Stochastic event alters gelatinous zooplankton community structure: impacts of Hurricane Sandy in a Mid-Atlantic estuary

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ABSTRACT: Climate change has increased hurricane activity and intensity, leading to greater destructive forces impacting coastal communities. Barnegat Bay, New Jersey, USA, is a shallow Mid-Atlantic estuary with considerable anthropogenic development which shows vulnerability to elevated storm surges and coastal flooding. Gelatinous zooplankton were sampled monthly in the summer prior to Hurricane Sandy in October 2012, with the community dominated by 2 species, *Chrysaora quinquecirrha* and *Mnemiopsis leidyi*. These 2 species showed inverse distributions, with *C. quinquecirrha* dominating in the northern, lower-salinity region and *M. leidyi* abundant in the southern, high-salinity region of the estuary, with significant top-down control of *M. leidyi* by *C. quinquecirrha*. Following Hurricane Sandy, substantial changes in the community occurred, with a 64% increase in gelatinous zooplankton species richness. *C. quinquecirrha* population density significantly declined by more than 50% in 2013 (from 0.033 to 0.013 m^{-3}) and remained lower in 2014 (0.012 m^{-3}). Concomitantly, *M. leidyi* populations significantly increased from 2.4 to 5.4 m^{-3} in 2013 but dropped in 2014. The drop in 2014 was unexpected, as the *C. quinquecirrha* population remained low. However, the increasing density and diversity of other gelatinous species in 2013 and 2014, including *Salpa* sp., *Turritopsis nutricula*, *Nemopsis bachei*, *Bougainvillea muscus*, and *Rathkea octopunctata*, changed the community composition. Consequently, the destructive forces of Hurricane Sandy cascaded throughout the community by the elimination of polyp habitat for the dominant predator, thereby opening the system to community succession.

KEY WORDS: Jellyfish · Community structure · Hurricanes · Zooplankton

INTRODUCTION

Gelatinous zooplankton have shown increases in some marine ecosystems, possibly as a result of climate change, species introductions, and a number of anthropogenic alterations to coastal food webs that favor jellyfish and ctenophores (Sullivan et al. 2001, Purcell & Decker 2005, Richardson et al. 2009). One important driver of the shift toward greater abundance of gelatinous zooplankton is the construction of hard surfaces such as bulkheads, docks, and other shoreline modifications that provide suitable habitat for scyphozoan polyps (Duarte et al. 2013). Additionally, gelatinous zooplankton may benefit from bottom hypoxia driven by local eutrophication, since they are highly tolerant of low dissolved oxygen, giving them an advantage over prey species that may be more susceptible (Breitburg et al. 1997). Under these eutrophic conditions, gelatinous zooplankton experience elevated energy intake through reduced competition and increased prey capture efficiency, leading to increased reproductive capacity which

ultimately contributes to population growth (Purcell et al. 2001, 2007, Grove & Breitburg 2005, Wang et al. 2016). Large populations of jellyfish can be detrimental to fisheries because they are voracious predators of zooplankton and ichthyoplankton and are therefore both competitors and predators of fish (Brodeur et al. 2008, Uye 2008). Additionally, blooms can also impact power generation and manufacturing by clogging intake screens, reduce tourism, and drive additional hypoxia when they die. Consequently, understanding population and species changes over time is critical to assessing the current and future impacts of these species on food webs, nutrient cycling, fisheries, and economic development (Purcell et al. 2007, Pitt et al. 2014).

While increases in some species have been documented, there is no clear pattern of global escalations in jellyfish populations (Richardson et al. 2009, Sanz-Martín et al. 2016), and long-term monitoring of jellyfish communities may be necessary to elucidate global cycles or changes in relative abundance (Condon et al. 2013). Many investigated communities appear to be dominated by 1 or even a few species which appear to demonstrate bloom conditions (Richardson et al. 2009), suggesting that the community dynamics and pelagic trophic interactions may be dictated by only a few dominant species. Many of these communities show seasonal signals related to reproduction cycles of these dominant species (Sullivan et al. 2001, Molinero et al. 2008), but subsequent trophic interactions may mask the relative abundance of other pelagic species, leading to an incomplete assessment of gelatinous zooplankton community dynamics (Boero et al. 2008). While many scyphozoans are relatively large and conspicuous, their densities can be dwarfed by smaller hydrozoans (Sun et al. 2012, Nogueira et al. 2015). However, many diminutive species may be important in trophic webs (Mills 1995, Purcell & Arai 2001) and contribute to energy transfer and nutrient recycling (Robinson et al. 2015). Since many gelatinous zooplankton species exert substantial top-down pressure on various organisms (Feigenbaum & Kelly 1984), they have assumed apex predator status in some planktonic communities (Finenko et al. 2013, Robinson et al. 2014). As a result, changes in the density, distribution, and species composition of gelatinous zooplankton can substantially alter trophic webs, nutrient cycling, and fisheries yields, but we need careful assessment of data sets and results to ensure accuracy before asserting global patterns (Sanz-Martín et al. 2016).

