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Top-Down Impacts of Sea Nettles (*Chrysaora quinquecirrha*) on Pelagic Community Structure in Barnegat Bay, New Jersey, U.S.A.

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ABSTRACT

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Coastal communities are substantially affected by human activities and create environments conducive to opportunistic species and structural changes in food webs. The Mid-Atlantic coast of the United States is highly urbanized with significant landscape modification and elevated pollutant loads. The appearance and development of resident populations of the Atlantic sea nettle (*Chrysaora quinquecirrha*) in Barnegat Bay, New Jersey demonstrates a successful establishment to this estuary. This research indicates that two species of gelatinous zooplankton (*Mnemiopsis leidyi*, *C. quinquecirrha*) play important structuring roles in the pelagic community. Specifically, *M. leidyi* exerts significant top-down control of calanoid copepods, cladocerans, fish eggs, and fish larvae, whereas *C. quinquecirrha*'s impact is felt through control of *M. leidyi*, whose density is two orders of magnitude greater. It was expected that if *C. quinquecirrha* exerted top-down control of *M. leidyi*, then a trophic cascade would result. However, no trophic cascade was observed, as *C. quinquecirrha* demonstrated broad control of pelagic community structure as a nonspecific, generalist predator. Consequently, the strength of *M. leidyi*'s ability to exert predation pressure is mediated by the development of the *C. quinquecirrha* bloom, but pelagic community structure is broadly defined by the combined impact of these predators within the system.

ADDITIONAL INDEX WORDS: Jellyfish, ctenophores, *Mnemiopsis*, *Scyphozoa*.

INTRODUCTION

Increasing coastal development has created environments that favor species that are tolerant of various pollutants and degraded water quality (Rosenberg *et al.*, 2004). Additionally, the hardening of shorelines and elimination of natural vegetated regions create the potential that tolerant fouling organisms can colonize and expand in these degraded systems (Simkanin *et al.*, 2012). Many coastal estuaries are plagued by poor water quality and increasing inclusion of nonnative species (Dafforn, Glasby, and Johnston, 2009). As such, developed coastal estuaries are being defined by lowered species richness and diversity as invaders monopolize available space (Cohen and Carlton, 1998; Ruiz *et al.*, 1997), the quantity and toxicity of pollutants (Long *et al.*, 1996), the loss of natural habitats (Lathrop and Bogner, 2001), and simplification of food webs through redirection of energy, species introduction, and overfishing (Byrnes, Reynolds, and Stachowicz, 2007). In particular, the relative increase in gelatinous zooplankton in many regions of the ocean has led to a phase shift from “textbook” planktonic communities dominated by zooplanktivorous fish and higher apex predators (Reid *et al.*, 2000) to ones dominated by ctenophores, cnidarians, and pelagic tunicates (Purcell, Uye, and Lo, 2007). Although the apparent global

increase in gelatinous zooplankton is actively debated (see Brotz *et al.*, 2012; Condon *et al.*, 2013), many specific regional locations have strong documentation of elevated abundances (Fuentes *et al.*, 2010) often leading to food-web disruption and fisheries crashes (Roohi *et al.*, 2010).

Perhaps the strongest evidence of gelatinous zooplankton-affected communities comes from the invasion of *Mnemiopsis leidyi* (Agassiz, 1865) in the Black, Caspian, Mediterranean, and North seas. In all of these systems, human influences relating to eutrophication and overfishing have fueled the degradation of these communities, thus altering food webs (Finenko *et al.*, 2013; Llope *et al.*, 2011). Consequently, *M. leidyi* introductions have demonstrated this species' ability to significantly affect pelagic food webs, devastate fisheries, and alter community structure through invasions and expansions. Specifically, in the Black Sea *M. leidyi* has caused rapid community shifts and depletion of fish stocks (Oguz and Gilbert, 2007). More recently, their proliferation in the North and Baltic seas has generated substantial research into the potential top-down and competitive structuring forces in pelagic food webs (Hosia and Titelman, 2011; Javidpour *et al.*, 2009; Kellnreitner *et al.*, 2013; but see Hamer, Malzahn, and Boersma, 2011; Jaspers *et al.*, 2011) and species interactions between *M. leidyi* and other gelatinous zooplankton species (Riisgård, Barth-Jensen, and Madsen, 2010; Riisgård *et al.*, 2012). Within its native range, *M. leidyi* has always played an important role in pelagic food webs (Deason and

