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Zooplankton Community Dynamics in a Western Mid-Atlantic Lagoonal Estuary

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ABSTRACT

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Zooplankton are an integral component of the food web in estuarine ecosystems. The most recent studies of zooplankton in Barnegat Bay, New Jersey, occurred almost 40 years ago. Since then, this coastal lagoon estuary has been affected by anthropogenic impacts that threaten its ecological integrity, including nutrient enrichment, algal blooms, alterations of freshwater inputs, and extensive development around the bay and its watershed. Assessing the zooplankton community in this ecosystem provided updated information on the status of this important component of the bay's living resources. Zooplankton samples were collected from the upper meter of the water column with horizontal surface net tows using bongo plankton nets monthly during the winter and twice a month during spring, summer, and fall. Sites were located along a longitudinal transect in the bay. Data included abundance and distribution of copepods, gelatinous macrozooplankton, bivalves, and decapods. The zooplankton community was characterized by strong spatial, seasonal, and interannual trends in abundance and diversity. Spatial variability is most apparent between the northern and southern sections of the bay. The northern bay was characterized by higher nitrogen and chlorophyll *a*; high abundances of copepods, ctenophores, and barnacle larvae; and lowest species diversity. Alkalinity, phosphate, and species diversity were higher in the southern bay. This was a typical pattern for the study, remaining stable even between seasons. It is apparent that direct and/or indirect effects of weather and climate affect zooplankton abundance in Barnegat Bay. Such sensitivity to changes in weather patterns has the potential to cause long-term shifts in the zooplankton community as a result of climate change.

ADDITIONAL INDEX WORDS: *Spatial and seasonal trends, copepods, ctenophores, water quality.*

INTRODUCTION

Plankton form the base of the food web in temperate estuarine ecosystems. Zooplankton provide an important link in the transfer of energy from phytoplankton to higher trophic levels in the estuarine food web (Gewant and Bollens, 2005). The estuarine zooplankton community includes holoplanktonic taxa that remain their entire lives as part of the plankton community and act as an important food resource for larger invertebrates and fishes (Houde and Rutherford, 1993), as well as meroplanktonic larvae of benthic and pelagic taxa, including commercially and recreationally important fishery species (Redden *et al.*, 2009).

As is typical for estuarine organisms, zooplankton are subject to temporally and spatially variable environmental stressors such as temperature and salinity. Impacts may be ameliorated by nutrient input that fuels population growth or may be exacerbated by anthropogenic non–point source nutrient loading that leads to eutrophication, uncontrolled blooms, and subsequent habitat deterioration (Kennish, 1992). Such parameters vary on diel and seasonal scales in temperate estuaries and act to regulate zooplankton abundance and distribution (Morgan, 1995; Rissik *et al.,* 2009). Physical conditions may impact zooplankton community dynamics at scales varying from small, *e.g.*, entrainment in localized eddies, to large, *e.g.*, advection out of the system due to weather-induced changes in current patterns (Shanks, 1995). Zooplankton communities are therefore characteristically dynamic and very patchy (Miller and Wheeler, 2012; Suthers *et al.,* 2009).

In a southeastern U.S. estuary, zooplankton abundance was correlated with temperature (Fulton, 1984; Mallin, 1991). Zooplankton communities were defined by temperature and salinity in a southern California estuary (Elliott and Kaufmann, 2007) and in the Gulf of Mexico (Holt and Strawn, 1983). In the Pacific Northwest, seasonality of zooplankton communities was correlated with the salinity gradient resulting from riverine flow in the Columbia River estuary (Breckenridge *et al.*, 2015), but temperature was the primary parameter affecting zooplankton abundance and distribution in Willapa Bay, Washington (Graham and Bollens, 2010).

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Biotic impacts such as competition and predation may enhance or worsen the impacts of abiotic parameters on zooplankton communities. In Tomales Bay, California, the pattern of copepod distribution was due to size-selective predation (Kimmerer, 1993), while in the upper San Francisco estuary, Winder and Jassby (2011) attributed interannual differences in the zooplankton community to impacts from invasive species as well as salinity changes from long-term drought. Although zooplankton abundance was correlated with temperature in a central California estuary, chlorophyll *a*, a proxy for phytoplankton abundance, was also important (Orsi and Mecum, 1986). However, copepod density was not correlated with chlorophyll *a* in a North Carolina estuary (Mallin, 1991).

Barnegat Bay–Little Egg Harbor (Barnegat Bay), New Jersey, is a shallow coastal estuary in the mid-Atlantic region of the United States (Figure 1; Kennish, 2001) and is characterized by a longitudinal gradient of anthropogenic nutrient loading, eutrophication, and poor tidal flushing, with impacted conditions prevalent in the northern bay (Defne and Ganju, 2015; Kennish *et al*., 2007). There are three inlets to the bay (Figure 1), two along the barrier island (Barnegat Inlet and Little Egg Harbor Inlet) and one from a man-made canal (Point Pleasant Canal). Tatham *et al*. (1977, 1978) studied the zooplankton community in the central region of Barnegat Bay; plankton abundance peaked in spring and summer but was characterized by strong temporal variability. Other studies in Barnegat Bay and the region have noted strong seasonal trends (Cronin, Daiber, and Hulbert, 1962; Knatz, 1978; Mountford, 1980; Sage and Herman, 1972; Steinberg and Condon, 2009; Turner, 1982), spatial variability (Yamazi, 1966), and the importance of anthropogenic impacts (Rothenberger *et al*., 2014; Shaheen and Steimle, 1995) on estuarine zooplankton communities.

Suburban and urban development in the Barnegat Bay watershed has increased substantially since the Tatham (1977, 1978) study, leading to increased non–point source input of nutrients and a concomitant increase in frequency of algal blooms (Barnegat Bay Partnership, 2016). Conversely, numerous wastewater treatment discharges into the bay were eliminated by 1979. Blooms of gelatinous species, *e.g*., sea nettle *Chrysaora quinquecirrha* and ctenophore *Mnemiopsis leidyi*, have become more abundant in the estuary in recent years (Bologna, Gaynor, and Meredith, 2017). Since gelatinous taxa, especially ctenophores, are important predators on other zooplankton (Costello *et al.,* 2012), an increase in occurrence of blooms has implications on overall zooplankton community structure.

The current study is a comprehensive assessment of Barnegat Bay zooplankton over a 3 year period. The objectives of this study were to characterize the zooplankton community in the bay; to elucidate trends in the occurrence, distribution, and abundance of dominant zooplankton taxa; and to examine the contributions of environmental parameters to the observed community patterns.

METHODS

Techniques used in this study were tailored for the study location (*i.e*. shallow water) with sampling stations along the long axis of the bay. Sampling was conducted each month, and resultant data were analyzed as described in the following sections.

Study Location

The study was conducted in Barnegat Bay, New Jersey, a 167 km^2, shallow coastal lagoon estuary in the mid-Atlantic characterized by poor tidal flushing, limited freshwater input, non–point source nutrient pollution, and mixed-use development within the approximately 1,700 km^2 watershed. Anthropogenic impacts decrease along a latitudinal gradient in the bay, with higher input in the northern bay. Study sites corresponded to New Jersey Department of Environmental Protection water quality sampling sites for better comparisons with other studies conducted concurrently in the bay (Figure 1).

Sampling Protocol

Sampling was conducted at each of three sites, BB02, BB05a, and BB12, from May 2012 to September 2012. Two additional sites, BB07a and BB10, were added in September 2012, so that all subsequent regular sampling events through April 2015 were conducted at all five sites. For the entire 3 year study, 54 regular sampling events were conducted during May 2012–April 2015, with 501 samples collected and processed.

Zooplankton were collected from the upper meter of the water column with horizontal surface net tows using two 0.5 m diameter bongo plankton nets. The water column was generally 1–3 m in depth. A sample tow was defined as a replicate pair of 500 µ nets followed by a replicate pair of 202 µ nets for each site, along with the measurement of abiotic water quality parameters. A flow meter was attached to each net for each tow to determine the volume of water sampled. The abiotic parameters water temperature, salinity, conductivity, dissolved oxygen (DO) mg/L, DO % saturation (% sat), and pH were measured with a calibrated YSI 600XL datasonde multiparameter water quality probe; water depth was measured with the vessel depth finder; water transparency was measured with a 20 cm Secchi disc.

A sampling event was the collection of sample tows at all sites, typically over a 1- or 2-day period. Sampling events occurred twice monthly during March–September and once monthly during November–February with some exceptions due to weather.

Each zooplankton sample was passed through a 4 mm mesh sieve to remove macrozooplankton and debris. Targeted gelatinous species in the macrozooplankton (*M. leidyi*, *Beroe ovata*, and *C. quinquecirrha*) were immediately identified and enumerated. Data collected on the gelatinous species included total volume per tow, total count per tow, and lengths (*M. leidyi* and *B. ovata*) and bell width (*C. quinquecirrha*) of 20 haphazardly selected individuals from each sample. Ichthyoplankton were removed for a separate study. Sieved mesozooplankton samples were preserved in 5% buffered formalin. Each 202 µ sample was separated with a 500 µ and a 202 µ sieve to produce a 202–500 µ fraction; this was designated the "200 µ" sample. One each of the two replicate 500 µ and 200 µ samples for each site for every sampling event was selected randomly for transport to a zooplankton processing laboratory, Morski Instytut Rybacki–Państwowy Instytut Badawczyi

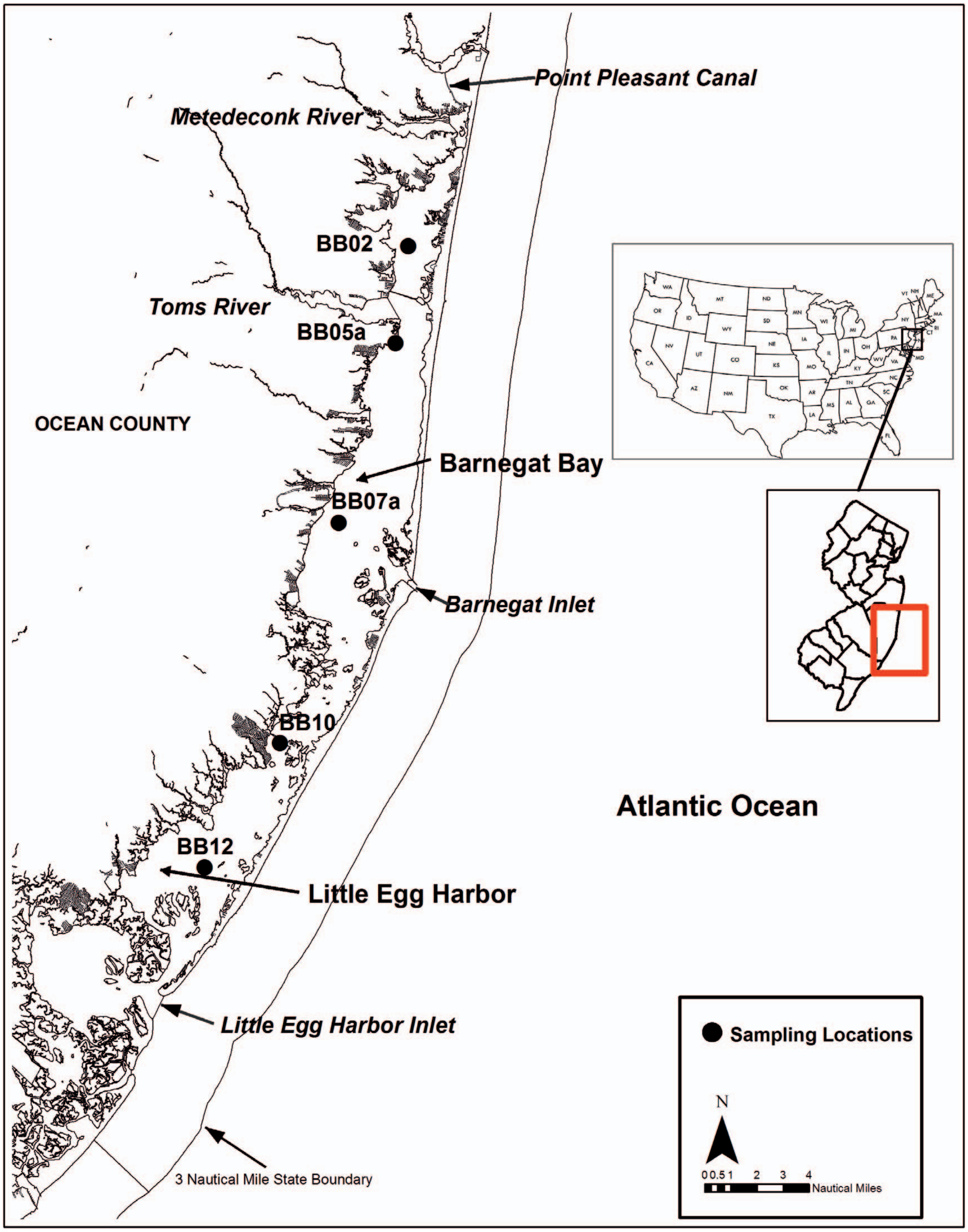

Figure 1. Zooplankton sampling Locations in Barnegat Bay–Little Egg Harbor, New Jersey.

(MIR), Zakład Sortowania i Oznaczania Planktonu (ZSIOP) in Poland.

Samples were processed at ZSIOP according to established protocols used with National Oceanic and Atmospheric Administration (NOAA) samples for 40+ years. Specimens were identified to the lowest possible taxonomic level.

Analyses

In total, 501 samples were collected, identified, and analyzed. All taxa present in $\geq 5\%$ of samples were included in the analyses. Mean abundance data were calculated as number of individuals per 100 m^3 of water (100 m^{-3}). Primer-E software

(v. 6.1.15; Clarke and Warwick, 2001) was used to examine the similarities and differences between zooplankton communities across samples, seasons, and sites. Abundance data were fourth-root transformed to decrease the weight of high-abundance taxa (*e.g.*, *Acartia* spp.). The resultant data were converted to a resemblance matrix using a Bray-Curtis similarity index. Nonmetric multidimensional scaling (MDS) plotted resemblance matrix data such that distance reflects dissimilarity; analysis of similarities (ANOSIM) tested the similarities of the zooplankton assemblages; and similarity percentage analysis (SIMPER) determined how taxa contributed to those similarities. Species diversity indices [species richness (Margalef), Shannon index, Pielou's evenness, and Simpson index] were calculated for each sample then averaged over site, month, and season. Season (astronomical) was determined by sample date.

RESULTS

Details on the data and findings of the 3 year study follow and include water quality, zooplankton abundance, community dynamics, and gelatinous macrozooplankton. Data analyses including statistical results are presented to describe the relative strength of the results.

Water Quality Data

Water temperature during the study period followed trends expected with seasonal changes. Water temperature trends were similar across all five stations (Figure 2a), although temperature was slightly cooler in the summer of 2014 than in the two previous summers. The winters of 2013–2014 and 2014–2015 were unusually cold in New Jersey, preventing sampling in some months. Salinity generally remained higher at BB07a, BB10, and BB12 throughout the sampling period. Salinity is lower in the northern bay (BB02 and BB05a) because of riverine input (Figure 2b). Dissolved oxygen (DO) levels were greatest in winter 2014–2015 but were also comparably high in the two previous winters of the study (Figure 2c). It is likely that the high DO levels are due to the decrease in temperature, since cold water holds more oxygen than warm water. Secchi transparency (water clarity) is inversely related to turbidity. Wind may mix particulate organic matter in the water column, or biological factors such as phytoplankton or zooplankton blooms may increase turbidity. Water clarity was variable over much of this study period but was generally highest in October, *e.g.*, October 2014 at BB10 (Figure 2d).

Zooplankton Abundance

Zooplankton abundance was quantified for each sampling site for each size fraction and for combined fractions. Bimodal seasonality was apparent in 2012 and 2014, with a very strong bloom at the most northern and southern sites in late spring 2012 followed by a smaller pulse in September/October 2012 (Figure 3). A strong bloom occurred again in November/December 2012 at all sites. The following spring a protracted but less intense bloom occurred across all sites. A fall bloom did not occur that year, however. Abundance in 2014 was characterized by an intense bloom in the spring followed by moderate numbers during the summer throughout the bay. A late summer pulse occurred in the lower bay, but zooplankton abundance declined into the fall of that year. Low densities of zooplankton were observed in the bay throughout the winter and early spring of 2014–2015. Abundance patterns observed for the 200–500 μ fraction (Figure 3a) and a smaller contribution by the >500 μ fraction (Figure 3b) were merged to exhibit the patterns of abundance for the combined fractions (Figure 3c). The mesoplankton and macroplankton of the >500 μ fraction produced small blooms in early spring of 2013 and 2014, but their abundance was much lower in spring 2015.

The intense bloom in spring 2012 at BB02 and BB12 was dominated by *Acartia* spp. This copepod comprised 77% of the bloom at BB02 and 60% of the bloom at BB12. Balanidae (barnacles) contributed 5% of the total abundance of zooplankton at BB02, while gastropods made up 3% of the total at BB02 and 16% at BB12. Distinctive peaks in abundance appeared at BB07 in April 2013 and 2014 but were produced by different species. The 2013 bloom was caused by several copepod species, including *Centropages*, *Eurytemora*, *Oithona*, and *Acartia* spp., as well as barnacle nauplii. The April 2014 bloom was made up almost entirely of *Eurytemora*.

The distinctive blooms of the >500 μ fraction in 2013 and 2014 were produced by copepods, including *Centropages hamatus* (53%) and *Eurytemora* spp. (31%) at BB10 in March 2013. In 2014, *Eurytemora* was the dominant copepod at BB02, BB05a, BB07a, and BB10 (87%, 63%, 88%, and 94% of entire sample, respectively), but *Acartia* was the dominant taxon at BB12, comprising 55% of the abundance for the >500 μ fraction, and *Eurytemora* abundance was <0.1%.