A critical global factor impacting gelatinous zooplankton communities is climate change (Doney et al. 2012). From an oceanic standpoint, increasing water temperature has allowed the migration of species into new regions (Hoegh-Guldberg & Bruno 2010) and also impacted organismal basal metabolic rates, energy demand, and ultimately oxygen consumption (Pörtner 2010). Warming ocean waters also play a critical role in the formation and intensification of hurricanes (Webster et al. 2005, Vecchi et al. 2008), with increasing destructiveness (Emanuel 2005). Hurricanes and severe storms negatively impact coastal communities directly through physical destruction of habitats and infrastructure as well as indirectly through elevated rainfall and coastal flooding (see Greening et al. 2006 and references within). As these storms gain energy, their destructive force increases and can lead to escalating economic damage (Akhtar & Santos 2013). Hurricane Sandy in October 2012 entered the Mid-Atlantic Ocean and devastated coastal New York and New Jersey, USA. The storm possessed a storm surge greater than 2.5 m (Sweet et al. 2013), which destroyed buildings, caused massive flooding, and breached barrier islands, leading to an economic loss estimated at more than US$75 billion, the direct loss of 147 lives (see Henry et al. 2013), and significant losses of ecosystem services (Hauser et al. 2015). One region particularly impacted was northern Barnegat Bay, NJ, where the storm surge produced an island breach, inundated coastal communities, and destroyed buildings and structural features such as marinas, docks, and bulkheads. While the breach was repaired immediately, debris removal continued well into 2013 and beyond. This region of the bay also maintains the highest densities of adult *Chrysaora quinquecirrha* (Bologna et al. 2017) and larval recruitment to hard substrates (Bologna 2011, Soranno 2016). Given the importance of polyp habitat for the life history and population dynamics of scyphozoans (Lucas et al. 2012), Hurricane Sandy had the potential to dramatically change community dynamics by impacting polyp substrate for *C. quinquecirrha* and subsequently their density and distribution. This research assessed the impacts of an extreme stochastic event on gelatinous zooplankton community structure.

MATERIALS AND METHODS

Study area

This project focused on Barnegat Bay, NJ, USA (39° N, 74° W), a Mid-Atlantic estuarine system iso-

lated from the Atlantic Ocean by 2 barrier islands, representing a lagoonal-type estuary. Barnegat Bay has 2 natural inlets in the central and southern reaches but also has a northern man-made tidal inlet associated with the Intracoastal Waterway maintained for navigation. It is designated both as a NOAA National Estuarine Research Reserve (NERR) (Jacques Cousteau NERR) and as a US Environmental Protection Agency National Estuary Program site (Barnegat Bay Partnership). It is shallow (1.5 m average depth) and well mixed (Kennish 2001). The northern reaches of the watershed are highly developed (Lathrop & Bognar 2001), with 2 major rivers (Toms and Metedeconk) contributing substantial freshwater and nutrients to the bay (Wieben & Baker 2009). The middle and southern reaches of the bay have less development and freshwater inputs, but overall, the bay has been described as highly eutrophic (Kennish et al. 2007), with evidence of hypoxia in regions of poor circulation (Sugihara et al. 1979). Sixteen sampling sites were established in the bay using a stratified bay-wide design to assess the spatial distribution of organisms throughout Barnegat Bay (Fig. 1). Sampling occurred monthly during the summer (May/June through September) at these 16 sites in 2012, 2013, and 2014. During sampling events, water quality (e.g. salinity, temperature, and dissolved oxygen) data were collected using a YSI® Professional Plus Multi-Parameter meter calibrated and certified by the New Jersey Department of Environmental Protection. Coordinates for sampling stations are provided in the Appendix.

Gelatinous macro-zooplankton sampling

Large gelatinous zooplankton were collected using lift nets (3.2 mm mesh, 0.836 m^2) from each station during each sampling event (n = 10 per site, per sampling event: N = 2977). Sampling occurred by allowing the lift net to settle to the bottom and remain undisturbed for at least 30 s. Lift nets were then raised directly through the water column, and all organisms were lifted to the surface. Once on deck, samples were transferred to a holding bin, where all gelatinous zooplankton were identified and enumerated. Water depth was recorded for each lift net sample, and the lift net area was then multi-
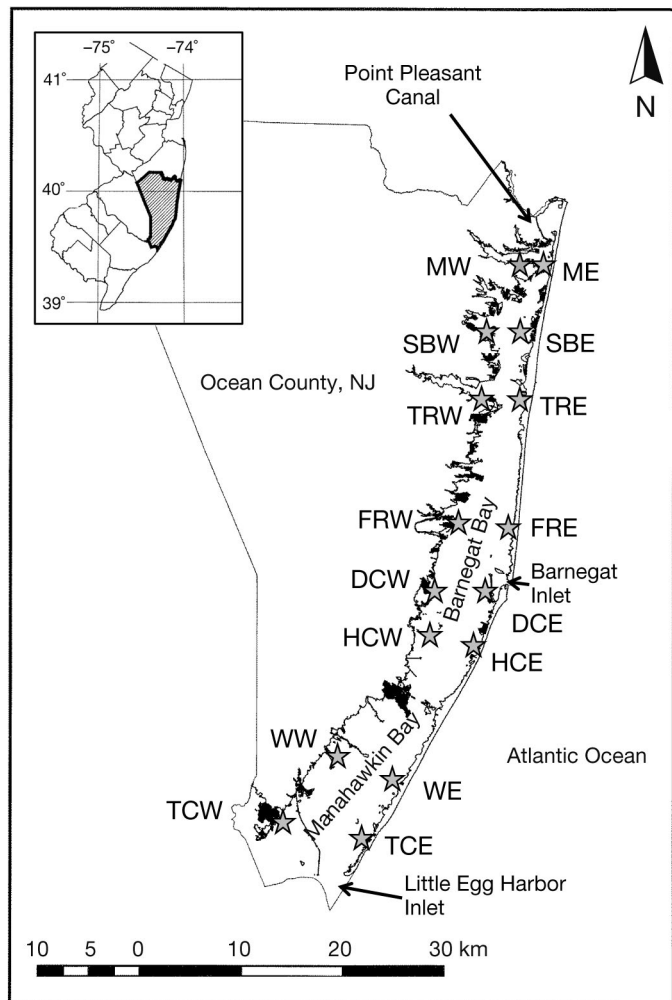