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Smayda, 1982; Mountford, 1980; Nelson, 1925), but with increasing anthropogenic stresses related to eutrophication and overfishing, their relative abundance and influence on communities has led to broader structuring effects in coastal communities (Breitburg *et al.*, 2010; McNamara, Lonsdale, and Cerrato, 2010; 2013). Often, it is the interactions and predator-prey relationships of other gelatinous zooplankton that seem to balance communities or minimize the impacts of *M. leidyi* as a keystone species (Hosia and Titelman, 2011; Purcell and Cowan, 1995; Tilves *et al.*, 2013).

In a similar manner, scyphozoan jellyfish have had regional increases affecting food webs and recreational use of coastal waters. The recent increases in many of these species have been hypothesized to result from eutrophication and coastal development (Duarte *et al.*, 2012; Purcell, 2012). Blooms of *Pelagia noctiluca* (Forskål, 1775) in the Mediterranean (Ferraris *et al.*, 2012), *Nemopilema nomurai* (Kishinouye, 1922) in the west Pacific (Uye, 2008), and *Chrysaora quinquecirrha* (Desor, 1848) and *Aurelia aurita* (Linnaeus, 1758) in the Gulf of Mexico (Graham, 2001) have been favored under eutrophic conditions and food-web simplification from overfishing. These have accentuated the impacts that humans are having on the oceans on a global level (Duarte *et al.*, 2012). It is now recognized that the expansion and continuation of gelatinous zooplankton blooms have the potential to significantly affect communities and under introduction to nonnative systems, their potential to permanently disrupt natural food webs has been demonstrated (Oguz *et al.*, 2012). Concurrently, the long-term impacts to commercially important fisheries species is occurring through direct consumption of fish eggs, larvae, and juveniles (Finenko *et al.*, 2013). Additionally, indirect impacts are occurring through competitive interactions for planktonic food resources with these same life-history stages (Purcell *et al.*, 2001).

Barnegat Bay, New Jersey is a shallow, eutrophic coastal lagoon system in the Mid-Atlantic region of the United States (Kennish *et al.*, 2007) with significant urbanization and land-use changes in its watershed (Lathrop and Bognar, 2001). Although *M. leidyi* has been reported as an important component of the pelagic community for the last century (Mountford, 1980; Nelson, 1925; Sandine, 1984), the recent establishment of reproductive populations of the scyphozoan *C. quinquecirrha* during the last decade (Bologna 2011) may be a result of the development and eutrophication of the system (*sensu* Duarte *et al.*, 2012) providing a favorable habitat for establishment. Bologna (2011) showed that larval recruitment to settling plates was highly localized in northern portions of the bay where development is high and salinity is reduced from two large rivers. As these jellyfish have become established in the region over the last decade, their impacts at the community level have yet to be evaluated; even though their increasing abundance has led to reduced recreational use of the bay. Conceptually, the establishment of *C. quinquecirrha* could initiate a trophic cascade as they exert top-down pressure on *M. leidyi* populations, similar to the findings of Purcell and Decker (2005) and Breitburg and Burrell (2014) in the Chesapeake Bay, where both species are present. This research addressed the following two hypotheses: establishment of *C. quinquecir-*