Zooplankton Community Dynamics

In general, interannual variability was observed in the intensity of spring and fall blooms as measured by abundance. There also appeared to be spatial variability in the blooms, with no consistent pattern in the intensity or location of blooms. *Acartia* was the most abundant taxon in the samples, with locally intense periodic blooms. Coastal copepod species were most often collected at BB07a, BB10, and BB12, which are exposed to more oceanic influence. However, to examine trends in the overall zooplankton community structure, a nonparametric multivariate approach was employed.

Zooplankton Community Metrics

When zooplankton taxonomic data from all routine samples were totaled (combined fractions), 34 taxa appeared in at least 5% of all samples (Table 1). Mean abundance of each taxon within each sample was then totaled to determine total mean abundance for each sample. For the combined fractions, the total mean abundance was 64,992 specimens. The copepod genus *Acartia* occurred in 91% of the samples and comprised 56.7% of the total mean abundance. *Acartia* spp. and the copepod genus *Eurytemora* together made up 71.8% of the total mean abundance. The most commonly occurring noncopepod taxon was Balanidae (acorn barnacles), which appeared in 63% of the samples and comprised 3.8% of the total mean abundance.

When the >500 μ fraction was analyzed separately from the 200–500 μ fraction, 31 taxa were present in the samples at or greater than a 5% frequency. In this case *Acartia* was not the dominant taxon, probably because of size differences in the copepod groups. *Eurytemora* spp. made up 41.8% of the total,

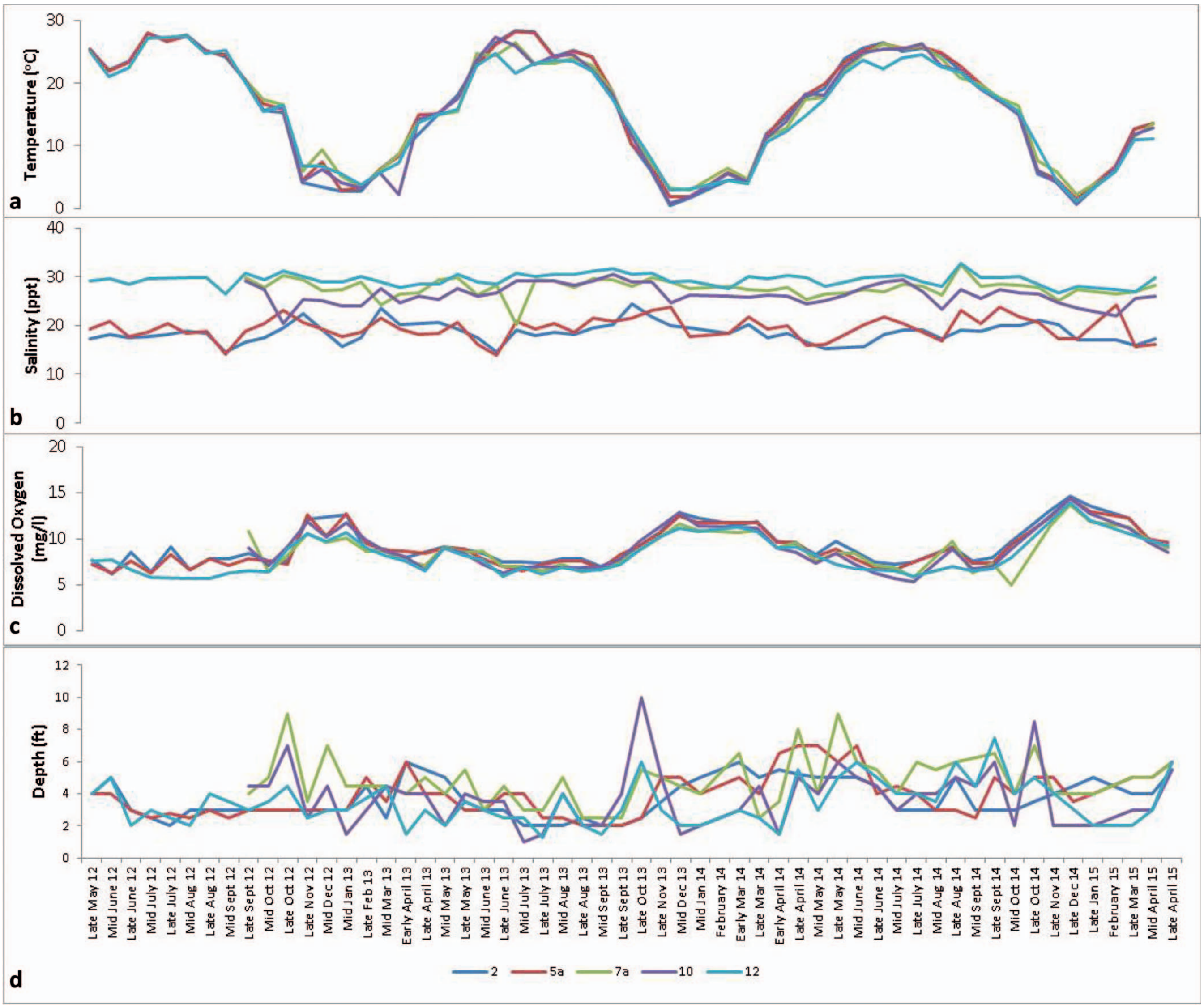

Figure 2. Abiotic data collected at Sites BB02, BB05a, BB07a, BB10, and BB12 in May 2012–April 2015. (a) temperature (°C); (b) salinity (ppt); (c) dissolved oxygen (mg/L); (d) Secchi transparency (ft). Sites 7a and 10 were added in late September 2012.

and when combined with two other copepod species, *Centropages hamatus* and *Temora longicornis*, comprised 81% of the total number of individuals in this collection (Table 2). Although *Acartia* was not as abundant in this fraction, it still appeared quite often, with a frequency of 85.7%. This is in contrast with the three most numerically abundant taxa in this group, which each appeared in less than 50% of the samples (*Eurytemora* spp., 30.3%; *C. hamatus*, 45.8%; *T. longicornis*, 36.3%). This pattern reflects the seasonality of population growth of these three coastal taxa within the estuary, while it is apparent that the estuarine *Acartia* is a commonly occurring resident in Barnegat Bay.

Although 27 taxa appeared in ≥5% of samples in the 200–500 μ fraction, *Acartia* spp. dominated the collection (Table 3). The copepod genus appeared in 97.2% of all routine samples of this fraction and made up 65.3% of the total mean abundance of 111,018 individuals. *Acartia* spp. and *Eurytemora* spp. together comprised 75.6% of the total mean abundance. Acorn barnacles (Balanidae) and snails (Gastropoda) also commonly occurred, with frequencies of 81.6% and 58%, respectively.

Similarity/Dissimilarity of Zooplankton Communities

Taxonomic mean abundances were compared across sampling date, season, and site in order to test for similarities and differences in the zooplankton community. Zooplankton community structure differed throughout the 3 years of the study ($R = 0.204, p < 0.001$), and seasonality was evident ($R = 0.204, p < 0.001$). Differences were especially marked between summer and winter ($R = 0.491, p < 0.001$) and were significant, but not as strongly dissimilar, between most other seasonal combina-

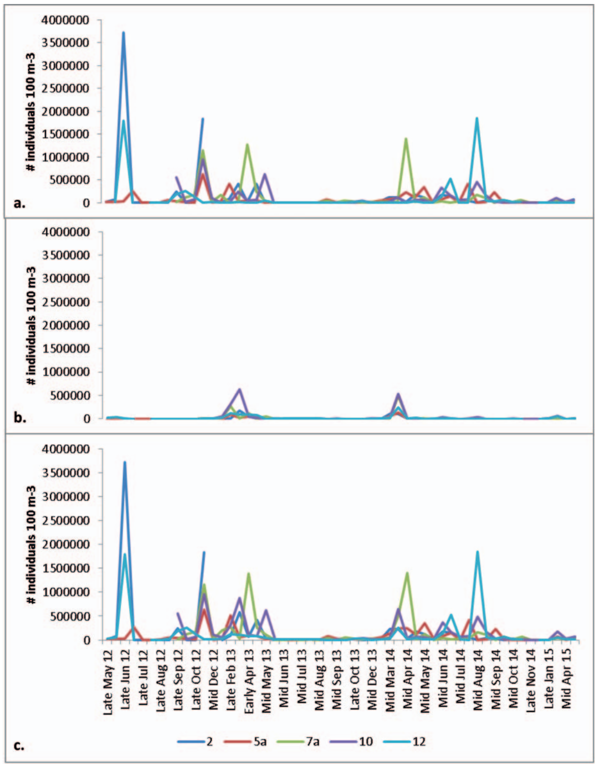

Figure 3. Zooplankton abundance for (a) 200–500 μ (b) >500 μ fraction, and (c) total abundance (combined fractions) collected at Sites BB02, BB05a, BB07a, BB10, and BB12 in May 2012–April 2015.

tions (*e.g.,* spring/summer, spring/fall, *etc*.). The only nonsignificant pairing was that of spring and winter. Community structure of the combined zooplankton fractions was weakly significantly different across sites ($R = 0.025$, $p = 0.003$). The combinations of BB02/BB12, BB05a/BB12, and BB05a/BB07a were significantly different ($p < 0.001$, <0.001, $= 0.029$, respectively).

Samples were too numerous to provide meaningful results when each sample community was analyzed for percentage similarity/dissimilarity. Within-site similarity indices indicate that community structure at each site was variable throughout the 3 year sampling period.

Because significant differences in community structure were observed, it is useful to determine which taxa are the most important contributors to those differences. Community structure of each sample was compared within and across sites, and within and across seasons. Community structure for each sample was compared for similarity within each treatment (site, season), and then between sites or seasons for dissimilarity. The top five contributing taxa to each comparison were determined, as well as percentage contribution.

Within-site similarities (Table 4) were lowest in the >500 μ fraction (16.9–22.5%) and highest in the samples from the 200–500 μ fraction (36.3–46.7%). The smaller plankton appear to create a more stable community at each site (less variability over the 3 year sampling period), which may be because 200–500 μ plankton tend to be holoplanktonic and remain more consistently associated with the planktonic community, whereas larger plankton (*e.g.*, Brachyura) are meroplankton that are transient in the planktonic community.

Table 1. *Zooplankton taxa collected in Barnegat Bay, New Jersey, May 2012–April 2015. Fractions (>500 μ, 200–500 μ) were combined.*

Taxon	Total Mean Abundance (No. individuals 100 m^{-3})	% of Total	Cumulative %	Frequency (% Occurrence in samples)
Acartia spp.	36,550	56.7	56.7	91.4
Eurytemora spp.	9747	15.1	71.8	33.3
Centropages hamatus	2447	3.8	75.6	37.1
Balanidae	2433	3.8	79.4	63.1
Temora longicornis	2390	3.7	83.1	31.9
Gastropoda	2295	3.6	86.6	46.3
Centropages spp.	1706	2.6	89.3	25.7
Calanoida	1309	2.0	91.3	60.5
Podon spp.	1062	1.6	92.9	12.4
Oithona spp.	957	1.5	94.4	36.5
Polychaeta	891	1.4	95.8	33.7
Coelenterata	614	<1	96.8	44.3
Brachyura	445	<1	97.4	31.7
Evadne spp.	437	<1	98.1	24.4
Harpacticoida	334	<1	98.6	48.9
Centropages typicus	255	<1	99.0	27.1
Copepoda	223	<1	99.4	24.2
Bivalvia	212	<1	99.7	22.8
Decapoda	202	<1	99.9	31.5
Paracalanus spp.	163	<1	99.9	9.4
Temora spp.	85	<1	99.9	7.2
Cyclopoida	40	<1	99.9	16.8
Caridea	35	<1	99.9	19.8
Isopoda	27	<1	99.9	17.4
Pseudocalanus minutus	24	<1	99.9	8.8
Tortanus discaudatus	24	<1	99.9	10.6
Calanus finmarchicus	21	<1	99.9	8.4
Foraminifera	18	<1	99.9	7.2
Ostracoda	9	<1	99.9	8.2
Gammaridea	8	<1	99.9	14.6
Mysida	8	<1	99.9	12.0
Pontellidae	8	<1	99.9	11.8
Chaetognatha	7	<1	99.9	5.8
Amphipoda	6	<1	100.0	13.2
Total	64,992			

Within-season similarities (Table 4) exhibited a pattern similar to that of within-site similarities described above. The 200–500 μ fraction maintained a more stable planktonic community (more similar community structure) within each season. Larger plankton, typically meroplanktonic, often appeared in the samples in pulses (*e.g.*, Decapoda, Brachyura, Bivalvia). Although holoplanktonic copepods were most abundant in blooms, some genera such as *Acartia* and *Eurytemora* were common in most samples.

Community structure was compared between sites and between seasons to evaluate differences and examine taxa contributing to those differences. There were strong differences in communities between sites (Table 5), especially for the >500 μ size fraction. The presence of taxa such as *Eurytemora* spp., *C. hamatus*, Coelenterata, and Brachyura contributed to those differences in community structure between sites. Since the 200–500 μ taxa are smaller, they may be more likely to be advected throughout the bay than larger taxa; thus the

Table 2. *Zooplankton taxa collected in Barnegat Bay, New Jersey, May 2012–April 2015. >500 μ fraction.*

Taxon	Total Mean Abundance (No. individuals 100 m^{-3})	% of Total	Cumulative %	Frequency (% Occurrence in samples)
Eurytemora spp.	7981	41.8	41.8	30.3
Centropages hamatus	4072	21.3	63.1	45.8
Temora longicornis	3414	17.9	81.0	36.3
Coelenterata	897	4.7	85.7	64.9
Acartia spp.	779	4.1	89.8	85.7
Brachyura	509	2.7	92.5	45.8
Centropages typicus	431	2.3	94.7	41.4
Balanidae	338	1.8	96.5	44.6
Decapoda	197	1.0	97.5	50.2
Gastropoda	87	<1	98.0	33.5
Caridea	56	<1	98.3	32.3
Centropages spp.	46	<1	98.5	8.4
Calanus finmarchicus	41	<1	98.7	16.3
Evadne spp.	39	<1	98.9	23.5
Tortanus discaudatus	37	<1	99.1	17.1
Calanoida	34	<1	99.3	43.4
Copepoda	18	<1	99.4	12.0
Mysida	16	<1	99.5	23.1
Chaetognatha	16	<1	99.6	9.6
Gammaridae	15	<1	99.7	27.9
Polychaeta	12	<1	99.7	19.5
Pontellidae	11	<1	99.8	17.9
Pseudocalanus minutus	7	<1	99.8	8.4
Cyclopoida	6	<1	99.8	6.0
Bivalvia	6	<1	99.9	15.9
Harpacticoida	6	<1	99.9	21.5
Isopoda	5	<1	99.9	30.3
Amphipoda	5	<1	99.9	22.3
Oithona spp.	4	<1	99.9	16.3
Ostracoda	0	<1	99.9	6.0
Cumacea	0	<1	100.0	7.2
Total	19,088			

Table 3. *Zooplankton taxa collected in Barnegat Bay, New Jersey, May 2012–April 2015. 200–500 μ fraction.*

Taxon	Total Mean Abundance (No. individuals 100 m^{-3})	% of Total	Cumulative %	Frequency (% Occurrence in samples)
Acartia spp.	72,464	65.3	65.3	97.2
Eurytemora spp.	11,520	10.4	75.6	36.4
Balanidae	4536	4.1	79.7	81.6
Gastropoda	4513	4.1	83.8	58
Centropages spp.	3372	3.0	86.8	43.2
Calanoida	2595	2.3	89.2	72.8
Podon spp.	2128	1.9	91.1	20.4
Oithona spp.	1913	1.7	92.8	56.8
Polychaeta	1773	1.6	94.4	48.4
Temora longicornis	1363	1.2	95.6	27.6
Evadne spp.	836	<1	96.4	25.2
Centropages hamatus	815	<1	97.1	28.4
Harpacticoida	664	<1	97.7	74
Copepoda	429	<1	98.1	38.8
Bivalvia	419	<1	98.5	29.6
Brachyura	382	<1	98.8	17.6
Coelenterata	329	<1	99.1	22.8
Paracalanus spp.	326	<1	99.4	15.6
Decapoda	207	<1	99.0	12.8
Temora spp.	170	<1	99.0	12
Centropages typicus	78	<1	99.0	12.8
Cyclopoida	75	<1	99.0	27.6
Pseudocalanus minutus	41	<1	99.0	9.2
Foraminifera	36	<1	99.0	12
Ostracoda	17	<1	99.0	10.4
Caridea	14	<1	99.0	7.2
Pontellidae	4	<1	100.0	5.6
Total	111,018			

community structure for smaller taxa is more spatially uniform.

Seasonal differences were very strong for the >500 μ fraction, since larger coastal copepods (*e.g.*, *C. hamatus*) are abundant in the winter in Barnegat Bay, and meroplankton exhibit strong seasonal spawning pulses (Table 6). The greatest differences in community structure were between summer and winter communities for all samples. The 200–500 μ fraction again exhibited a more stable and uniform planktonic community compared to the larger fraction.

Relationships in the taxonomic data were visualized by analyzing the Bray-Curtis resemblance matrix with principal coordinates analysis (PCO). PCO is similar to principal components analysis (PCA) but more appropriate for biological community data, which even with transformations is typically nonnormally distributed. Taxa (Table 7) were evaluated with multiple correlations on the PCO plots. Taxa with correlations $\geq$0.25 are represented by vectors on the plots to better evaluate those driving the variability in the community data.

The PCO of the entire zooplankton data set did not group the communities according to site but did exhibit a trend in the data along the PCO1 axis, with variability (23.1%) driven primarily by seasonal differences in the zooplankton communities (Figure 4). PCO2 (18%) varied somewhat with sampling year. The most important taxa (correlation $\geq$0.25) driving the seasonal trend were the copepods *C. hamatus*, *Centropages typicus*, *T. longicornis*, and *Eurytemora* sp., which appeared regularly in the winter and early spring samples. The extremely elevated abundances of *Acartia* spp. in 2012–2013 were responsible for the high correlation between that taxon and the PCO2 axis.

