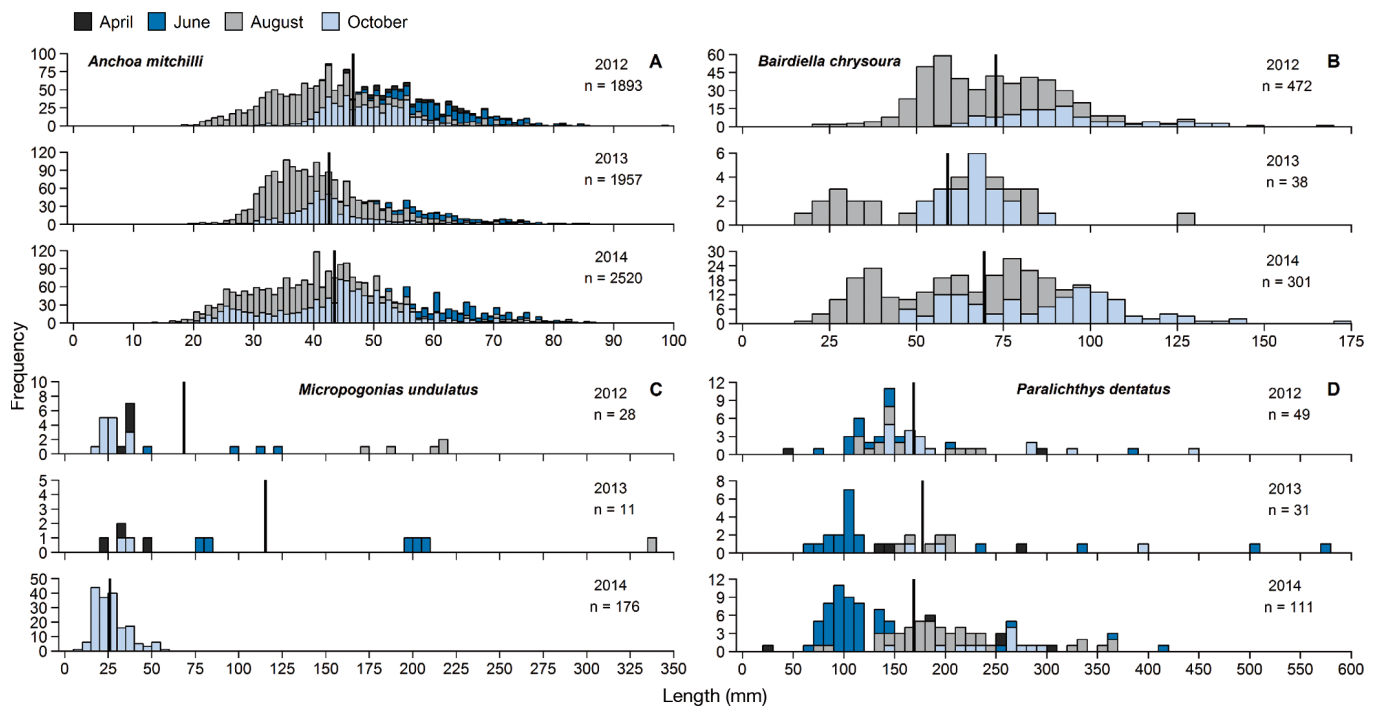


Fig. 3. Length frequency plots broken up by year (2012: pre-Sandy; 2013: 1 yr post-Sandy; 2014: 2 yr post-Sandy) for select estuarine transient species. See Table 4 for additional species characteristics. Black vertical lines indicate yearly mean length for each species