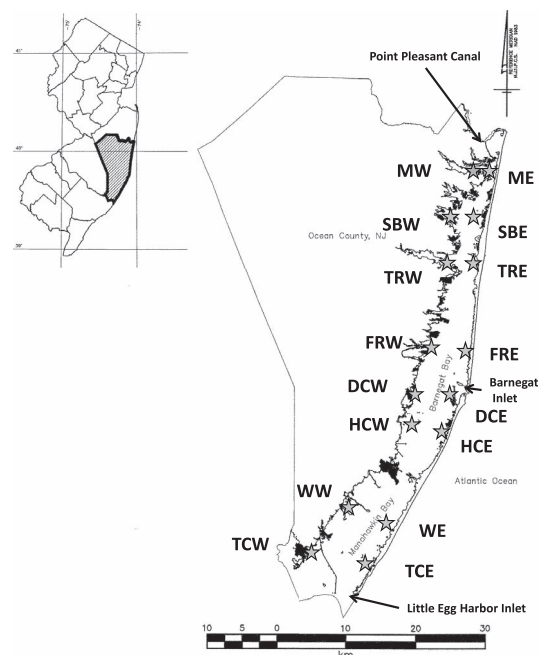


Figure 1. Map of Barnegat Bay, New Jersey identifying the eight paired sampling stations throughout the bay and the three tidal inlets. Map abbreviations as follows: ME = Metedeconk River East (site depth 1.4 m), MW = Metedeconk River West (1.5 m), SBE = Silver Bay East (1.3 m), SBW = Silver Bay West (1.9 m), TRE = Toms River East (2.25 m), TRW = Toms River West (1.4 m), FRE = Forked River East (1.6 m), FRW = Forked River West (1.3 m), DCE = Double Creek East (1.6 m), DCW = Double Creek West (1.67 m), HCE = Harvey Cedars East (2.03 m), HCW = Harvey Cedars West (1.2 m), WE = Westecunk Creek East (1.2 m), WW = Westecunk Creek West (1.56 m), TCE = Tuckerton Creek East (1.36 m), TCW = Tuckerton Creek West (2.1 m).

rha will (1) demonstrate top-down control of *M. leidyi* and (2) invoke a trophic cascade.

METHODS

Study Area

The geographic focus for this research was Barnegat Bay, New Jersey (39° N, 74° W), located just south of the Mid-Atlantic Bight (Figure 1). Barnegat Bay is a barrier island lagoon estuary with three tidal inlets and is designated both as a National Oceanic and Atmospheric Administration National Estuarine Research Reserve and a U.S. Environmental Protection Agency National Estuary Program site. Kennish *et al.* (2007) have described the bay as highly eutrophic, but it maintains the only known eelgrass (*Zostera marina* L. 1753) populations in the state of New Jersey. It is shallow with an average depth of 1.5 m and is well mixed (Kennish 2001). It also has experienced substantial development in the northern portion of the bay watershed (Lathrop and Bognar 2001). Eight paired sampling sites ($N = 16$) were established in Barnegat Bay matching eastern and western sides of the bay in a given region (Figure 1). Site selection incorporated stratified samples throughout the bay, but focused on major freshwater inputs, which may provide preferred habitat for *C. quinquecir-*

rha. These sites were selected to be representative of the various environmental conditions that exist in the bay and comprehensive coverage of sites throughout the bay. Field research was initiated in May 2012 and concluded in September 2012. During this time, sites were sampled on eight dates approximately 2 weeks apart to assess spatial and temporal plankton community structure. During sampling events, larger gelatinous zooplankton were sampled using lift nets, the pelagic zooplankton community ($>363\ \mu\text{m}$) was sampled using a towed plankton net, and water quality was monitored for salinity, temperature, and dissolved oxygen using a YSI® Professional Plus multiparameter meter calibrated and certified by the New Jersey Department of Environmental Protection. Water-quality data indicated a typical seasonal temperature pattern, with a seasonal range of 18.6°C in early June to a peak of 29.9°C in July. Since sampling occurred during the day, dissolved oxygen values were generally high, but ranged from $4.23\ \text{mg/L}$ to supersaturation values at $11.09\ \text{mg/L}$. Salinity did not show any seasonal patterns, but data indicate a strong spatial distribution, with substantially lower values recorded at the six northerly sites (mean = 18.9 parts per thousand [ppt]) compared with the other 10 sites (mean = 27.5 ppt, Supplementary Figure 1). This was due to the freshwater inputs of the two major rivers in the bay, the Metedeconk and Toms rivers.