Fig. 1. Eight paired sampling stations in Barnegat Bay, NJ, and the 3 tidal inlets. Map abbreviations and site depths as follows: ME: Metedeconk River East (site depth 1.4 m); MW: Metedeconk River West (1.5 m); SBE: Silver Bay East (1.3 m); SBW: Silver Bay West (1.9 m); TRE: Toms River East (2.25 m); TRW: Toms River West (1.4 m); FRE: Forked River East (1.6 m); FRW: Forked River West (1.3 m); DCE: Double Creek East (1.6 m); DCW: Double Creek West (1.67 m); HCE: Harvey Cedars East (2.03 m); HCW: Harvey Cedars West (1.2 m); WE: Westecunk Creek East (1.2 m); WW: Westecunk Creek West (1.56 m); TCE: Tuckerton Creek East (1.36 m); TCW: Tuckerton Creek West (2.1 m)

plied to determine the volume of water sampled. All samples were then standardized to ind. m^{-3} and compared among years. In 2012, 1394 lift net samples were collected; 823 in 2013, and 760 in 2014.

Gelatinous micro-zooplankton sampling

In addition to the lift net sampling for larger gelatinous zooplankton, triplicate 363 µm surficial

zooplankton nets (30 cm diameter) were towed at each location (N = 819). Tows were conducted at minimally engaged engine speed for 1 min. Length of tow was measured using a mechanical flow meter (General Oceanics Model 2030R) to calculate the distance traveled using the manufacturer's conversion constant. Sample volume was then calculated for each tow, and samples were standardized to ind. m^{-3} prior to analysis. Since Barnegat Bay is a well-mixed, shallow system (mean depth = 1.5 m), these samples are representative of the overall water column. After field collection, ctenophores were immediately sieved (4 mm) and counted in a manner similar to Purcell & Decker (2005). This method was performed to specifically evaluate the ctenophore *Mnemiopsis leidyi* populations, since they do not preserve well. Employing this method was necessary to obtain an accurate assessment of their distribution in the plankton tows. Zooplankton samples were then preserved in ethanol, stained with rose bengal, and returned to the laboratory for later identification (lowest reasonable taxonomic level) and enumeration. In 2012, 369 zooplankton samples were collected; 218 in 2013, and 232 in 2014.

Statistical analyses

To evaluate the impacts of Hurricane Sandy, data were pooled by year to evaluate changes. Specifically, 1-way ANOVAs were conducted using PROC GLM (SAS® ver. 9.3, SAS Institute), with year as the independent variable and water quality parameters and organismal density from lift nets and plankton tow samples of each taxon as dependent response variables in the model. Discrimination of significant differences among years was accomplished by using the LSMEANS method in SAS®. Organismal density for each taxon was square root transformed prior to analysis to eliminate heteroscedasticity.

The zooplankton tow data were also analyzed for community structure using a 2-way ANOSIM procedure in Primer® on 4th root Bray-Curtis transformed data (Clarke & Gorley 2006), using year and month of collection as factors to determine seasonal and annual changes in the gelatinous zooplankton community. Additionally, a principal component analysis (PCA) was completed to assess the primary taxa responsible for driving annual community structure patterns.

RESULTS

Water quality

While average salinity did not change significantly from 2012 to 2014 (Fig. 2A), both temperature and dissolved oxygen changed significantly, coinciding with Hurricane Sandy (Fig. 2B,C). Specifically, average temperature significantly declined each year ($F_{2,273}$ = 17.1, p < 0.0001) from an average of 24.7°C in 2012 to 22.1°C in 2014 (Fig. 2B). Similarly, and most likely related to the lower temperatures, dissolved oxygen was significantly greater ($F_{2,273}$ = 27.7, p < 0.0001) in both 2013 and 2014 compared to 2012 (Fig. 2C).