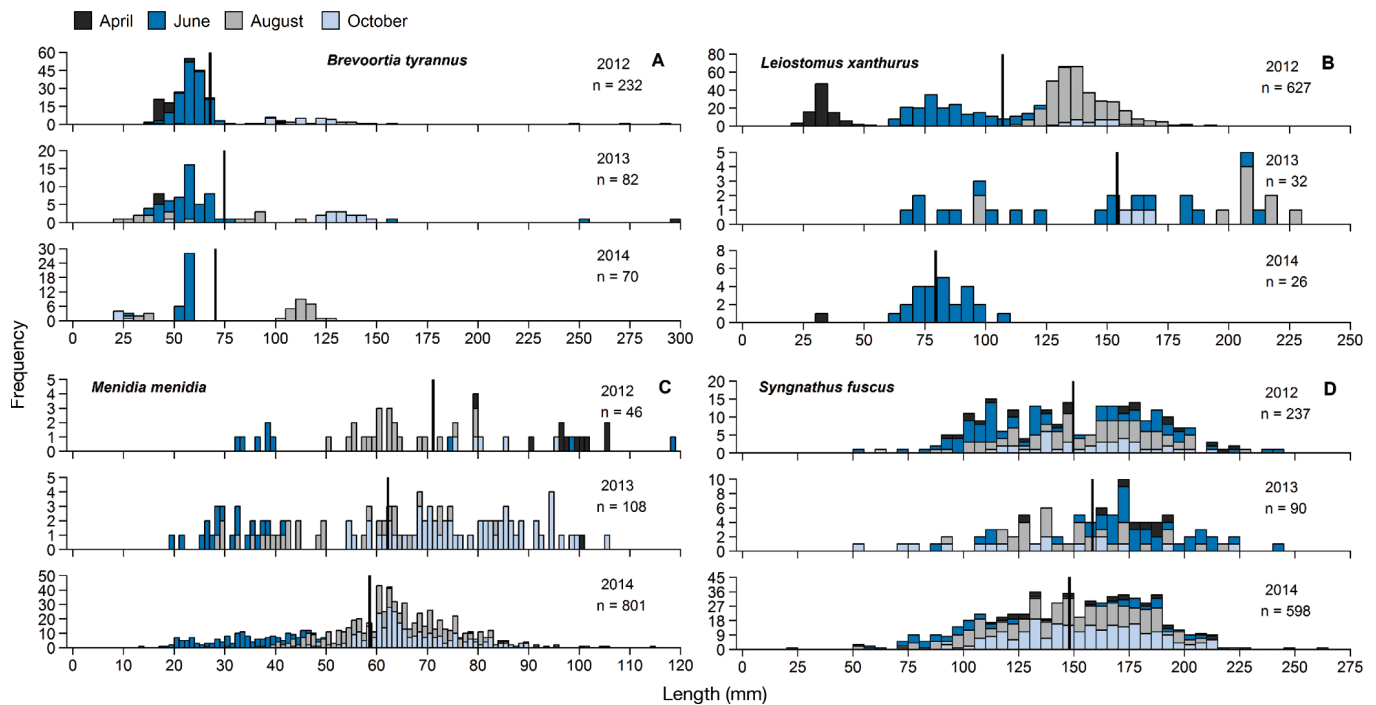


Fig. 4. Length frequency plots broken up by year (2012: pre-Sandy; 2013: 1 yr post-Sandy; 2014: 2 yr post-Sandy) for select estuarine transient species. See Table 4 for additional species characteristics. Black vertical lines indicate yearly mean length for each species

3.5. Assemblage composition

The fish fauna inhabiting Barnegat Bay encompassed various estuarine resident (e.g. *G. bosc*) and transient (e.g. *Paralichthys dentatus*) species and included southern stray (e.g. crevalle jack *Caranx hippos*) and shelf stray (e.g. butterflyfish *Peprilus triacanthus*) species (Table 3). The first 2 axes of the NMDS analysis indicated overall similarity in annual assemblage composition, with only slight separation of 2014 samples (2 YPS) from 2012 (pre-Sandy) and 2013 (1 YPS) samples along the second axis; however, seasonal shifts in assemblage composition were evident along the first axis (Fig. 5). The third axis did not add any additional information to the interpretation and therefore is not discussed.