Lift Nets

Gelatinous zooplankton (e.g., pelagic cnidarians and ctenophores) tend to be rather delicate and are frequently mangled and destroyed in standard plankton tows. Ten to 12 lift-net samples were collected from each site during every sampling event ($N = 1394$) by allowing the lift net to settle to the bottom and remain undisturbed for 30 seconds. Lift nets ($0.836\ \text{m}^2$, 3.2-mm mesh) were then raised directly through the water column and all organisms were lifted to the surface. Depths varied among sites (range: $1.24\text{--}2.3\ \text{m}$, Figure 1), but since the bay is relatively shallow (average: $1.5\ \text{m}$), these samples are representative of the entire well-mixed water column at each site. Once on deck, samples were transferred to a holding bin where all gelatinous zooplankton were identified and enumerated. Water depth was recorded for each lift-net sample and the lift-net area was then multiplied to determine the volume of water sampled. All samples were then standardized to number per cubic meter and compared among sites and dates of collection.

Zooplankton Tows

During each sampling event, triplicate $363\text{-}\mu\text{m}$ zooplankton nets (30-cm diameter) were towed at each location ($N = 370$). Surficial tows were conducted at minimally engaged engine speed for 1 minute while a mechanical flow meter (General Oceanics mechanical flowmeter model 2030R) was deployed to measure length of each tow. We used the manufacturer's empirical conversion constant to calculate the tow length (m) and multiplied distance traveled with net area to calculate the volume sampled in cubic meters. Since this is a shallow, well-mixed system, these samples are representative of the entire water column. After collection, the sample was passed through a coarse (4-mm) sieve to remove ctenophores and any sea nettles. These were washed and counted while the sample was fresh in a manner similar to that of Purcell and Decker (2005).

The remaining zooplankton were then preserved in ethanol and stained with rose bengal for ease of identification and quantification in the laboratory. Samples were returned to the lab for identification and enumeration to lowest reasonable taxonomic unit. All samples were standardized to number per cubic meter and compared among sites and dates of collection.

Statistical Analyses

Because of the seasonality of communities, primary analyses of data sets were conducted using analysis of covariance (ANCOVA) (SAS®, 2002–10) with site as the independent variable and date of collection as the covariate in the model using PROC GLM and organismal density of each taxon as dependent response variables in the model. Discrimination of significant differences among sites and dates of collection were accomplished by using the REGWQ method in SAS. Organismal density for each taxon was square-root transformed before analysis to eliminate heteroscedasticity. Correlation analysis was conducted with both data sets to assess significant relationships among taxa sampled. To fully assess and test the hypothesis that *C. quinquecirrha* is exerting top-down pressure on *M. leidyi* beyond simple correlation, the density distributions of both species were plotted against each other. To analyze the distribution, a PROC REG analysis was conducted in SAS to estimate the observed negative exponential function for both lift-net and plankton-tow data. Before analysis, samples containing neither species were eliminated from the analysis. Samples were then transformed by the addition of 0.000001 to allow for the analysis when one species was present but the other was not, and approximates a density of zero. This resulted in 816 valid data points for lift nets and 229 for zooplankton tows. Additionally, to assess the overall top-down impacts of the two dominant gelatinous zooplankton species, a correlation matrix was generated between *M. leidyi* and *C. quinquecirrha* with the other zooplankton taxa collected in the plankton tows. These matrix values were then analyzed using a nonparametric sign test for potential prey items using their positive or negative sign as a designation of trophic interaction using the large sample approximation (Sokal and Rohlf, 1995), with the *a priori* null hypothesis that these species have no impact on the other taxa. Last, the zooplankton-tow data were analyzed for community structure and similarity using the SIMPER and two-way analysis of similarity (ANOSIM) (site and collection date as factors) procedures in Primer® on fourth-root-transformed data (Clarke and Gorley, 2006).