Gelatinous macro-zooplankton sampling

During lift net sampling for larger individuals (i.e. >3.2 mm), 6 species of gelatinous zooplankton were collected, including the scyphozoans *Chrysaora quinquecirrha*, *Aurelia aurita*, and *Cyanea capillata* and the ctenophores *Mnemiopsis leidyi*, *Beroe ovata*,
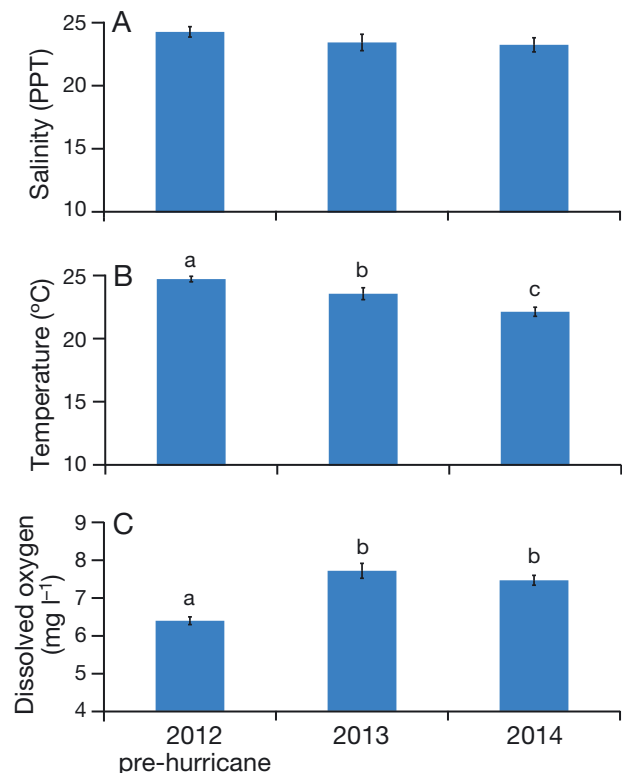

Fig. 2. Yearly mean ± SE water quality results from the combined 16 sampling stations in Barnegat Bay. (A) Salinity, (B) temperature, and (C) dissolved oxygen. Different letters above bars indicate significant differences (p < 0.05)

and *Pleurobrachia pileus*. The 2 most numerically abundant species were *M. leidyi* and *C. quinquecirrha* and accounted for >90% of all organisms sampled. During our investigation, density of *C. quinquecirrha* and *M. leidyi* changed dramatically among years. For *C. quinquecirrha*, density was significantly higher in 2012 compared to both 2013 and 2014 ($F_{2,2974} = 6.27$, p < 0.002; Fig. 3A). One feature of the decline in sea nettle populations in 2013 is the signif-

icant increase in *M. leidyi* densities during that year ($F_{2,2974} = 32.4$, p < 0.0001; Fig. 3B). However, in 2014, *M. leidyi* densities significantly declined by half. The only other species to show significant changes in its density was the sea gooseberry *P. pileus*, which showed a significant decline in population density in 2013 following the storm ($F_{2,2974} = 4.23$, p < 0.015) but then returned to pre-hurricane densities in 2014 (Fig. 3C).
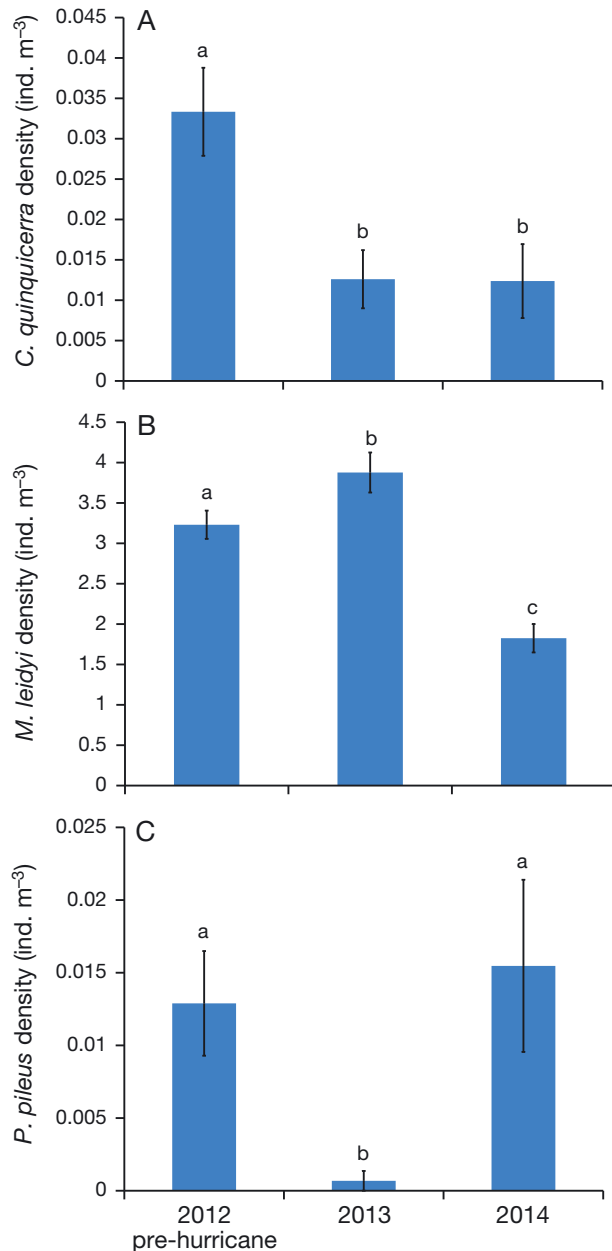
Gelatinous micro-zooplankton sampling