4. DISCUSSION

Recruitment dynamics of the fish assemblage inhabiting Barnegat Bay, as measured by select structural characteristics (CPUE, diversity, richness, composition), remained relatively stable over a 3 yr period encompassing the large episodic disturbance of Hurricane Sandy. Although the analyzed struc-

tural characteristics occasionally had higher odds of occurrence or were larger pre-Sandy (2012) and 2 YPS (2014) relative to 1 YPS (2013), this trend was not consistent across seasons or between structural characteristics, making it difficult to attribute these differences in assemblage dynamics solely to Hurricane Sandy. However, Meléndez-Vázquez et al. (2019) documented a similar high-low-high or 'boomerang' pattern in fish assemblage dynamics following Hurricane Maria, suggesting that the interannual trends observed in this study may be in part related to hurricane passage, although this is challenging to conclude, especially given that the ecological mechanism driving this disturbance-induced 'boomerang' pattern is unknown (Miller et al. 2011, Hall et al. 2012, Fox 2013). The apparent absence of a pronounced hurricane effect 1 to 2 yr after the event was also evident in the Barnegat Bay benthic community. Comparison of the benthic community 3.5 mo before and 8 mo after Sandy yielded minimal noticeable differences in benthic community dynamics (Taghon et al. 2017). This is particularly relevant because many fish species collected in this study rely on benthic food sources (Festa 1979).

The absence of a pronounced hurricane effect and the observed stability in fish assemblage dynamics

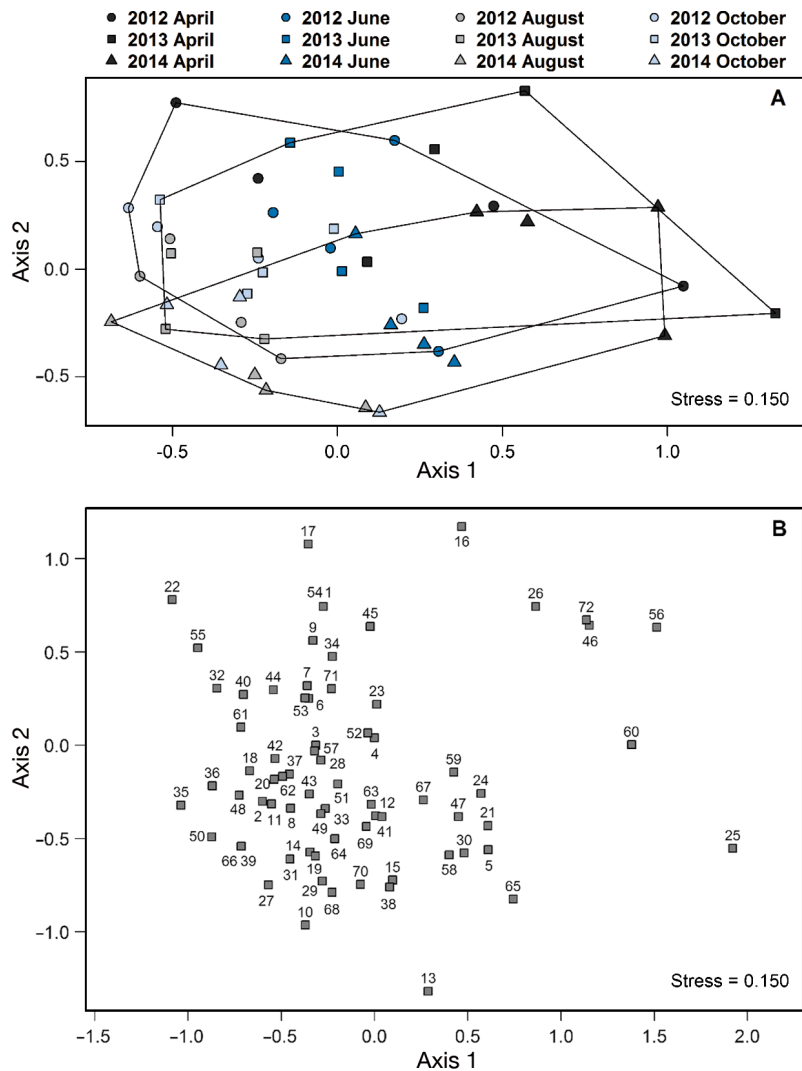


Fig. 5. (A) Non-metric multidimensional scaling (NMDS) sample plot. Assemblage similarity decreases by half per one unit change. Convex polygons enclose samples taken in the same year (2012: pre-Sandy; 2013: 1 yr post-Sandy; 2014: 2 yr post-Sandy). (B) NMDS species plot which is in the same dimensions as the previous sample plot, but was separated for legibility. Species are coded by number for clarity (see Table 3 for pairings), and their locations are based on weighted averages. Only the first 2 axes of the NMDS are shown. Note the difference in scale between axes from the 2 plots