To assess the potential trophic cascade and time-dependent changes in planktonic communities, Barnegat Bay was subdivided into two regions: the northern, low-salinity region comprising six sites including Toms River to the Metedeconk River sites and the southern, high-salinity region comprised of the remaining 10 sites (see Supplemental Figure 1). This designation was established on the basis of the general salinity pattern observed in the field and the overall density patterns of *C. quinquecirrha*, leading to either a high-density or low-density region. Data regarding *M. leidyi*, *C. quinquecirrha*, and calanoid copepods were pooled by date and averaged for each region, then plotted to assess the temporal density patterns to test the trophic cascade hypothesis.

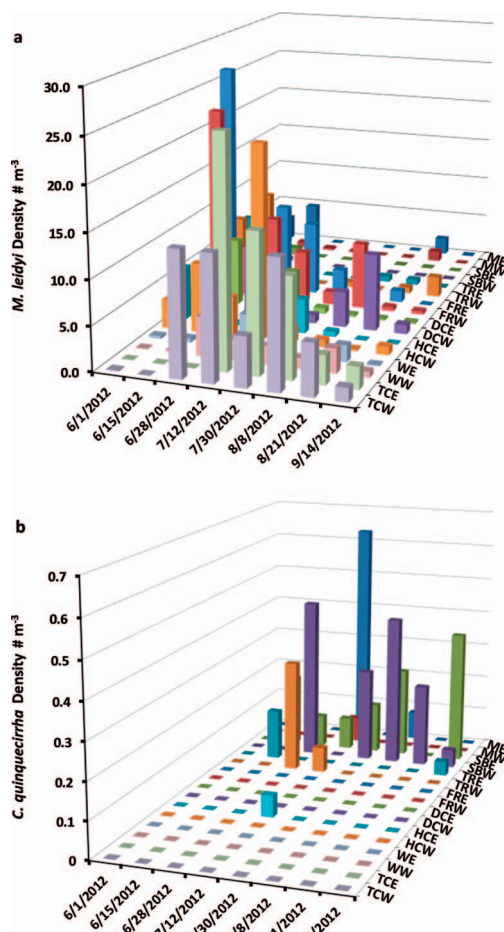


Figure 2. Comparative spatial and temporal distributions of (a) *Mnemiopsis leidyi* and (b) *Chrysaora quinquecirrha* collected from lift-net samples. Z-axis orients north to south of sampling stations.

RESULTS

Lift Nets

During lift-net sampling, six species of gelatinous zooplankton were collected and include *C. quinquecirrha*, *M. leidyi*, *Beroe ovata* (Bruguiere, 1789), *Pleurobranchia pileus* (O.F. Muller, 1776), *Aurelia aurita*, and *Cyanea capillata* (L., 1758). ANCOVA results indicate significant differences among sites of collection for *C. quinquecirrha* density ($F_{15,1377} = 7.67$, $p < 0.0001$), but no difference among dates, whereas *B. ovata*, *M. leidyi*, and *P. pileus* showed significant differences among sites and dates of collection (*B. ovata* [$F_{15,1377} = 4.45$, $p < 0.0001$; $F_{1,1377} = 11.21$, $p < 0.001$], *M. leidyi* [$F = 17.64$, $p < 0.0001$; $F = 69.4$, $p < 0.0001$], and *P. pileus* ($F = 1.81$, $p < 0.03$; $F = 16.6$, $p < 0.0001$)). *Aurelia aurita* and *C. capillata* showed no difference among sites because each was encountered only once during sampling. Numerically, *M. leidyi* and *C. quinquecirrha* were one to three orders of magnitude greater in abundance than the other four species and showed disjunct distributions in the bay, with *C. quinquecirrha* dominating in the northern portion of the bay (Figure 2b), but relatively absent from the southern