The results of the PCO for the 200–500 μ zooplankton community was similar to those PCO plots created for the complete dataset, with PCO1 (22.4%) affected mainly by seasonal differences, while PCO2 (18%) varied with sampling year (Figure 5). The zooplankton community did not differentiate strongly according to site. *Centropages hamatus*, *T. longicornis*, *Eurytemora* spp., and additional copepods *Centropages* spp. and *Oithona* spp., are correlated with seasonal differences; as in this study they were most typically found in the winter/early spring zooplankton community. Highest abundances of *Acartia* spp. and snails *Gastropoda* (order of magnitude greater than the other years) occurred in 2012–2013; they are likely important in driving the interannual trends in this dataset.

The $\geq$500 μ zooplankton fraction exhibited similar trends in the PCO as the previous two data sets (Figure 6). PO1 contributed 22.2% of the variability, while PCO2 was responsible for only 10.9%. Sites were not strongly differentiated in this data set. *Centropages hamatus*, *C. typicus*, *T. longicornis*, *Eurytemora* spp., and the cladoceran genus *Evadne* spp. were again typical of the winter/spring community. These copepod

Table 4. *Similarity indices comparing community structure of samples across sites and seasons.*

	Combined Fractions				>500 Fraction				200–500 Fraction			
	Group Avg. Sim.	Taxon	Avg. Sim.	% Contrib.	Group Avg. Sim.	Taxon	Avg. Sim.	% Contrib.	Group Avg. Sim.	Taxon	Avg. Sim.	% Contrib.
Site												
2	23.8	*Acartia* spp.	8.7	36.5	16.9	*Acartia* spp.	5.2	30.9	36.3	*Acartia* spp.	14.5	39.9
		Balanidae	3.5	14.7		Coelenterata	2.1	12.4		Balanidae	7.4	20.4
		Gastropoda	1.6	6.6		Brachyura	1.9	11.1		Gastropoda	3.5	9.6
		Calanoida	1.5	6.1		Decapoda	1.1	6.5		Harpacticoida	2.8	7.6
		Coelenterata	1.2	5.2		Caridae	1.0	5.6		Calanoida	2.7	7.3
				69.1				66.5				84.8
5a	28.0	*Acartia* spp.	11.1	39.5	19.1	*Acartia* spp.	7.0	36.7	46.7	*Acartia* spp.	18.6	39.8
		Balanidae	4.8	17.2		Brachyura	2.5	13.0		Balanidae	10.4	22.3
		Gastropoda	1.6	5.9		Coelenterata	2.2	11.6		Gastropoda	3.4	7.3
		Coelenterata	1.4	5.0		Balanidae	1.3	6.6		Calanoida	3.4	7.2
		Calanoida	1.2	4.2		Decapoda	1.1	5.5		Harpacticoida	2.3	4.8
				71.8				73.4				81.4
7a	27.5	*Acartia* spp.	8.1	29.3	19.8	*Acartia* spp.	4.0	20.0	41.2	*Acartia* spp.	13.9	33.8
		Balanidae	2.6	9.6		*C. hamatus*	2.4	12.2		Harpacticoida	4.1	9.9
		C. hamatus	1.6	5.8		Decapoda	2.3	11.4		Balanidae	3.9	9.5
		Calanoida	1.5	5.5		Brachyura	2.1	10.8		Calanoida	3.4	8.3
		T. longicornis	1.5	5.3		*C. typicus*	2.1	10.4		*Oithona* spp.	2.7	6.5
				55.5				64.8				68.0
10	30.2	*Acartia* spp.	11.0	36.4	19.6	*Acartia* spp.	6.3	32.1	44.6	*Acartia* spp.	16.4	36.8
		Calanoida	2.8	9.2		Coelenterata	2.5	12.8		Harpacticoida	5.9	13.1
		Harpacticoida	2.3	7.7		*C. hamatus*	2.0	10.4		Calanoida	5.7	12.9
		Eurytemora spp.	1.6	5.2		Brachyura	1.8	9.1		Gastropoda	2.5	5.6
		Balanidae	1.6	5.2		Decapoda	1.5	7.6		Balanidae	2.4	5.3
				63.7				72.0				73.7
12	30.3	*Acartia* spp.	8.0	26.4	22.5	*Acartia* spp.	4.2	18.6	44.4	*Acartia* spp.	11.8	26.6
		Calanoida	2.6	8.4		Brachyura	3.7	16.3		Calanoida	6.4	14.3
		Balanidae	2.2	5.6		Decapoda	2.9	13.1		Harpacticoida	4.8	10.7
		C. hamatus	1.7	5.6		*C. hamatus*	2.3	10.3		Balanidae	4.3	9.6
		Brachyura	1.6	5.2		Coelenterata	2.1	9.1		*Oithona* spp.	2.9	6.5
				51.2				67.3				67.7
Season												
Spring	31.2	*Acartia* spp.	8.0	25.5	22.8	*C. hamatus*	4.1	18.2	42.9	*Acartia* spp.	13.3	31.1
		Balanidae	3.2	10.3		*Acartia* spp.	3.7	16.2		Balanidae	5.1	11.9
		C. hamatus	3.2	10.2		Coelenterata	3.1	13.4		*Eurytemora* spp.	4.5	10.6
		Eurytemora spp.	2.9	9.3		*C. typicus*	2.4	10.3		Harpacticoida	3.0	7.0
		Coelenterata	2.1	6.6		*T. longicornis*	1.7	7.6		*Centropages* spp.	3.0	7.0
				61.9				65.7				67.6
Summer	33.7	*Acartia* spp.	10.2	30.3	29.7	Brachyura	11.2	37.8	48.8	*Acartia* spp.	18.3	37.5
		Gastropoda	5.0	14.8		*Acartia* spp.	5.4	18.3		Gastropoda	9.3	19.1
		Brachyura	4.9	14.6		Decapoda	4.5	15.1		Balanidae	7.1	14.6
		Balanidae	2.9	8.5		Coelenterata	2.3	7.7		Calanoida	5.6	11.4
		Calanoida	2.3	6.8		Gastropoda	1.7	5.8		Harpacticoida	3.6	7.4
				75.0				84.7				90.0
Fall	27.8	*Acartia* spp.	11.0	39.7	20.9	*Acartia* spp.	8.7	41.7	47.5	*Acartia* spp.	17.2	36.3
		Calanoida	3.6	12.9		Coelenterata	2.2	10.5		Calanoida	6.8	14.2
		Harpacticoida	2.1	7.5		Calanoida	1.6	7.6		Harpacticoida	6.0	12.5
		Balanidae	1.9	6.7		Decapoda	1.4	6.5		Balanidae	4.1	8.6
		Oithona spp.	1.2	4.4		*C. hamatus*	1.1	5.1		*Oithona* spp.	3.6	7.6
				71.2				71.4				79.2
Winter	42.0	*Eurytemora* spp.	7.5	18.0	34.9	*C. hamatus*	9.6	27.6	45.9	*Acartia* spp.	8.0	17.3
		Acartia spp.	7.4	17.5		*T. longicornis*	8.1	23.3		*Eurytemora* spp.	7.4	16.1
		T. longicornis	6.8	16.3		*Eurytemora* spp.	6.8	19.4		*Centropages* spp.	6.0	13.1
		C. hamatus	5.6	13.2		*Acartia* spp.	4.1	11.8		Balanidae	4.7	10.3
		Balanidae	5.0	11.8		Balanidae	2.5	7.2		*T. longicornis*	4.4	9.5
				76.8				89.3				66.3

Group Avg Sim = group average similarity index—how similar are the community structures of the samples within the treatment. Avg Sim = average similarity of taxon among samples. % Contrib = percentage contribution of that taxon to the Group Average Similarity.

species were collected in both size fractions, as both larval stages and adults were identified and enumerated in this study. The meroplankton taxa Brachyura, Decapoda, and Isopoda were abundant in spring/summer samples. *Acartia* spp. and Bivalvia drove interannual variability. The spring samples for the $\geq$500 μ zooplankton fraction were more spread out on the plot, indicating a lower similarity than was evident in the other data sets. This may be due to a higher prevalence of meroplankton, which tend to spawn in pulses. Samples were only collected monthly (early spring) or every 2 weeks (late

Table 5. *Dissimilarity indices comparing community structure of samples between sites. Group Avg Dis = group average dissimilarity index—how different are the community structures of the samples between the treatments.*

	Combined Fractions				>500 Fraction				200–500 μ Fraction			
Sites	Group Avg. Dis.	Taxon	Avg. Dis.	% Contrib.	Group Avg. Dis.	Taxon	Avg. Dis.	% Contrib.	Group Avg. Dis.	Taxon	Avg. Dis.	% Contrib.
2 *vs.* 5a	74.0	*Acartia* spp.	10.5	14.2	81.5	*Eurytemora* spp.	10.0	12.3	58.9	*Acartia* spp.	8.5	14.4
		Balanidae	6.6	8.9		*Acartia* spp.	9.9	12.2		*Eurytemora* spp.	5.6	9.5
		Eurytemora spp.	6.0	8.1		Coelenterata	7.3	9.0		Gastropoda	5.5	9.3
		Gastropoda	5.1	6.9		*C. hamatus*	7.0	8.5		Balanidae	5.3	9.0
		Calanoida	3.8	5.2		Brachyura	6.8	8.3		Calanoida	3.9	6.6
				43.3				50.3				48.8
2 *vs.* 7a	75.6	*Acartia* spp.	9.2	12.1	82.9	*C. hamatus*	9.7	11.7	63.8	*Acartia* spp.	8.0	12.5
		Eurytemora spp.	5.4	7.1		*Eurytemora* spp.	8.1	9.7		*Eurytemora* spp.	5.3	8.3
		Balanidae	4.8	6.4		*T. longicornis*	7.2	8.7		Balanidae	4.3	6.8
		C. hamatus	4.2	5.6		*Acartia* spp.	7.1	8.5		*Centropages* spp.	4.2	6.5
		T. longicornis	4.0	5.3		Brachyura	6.5	7.8		Gastropoda	4.1	6.4
				36.5				46.4				40.5
2 *vs.* 10	74.0	*Acartia* spp.	9.8	13.2	82.7	*Eurytemora* spp.	10.5	12.7	62.3	*Acartia* spp.	9.0	14.5
		Eurytemora spp.	6.2	8.4		*Acartia* spp.	10.0	12.1		*Eurytemora* spp.	5.7	9.2
		Balanidae	4.6	6.2		*C. hamatus*	9.4	11.3		Gastropoda	4.9	7.9
		Gastropoda	4.5	6.0		Coelenterata	8.0	9.7		Balanidae	4.7	7.6
		C. hamatus	4.3	5.8		Brachyura	7.9	9.6		Calanoida	4.4	7.1
				39.5				55.4				46.3
2 *vs.* 12	74.7	*Acartia* spp.	8.5	11.3	82.6	*C. hamatus*	9.7	11.7	63.2	*Acartia* spp.	8.4	13.3
		Balanidae	4.5	6.0		Brachyura	9.4	11.4		Calanoida	5.0	7.9
		Calanoida	4.4	6.0		Decapoda	7.4	8.9		Gastropoda	4.6	7.4
		C. hamatus	4.2	5.6		*T. longicornis*	7.1	8.6		Balanidae	4.2	6.7
		Eurytemora spp.	4.1	5.5		*Acartia* spp.	7.1	8.6		*Eurytemora* spp.	4.1	6.6
				34.4				49.2				41.9
5a *vs.* 7a	73.4	*Acartia* spp.	8.7	11.8	82.1	*C. hamatus*	9.9	12.1	58.4	*Acartia* spp.	6.23	10.7
		Eurytemora spp.	5.1	6.9		*Eurytemora* spp.	8.13	9.9		*Eurytemora* spp.	4.84	8.3
		Balanidae	5.0	6.8		*T. longicornis*	7.4	9.0		Balanidae	4.3	7.3
		Gastropodapoda	4.0	5.5		*Acartia* spp.	7.0	8.5		Gastropoda	4.1	7.0
		C. hamatus	4.0	5.4		Brachyura	6.5	7.9		*Centropages* spp.	4.0	6.9
				36.4				47.4				40.2
5a *vs.* 10	72.1	*Acartia* spp.	9.0	12.5	82.1	*Eurytemora* spp.	10.5	12.8	57.4	*Acartia* spp.	7.0	12.2
		Eurytemora spp.	5.8	8.1		*Acartia* spp.	9.8	12.0		*Eurytemora* spp.	5.1	8.9
		Balanidae	4.9	6.8		*C. hamatus*	9.5	11.6		Balanidae	5.1	8.8
		Gastropoda	4.5	6.2		Coelenterata	8.3	10.2		Gastropoda	4.8	8.3
		C. hamatus	4.1	5.6		Brachyura	7.9	9.6		*Centropages* spp.	3.7	6.4
				39.2				56.2				44.6
5a *vs.* 12	72.8	*Acartia* spp.	8.0	11.0	82.2	*C. hamatus*	9.8	12.0	58.4	*Acartia* spp.	7.1	12.2
		Balanidae	4.8	6.5		Brachyura	9.3	11.3		Gastropoda	4.5	7.7
		Calanoida	4.2	5.7		*T. longicornis*	7.2	8.8		Balanidae	4.3	7.4
		Gastropoda	4.1	5.7		Decapoda	7.1	8.6		Calanoida	4.2	7.2
		C. hamatus	3.9	5.4		*Acartia* spp.	7.0	8.6		*Eurytemora* spp.	3.8	6.4
				34.3				49.3				40.9
7a *vs.* 10	71.8	*Acartia* spp.	8.2	11.4	81.2	*C. hamatus*	10.8	13.3	58.0	*Acartia* spp.	6.8	11.8
		Eurytemora spp.	5.4	7.5		*Eurytemora* spp.	9.0	11.1		*Eurytemora* spp.	5.0	8.5
		C. hamatus	4.6	6.4		*Acartia* spp.	8.0	9.8		*Centropages* spp.	4.4	7.6
		Calanoida	3.7	5.2		Brachyura	7.3	9.0		*Oithona* spp.	3.7	6.4
		T. longicornis	3.7	5.2		Coelenterata	6.6	8.1		Gastropoda	3.5	6.1
				35.7				51.3				40.4
7a *vs.* 12	71.3	*Acartia* spp.	7.2	10.1	79.1	*C. hamatus*	11.1	14.0	57.9	*Acartia* spp.	6.8	11.7
		C. hamatus	4.4	6.2		*T. longicornis*	8.5	10.7		*Centropages* spp.	4.2	7.2
		T. longicornis	4.1	5.8		Brachyura	8.3	10.5		Calanoida	3.8	6.6
		Calanoida	3.9	5.5		Decapoda	7.3	9.2		*Oithona* spp.	3.6	6.3
		Eurytemora spp.	3.6	5.0		*C. typicus*	6.5	8.2		*Eurytemora* spp.	3.6	6.2
				32.6				52.6				38.0
10 *vs.* 12	70.3	*Acartia* spp.	7.6	10.8	79.5	*C. hamatus*	10.6	13.3	56.3	*Acartia* spp.	7.6	13.5
		C. hamatus	4.5	6.4		Brachyura	8.9	11.3		*Centropages* spp.	4.0	7.2
		Eurytemora spp.	4.3	6.1		*Acartia* spp.	7.6	9.5		Gastropoda	4.0	7.2
		Calanoida	4.1	5.8		*Eurytemora* spp.	7.0	8.8		*Eurytemora* spp.	3.9	7.0
		Gastropoda	3.7	5.2		*T. longicornis*	6.1	7.7		Calanoida	3.9	6.8
				34.3				50.6				41.7

Avg. Dis. = average dissimilarity of taxon between samples. % Contrib = percentage contribution of that taxon to the Group Average Dissimilarity.