likely emerged from many interacting factors. Estuaries worldwide are known for supporting relatively stable fish assemblages; although species abundances may fluctuate annually, species composition is fairly consistent across years (Jackson & Jones 1999, Garcia et al. 2001, Griffiths 2001, James et al. 2008). Annual stability in species composition has been observed for fish larval supply to Barnegat Bay (Witting et al. 1999, Able et al. 2017) and in the juvenile fish assemblage inhabiting the bay (this study). The inherent stability of the Barnegat Bay fish assemblage may help diminish the potential for struc-

tural changes to the fish assemblage, external to typical interannual variability, following episodic storm events, such as Hurricane Sandy.

Further, fish are often capable of relocating from areas of unsuitable habitat, and have been documented doing so in reference to changes in salinity, DO, and barometric pressure caused by storms (Heupel et al. 2003, Houde et al. 2005, Udyawer et al. 2013, Massie et al. 2019), as seen for summer flounder *Paralichthys dentatus* in adjacent Great Bay (Sackett et al. 2007). In some cases, this relocation can occur for prolonged periods of time until water quality approximates pre-storm conditions (Knott & Martore 1991). In Barnegat Bay, although temporary movements and distribution shifts of fishes in the days immediately following the storm probably occurred, the absence of low salinity and DO conditions during and after Hurricane Sandy (Taghon et al. 2017), and the well-mixed nature of this shallow lagoonal estuary (Chizmadia et al. 1984, Defne & Ganju 2015), likely precluded any prolonged distribution shifts related to alterations in water quality. Moreover, the fact that Sandy occurred during the fall, in a period of declining temperature, made it less likely that abrupt changes in temperature and low DO could occur.

This lack of a shift in salinity and DO following Hurricane Sandy contrasts with observations following hurricanes that impacted other US east coast lagoonal estuaries. Pamlico Sound (North Carolina), the largest lagoonal estuary in the USA (Paerl et al. 2006),

has been affected by a multitude of hurricanes over the past few decades, with many storms resulting in salinity and DO shifts that consequently affected fish assemblages (Paerl et al. 2001, Adams et al. 2003, Burkholder et al. 2004). Potential drivers of the differing hurricane responses between these 2 lagoonal estuaries include the timing of the storms and larger freshwater influence, greater water depths on average, and a longer residence time in Pamlico Sound compared to Barnegat Bay (Paerl et al. 2001, 2010). Great South Bay (New York) was also impacted by Hurricane Sandy, resulting in a permanently open

breach through Fire Island (Aretxabaleta et al. 2014). This increased connectivity between Great South Bay and the ocean has resulted in altered water quality parameters and fish assemblage dynamics (Tinoco 2017, Olin et al. 2019). The differing hurricane effects in these studies suggest that estuarine and faunal responses to hurricanes are highly variable and depend heavily on the storm (e.g. path, wind speeds), estuary (e.g. freshwater input, potential for barrier island breaches), and watershed (e.g. urban versus rural) characteristics (Mallin & Corbett 2006).

In addition to intermittent movements related to habitat quality, many of the fishes inhabiting Barnegat Bay also undergo annual seasonal migrations (as observed in this study), entering or recruiting as larvae to the estuary as the water warms during the spring and leaving as the water cools in the fall (Able & Fahay 2010). Since Hurricane Sandy made landfall late in October, many estuarine transient species had likely already migrated into the ocean, reducing the number of individuals enduring the full force of the storm while confined to this extremely shallow, estuarine habitat. However, estuarine resident species (e.g. naked goby *Gobiosoma bosc*, oyster toadfish *Opsanus tau*, winter flounder *Pseudopleuronectes americanus*) did not appear differentially affected by the storm compared to estuarine transients (e.g. Atlantic silverside *Menidia menidia*, northern pipefish *Syngnathus fuscus*), potentially due to the inherent adaptability of estuarine species to environmental perturbations (Elliott & Quintino 2007).