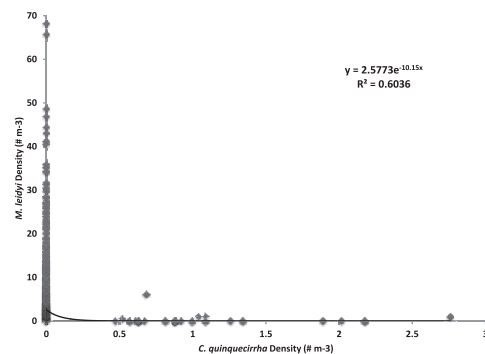


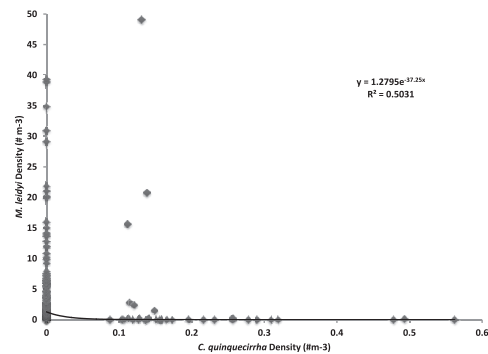
Figure 3. Inverse exponential relationship between *Chrysaora quinquecirrha* and *Mnemiopsis leidyi* density collected from lift-net samples.

region, which was dominated by *M. leidyi* (Figure 2a). Although this pattern was generally observed when *C. quinquecirrha* were abundant, on dates when they were absent from northerly sites, *M. leidyi* was present and as abundant as samples collected on the same date from sites farther south (Figure 2a), indicating predatory control. Integrally, this suggests that the disjunct distribution reflects a predator–prey interaction, as a significant negative correlation occurred between these two species ($p < 0.005$), but clearly the relationship is not linear. Results from the regression analysis showed a significant negative exponential relationship between *C. quinquecirrha* and *M. leidyi* density ($F_{1,815} = 1240.8$, $p < 0.0001$; Figure 3), demonstrating the top-down effect and allowing us to reject the null hypothesis of no predatory impact. ACOVA showed a significant difference among sites for *C. quinquecirrha*, with significantly greater densities occurring at Silver Bay East and West compared with other sites; whereas *M. leidyi* distribution reflects proximity to oceanic inlets, showing significantly greater densities at Tuckerton Creek East and West, Forked River East and West, and Harvey Cedars West compared with other sites, and lowest densities occurring in regions where *C. quinquecirrha* densities were high (Figure 2a,b).

Zooplankton Tows

A total of 64 taxonomic groups was identified from plankton net samples and included two distinct life-history stages of *C. quinquecirrha* (i.e. juvenile medusae and ephyrae). Average density for the most numerically dominant groups include *Brachyura* larvae (830 m^{-3}), calanoid copepods (27.9 m^{-3}), fish eggs (4.8 m^{-3}), Caridea larvae (4.1 m^{-3}), and *M. leidyi* (2.4 m^{-3}). The *Brachyura* density pattern was predominantly driven by the presence of *Callinectes sapidus* (Rathburn, 1896) in samples collected on 30 July from our Westcunk Creek West site, where average density on that date was $99,873 \text{ m}^{-3}$!