Table 6. *Dissimilarity indices comparing community structure of samples between seasons.*

	Combined Fractions				>500 Fraction				200–500 μ Fraction			
Seasons	Group Avg. Dis.	Taxon	% Contrib.	Avg. Dis.	Group Avg. Dis.	Taxon	% Contrib.	Avg. Dis.	Group Avg. Dis.	Taxon	% Contrib.	Avg. Dis.
Spring *vs*. Summer	75.9	*Acartia* spp.	8.5	11.2	83.2	*C. hamatus*	9.9	11.9	63.2	*Acartia* spp.	7.4	11.7
		Eurytemora spp.	5.8	7.7		Brachyura	9.7	11.7		*Eurytemora* spp.	6.4	10.1
		Gastropoda	5.0	6.6		Coelenterata	8.2	9.8		Gastropoda	5.4	8.6
		Balanidae	4.8	6.3		*Eurytemora* spp.	7.5	9.0		Balanidae	4.3	6.7
		C. hamatus	4.8	6.3		Decapoda	6.8	8.2		*Centropages* spp.	4.2	6.7
				38.1				50.6				43.8
Spring *vs*. Fall	74.8	*Acartia* spp.	8.2	10.9	83.9	*C. hamatus*	11.2	13.4	59.7	*Acartia* spp.	6.7	11.2
		Eurytemora spp.	6.0	8.0		Coelenterata	8.7	10.4		*Eurytemora* spp.	5.8	9.8
		C. hamatus	4.8	6.5		*Eurytemora* spp.	8.3	9.9		*Centropages* spp.	4.1	6.9
		Balanidae	4.4	5.9		*Acartia* spp.	6.6	7.8		Balanidae	3.9	6.5
		Coelenterata	3.9	5.2		*C. typicus*	6.5	7.7		Calanoida	3.8	6.4
				36.5				49.2				40.8
Spring *vs*. Winter	66.3	*Eurytemora* spp.	7.5	11.3	77.5	*Eurytemora* spp.	15.4	19.9	58.0	*Eurytemora* spp.	6.5	11.3
		Acartia spp.	5.7	8.6		*C. hamatus*	13.6	17.5		*Acartia* spp.	6.4	11.1
		T. longicornis	5.6	8.4		*T. longicornis*	12.2	15.7		*Centropages* spp.	4.6	7.9
		C. hamatus	5.4	8.2		*Acartia* spp.	6.0	7.7		*T. longicornis*	3.9	6.7
		Centropages spp.	3.9	5.8		Coelenterata	5.4	6.9		*Oithona* spp.	3.4	5.9
				42.3				67.7				42.9
Summer *vs*. Fall	73.5	*Acartia* spp.	11.1	15.1	81.7	Brachyura	13.4	16.4	57.0	*Acartia* spp.	8.6	15.0
		Gastropoda	5.8	7.9		*Acartia* spp.	11.2	13.7		Gastropoda	5.7	10.0
		Calanoida	5.3	7.3		Decapoda	8.7	10.7		Calanoida	4.6	8.1
		Balanidae	5.1	7.0		Gastropoda	5.1	6.3		Balanidae	4.5	7.8
		Brachyura	4.7	6.4		Coelenterata	4.8	5.9		*Oithona* spp.	3.7	6.5
				43.7				53.0				47.4
Summer *vs*. Winter	81.1	*Eurytemora* spp.	9.1	11.3	93.3	*C. hamatus*	17.7	19.0	70.4	*Acartia* spp.	8.3	11.8
		Acartia spp.	7.5	9.2		*Eurytemora* spp.	16.8	18.0		*Eurytemora* spp.	7.9	11.2
		T. longicornis	7.5	9.2		*T. longicornis*	15.2	16.3		Gastropoda	6.3	8.9
		C. hamatus	6.9	8.6		*Acartia* spp.	8.2	8.8		*Centropages* spp.	5.7	8.1
		Balanidae	4.5	5.5		Brachyura	5.2	5.6		*T. longicornis*	4.6	6.6
				43.8				67.7				46.6
Fall *vs*. Winter	75.2	*Eurytemora* spp.	8.6	11.4	87.8	*C. hamatus*	17.9	20.4	62.3	*Acartia* spp.	7.7	12.3
		Acartia spp.	7.2	9.6		*Eurytemora* spp.	17.4	19.9		*Eurytemora* spp.	6.8	11.0
		T. longicornis	7.2	9.5		*T. longicornis*	15.6	17.8		*Centropages* spp.	4.9	7.9
		C. hamatus	6.6	8.8		*Acartia* spp.	8.5	9.7		*T. longicornis*	4.3	6.9
		Balanidae	4.2	5.6		Balanidae	4.8	5.4		Calanoida	3.9	6.2
				44.9				73.2				44.3

Group Avg. Dis. = group average dissimilarity index—how different are the community structures of the samples' between the treatments. Avg. Dis. = average dissimilarity of taxon between samples. % Contrib. = percentage contribution of that taxon to the Group Average Dissimilarity.

spring/summer); sampling at a higher frequency may smooth the variability.

Species Diversity

Species diversity indices were calculated to examine overall diversity of the zooplankton in Barnegat Bay. Although this does not provide specific information about community structure, it does provide a comparison of overall diversity.

Total taxa and mean abundance were provided previously (Tables 1–3). Diversity increased with decreasing latitude (Figure 7), which is as expected, since the southern bay is more pristine and is subjected to greater oceanic impact. Copepod taxa most often collected in coastal ocean habitats (*e.g.*, *Centropages* spp., *Calanus finmarchicus*) were more abundant at BB07a, BB10, and BB12. The Simpson index rose slightly as latitude decreased, while the Pielou's evenness index remained stable.

Samples were parsed into month and season to examine temporal changes in species diversity (Figure 8). A variable pattern was evident, especially in species richness and the Shannon index, with highest values of species richness in May and December, and Shannon in December–February (Figure 8a). Pielou's and Simpson's indices were lower and more stable than the other two indices (Figure 8a,b).

While species richness values are similar in the spring and winter, the Shannon index is much higher than species richness in the winter (Figure 8b). The Shannon index incorporates both species richness and abundance ("evenness") of each taxon; this indicates that the winter community is more biodiverse than that of the spring. Although many taxa may be present, a lower Shannon index in the spring is likely due to uneven abundance patterns, particularly the dominance of a few taxa (*e.g.*, *Acartia* spp.) associated with blooms. A higher Shannon index coupled with higher species richness in the winter indicates that abundances are more evenly distributed among the taxa, and one taxon is not highly dominant, which is likely driven by the winter appearance of coastal copepod species.

Distribution and Abundance of Taxa

The zooplankton community in Barnegat Bay was dominated by copepods, and the distribution and abundance for the duration of the study are described below. Decapods and

Table 7. *Key to taxa in PCO and dbRDA plots created to examine the relationships in zooplankton community data in Barnegat Bay.*

Assigned Number	Taxon
1	*Calanus finmarchicus*
2	*Centropages hamatus*
3	*Centropages typicus*
4	*Pseudocalanus minutus*
5	*Temora longicornis*
6	*Acartia* spp.
7	Calanoida
8	*Centropages* spp.
9	Copepoda
10	Cyclopoida
11	*Eurytemora* spp.
12	Harpacticoida
13	*Oithona* spp.
14	*Paracalanus* spp.
15	Pontellidae
16	*Temora* spp.
17	*Tortanus discaudatus*
18	Amphipoda
19	Balanidae
20	Brachyura
21	Caridea
22	Chaetognatha
23	Coelenterata
24	Decapoda
25	*Evadne* spp.
26	Foraminifera
27	Gammaridea
28	Gastropoda
29	Isopoda
30	Mysida
31	Ostracoda
32	Bivalvia
33	*Podon* spp.
34	Polychaeta

bivalves, important ecosystem and commercial/recreational species were also detected, albeit in generally lower numbers.

Copepods

Over 32,500,000 individual zooplankters were collected over the duration of the study, with a mean total per tow (200 μ and 500 μ nets) of 65,093 individuals 100 m^{-3}. For the 200 μ tows over 27,700,000 specimens were collected, and each tow averaged 111,086 individuals 100 m^{-3}. Over 4,700,000 zooplankters were collected in the 500 μ tows, with a mean total of 19,081 individuals 100 m^{-3} per tow. These mean abundance values differ slightly from those presented in Tables 1–3, since those tables included only the taxa that appeared in $\geq$5% of all samples. Copepods, an integral component of the holoplankton and the most important estuarine primary consumer, comprised 86.6% of the total zooplankton collected. The calanoid copepod *Acartia* was the most abundant copepod taxon, comprising 56% of all zooplankton specimens collected, while another calanoid copepod taxon, *Eurytemora* (15% of total zooplankton), was the second most abundant taxonomic group. No other taxonomic group was above 4% in total abundance.

Trends in abundance indicate that *Acartia* was especially associated with spring and fall blooms in Barnegat Bay (Figure 9a). *Acartia* spp. abundance was highest in late June 2012, very abundant in the spring and fall of 2012, and moderately abundant in the spring of 2013. However, *Acartia* spp. did not reappear for the fall bloom of 2013. The spring bloom of 2014 was delayed, with greatest numbers of *Acartia* spp. seen during June and July of that year. The delay in the appearance of the *Acartia* spp. bloom in spring 2014 may have been a result of overwintering *Acartia* spp. being adversely affected by the extreme cold of the 2013–2014 winter, or may have been related to phytoplankton abundance. That seemingly anomalous summer bloom extended into the early fall of 2014 but did not maintain enough intensity to produce a true fall bloom, such as the bloom observed in fall 2013. Since sampling for this study was completed in April 2015 with no evidence of a spring bloom, it is suggested that, due to the extreme cold of the 2014–2015 winter, the spring bloom may again have been delayed.

NOAA monitors several common coastal species in the mid-Atlantic bight (MAB), including *T. longicornis, C. finmarchicus, Pseudocalanus minutus, C. hamatus*, and *C. typicus*. Although these species are common along the coast, they are not as abundant in Barnegat Bay. When they do occur, their occurrence is most often associated with the spring zooplankton bloom (Figure 9b–f). *Centropages typicus,* in particular, is strongly associated with the spring bloom in Barnegat Bay (Figure 9f).

To quantify the trends in abundance demonstrated graphically, as well as to examine the importance of specific copepod taxa such as *Acartia* spp., *Eurytemora* spp., and NOAA-monitored species to the Barnegat Bay zooplankton community, total abundance and mean abundance of copepod taxa were calculated for each year, each season, and each site. Percentage abundance of each copepod taxon relative to total copepod abundance was also calculated for each of the aforementioned parameters. Total and mean abundance varied annually, with the highest numbers collected in 2012 (total = 10,459,280; mean = 222,538), and the lowest in 2015 (total = 658,360; mean = 32,918). In 2014 the total number of copepods collected was comparable to that in 2012 (10,271,778), although the mean abundance was half of that in 2012 (109,274). However, it is important to note that the duration and timing of sampling effort differed in 2012 and 2015: samples were collected May–December in 2012, but January–April in 2015. Copepod abundance in 2012 is therefore extremely high even with a shortened (May–December) sampling period, when compared with 2014.

Acartia was the dominant copepod taxon over the entire study, comprising 64.9% of the total collection of copepods, with contributions from *Eurytemora* spp. (17.3%) and several other taxa below 5% abundance. Although *Acartia* is the most important copepod taxon in Barnegat Bay in terms of total numbers and mean abundance, several other taxa are also prevalent at certain times of the year and in certain locations. In 2012, mean abundance of *Acartia* spp. relative to all other copepods reached 91.1%, while the taxon's contribution to mean total abundance of copepods varied greatly in 2013, 2014, and 2015 (35.6%, 60.3%, and 25.3%, respectively). In 2013, *Eurytemora* spp. (20.1%), *C. hamatus* (14.4%), and *T. longicornis* (12.5%) were also prevalent in the bay. *Eurytemora* was also abundant in 2014 (30.7%), and in 2015 was more abundant (50.9%) than *Acartia* spp. (25.3%). For comparison purposes, total and mean abundance were therefore split into similar time periods in 2013 and 2014. For the January–April time

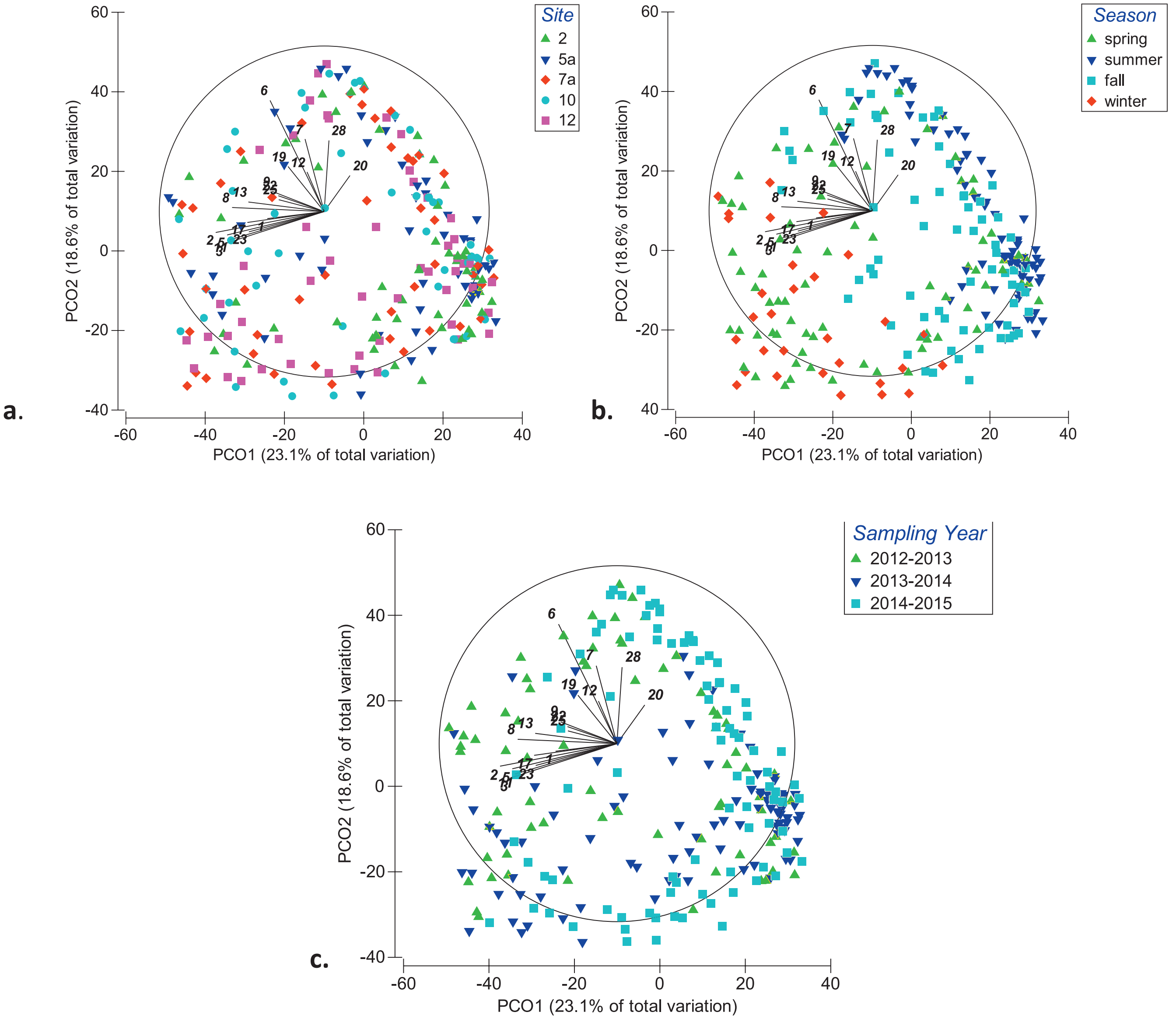

Figure 4. PCO of zooplankton community taxa for both the 200–500 µ and >500 µ fractions for each sampling event. Each data set is organized by (a) site, (b) season, and (c) sampling year. Vectors are zooplankton taxa that are correlated at or above 0.25. Taxa are identified by numbers as in Table 7. PCO1 = 23.1%, PCO2 = 18.6%.

period (2013–2015), total copepod abundance was highest in 2013 (5,563,818) and almost an order of magnitude less in 2015 (658,360). Mean abundance was also considerably higher in 2013 (222,553) than in 2015 (32,918), likely due to the lack of an early spring bloom in 2015. When considering the three sampling years during the January–April time period, it became apparent that *Acartia* was not always the dominant copepod taxon in the bay. For the January–April 2013 sampling period, *Acartia* (27.4%) was only slightly more abundant than *Eurytemora* spp. (23.9%), while *C. hamatus* (16.9%) and *T. longicornis* (15.1%) were also somewhat abundant. In that sampling period in 2014, *Eurytemora* (71.4%) was by far the dominant taxon, although *Acartia* spp. (13.5%) and *T. longicornis* (7.1%) both added to the total abundance. January–April was the only sampling period in 2015; in this time period *Eurytemora* (50.9%) was twice as abundant as *Acartia* spp. (25.3%). For the May–December time period in 2012–2014, total abundance in 2012 (10,459,280) was twice as high as 2014 (5,585,901) and much greater than 2013 (571,706). *Acartia* was the dominant taxon for May–December 2012 (91.1%) and 2014 (98.6%). However in 2013, in addition to *Acartia* spp. (70.9%), the cyclopoid copepod *Oithona* (7.9%) contributed to the total copepod abundance, as did calanoid (8.3%) and harpacticoid copepods (5.9%). Calanoida are

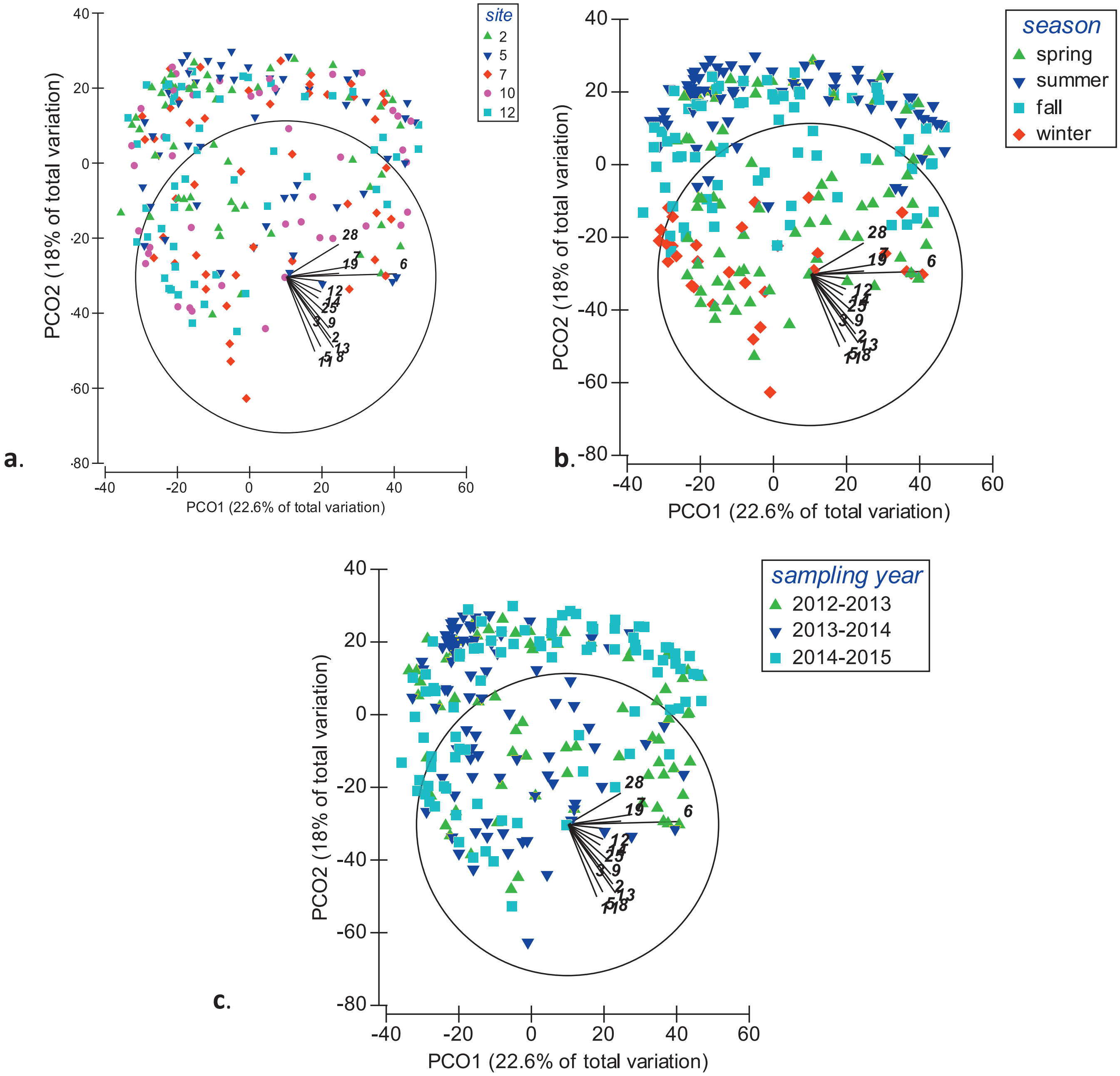

Figure 5. PCO of zooplankton community taxa for the 200–500 µ fraction for each sampling event. Each data set organized by (a) site, (b) season, and (c) sampling year. Vectors are zooplankton taxa that are correlated at or above 0.25. Taxa are identified by numbers as in Table 7. PCO1 = 22.6%, PCO2 = 18.0%.

calanoid copepods that could not be identified to a lower taxon; therefore, it is unknown whether they were *Acartia* spp. or another calanoid copepod genus.