Seventeen different gelatinous zooplankton taxa were collected from plankton tow samples, with representatives from Scyphozoa (4 taxa), Hydrozoa (10), Tentaculata (2), and a single Thaliacea (*Salpa* sp.), as well as a few unidentifiable ephyrae. Of the taxa identified, 8 showed significant density differences among years. Results from the plankton net samples, however, showed no significant difference in *C. quinquecirrha* densities among years compared to results from the lift net samples, which showed significant declines post-hurricane. This result was not unexpected, as plankton nets poorly sample adult *C. quinquecirrha*. For *M. leidyi*, we observed a significant increase in 2013 ($F_{2,816} = 14.18$, p < 0.0001) and then a dramatic decline in 2014 (Fig. 4), similar to the results seen from the lift net samples. A similar pattern was observed with *P. pileus*, with a significant increase in density in 2013 ($F_{2,816} = 7.54$, p < 0.0006). One outstanding result from 2013 was the massive and significant increase in *Salpa* sp. (Fig. 5A), which is a coastal/open ocean species rarely encountered in
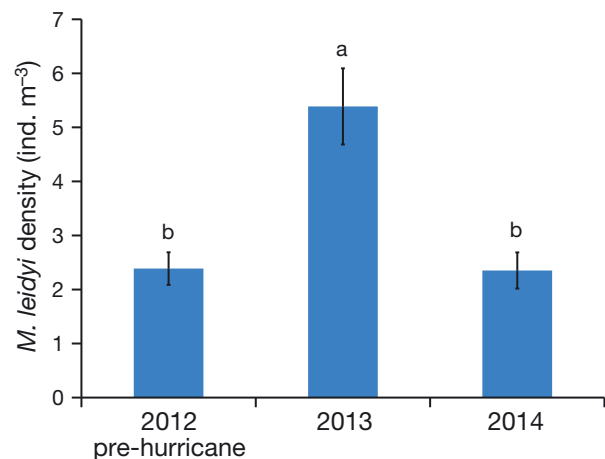

Fig. 3. Yearly mean ± SE densities from the combined 16 sampling stations in Barnegat Bay collected from lift nets. Density comparisons for (A) *Chrysaora quinquecirrha*, (B) *Mnemiopsis leidyi*, and (C) *Pleurobrachia pileus*. Different letters above bars indicate significant differences (p < 0.05)

Fig. 4. Yearly mean ± SE *Mnemiopsis leidyi* densities from the combined 16 sampling stations in Barnegat Bay collected from plankton nets. Different letters above bars indicate significant differences (p < 0.0001)

sheltered lagoon systems ($F_{2,816} = 18.8$, p < 0.0001). *Turritopsis nutricula* and *Nemopsis bachei* showed significant increases in 2013 following Hurricane Sandy ($F_{2,816} = 11.24$, p < 0.0001, and $F_{2,816} = 10.96$, p < 0.0001, respectively), while *Rathkea octopunctata* and *Bougainvillea muscus* both showed significant increases in 2014 (Fig. 5B), coinciding with declines in *M. leidyi* populations ($F_{2,816} = 3.6$, p < 0.03, and

$F_{2,816} = 12.82$, p < 0.0001, respectively). The only other taxa to show significant declines post-hurricane was *Clytia* sp., which showed significant declines in 2013 and was absent from samples in 2014 ($F_{2,816} = 8.39$, p < 0.0002). This pattern was true for *Aequora* sp., albeit not significantly ($F_{2,816} = 1.34$, p > 0.26). Overall, comparisons among years showed a species richness increase of 64% in 2013, with continued higher species richness in 2014.