Similar to lift nets, *C. quinquecirrha* densities were greater in the northern portion of the bay; however, juveniles and ephyrae were collected in the southern regions of the bay (Figure 4b), even though adults were not observed. Additionally, 16 taxa collected showed significant density differences among sites (Table 1), including *C. quinquecirrha* ($F_{15,361} = 5.98$, $p < 0.0001$), *M. leidyi* ($F = 5.6$, $p < 0.0001$), *Turritopsis nutricula* (McCrary, 1857) ($F = 4.49$, $p < 0.0001$), calanoid



$p < 0.0001$), and fish larvae ($F = 1.88$, $p < 0.03$). *Chrysaora quinquecirrha* was significantly greater at our Silver Bay East site, with an average density of 0.23 m^{-3} and a maximum density of 0.56 m^{-3} . Ephyrae were identified throughout the bay and there appear to have been several pulses into the system including mid-June, followed by sporadic site-specific pulses in July and August (Figure 4c). The collection of ephyrae in the southern reaches of the estuary on several dates, and at multiple sites, suggests that there are proximal polyp populations in this region and these collections do not reflect a single random export of ephyrae from northern portions of the bay. *Mnemiopsis leidyi* distributions were characterized by higher densities in the southern region of the bay and they were relatively absent in the northern bay, except on dates when *C. quinquecirrha* was absent (Figure 4a). When the densities of *C. quinquecirrha* and *M. leidyi* for individual samples were plotted against each other, a significant negative exponential relationship existed ($F_{1,228} = 230.8$, $p < 0.0001$; Figure 5), similar to that observed in the lift nets.

Collectively, many organisms were positively correlated with each other and relate to generalized pelagic communities and larval distribution (*e.g.*, calanoid copepods with crab larvae ($r = 0.25, p < 0.0001$), Caridea larvae ($r = 0.5, p < 0.0001$)), and life-history stages (*e.g.*, fish eggs and larvae [$r = 0.44, p < 0.0001$], *C. quinquecirrha* ephyrae, and juveniles ($r = 0.14, p < 0.007$)). One unique group of organisms displaying distributions highly

copepods ($F=3.67, p < 0.0001$), Brachyura larvae ($F=2.24, p < 0.005$), Caridea larvae ($F=4.3, p < 0.0001$), fish eggs ($F=3.43,$

Table 1. Average densities (# m⁻³) of taxa exhibiting significant differences among sites. Site designation identifiers follow those given in Figure 1. Differing letters next to density values indicate significant differences in means among sites for taxa.

Species Sites	MW	ME	SBW	SBE	TRW	TRE	FRW
Brachyura larvae***	0.83 b	1.55 b	0.97 b	0.98 b	0.58 b	0.85 b	2.12 b
Calanoid Copepods***	2.36 bcde	3.46 abcde	1.19 e	2.06 cde	2.52 abcde	0.69 e	1.14 e
Fish Eggs***	0.10 b	1.52 b	1.69 ab	1.63 ab	0.90 b	1.24 b	1.08 b
Caridea Larvae***	1.32 abcdef	1.87 abcd	0.51 ef	0.83 cdef	0.34 f	0.68 ef	0.79 def
<i>Mnemiopsis leidyi</i> ***	0.53 cde	0.27 de	0.13 e	0.16 e	0.47 cde	0.54 cde	0.96 bcde
<i>Turritopsis nutricula</i> ***	0.01 c	0.00 c	0.00 c	0.00 c	0.04 c	0.00 c	0.01 c
Mellitidae***	0.06 bc	0.08 bc	0.02 c	0.13 bc	0.07 bc	0.07 bc	0.03 c
Fish Larvae***	0.10 bcd	0.04 d	0.17 abcd	0.05 cd	0.21 abcd	0.13 bcd	0.08 bcd
<i>Idotea baltica</i> ***	0.06 e	0.02 e	0.00 e	0.02 e	0.00 e	0.02 e	0.16 bcde
Ostrococha**	0.03 b	0.14 b	0.07 b	0.14 b	0.05 b	0.02 b	0.06 b
<i>Gammarus</i> **	0.00 b	0.00 b	0.05 ab	0.22 ab	0.03 ab	0.15 ab	0.08 ab
Caprellidae***	0.00 b	0.03 b	0.00 b	0.16 ab	0.00 b	0.00 b	0.02 b
Pycnogonidae***	0.00 b	0.00 b	0.00 b	0.00 b	0.00 b	0.00 b	0.00 b
<i>Chrysaora</i>	0.02 c	0.11 bc	0.16 ab	0.23 a	0.03 c	0.03 c	0.00 c
<i>quinquecirrha</i> ***							
<i>Stegastes fuscus</i> *	0.00 b	0.00 b	0.00 b	0.00 b	0.00 b	0.00 b	0.00 b
<i>Eutima</i> **	0.00 b	0.00 b	0.03 ab	0.00 b	0.00 b	0.00 b	0.01 ab