Copepod total and mean abundances were calculated for season (astronomical). Since sampling effort differed between November–March and April–October, mean abundances, rather than total abundances, are the only appropriate metric for comparison. Contrary to the paradigm of the temperate zone spring bloom, the spring copepod mean abundance was slightly less than the summer value (114,704 and 120,673, respectively); additionally, the fall temperate zone bloom was not as apparent in this study, since the overall winter mean abundance (126,350) was considerably higher than that of the fall (94,083) (Table 8). This disparity is likely due to the influence of a large copepod bloom 1–2 months after Superstorm Sandy. The copepod community differed seasonally as well, with the contribution of *Acartia* spp. much lower in the spring (35.2%) than in the summer (94.7%), with *Eurytemora*

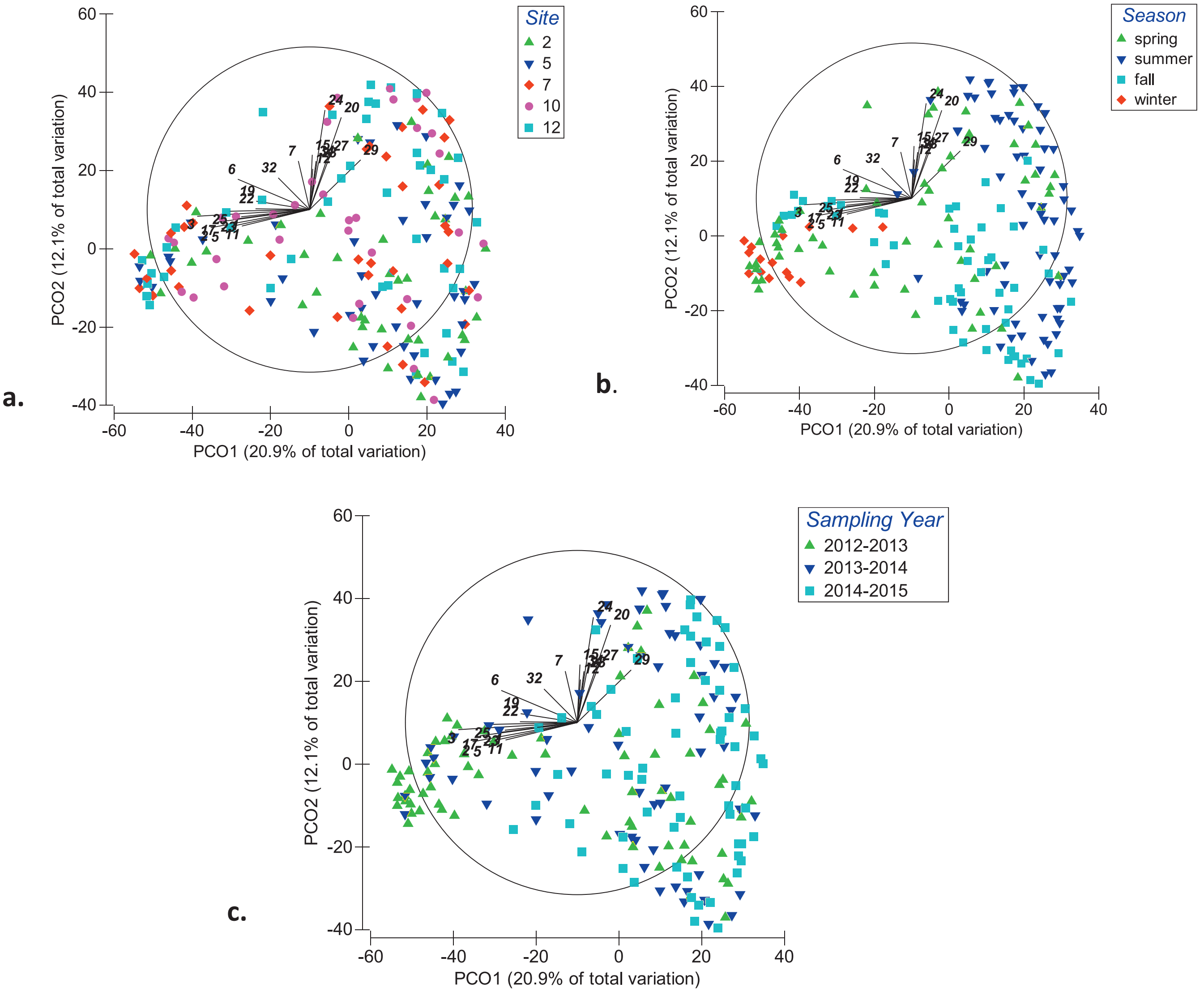

Figure 6. PCO of zooplankton community taxa for the ≥500 μ fraction for each sampling event. Each data set organized by (a) site, (b) season, and (c) sampling year. Vectors are zooplankton taxa that are correlated at or above 0.25. Taxa are identified by numbers as in Table 7. PCO1 = 22.2%, PCO2 = 10.9%.

(41.6%) more abundant than *Acartia* spp. in the spring. *Acartia* spp. remained prevalent in the fall (88%), but abundance declined in the winter (20.9%), with other taxa in the community contributing to the overall copepod abundance, *e.g.*, *Eurytemora* spp. (32.3%), *C. hamatus* (18.8%), *T. longicornis* (16.9%), and *Centropages* spp. (5.7%).

Sampling effort was similar for all sites, facilitating comparisons of total abundance as well as mean abundance between them. Copepod total and mean abundance were similar at BB02, BB07a, and BB10 (total ≈ 6,000,000, mean ≈ 130,000) and slightly less at BB12 (total = 5,486,133, mean = 105,503), but only about half of those values at BB05a (total = 3,425,868, mean = 63,442) (Table 9). *Acartia* was the dominant taxon at BB02 (80.5%), BB05a (71.9%), and BB10 (61%) while *Eurytemora* was the other prevalent species at these locations (11%, 15.9%, and 21.5%, respectively). *Acartia* was also dominant at BB12 (76.6%); however, the other important contributors to overall abundance were unidentified calanoid copepods (6.5%), *T. longicornis* (5.9%), and *C. hamatus* (5.0%). The copepod community characteristics differed at BB07a, with *Acartia* spp. and *Eurytemora* spp. being similarly abundant (37.6%, 35.2%), but *Centropages* spp., *T. longicornis*, and *Oithona* spp. contributing 4%–8% each.

Decapods and Bivalves

Although decapod and brachyuran specimens were not identified to species, the overall trend in both taxonomic groups shows highest abundances in the spring and summer (Figure 10). The order Decapoda includes shrimp, lobster, hermit crabs, and other crustacean taxa with 10 legs, while the infraorder Brachyura within Decapoda includes the true

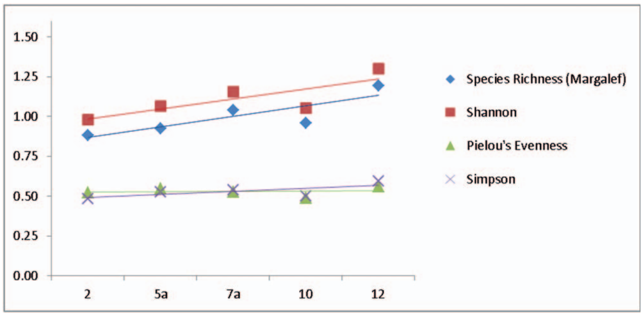

Figure 7. Species diversity analyses for zooplankton samples collected in Barnegat Bay, New Jersey, May 2012–April 2015. Taxa were present in $\geq$5% of samples. Species richness: $R^2 = 0.7228$, $y = 0.066x + 0.0812$. Shannon: $R^2 = 0.6518$, $y = 0.0629x + 0.9206$. Pielou's: $R^2 = 0.0131$, $y = 0.0021x + 0.5228$. Simpson: $R^2 = 0.5226$, $y = 0.0196x + 0.4716$.

crabs. For this study, brachyurans were enumerated separately from the decapods. Peak abundance of decapod and brachyura larvae occurred in the summers of 2012 and 2014. The largest spawning pulse of this study occurred in the summer of 2012 at BB12 in the southern bay. Decapod samples rose to over 35,000 individuals 100 m^{-3}, while brachyuran abundance was also extremely high at over 85,000 individuals 100 m^{-3}. Intensity and timing of these spawning pulses varied over the course of the study. The intense pulse in June 2012 may have been due to the warm winter of 2012–2013, while the later, less intense pulses observed in 2013 and 2014 may have been the result of the anomalously cold winters of 2013–2014 and 2014–2015.

Since the brachyuran blue crab *Callinectes sapidus* is a valuable fishery stock, taxonomic analysis with higher resolution than presented in this study would be useful in reaffirming the value of Barnegat Bay as a nursery ground for the species. However, further examination of the interaction between environmental factors and the timing and intensity of spawning pulses is warranted to determine the extent of density-independent population dynamics.

Several bivalve spawning events occurred during this study. Approximately 10,000 individuals 100 m^{-3} were collected at BB02 in June 2012, with lower abundances collected at BB05a and BB12 as well (BB07 and BB10 were not sampled until September 2012) (Figure 11). A relatively small spawning event occurred in June–August 2013 at BB02 and BB07a, but that was followed by a larger pulse during the same time period in 2014, with highest abundance at BB05a. Greatest abundance of bivalve larvae occurred in Fall 2012, one month after Superstorm Sandy, with an extremely large event evident in November and a smaller pulse in January. These two blooms were at BB07a, the station closest to Barnegat Inlet, so it is unclear whether these bivalve larvae are from the bay or from coastal populations. Another bloom in the same location occurred in December of the following year, but on a smaller scale. Bivalve abundance throughout the rest of the study was low relative to the numbers seen during the spawning events.

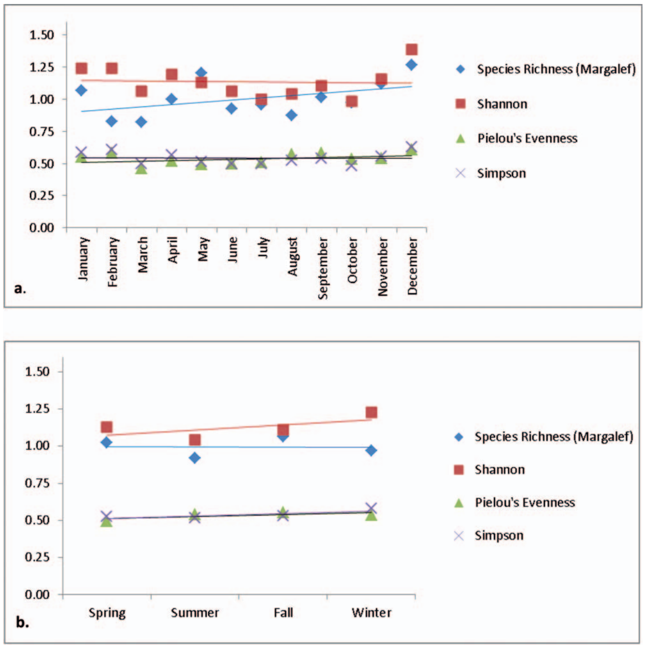

Figure 8. Species diversity analyses for zooplankton samples collected in Barnegat Bay, New Jersey, May 2012–April 2015. Taxa were present in $\geq$5% of samples. (a) Species diversity indices sorted by month. Species richness (Margalef): $R^2 = 0.2027$, $y = 0.0175x + 0.8888$; Shannon: $R^2 = 0.0036$, $y = -0.0019x + 1.1447$; Pielou's Evenness: $R^2 = 0.1462$, $y = 0.0046x + 0.5054$; Simpson: $R^2 = 0.0032$, $y = -0.0007x + 0.5458$. (b) Species diversity indices sorted by season. Species richness (Margalef): $R^2 = 0.0017$, $y = -0.002x + 1.0011$; Shannon: $R^2 = 0.363$, $y = 0.0354x + 1.0381$; Pielou's Evenness: $R^2 = 0.5059$, $y = 0.0137x + 0.4975$; Simpson: $R^2 = 0.6592$, $y = 0.0178x + 0.4937$.

Effects of Environmental Parameters on Zooplankton Community Dynamics

Zooplankton community data matrices were linked to those for environmental data. The RELATE and BioENV routines were first used to determine relatedness of the data sets; distance-based linear models (DistLM) and distance-based redundancy analyses (dbRDA) with multiple correlations were then used to determine the most parsimonious set of environmental factors contributing the most variability to the data. The New Jersey Department of Environmental Protection (NJDEP) collected "nutrient" environmental data (alkalinity, chlorophyll *a*, nitrogen, phosphorus, and total suspended solids) that covered 80% of this study's sampling events (Water Quality Portal, 2017); therefore, sampling events that did not have associated nutrient data were discarded (primarily late fall/winter 2013–2014 and 2014–2015). "Abiotic" environmental data (temperature, salinity, DO % saturation, pH, transparency, and water depth) were collected in the present study and thus represented 100% of the sampling events. When nutrient and abiotic environmental data were analyzed together, those sampling events that did not have associated nutrient data were discarded. These analyses were conducted for each sample type: 200 μ, 500 μ, and combined fractions (Table 10). This approach was taken to enable a comprehensive evaluation of the available data and to determine whether the

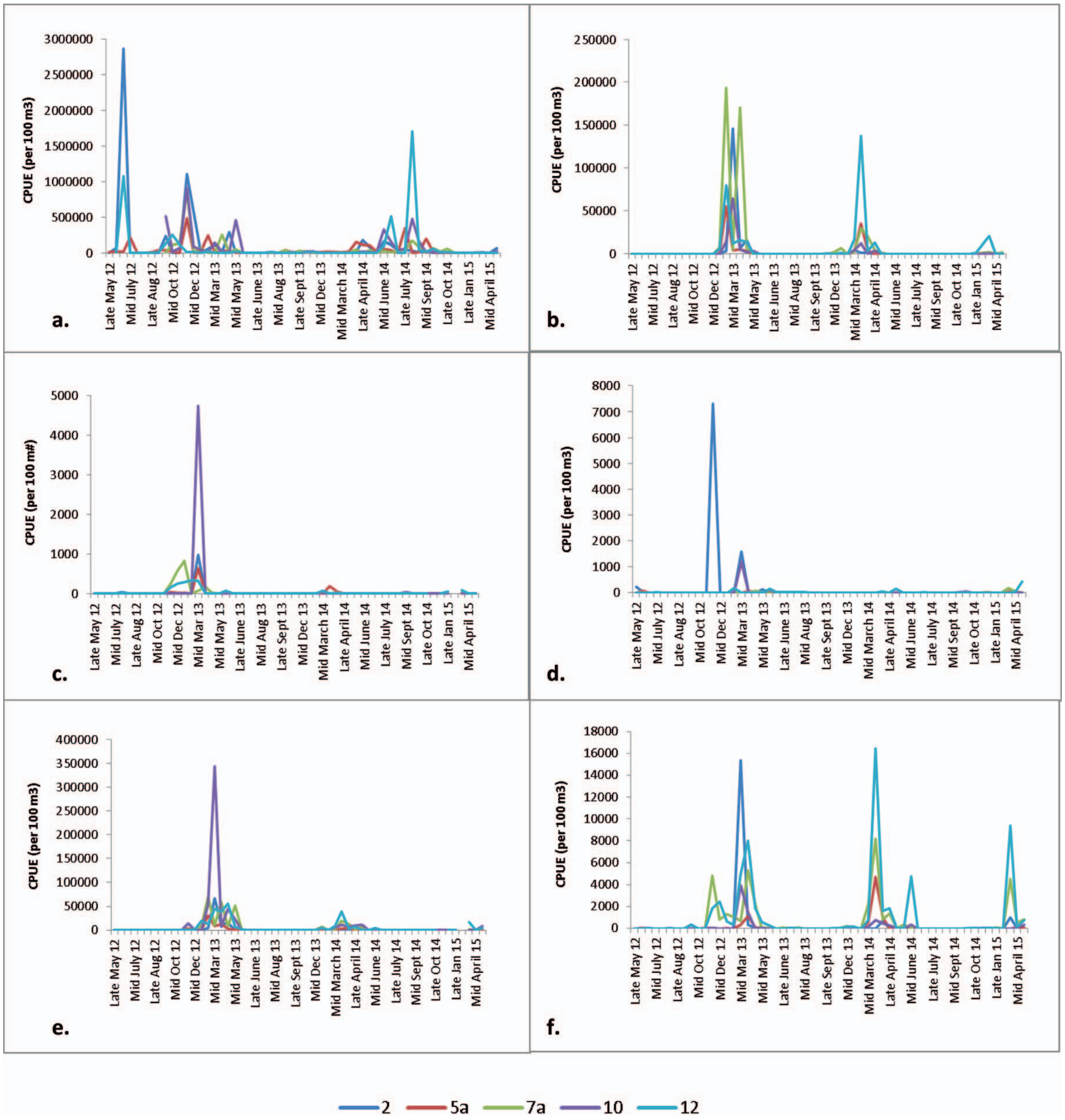

Figure 9. Abundance of copepod species collected at Sites BB02, BB05a, BB07a, BB10, and BB12 in May 2012–April 2015. Sites BB07a and BB10 were added in late September 2012. (a) *Acartia* sp., (b) *Temora longicornis*, (c) *Calanus finmarchicus*, (d) *Pseudocalanus minutus*, (e) *Centropages hamatus*, (f) *Centropages typicus*. CPUE = catch per unit effort.

nutrient and abiotic data could be combined into one analysis for each sample type.