Community dynamics

Overall, the analysis of community structure showed significant differences among year comparisons in the 2-way ANOSIM (global R = 0.143, p < 0.001) as well as significant differences among months of collection (global R = 0.079, p < 0.001). For monthly contrasts, all pair-wise comparisons were significantly different (p < 0.05) from each other except for May when compared to samples from June, July, and August. This indicates that a seasonal signal in community structure exists, which is typical in temperate estuaries. Results from the PCA demonstrate clear patterns of individual species driving community structure among years. Since *M. leidyi* density is often an order of magnitude greater than all other species, its abundance drives the majority of loading on PC 1 (Table 1). As such, discrimination of
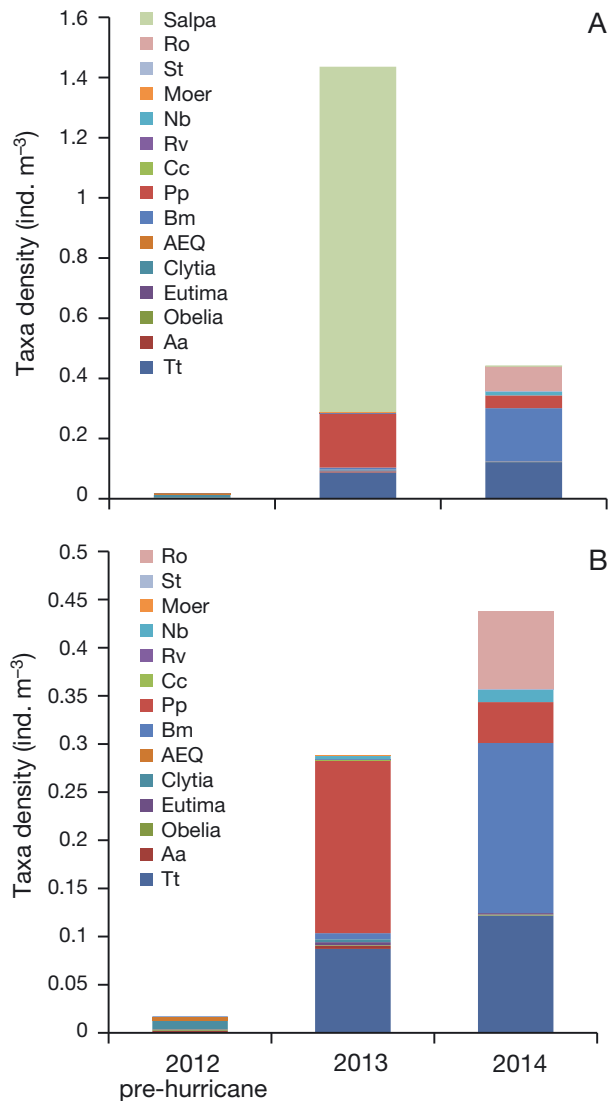

Fig. 5. Yearly averaged gelatinous zooplankton densities from the combined 16 sampling stations in Barnegat Bay collected from plankton nets with *Chrysaora quinquecirrha* and *Mnemiopsis leidyi* excluded. (A) All taxa present in samples and (B) all taxa present with *Salpa* sp. removed. Shown are means for each taxon. Salpa: *Salpa* sp.; Ro: *Rathkea octopunctata*; St: *Sarsia tubulosa*; Moer: *Moerisia* sp.; Nb: *Nemopsis bachei*; Rv: *Rhopilema verri*; Cc: *Cyanea capillata*; Pp: *Pleurobrachia pileus*; Bm: *Bougainvillea muscus*; AEQ: *Aequora* sp.; Clytia: *Clytia* sp.; Eutima: *Eutima* sp.; Obelia: *Obelia* sp.; Aa: *Aurelia aurita*; Tt: *Turritopsis nutricula*

Table 1. Individual principal component analysis loading values for the taxa identified in samples associated with the first 3 principal components (PCs). Eigenvalue (E) and relative contribution (%) are provided for each PC

| Taxon	PC1 ($E = 3.9$, 52.5%)	PC2 ($E = 1.01$, 13.4%)	PC3 ($E = 0.6$, 8.2%)
Mnemiopsis leidyi	0.979	−0.055	0.072
Chrysaora quinquecirrha	−0.158	−0.042	0.479
Turritopsis nutricula	−0.035	−0.015	−0.771
Aurelia aurita	−0.009	−0.002	−0.047
Obelia spp.	0.005	−0.004	−0.006
Eutima mira	−0.012	−0.003	−0.024
Clytia spp.	−0.004	0.018	0.005
Aequora spp.	0.002	−0.003	0.002
Bougainvillea muscus	−0.062	0.007	−0.183
Pleurobrachia pileus	0.052	−0.073	−0.174
Cyanea capillata	0.002	−0.001	0.001
Rhopilema verrilli	−0.001	−0.001	−0.015
Nemopsis bachei	−0.005	−0.013	−0.054
Salpa spp.	0.049	0.994	0.008
Moerisia spp.	0.003	0.017	0.002
Sarsia tubulosa	0.001	−0.002	−0.001
Rathkea spp.	0.019	−0.014	−0.026
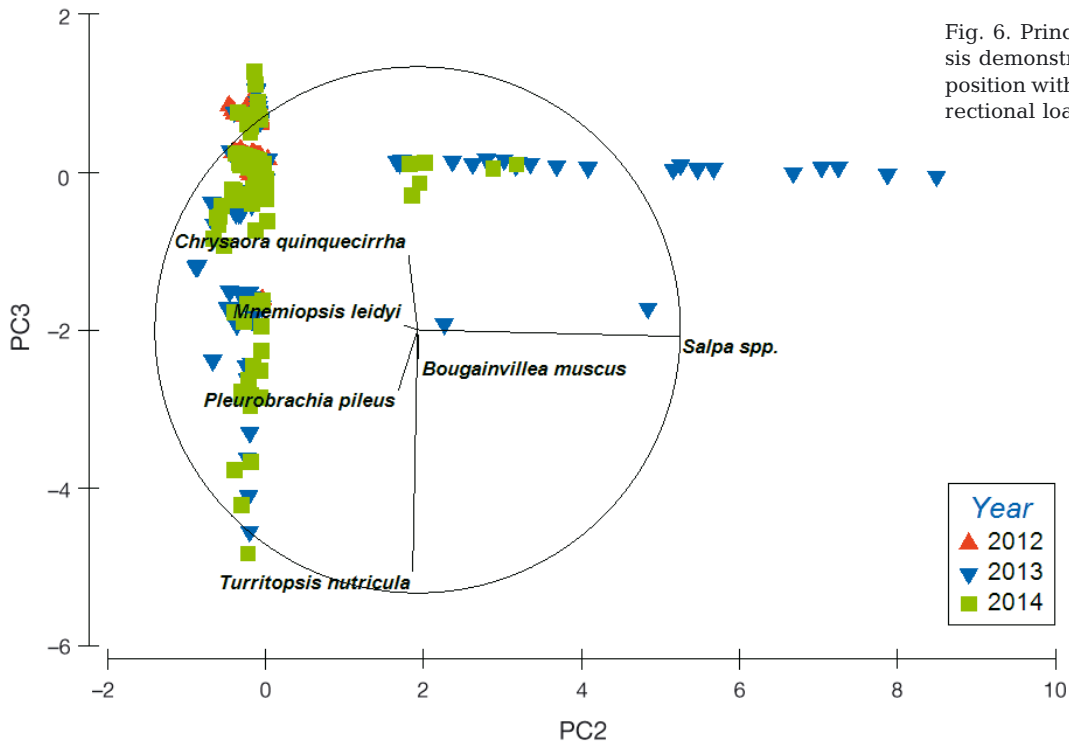
Fig. 6. Principal component analysis demonstrating community composition with critical species and directional loading on PC 2 and PC3