Although many transient species likely migrated from the estuary, in a seasonal pattern (Able & Fahay 2010), prior to the storm, hurricanes have the potential to influence estuarine larval supply by temporarily altering hydrodynamics (Hoagman & Merriner 1977), as was observed for New Jersey coastal ocean circulation during Sandy (Miles et al. 2017), which could result in subsequent recruitment effects. With regards to Hurricane Sandy, larval supply of species that spawn in fall/early winter, such as the estuarine transients bay anchovy *Anchoa mitchilli*, Atlantic menhaden *Brevoortia tyrannus*, spot *Leiostomus xanthurus*, Atlantic croaker *Micropogonias undulatus*, and *Paralichthys dentatus* (Able & Fahay 1998, 2010), were most likely to be affected by the storm. However, abundances of larvae in Barnegat Bay typically exhibit some interannual variation (Witting et al. 1999, Able et al. 2017), and hurricane-induced alterations in larval supply do not necessarily directly translate to observable changes in juvenile recruitment, at least not in the larger Chesapeake Bay (Montane & Austin 2005). Effects of Hurricane Sandy

on *A. mitchilli*, *B. tyrannus*, *M. undulatus*, and *P. dentatus* recruitment dynamics were not evident as YOY of these species were present in samples 1 YPS, and CPUE occurrence odds and length frequency distributions for these species 1 YPS relative to pre-Sandy and 2 YPS did not indicate the existence of a defined hurricane effect. *L. xanthurus* had variable yearly length frequency distributions and higher CPUE occurrence odds pre-Sandy relative to 1 and 2 YPS, but large annual fluctuations in *L. xanthurus* larval and juvenile abundances within New Jersey estuaries is normal (Able & Fahay 1998, 2010, Able et al. 2017).

Silver perch *Bairdiella chrysoura* and fourspine stickleback *Apeltes quadracus* had lower odds of occurrence 1 YPS compared to pre-Sandy and 2 YPS. Similarly to *L. xanthurus*, *B. chrysoura* exhibit large annual fluctuations in larval (Able & Fahay 1998, Able et al. 2017) and juvenile (Able & Fahay 2010) abundances within New Jersey estuaries, so the lower odds of occurrence observed 1 YPS may not be attributable to the hurricane. *A. quadracus* are estuarine residents that spawn in the late spring/early summer (Able & Fahay 2010); the cause of the lower CPUE occurrence odds 1 YPS compared to pre-Sandy and 2 YPS is unclear.

The ability to discern temporal trends in species and assemblage dynamics is hindered by a general lack of studies encompassing prolonged time scales (Magurran et al. 2010). This lack of long-term data becomes problematic when trying to discern the influence of anthropogenic impacts or episodic events, such as hurricanes, from natural annual variation in fish dynamics (Desmond et al. 2002, Houde et al. 2005, Magurran et al. 2010, Izzo et al. 2016). Although the time series analyzed in this study spanned 1 yr pre-Sandy to 2 YPS, interannual variability in recruitment dynamics occurs without hurricane influences, making it difficult to discern long-term hurricane effects from interannual variation. A long-term monitoring program would have assisted in putting the observed 'highs' and 'lows' in perspective, as was done by Greenwood et al. (2006). The utility of long-term time series in attempting to understand the complex dynamics of the natural world has been stressed in the past (Callahan 1984, Franklin 1989, Cody 1996) and in more recent years (Hobbie et al. 2003, Magurran et al. 2010, Lindenmayer et al. 2012, Able 2016) and will continue to be important for understanding effects of episodic events, such as hurricanes, especially in the face of climate change, which may drastically alter processes driving observed phenomena (Walther et al. 2002, Colbert et al. 2013, Walsh et al. 2016).

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