Although none of the R^2 values for BioENV or DistLM are high relative to the maximum of 1, in the context of the study, highest R^2 values are seen in the abiotic data sets, driven by temperature (Table 10). Although several variables created the most parsimonious set, temperature is by far the most important factor driving variability in the Barnegat Bay zooplankton community. The R^2 value for this factor was always an order of magnitude higher than the other factors, whether analyzed only with the abiotic group or combined with the nutrient group. Although the nutrient R^2 values are low relative to temperature, the highest variability in this group can be attributed to alkalinity, nitrogen, and phosphorus.

Since the analyses showed that there was not a large difference in the DistLM R^2 between abiotic (100% of samples) and abiotic + nutrient (80%) of samples, only the abiotic + nutrient analyses were used in subsequent analyses. The dbRDA results for the impacts of all environmental parameters

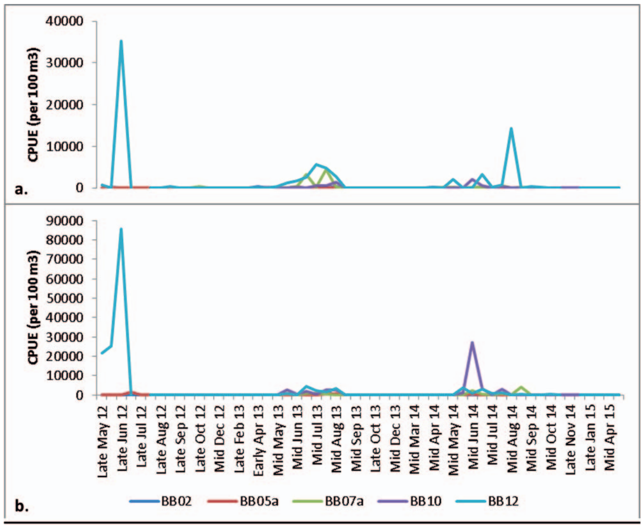

Figure 10. Abundance of arthropod larvae collected at Sites BB02, BB05a, BB07a, BB10, and BB12 in May 2012–April 2015. (a) Decapoda (b) Brachyura (crabs). Sites BB07a and BB10 were added in late September 2012.

on zooplankton community structure were therefore plotted for the combined fractions to examine variability in the context of sites and season (Figure 12). Variability across sampling year was not examined because of the elimination of several sampling events in 2013–2014 and 2014–2015, as described previously.

On the dbRDA2 axis, the data trend was along a spatial gradient, with variability in BB02 and BB05a (northern bay) driven by nitrogen and chlorophyll *a*, and variability in BB07a, BB10, and BB12 driven by alkalinity and salinity (Figure 12a). Temperature was the strongest contributor of variability in community structure across seasons. Winter and summer communities differed most strongly from each other; spring and fall communities were more similar to each other (Figure 12b).

Because of the strong effect of temperature on zooplankton community structure, the data were parsed into seasons and analyzed with the statistics reported above. Although temperature remained the environmental parameter driving variability in the spring and fall samples, phosphorus was important in the fall as well. During summer and winter months when temperature remained stable, other variables became important, *e.g.*, total suspended solids and transparency; the presence of both as important variables is not surprising given their relationship (Table 11). The impacts of environmental parameters on the combined fractions of summer zooplankton community data were plotted (Figure 13). Zooplankton community structure was sorted according to latitudinal gradient, with BB02 and BB05a similar to each other and strongly associated with nitrogen and chlorophyll *a*. This grouping was strongly negatively correlated with transparency. The summer communities at BB07a, BB10, and BB12 were similar to each other; this grouping was driven by alkalinity and salinity, with less important impact by total suspended solids and phosphorus (Figure 13a).

Summer zooplankton community structure differed across sampling years. The 2012–2013 and 2013–2014 sampling years were more closely associated with each other than with the 2014–2015 sampling year and were strongly negatively correlated with transparency (Figure 13b).

Correlations of zooplankton taxa with summer community structure were overlaid on the dbRDA plots. Taxa driving the groupings included barnacles and polychaetes in the northern bay and decapods and gammarids in the southern bay. Caridean shrimp, *Evadne* spp., isopods, and gammarids were more common in the final year of sampling.

Gelatinous Macrozooplankton

Targeted gelatinous macrozooplankton included the ctenophores *M. leidyi* and *B. ovata*, as well as the cnidarian scyphozoan *C. quinquecirrha*. Although initially abundant in the spring and fall of 2012, *M. leidyi* abundance declined over the duration of the study (Figure 14). Although abundance was also high in the winter of 2012–2013, *M. leidyi* was not collected during the two subsequent winters. In 2014, the ctenophore did not appear in samples until May, which was later than the previous spring; abundance during summer 2014 was also lower than in previous summers. *Mnemiopsis leidyi* was not collected in 2015 before sampling was completed in April 2015.

The uneven temporal distribution of *M. leidyi* was highly significant in a two-way analysis of variance (ANOVA) of date *vs*. site on abundance ($F = 2.205$, $p < 0.001$), probably because none were collected in the winters of 2013–2014 and 2014–2015. Although abundance patterns were generally uneven throughout the bay (Figure 14), site was not significant in this analysis ($F = 0.774$, $p = 0.543$). However, the interaction of date and site was highly significant ($F = 10{,}164$, $p < 0.001$), most likely due to the great abundance of *M. leidyi* collected in the northern bay in the spring and summer of 2012.

A predator of *M. leidyi*, the sea nettle *C. quinquecirrha*, was collected in small numbers during each summer of the study (Figure 15). Abundance was highest in the northern bay in 2012 and 2013 but was also found at BB12 in the southern bay in summer 2013 and spring 2014. The ctenophore predator *B. ovata* often cooccurs with its preferred prey *M. leidyi*. However, *B. ovata* occurred only rarely in the bay and was only collected in very small numbers in the northern bay during periods of largest *M. leidyi* abundance, spring and summer of 2012 (Figure 15).

DISCUSSION

The Barnegat Bay zooplankton community was characterized in a 3 year study examining temporal and spatial trends in abundance and distribution. The most recent available study (Tatham *et al*., 1977, 1978) provided an assessment of two size fractions of the zooplankton community in one location in the central bay. Bologna, Gaynor, and Meredith, (2017) focused on gelatinous zooplankton but also provided data on the zooplankton community. The current study presents analyses of over 500 samples collected continuously over 3 years, at five sites along a north/south transect in the bay. Further, statistical techniques designed specifically for large sets of biological community data were employed in this study to

Table 8. *Total, mean, and percentage abundances of Barnegat Bay copepods by season. Although total abundance is provided, sampling effort differed between the two time periods November–March and April–September. Units are individuals 100* m^{-3} *of water.*

Season	*Acartia* spp.	Calanoida	*Calanus finmarchicus*	*Centropages hamatus*	*Centropages typicus*	*Centropages* spp.	Copepoda	Cyclopoida	*Eurytemora* spp.
Spring									
Total	3,070,301	36,555	609	482,869	83,352	514,357	21,358	6203	3,624,511
Mean	40,399	481	8	6354	1097	6768	281	82	47,691
% Abundance	35	<1	<1	6	1	6	<1	0	42
Summer									
Total	8,803,452	396,869	62	609	205	634	9716	4748	2
Mean	114,331	5154	1	8	3	8	126	62	<1
% Abundance	95	4	<1	<1	<1	<1	<1	<1	<1
Fall									
Total	5,644,157	204,365	1348	29,934	11,423	122,853	58,510	7126	35,883
Mean	83,002	3005	20	440	168	1807	860	105	528
% Abundance	88	3	<1	<1	<1	2	1	<1	1
Winter									
Total	793,547	18,213	8360	712,428	32,682	216,834	22,074	2122	1,222,789
Mean	26,452	607	279	23,748	1089	7228	736	71	40,760
% Abundance	21	<1	<1	19	1	6	1	<1	32

examine the effects of environmental parameters and taxa driving the variability in the zooplankton community.

Trends in Zooplankton Abundance and Diversity

The zooplankton community in Barnegat Bay is characterized by strong spatial, seasonal, and interannual trends in abundance and diversity. Spatial variability is most apparent between the northern and southern regions of the bay, with a characteristic suite of water quality parameters and taxa in each region. Seasonal and interannual differences are strongly associated with temperature, and to a lesser extent other environmental parameters, but are likely also due to predation and interactions with the phytoplankton community that were not addressed in this study. Variability in abundance of dominant taxa, *e.g.*, *Acartia* spp. and *M. leidyi*, was evident over the 3 years of this study.

It is apparent that direct and/or indirect effects of weather patterns, *i.e.* seasons, affect zooplankton abundance in Barnegat Bay. Density-independent factors (*e.g.*, temperature) contribute strongly to interannual variability in biological systems. This effect may serve to render the zooplankton community (and thus the food web) highly vulnerable to secondary, sublethal factors, potentially resulting in additional impacts to the community, *e.g.*, a zooplankton community with low abundance or diversity as a result of several extreme winters is then subjected to a sublethal anthropogenic factor such as nutrient-driven decreased DO. Such sensitivity to changes in weather patterns has the potential to cause long-term shifts in the zooplankton community as a result of climate change.

The northern bay (BB02, BB05a) is characterized by high nitrogen and chlorophyll *a*, a few dominant species such as *Acartia* spp. and *M. leidyi*, and the lowest species diversity of zooplankton in the bay, all indicative of a stressed community. Alkalinity and phosphorus were higher in the southern bay (BB07a, BB10, BB12), as was zooplankton species diversity. This was a typical pattern throughout the study and remained stable even between seasons.

Table 9. *Total, mean, and percentage abundances of Barnegat Bay copepods by site. Units are individuals 100* m^{-3} *of water.*

Site	*Acartia* spp.	Calanoida	*Calanus finmarchicus*	*Centropages hamatus*	*Centropages typicus*	*Centropages* spp.	Copepoda	Cyclopoida	*Eurytemora* spp.
2									
Total	5,568,161	132,765	1002	105,978	18,076	45,295	3380	1380	762,983
Mean	105,060	2505	19	2000	341	855	64	26	14,396
% Abundance	81	2	<1	2	<1	1	<1	<1	11
5a									
Total	2,463,316	55,314	882	65,810	6975	79,280	9526	841	545,080
Mean	45,617	1024	16	1219	129	1468	176	16	10,094
% Abundance	72	2	<1	2	<1	2	<1	<1	16
7a									
Total	2,351,750	38,793	1996	229,801	37,269	497,620	56,564	3124	2,201,051
Mean	51,125	843	43	4996	810	10,818	1230	68	47,849
% Abundance	38	1	<1	4	1	8	1	<1	35
10									
Total	3,727,394	73,777	4910	550,325	8060	166,110	27,444	6458	1,313,051
Mean	81,030	1604	107	11,964	175	3611	597	140	28,545
% Abundance	61	1	<1	9	<1	3	<1	<1	21
12									
Total	4,200,836	355,354	1590	273,928	57,281	66,374	14,745	8396	61,019
Mean	80,785	6834	31	5268	1102	1276	284	161	1173
% Abundance	77	6	<1	5	1	1	<1	<1	1

Table 8. *Extended.*

Harpacticoida	*Oithona* spp.	*Paracalanus* spp.	Pontellidae	*Pseudocalanus minutus*	*Temora longicornis*	*Temora* spp.	*Tortanus discaudatus*	Grand Total
54,511	239,765	4059	2530	1827	554,491	14,962	5269	8,717,532
717	3155	53	33	24	7296	197	69	114,704
1	3	<1	<1	<1	<1	<1	<1	
58,619	15,991	252	406	33	181	47	0	9,291,827
761	208	3	5	0	2	1	0	120,673
1	<1	<1	<1	<1	<1	<1	<1	
47,881	148,810	71,687	846	7429	3884	1429	73	6,397,638
704	2188	1054	12	109	57	21	1	94,083
1	2	1	<1	<1	<1	<1	<1	
6448	74,862	5460	0	2943	638,893	26,250	6598	3,790,504
215	2495	182	0	98	21,296	875	220	126,350
<1	2	<1	<1	<1	17	1	<1	

Poor water quality in the northern bay is likely because of increased urbanization coupled with poor tidal flushing and elevated nutrient input from the watershed during the spring freshet, resulting in an impacted zooplankton community with a few dominant taxa, at the expense of species diversity. Such communities lack resilience to ecosystem fluctuations.

Changes in the Barnegat Bay zooplankton community are evident in the almost 40 years since the previous study was conducted in the bay (Tatham, 1977, 1978). One important difference is that in the previous study, the calanoid copepod *Acartia* was dominant one year, while the cyclopoid copepod *Oithona* was dominant another year. Whether the low abundance of *Oithona* in the present study is due to natural cycles, urbanization in the bay watershed, changes in nutrient load, predation, or differential feeding by *M. leidyi* is difficult to answer.

Direct comparisons with the previous studies are challenging, since Tatham (1977, 1978) employed 80 µ and 500 µ towed nets, while Bologna, Gaynor, and Meredith (2017) used a 363 µ towed net and a 3.2 mm lift net. The zooplankton taxa that were collected differed somewhat from the current study. Copepod abundance was substantially higher in Tatham (1977, 1978) than in the current study, but the smaller mesh net undoubtedly collected more small life stages of copepod species as well as rotifers. No copepods were collected in their 500 µ net; no rotifers were collected at all in the present study. One taxonomic group, the polychaetes, was 10 times greater in abundance in the present study, while chaetognaths were almost identical between 1 year of that study and the 3 year average of this study.

Copepods

Although *Acartia* is the most abundant copepod in the bay, its dominance was highly variable spatially and temporally, and other copepod taxa were occasionally more numerous. This trend was apparent in a previous study, as *Acartia* spp. accounted for 63% of mean annual abundance of all copepods in

Table 9. *Extended.*

Harpacticoida	*Oithona* spp.	*Paracalanus* spp.	Pontellidae	*Pseudocalanus minutus*	*Temora longicornis*	*Temora* spp.	*Tortanus discaudatus*	Grand Total
17,815	47,351	19,867	18	9425	181,698	806	799	6,916,798
336	893	375	<1	178	3428	15	15	130,506
<1	1	<1	<1	<1	3	<1	<1	
10,702	33,183	5218	107	257	115,546	33,178	652	3,425,868
198	614	97	2	5	2140	614	12	63,442
<1	1	<1	<1	<1	3	1	<1	
17,859	299,752	46,916	526	245	462,344	6705	4225	6,256,539
388	6516	1020	11	5	10,051	146	92	136,012
<1	5	1	<1	<1	7	<1	<1	
63,036	52,066	1331	545	1265	113,413	1259	1718	6,112,162
1370	1132	29	12	27	2466	27	37	132,873
1	1	<1	<1	<1	2	<1	<1	
58,049	47,077	8125	2586	1039	324,447	741	4547	5,486,133
1116	905	156	50	20	6239	14	87	105,503
1	1	<1	<1	<1	6	<1	<1	

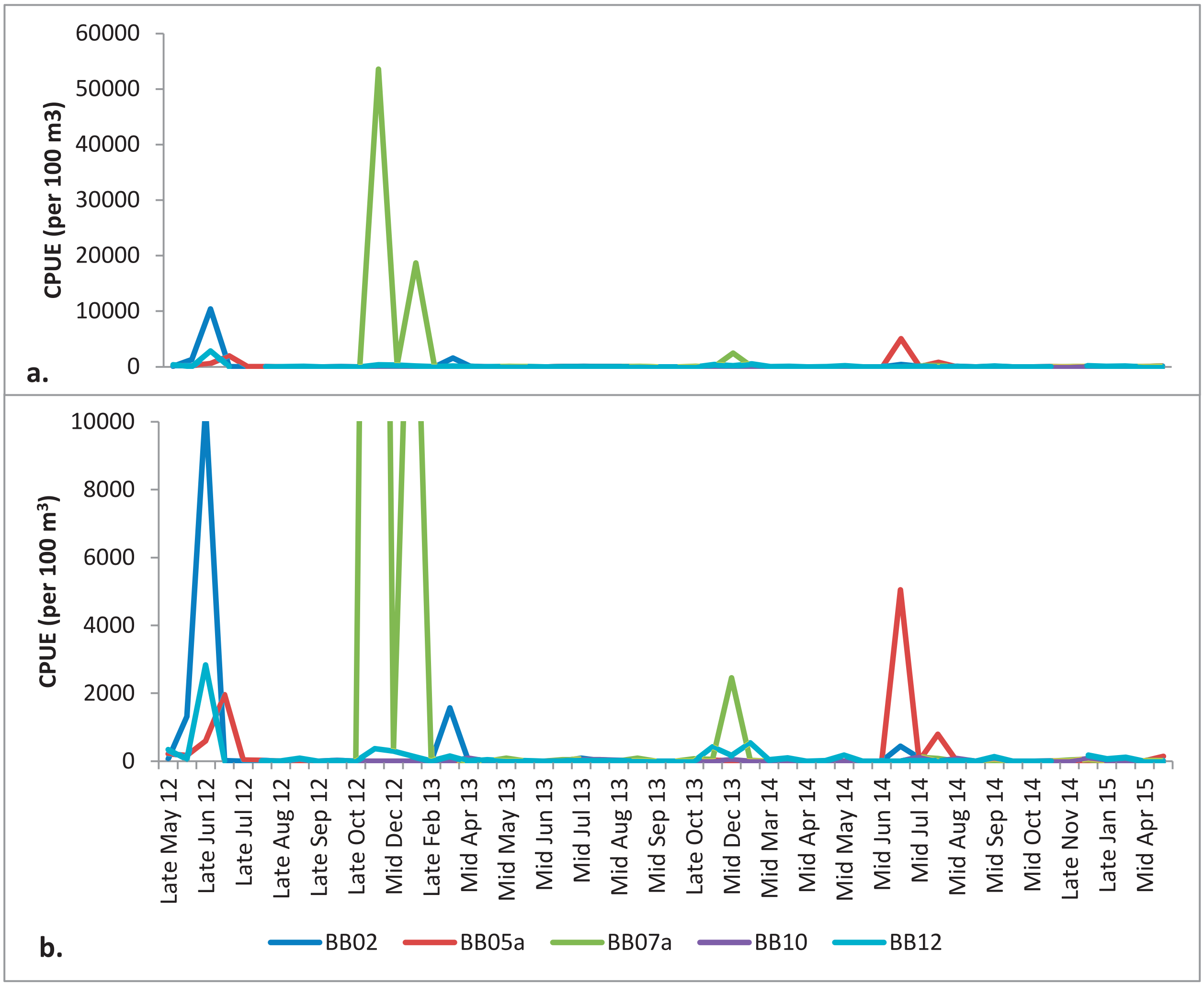

Figure 11. Abundance of bivalve veliger larvae collected at Sites BB02, BB05a, BB07a, BB10, and BB12 in May 2012–April 2015. Sites BB07a and BB10 were added in late September 2012. (a) *Y* axis maximum set at 60,000. (b) *Y* axis maximum set at 10,000.