the community is better represented from loading factors on PC2 and PC3 (Fig. 6). Specifically, *Salpa* sp. strongly describes the sample community in 2013 with high loading on PC2, while *C. quinquecirrha* drives community development in 2012 with high loading on PC3 (Table 1). *P. pileus, T. nutricula*, and *B. muscus* densities played critical roles in defining differences between pre- and post-hurricane communities, showing discrimination along the PC3 axis (Fig. 6).

DISCUSSION

Community structure is typically defined by the dominant species present or those that structure or engineer the system (Breitburg et al. 2010). In Barnegat Bay, the increase in abundance of *Chrysaora quinquecirrha* over the last decade has changed the pelagic trophic structure to where this species assumed the role of an apex predator and exerted strong top-down control of the food web (Bologna et al. 2017). The appearance of established *C. quinquecirrha* populations in Barnegat Bay is a relatively new phenomenon, as they were never recorded in previous evaluations of gelatinous zooplankton (Nelson 1925, Mountford 1980, Sandine 1984), although this is within their established range (Morandini & Marques 2010). The most probabilistic mechanism in the establishment of polyp populations is the sub-

stantial development in the northern part of the bay over the last 40 yr. This has led to changes in land use and loss of coastal wetlands (Lathrop & Bognar 2001), elevated nutrient loading (Wieben & Baker 2009), and substantial increases in hard substrates (e.g. docks, bulkheads), which has led to high levels of larval settlement and polyp recruitment (Bologna 2011, Soranno 2016). However, Hurricane Sandy in October 2012 significantly impacted Barnegat Bay, causing an island breach to develop in the northern region of the bay, and destroyed homes, roads, and businesses (Henry et al. 2013). These impacts had unanticipated consequences, as the elimination of floating docks, bulkheads, and other hard surfaces in the bay destroyed polyp/podocyst habitat for *C. quinquecirrha*. At the time of the storm, adult *C. quinquecirrha* populations had senesced; therefore, continued larval production and recruitment could not occur. We theorize this event caused the significant decline in their densities seen in 2013 and 2014 (Fig. 3A) and was a result of the destroyed structures which supported existing polyps and generated a population check in the years following the storm. Additionally, large-scale changes in tidal exchange with the coastal ocean and elevated water levels were seen after the storm (Aretxabaleta et al. 2014). Subsequent changes led to the observed shifts in water quality (Fig. 2) and an increase in the frequency of novel coastal ocean species like salps. Our data demonstrate that the significant increase in

Salpa sp. in 2013 following the storm showed that Barnegat Bay was undergoing a substantial change in the gelatinous zooplankton community (Figs. 5A & 6). It is possible that the observed changes and increased abundance of coastal ocean species correspond to physical and environmental shifts potentially linked to coastal oceanographic mechanisms. One potential mechanism which could elevate coastal sea levels (SLs) along the western Mid-Atlantic is change in the strength and stability of the Gulf Stream coupled with atmospheric forcing. Andres (2016) describes the recent destabilization of the Gulf Stream and its westward movement toward the Mid-Atlantic Bight coastal shelf, which impacts both surface and deep water currents. The location and strength of the Gulf Stream coupled with the North Atlantic Oscillation have previously been tied to accelerated flooding along the east coast (Ezer & Atkinson 2014, Goddard et al. 2015), with Ezer (2016) describing a potential SL gradient mechanism driving short-term coastal SL rise. Additionally, Sheridan et al. (2017) and Sweet et al. (2009) have demonstrated that coastal wind patterns can cause elevated dynamic SL and subsequent coastal flooding. Little et al. (2017) describe potential interactions between the decline in the Atlantic meridional overturning circulation and dynamic SL, where long-term changes in coastal waters are likely linked, but local wind-driven forces can greatly impact local SL, and this is supported by Piecuch & Ponte (2015). These conditions were present in the system during the post-Sandy sampling and could support the increased abundance of coastal oceanic gelatinous zooplankton species observed and changes in water quality.