Barnegat Bay in September 1975–August 1976 (Tatham, 1977), but the following year *Oithona* was dominant (51% of total copepods) (Tatham, 1978). In the current study, *Acartia* was more prevalent in summer and fall than in winter and spring, when other copepod taxa, *e.g.*, *Eurytemora* spp. and *T. longicornis*, were more common. These coastal species are likely less tolerant of the warm summer temperatures characteristic of the bay's shallow waters. *Acartia* is abundant throughout the bay, except for BB07a. This location is close to Barnegat Inlet, which provides an opportunity for exchange with coastal waters; this is evident in the appearance of coastal taxa such as *Centropages* spp., *T. longicornis*, and *Oithona* at this site.

Comparing copepod abundance in Barnegat Bay with other estuaries is challenging, as there is inconsistency in methodologies (mesh size, sampling effort, *etc.*) in available studies. The copepods sampled in this study included larval (nauplii) and juvenile (copepodite) stages, as well as adults, combined into one total count for each taxon. As they are smaller than adults, more nauplii and copepodites were collected in the 200 μ net than the 500 μ net, but younger nauplii were likely missed since they are smaller than 200 μ.

However, copepod abundance in Barnegat Bay appears to be comparable to other MAB estuaries. The zooplankton community in a Long Island, New York, estuary was dominated by copepods and exhibited greatest abundance in early spring and summer (Turner, 1982). Copepods collected in a 202 μ net reached a maximum of 2,000,000 individuals 100 m^{-3} in August 1979, similar to the abundance of *Acartia* spp. at BB12 in late summer 2014 in this study. However, there is marked interannual variability in Barnegat Bay, and copepod abundances were much lower in a similar time period in the two previous years of the present study. Rothenberger *et al.* (2014) sampled Raritan Bay, New Jersey, with a Schindler-Patalas trap and undisclosed mesh size in April–November and found that zooplankton abundance reached a maximum of

Table 10. *Statistical tests examining the relationships between environmental variables and zooplankton community data.*

Statistical Test	200–500 µ Fraction		>500 µ Fraction		Both Fractions	
Nutrients						
PCO1,2 (%)	24.70	15.80	20.90	12.10	23.80	17.30
RELATE	$p = 0.016$		$p = 0.001$		$p = 0.007$	
BIOENV	$p = 0.001$	corr = 0.107	$p = 0.001$	corr = 0.107	$p = 0.001$	corr = 0.108
Most Pars.	4, 5		3, 4, 5		4, 5	
DistLM-Best						
AICc	1554.8		1631.3		1560.6	
R^2	0.102		0.087		0.124	
Most Pars.	1*, 2, 4*		1, 2, 4*, 5		1, 2, 3*, 4*, 5	
**Highest Indiv.* R^2	0.03		0.03		0.034	
dbRDA 1, 2						
Fitted %	6.03	2.22	5.74	2.09	6.63	2.72
Total %	59.25	21.83	65.55	23.93	53.3	21.89
Abiotic						
PCO1,2 (%)	22.60	18	22.20	11	23.10	19
RELATE	$p = 0.001$		$p = 0.001$		$p = 0.001$	
BIOENV	$p = 0.001$	corr = 0.298	$p = 0.001$	corr = 0.419	$p = 0.01$	corr = 0.358
Most Pars.	6		6		6	
DistLM						
AICc	1908.5		1999.5		1908.8	
R^2	0.21		0.2		0.23	
Most Pars.	*6*, 7, 8, 10, 11*		*6*, 7, 8, 9, 10*		*6*, 7, 8, 9, 10*	
**Highest Indiv.* R^2	0.12		0.15		0.14	
dbRDA 1, 2						
Fitted %	12.27	4.62	15.09	2.58	14.82	3.64
Total %	59.08	22.22	75.61	12.94	62.82	15.42
Nutrients and Abiotic						
PCO1,2 (%)	24.7	15.8	20.9	12.1	23.8	17.3
RELATE	0.001		$p = 0.001$		$p = 0.001$	
BIOENV	$p = 0.001$	corr = 0.259	$p = 0.001$	corr = 0.431	$p = 0.001$	corr = 0.341
Most Pars.	6		6		6	
DistLM						
AICc	1540.2		1606.8		1535.7	
R^2	0.19		0.2		0.226	
Most Pars.:	1, 2, 4, 6*, 7, 10		4, 6*, 7, 8, 9		3, 6*, 7, 8, 10	
**Highest indiv.* R^2	0.09		0.14		0.13	
dbRDA 1, 2						
Fitted %	53.75	25.11	71.45	14.54	60.26	13.61
Total %	10.24	15.02	14.58	2.97	14.99	3.39

Environmental data matched study sampling event (zooplankton collections) as follows: nutrient = 80%, abiotic = 100%, nutrient + abiotic = 80%. Unmatched sampling events were excluded from the analyses. Most pars. = most parsimonious match of variables. Highest indiv. R^2 *= starred variable in most parsimonious set of variables had the highest individual* R^2 *value. Variables are numbered as follows: 1 = alkalinity; 2 = chlorophyll* a*; 3 = total nitrogen; 4 = total phosphorus; 5 = total suspended solids; 6 = temperature; 7 = salinity; 8 = dissolved oxygen % saturation; 9 = pH; 10 = transparency; 11 = water depth.*

100,000 individuals 100 m^{-3} and was greatest in late spring/early summer. They report that rotifers, copepods, and copepod nauplii comprised most of the zooplankton community, which indicates that their mesh size was smaller than the present study, since rotifers were not collected in the 200 µ net. Thus maximum zooplankton abundance in Raritan Bay is considerably lower than the maximum seen in Barnegat Bay (>2,500,000 individuals 100 m^{-3} in May 2012), which may indicate lower secondary productivity in Raritan Bay. Shaheen and Steimle (1995) sampled the Navesink/Shrewsbury, New Jersey, estuary using a 203 µ net. Sampling occurred during one summer (May–July) and collected on average approximately 200,000 copepods 100 m^{-3}, which were higher than this study's Barnegat Bay summer average of 120,673 individuals 100 m^{-3}. A mean of 152,700 individuals 100 m^{-3} copepod adults and 70,100 individuals 100 m^{-3} nauplii were collected with an 80 µ net in Chesapeake Bay from May to October (Harding, 2001); adult copepod values were higher than average copepod values found in Barnegat Bay (Table 9). Elliot and Tang (2011) collected copepods in Chesapeake Bay with a 200 µ net with abundances ranging from <100,000 to 2,000,000 individuals 100 m^{-3} and found that copepod abundance, dominated by *Acartia* spp., peaked in March to June and July to October, and was lowest in winter. Average copepod abundance in Barnegat Bay in the present study exhibited strong interannual variability, with maxima observed in May and November/December in one year, late summer in another, and minima observed for nearly a year.

Copepods are the primary consumers in Barnegat Bay, and as such provide important food for a variety of organisms. Copepod total and mean abundance varied annually, seasonally, and spatially in this study. Although a pattern of spring and fall copepod blooms may be a paradigm typical of some MAB estuaries, the results of this study seem to suggest otherwise for Barnegat Bay and potentially other estuaries with similar features. Factors such as survivability of copepod overwintering stages, phytoplankton abundance, abundance of gelatinous predators, and nutrient loading may impact the

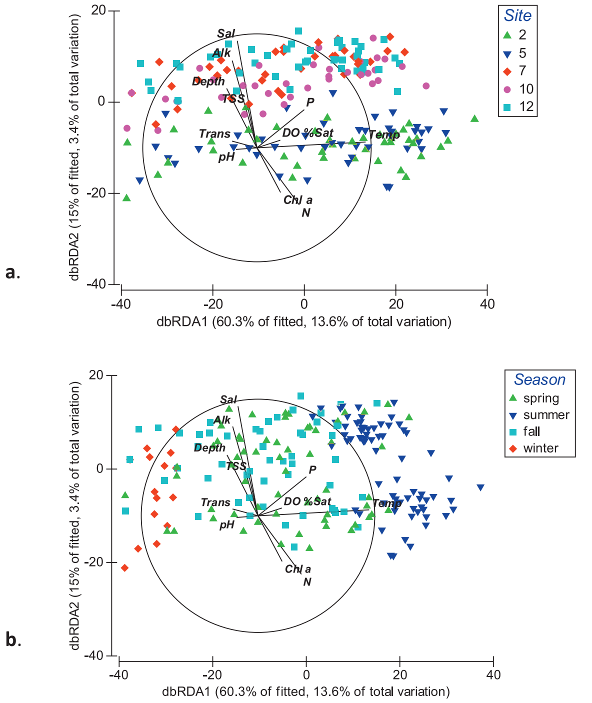

Figure 12. Distance-based redundancy analysis (dbRDA) plots of the zooplankton community data Bray-Curtis resemblance matrix for combined environmental variables (nutrient + abiotic) and combined fractions. (a) by site, (b) by season.

timing, intensity, and duration of blooms in the bay. Additionally, freshwater influence in the northern bay may result in a pulsed system that could affect bloom patterns of the zooplankton community, potentially causing an increase in zooplankton abundance (and secondary productivity) in response to an increase (Mann, 2000) or decrease (Boynton, Kemp, and Keefe, 1982; Day *et al.*, 1989) in freshwater input. Further analyses examining the linkages of phytoplankton (Ren, 2015) and gelatinous predators (present study; Howson and Nickels, unpublished data) to the Barnegat Bay zooplankton community are planned.

Gelatinous Macrozooplankton

Abundance and distribution of three species of gelatinous macrozooplankton were examined as part of this study. *Mnemiopsis leidyi* and *B. ovata* are important ctenophores in the mid-Atlantic; *M. leidyi* consumes mesozooplankton, including holoplanktonic crustaceans (*e.g.*, copepods), barnacles, and bivalve veligers (Larson, 1988; Mountford, 1980), the most numerous taxa in this study. *Beroe ovata* preys on ctenophores (Swanberg, 1974), as does the scyphozoan *C. quinquecirrha* (Purcell and Cowan, 1995). Another zooplanktivorous mid-Atlantic ctenophore, *Pleurobrachia pileus*, was collected only twice in this study.

While *M. leidyi* were numerous periodically throughout the study, *B. ovata* and *C. quinquecirrha* were collected only infrequently. Although the association of predator *B. ovata* and its prey *M. leidyi* has been documented in the mid-Atlantic (Burrell and Van Engel, 1976; Kremer and Nixon, 1976) and the Black Sea (Shiganova *et al.*, 2004) that relationship was not evident in this study. Few *B. ovata* were collected; several were associated with a large *M. leidyi* bloom in the northern bay, but the remainder were collected in the southern bay, not associated with the concurrent *M. leidyi* bloom in the northern bay. Although *C. quinquecirrha* have historically created blooms in the northern bay, they were not collected often in this study, and the predator/prey relationship observed in other systems such as the Chesapeake Bay was not apparent in this study (Purcell and Cowan, 1995). Although all size ranges of ctenophores are readily collected with a towed 0.5 m plankton net, adult *C. quinquecirrha* are probably not, as the net diameter might not be conducive to sampling larger sized individuals. However, juvenile *C. quinquecirrha* were also only rarely collected during the study; few *C. quinquecirrha* of any size were observed in the water during sampling. Purcell (1992) and Purcell, White, and Roman (1994) found that *C. quinquecirrha* were more commonly found in tributaries of the Chesapeake Bay than in open water habitat. This study was conducted in open water habitat within Barnegat Bay, likely leading to lower encounter rates with *C. quinquecirrha*.

Historically, *M. leidyi* has been a common and abundant resident in Barnegat Bay, producing strong blooms in the northern bay but exhibiting seasonal and interannual variability (Mountford, 1980; Nelson, 1925; Sandine, 1984; Tatham, 1977, 1978). Variability in *M. leidyi* populations has also been reported in other mid-Atlantic systems and has been attributed to predation (Purcell and Cowan, 1995), zooplankton abundance (Deason, 1982; Mountford, 1980), and environmental conditions (Costello *et al.,* 2012; Sullivan *et al.,* 2001).

Mnemiopsis leidyi is an important predator of zooplankton in mid-Atlantic estuarine systems and likely exhibits top-down control on the zooplankton community. When *M. leidyi* does bloom, the impact on zooplankton populations may be substantial due to the sheer numbers they consume: one adult ctenophore may eat up to 10 times its weight in zooplanktonic crustaceans per day (Suthers and Rissik, 2009). Close linkage between the *M. leidyi* population and zooplankton abundance has been reported in Barnegat Bay (Mountford, 1980; Tatham, 1977, 1978), Narragansett Bay, Rhode Island (Kremer, 1979; Sullivan *et al.,* 2001), Long Island Sound (Turner, 1982), and Chesapeake Bay (Purcell, White, and Roman, 1994).

Two strong *M. leidyi* blooms were observed in this study, both occurring in the first sampling year. The strong ctenophore bloom of spring 2012 was coupled with a large zooplankton bloom in the northern bay. The strong fall bloom of 2012 was associated with a small peak in zooplankton abundance, but well before the zooplankton bloom observed in November–December 2012. The *M. leidyi* population continued to produce the characteristic spring/fall bloom pattern the following year, as small increases in the population were observed in spring and fall of 2013 in conjunction with small zooplankton blooms. The increase in *M. leidyi* in spring 2013 at BB07 was likely supported by the earlier zooplankton bloom at the same location. A still smaller increase in the *M. leidyi* population occurred in late spring/early summer in 2014, likely fueled by the earlier zooplankton bloom. However, a second zooplankton bloom in late summer/early fall did not result in an increase in

Table 11. *Statistical tests examining the relationships between environmental variables and zooplankton community data for season and sample type. Environmental data included both NJDEP nutrient data and this study's abiotic data; data matched 80% of the study sampling events (zooplankton collections). Unmatched sampling events were excluded from the analyses.*

Statistical Test	200–500 μ Fraction		>500 μ Fraction		Both Fractions	
Spring						
PCO1,2 (%)	24.1	18.9	28.8	13.7	26.40	19.30
RELATE	$p = 0.001$		$p = 0.001$		0.001	
BIOENV	$p = 0.001$	corr = 0.302	$p = 0.001$	corr = 0.445	$p = 0.001$	corr = 0.360
Most Pars.	2, 6, 7, 10		6		6, 7	
DistLM-Best						
AICc	459.04		476.03		459.92	
R^2	0.24		0.299		0.335	
Most Pars.	6*, 7, 10		6*, 7, 8		6*, 7, 8, 10	
**Highest Indiv.* R^2	0.136		0.197		0.188	
dbRDA 1, 2						
Fitted %	60.53	23.03	67.67	24.63	57.92	19.63
Total %	14.53	5.53	20.21	7.36	19.4	6.57
Summer						
PCO1,2 (%)	31.8	16.1	25.0	12.0	30.70	15
RELATE	$p = 0.183$		0.125		$p = 0.106$	
BIOENV	$p = 0.57$	corr = 0.106	$p = 0.18$	corr = 0.154	$p = 0.001$	corr = 0.848
Most Pars.	1, 6, 7, 8, 10		2, 3, 5, 6		1, 2, 5, 8, 11	
DistLM						
AICc	550.06		567.12		546.06	
R^2	0.1		0.112		0.10392	
Most Pars.	*1, 10**		5*, 9, 10		1, 10*	
**Highest Indiv.* R^2	0.056		0.045		0.056	
dbRDA 1, 2						
Fitted %	58.3	41.17	73.12	17.39	54.31	45.69
Total %	5.89	4.12	8.19	1.95	5.64	4.75
Fall						
PCO1,2 (%)	33.0	17.2	23.5	10.2	31.0	16.4
RELATE	$p = 0.001$		$p = 0.002$		$p = 0.001$	
BIOENV	$p = 0.001$	corr = 0.390	$p = 0.001$	corr = 0.833	$p = 0.001$	corr = 0.407
Most Pars.	4, 6, 8, 11		2, 3, 4, 7, 9		5, 6, 8, 11	
DistLM						
AICc	403.4		430.3		402.5	
R^2	0.334		0.232		0.346	
Most Pars.	4*, 6*, 7, 8		4, 6*, 7		4*, 6, 7, 8, 10	
**Highest Indiv.* R^2	4 = 0.11, 6 = 0.12		0.144		0.104	
dbRDA 1, 2						
Fitted %	44.68	28.86	65.63	22.36	41.48	30.57
Total %	14.9	9.62	15.25	5.2	14.35	10.58
Winter						
PCO1,2 (%)	36.9	19.7	41.9	24.7	33.4	18.2
RELATE	$p = 0.11$		0.002		0.033	
BIOENV	$p = 0.15$	corr = 0.348	$p = 0.001$	corr = 0.531	$p = 0.04$	corr = 0.424
Most Pars.	1, 2, 7, 10		1, 6, 8, 10		1, 8	
DistLM						
AICc	119.49		114.17		114.27	
R^2	0.144		0.381		0.3	
Most Pars.	1*		1*,8		7*, 8*	
**Highest Indiv.* R^2	0.144		0.27		0.16	
dbRDA 1, 2						
Fitted %	100	0	100	0	100	0
Total %	14.4	0	26.98	0	18	0

Most pars. = most parsimonious match of variables. Highest indiv. R^2 *= starred variable in most parsimonious set of variables had the highest individual* R^2 *value. Variables are numbered as follows: 1 = alkalinity, 2 = chlorophyll* a, *3 = total nitrogen, 4 = total phosphorus, 5 = total suspended solids, 6 = temperature, 7 = salinity, 8 = dissolved oxygen % saturation, 9 = pH, 10 = transparency, 11 = water depth.*

M. leidyi abundance; the ctenophore population declined further and ultimately disappeared for the remainder of the year and did not reappear in 2015 before the study was completed in April.

Mnemiopsis leidyi has no specialized life stages for overwintering (Costello *et al.,* 2012). If a population dies or is advected out of the system, replenishment from another source would need to occur to reestablish the population. It appears that historically, Barnegat Bay has maintained an overwintering source population of *M. leidyi*, as is typified by the abundance patterns in this study over the winter of 2012–2013. However, anomalously cold temperatures occurred in the two subsequent winters of this study, with considerable portions of the bay frozen over for a period of time in both years. Barnegat Bay appears to have changed from a source to a sink for *M. leidyi* during this time. Although *M. leidyi* is characterized by a broad

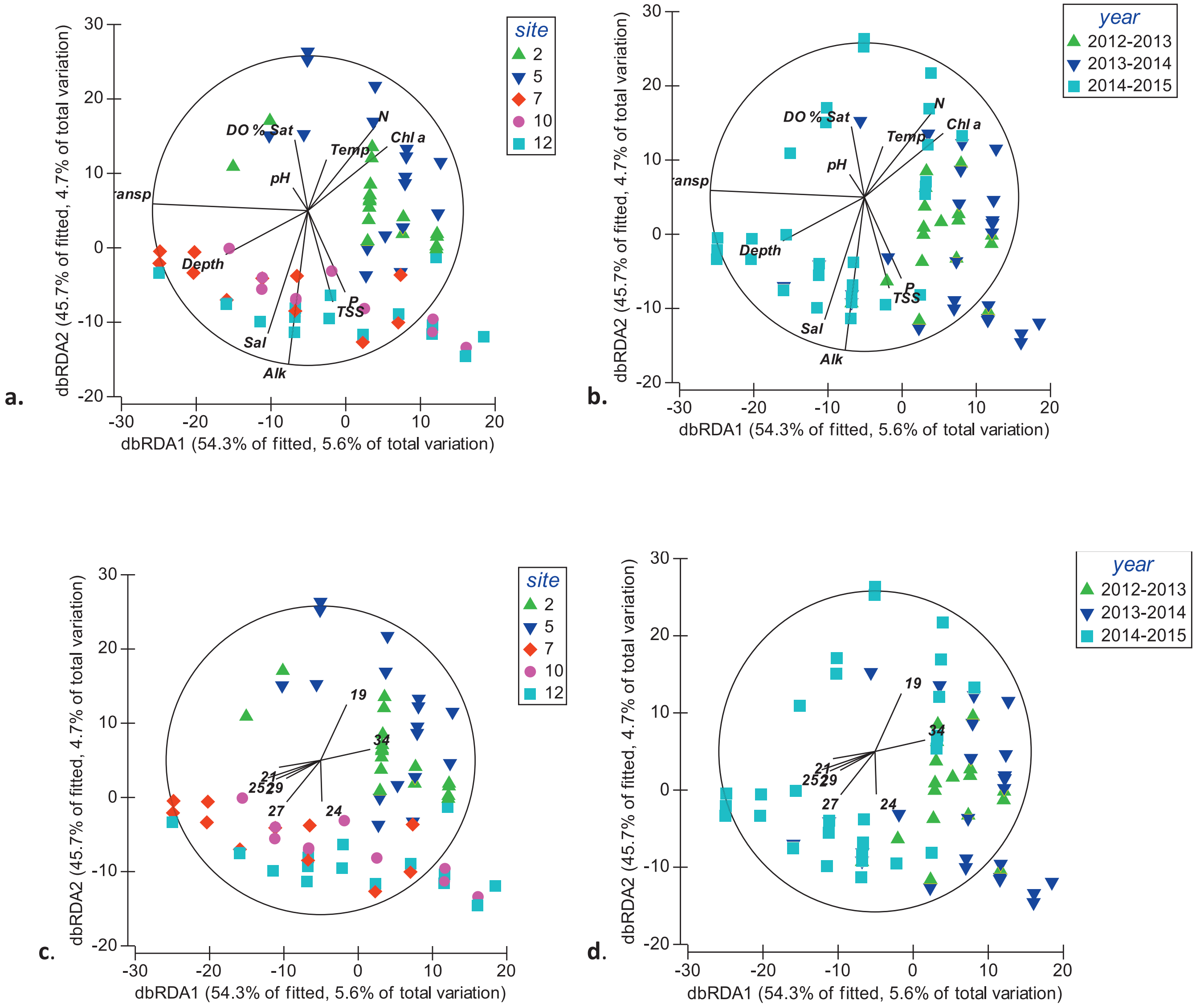

Figure 13. Distance-based redundancy analysis (dbRDA) plots of the zooplankton community data Bray-Curtis resemblance matrix for summer, combined fractions. (a) by site, with all environmental variables, (b) by sampling year, with all environmental variables, (c) by site, with zooplankton taxa, correlation = 0.25, numbered as in Table 7, (d) by sampling year, with zooplankton taxa, correlation = 0.25, numbered as in Table 7.

temperature tolerance range of 0–32°C, the lower thermal limit is raised when salinity decreases to below 20–22 ppt (Costello *et al.,* 2012). Survivability is thus impacted when water temperatures approach or reach freezing (–1.9°C for seawater at 35 ppt) and low salinity. Such conditions were typical of the upper bay during the latter two winters of this study, with measured water temperatures approaching 0°C and salinities often at or below 20 ppt. Reproduction in *M. leidyi* populations does not begin until temperatures reach 10–12°C. In late May 2012 when this study began, water temperatures were already above 25°C, so *M. leidyi* spring reproduction would have been well established by then. In subsequent springs during this study, water temperatures were 5–10°C lower at the same time of year.

Interannual and seasonal variability in ctenophore abundance may be due to differences in overwintering conditions coupled with availability of zooplankton prey such as copepods. The density-independent interannual variability of *M. leidyi* observed in this study may have the potential to impact zooplankton community dynamics. Elucidating the causal mechanisms of these blooms therefore becomes an important consideration in understanding the food web in mid-Atlantic estuaries.

Decapods and Bivalves

Decapods and bivalve zooplankton were evident in high densities during select periods during the 3 years of sampling. These periods coincided with spawning, which were typically

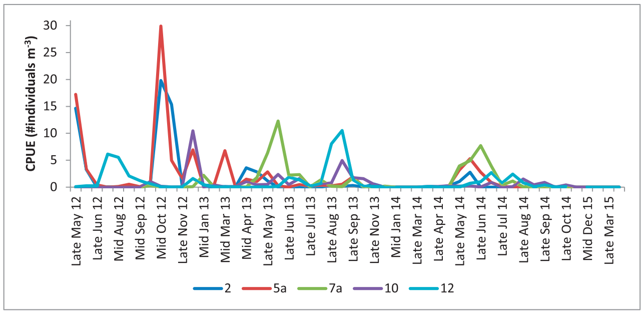

Figure 14. Abundance of *Mnemiopsis leidyi* collected at Sites BB02, BB05a, BB07a, BB10, and BB12 in May 2012–April 2015. Sites BB07a and BB10 were added in late September 2012.

late spring and summer for decapods. Abundance of bivalve larvae was highest in the fall–winter of 2012–13 with smaller pulses observed in spring–summer of 2012 and summer of 2014. Hard clam (*Mercenaria mercenaria*), an important commercial and recreational species in Barnegat Bay, typically start spawning in June, when water temperatures reach 20°C, and peak in July (Carriker, 1961) and were likely the species present during the summer months. However, the high densities of bivalve larvae at BB07 in November 2012 and January 2013 were likely another species, *Arctica islandica*, which spawns in coastal habitats from August to November (Jones, 1981; Mann, 1982). BB07 is located near Barnegat Inlet; veliger larvae of the species may have been brought into the bay with the Superstorm Sandy storm surge.

Superstorm Sandy

Superstorm Sandy made landfall on 29 October 2012, several miles south of Barnegat Bay. The bay was subjected to a storm surge up to 2.5 m. Two breaches occurred in the northern bay near Mantoloking, New Jersey, opening the bay up to the ocean for approximately 1 week before the breaches were closed. Project sampling occurred several days before and 1 month after landfall.

The storm had a considerable impact on water quality and the zooplankton community in Barnegat Bay. Nitrogen, phosphate, and total suspended solids were extraordinarily high throughout the bay in November 2012 after the storm (Water Quality Portal, 2017). The strong pulse in nutrient levels was coupled with an extremely dense bay-wide calanoid copepod bloom, dominated by *Acartia* spp., in November and December. Coastal populations of all *Acartia* species were relatively low at that time, with a mean of approximately 9500 individuals 100 m^{-3} at sampling stations along the New Jersey Coast in mid-November (Hare, 2017), making it unlikely that the bloom was caused by an influx of large numbers of these copepods through the breaches or natural inlets. The bloom may have been initiated by the storm's resuspension of nutrients and copepod resting cysts from bottom sediment. Ren (2015) indicated that the phytoplankton community in northern Barnegat Bay was significantly impacted after the storm (as compared to 2011), with substantially decreased phytoplankton densities observed in November and December 2012. The phytoplankton decline may have been a result of the decrease in available light due to the post-Sandy elevated turbidity in the bay coupled with the seasonal decline in light levels, as well as copepod predation of the phytoplankton standing stock. Calanoid copepods are opportunistic omnivores (Kleppel, 1993) that feed on phytoplankton and other food sources such as heterotrophic protozoans (Verity and Paffenhofer, 1996), especially when abundance of phytoplankton is low and concentration of heterotrophic protozoans is high (Kleppel 1992). Calanoid copepods exhibit higher clearance rates for heterotrophic protozoans than for phytoplankton (Castellani *et al*., 2005; Liu, Dagg, and Strom, 2005); heterotrophic protozoan abundance is an important driver of reproduction in *Acartia tonsa* in Chesapeake Bay (White and Roman, 1992). The surge in nutrient levels in the bay as a result of Superstorm Sandy may have led to an increase in protozoan populations, thereby fueling and sustaining the copepod bloom.

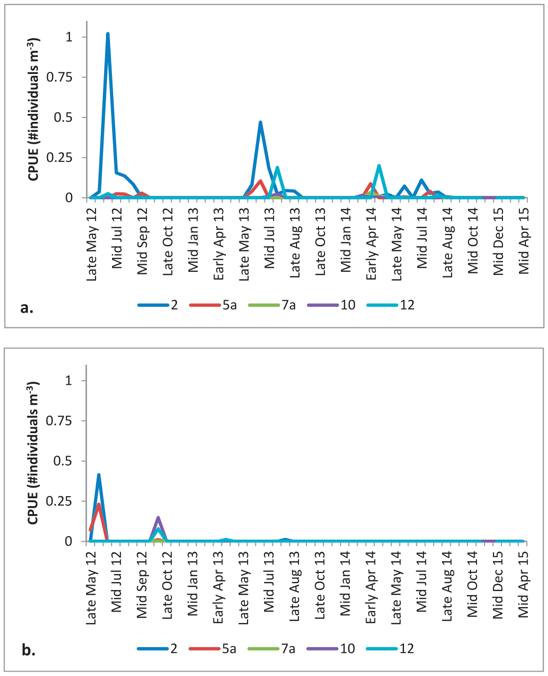

Figure 15. Abundance of (a) *Chrysaora quinquecirrha* and (b) *Beroe ovata* collected at Sites BB02, BB05a, BB07a, BB10, and BB12 in May 2012–April 2015. Sites BB07a and BB10 were added in late September 2012.

The coastal copepod *P. minutus* was absent in the bay throughout the fall of 2012 (prestorm), but increased only at BB02 in the northern bay to approximately 7300 individuals 100 m^{-3} in November 2012. Since *P. minutus* was not collected elsewhere in the bay and does not have a resting egg stage (Mauchline, 1998), the likely source of the copepod was from the coastal stock, through the breach in the northern bay. Low numbers (mean = 55 individuals 100 m^{-3}) were collected at stations near the New Jersey coast in mid-November 2012 (Hare, 2017); upon ingress into the bay, the high nutrient load in the bay likely provided conditions for the small bloom.

Owing to the exchange of coastal and estuarine water in the northern part of the bay, some *M. leidyi* may have been advected out of the system. The population of *M. leidyi* was substantially reduced in the northern bay immediately after Sandy, although numbers increased again in December at BB05a, possibly in response to the copepod bloom. Abundance data were not available for BB02 for December. The possible advection of *M. leidyi* from the system coupled with the rapid decline in water temperature during that time period may have reduced the overwintering population, resulting in a smaller population the following spring (2013). The two subsequent winters were severe, probably resulting in mortality of overwintering *M. leidyi* due to the physiologically stressful conditions of low temperature and low salinity observed in the northern bay. The synergistic effects of the reduction in population size due to advection from Superstorm Sandy coupled with mortality in subsequent winters likely led to the severe population decline observed in the final year of the study.

Long-Term Ecological Perspective

Variability in the Barnegat Bay zooplankton community was evident on a seasonal basis; a predictable observation. In addition, these intraannual differences were interannually regular, such that a community in the southern bay in winter occurred regularly over the 3 years of the study. The 3 years of data indicate that the bay could be divided into two regions, each with its characteristic zooplankton communities. The northern bay (BB02, BB05a) is characterized by *Acartia* spp. and Balanidae (acorn barnacles), lower salinity, and higher nitrogen and chlorophyll *a*, while sites in the southern bay (BB07a, BB10, BB12) are linked by the copepod community of *C. hamatus*, *C. typicus*, and *T. longicornis*, as well as higher salinity, alkalinity, and phosphorus. It appears that the communities within these two regions are resilient at least in the short term (duration of the study), since zooplankton community composition appeared to remain relatively stable with some exceptions because of Superstorm Sandy. The northern bay is already impacted (*e.g.*, developed watershed, elevated nitrogen) and is characterized by a few dominant euryhaline estuarine zooplankton taxa. The southern bay, however, is less developed and exhibits lower nitrogen levels and is characterized by a diverse zooplankton community characterized by more stenohaline coastal/oceanic copepod species.

New Jersey was marked by three climatic events during the study: Superstorm Sandy in October 2012, and two unusually severe winters in 2013–2014 and 2014–2015. The zooplankton community in Barnegat Bay exhibited responses to these events with fluctuations in abundance, timing of blooms, and species makeup of the community; these events were especially characterized by *Acartia* and several other species.

Zooplankton blooms in the bay exhibited strong temporal variability. An extremely dense bloom was seen in May 2012, followed by a somewhat smaller bloom in December and January after Superstorm Sandy, and an even smaller bloom in spring 2013. The spring bloom was substantially delayed after the severe winter of 2014, not appearing until the summer, and did not appear at all before the study ended in late April 2015. Overall copepod abundance was very low from May 2013 through March 2014.

Since an estuarine zooplankton community is typically tightly coupled with the phytoplankton community and supports the remainder of the food web, factors that affect the zooplankton community may ultimately affect the entire food web. Thus any factor that impacts zooplankton abundance will affect the food web and ultimately carbon cycling through the web. Further, this has important implications to the estuarine ecosystem when considered in the context of climate change, which may result in higher water temperatures in coastal lagoons as well as an increase in the frequency and duration of storms. The zooplankton community in Barnegat Bay therefore has the potential to be highly vulnerable based on the results of this study.

CONCLUSIONS

Changes in the Barnegat Bay zooplankton community are evident in the almost 40 years since the previous study was conducted in the bay. The zooplankton community in the present study was characterized by strong spatial, seasonal, and interannual trends in abundance and diversity. Spatial variability was most apparent between the northern and southern regions of the bay, with a characteristic suite of water quality parameters and taxa in each region. Seasonal and interannual differences were strongly associated with temperature and to a lesser extent other environmental parameters, but were likely also due to predation and interactions with the phytoplankton community. The zooplankton community consisted of common estuarine species, as well as taxa found only at specific locations at certain times of the year. Copepods were the most important primary consumers in the estuarine food web and provided food for a variety of species, including recreationally and commercially important fisheries species. The calanoid copepod *Acartia* was by far the most abundant zooplankton taxon in the bay and was ubiquitous throughout the bay, but its abundance was highly variable. This study determined that zooplankton community dynamics are closely tied to temperature and seasonal changes in the bay and are likely vulnerable to the environmental impacts of climate change.

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