While these physical oceanographic changes were likely responsible for the inclusion of coastal species in samples, the significant density reduction in *C. quinquecirrha* led to community shifts through trophic interactions. The significant increase in *Mnemiopsis leidyi* in 2013 is a direct result of *C. quinquecirrha* declines (Figs. 3B & 4), something that has been observed in other systems where *C. quinquecirrha* and *M. leidyi* are abundant (Feigenbaum & Kelly 1984, Purcell & Decker 2005). In addition, the 64% increase in gelatinous species richness in 2013 and the significant increase in the densities of 4 other species in the ensuing 2 yr (Fig. 5B) can be tied to the increasing densities of *Turritopsis nutricula, Bougainvillea muscus,* and *Rathkea octopunctata* following Hurricane Sandy (Fig. 6). These are relatively small gelatinous species and are potential prey items of *C. quinquecirrha* (Meredith et al. 2016). Consequently, the predation release due to the significant

decline in *C. quinquecirrha* (Fig. 3A) has opened the community to successional shifts, and this is clearly demonstrated in our results (Fig. 5B).

The keystone predator concept has been applied to *C. quinquecirrha* in the Chesapeake Bay, where the relative abundance of sea nettles among years has had a structuring force on the food web and initiated trophic cascades (Feigenbaum & Kelly 1984, Purcell & Decker 2005). Bologna et al. (2017) also demonstrated significant top-down control of food webs by *C. quinquecirrha*, but no trophic cascades were evident, as *C. quinquecirrha* actively fed on copepods (and reduced their densities) as well as on *M. leidyi*. Consequently, the dynamics of predator abundance in this system is quite complex, but the significant decline in *C. quinquecirrha* density has opened and expanded the ecological niches for other species, and results from our ANOSIM demonstrate significant differences in the community among years. It is interesting to evaluate the keystone predator designation of *C. quinquecirrha*, since its removal led to increased diversity rather than diversity loss (cf. Paine 1966, Estes & Palmisano 1974).

If we invoke the keystone predator concept for *C. quinquecirrha*, then its community structuring forces are more similar to communities that have seen introductions of non-native predatory species. For example, the introduction of *M. leidyi* into several systems has caused significant shifts in communities and concomitant fisheries collapses (Oguz & Gilbert 2007, Roohi et al. 2010, Oguz et al. 2012), and the introduction of Nile perch *Labrus niloticus* Linnaeus, 1758 to lakes in Africa has decimated native cichlid populations (Achieng 1990). The introduction of non-native species into new systems is one of the primary concerns in global conservation biology (Ruiz et al. 1997, Bax et al. 2003). Perhaps it is the fact that in Barnegat Bay, where *C. quinquecirrha* have become dominant, prior investigations did not even report their presence (Nelson 1925, Mountford 1980, Sandine 1984). What remains to be understood is whether *C. quinquecirrha* will become reestablished as the apex predator in this system or whether the increase in other taxa seen in 2013 and 2014 will lead to a new species equilibrium. The most likely scenario is that, as the infrastructure slowly returns and polyp habitat becomes available again, *C. quinquecirrha* populations will rebound, and they will eventually return to pre-storm densities and begin to exert top-down pressure on the planktonic community. However, large stochastic events can exert impacts on population genetics, which may slow or impede the reestablishment of this species (Banks et al. 2013, Mora et al. 2016).

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Appendix. Sampling stations and coordinates for the 16 sites used for data collection, coordinated from north to south

Bay-wide sampling site	Abbreviation	GPS coordinate N	GPS coordinate W
Metedeconk River West	MW	40.050983	−74.064300
Metedeconk River East	ME	40.045183	−74.054117
Silver Bay West	SBW	39.992217	−74.119350
Silver Bay East	SBE	39.933683	−74.092100
Toms River West	TRW	39.989917	−74.107567
Toms River East	TRE	39.925833	−74.084733
Forked River West	FRW	39.821333	−74.159667
Forked River East	FRE	39.815767	−74.122883
Double Creek East	DCE	39.787550	−74.153833
Double Creek West	DCW	39.786100	−74.182700
Harvey Cedars West	HCW	39.700733	−74.166050
Harvey Cedars East	HCE	39.698917	−74.146000
Westecunk Creek West	WW	39.620117	−74.259400
Westecunk Creek East	WE	39.598800	−74.229750
Tuckerton Creek West	TCW	39.578983	−74.324283
Tuckerton Creek East	TCE	39.556400	−74.254433