Significance: * = 0.05, ** = 0.01, *** = 0.0001.

correlated with one another consisted of benthic Peracarida associated with floating seagrass wrack in open water. When the 11 most abundant organisms in this group were analyzed using correlation analysis, 45 of 55 possible combinations showed significant positive correlations (Table 2). As these organisms are usually associated with benthic habitats, their collection within floating wrack suggests a strong, yet uninvestigated, benthic–pelagic coupling for these organisms. Some of these taxa (e.g., *Gammarus* spp., *Idotea baltica* Pallas, 1772, Mellitidae) were also important in defining the community structure in the SIMPER analysis for some sites.

Results from the SIMPER analysis indicate average similarities ranging from 35% to 53%, with between four and eight taxa contributing to >90% of the group similarity (Table 3). Overall, *C. quinquecirrha* was only represented in two of 16 sample sites as a discriminating species, whereas *M. leidyi* occurred in 13, which relates to its broad distribution and relative abundance in samples. Three crustacean groups were critical in defining community structure and included Caridea larvae, calanoid copepods, and Brachyura larvae. These were represented as fundamental taxa in all 16 sites and were in the top four of species contributions (Table 3). Fish eggs and larvae were also important, but their relative contributions were generally much smaller. The two-way ANOSIM indicated a global *R* of 0.628 ($p < 0.001$) for differences among sites and a global *R* of 0.706 ($p < 0.001$) for differences among dates. For all but one assessment between individual sites and dates, significance was < 0.001 ($p < 0.007$ for Silver Bay West and Toms River East) and individual *R* statistics ranged from 0.338 to 0.942 for sites and 0.4 and 0.94 for dates. Collectively, these results indicate relatively unique plankton community characteristics within this system, driven temporally by egg/larvae production of *C. sapidus*, Caridea, fish, and Polychaeta larvae, as well as seasonal spikes in calanoid copepods and naupli. Additionally, sites showed spatial differences through the disjunct distributions of *M. leidyi* and *C. quinquecirrha* within the bay, the relative abundance of various Peracarida associated with floating seagrass wrack in the system, and pulses of more oceanic organisms near the sites adjacent to tidal inlets.

Trophic Cascade Assessment

Although the sign test demonstrated significant top-down relationships between gelatinous zooplankton and other pelagic species, the analyses cannot document trophic cascades. To test the hypothesis of whether *C. quinquecirrha* was generating a trophic cascade (*sensu* Purcell and Decker, 2005), the temporal distribution of *C. quinquecirrha*, *M. leidyi*, and calanoid copepods were plotted on the basis of the N-S site designations. In the southern region where *C. quinquecirrha* is relatively absent (Figure 2b), no pattern is present between *C. quinquecirrha* and *M. leidyi* (Figure 6a), nor did *C. quinquecirrha* show a structuring pattern with copepods (Figure 6c). However, when addressing the distributional patterns between *M. leidyi* and copepods, a clear temporal top-down control pattern is evident in the results (Figure 6b). In the northern region where *C. quinquecirrha* density is significantly greater, we see strong top-down control of *M. leidyi* (Figure 6d), but no inverse or temporal relationship between *M. leidyi* and copepods (Figure 6e), which would infer a trophic cascade. Rather, copepod abundance was controlled in this region by *C. quinquecirrha* (Figure 6f). Consequently, *C. quinquecirrha* exerts significant top-down control of both *M. leidyi* and copepod populations and no large-scale trophic cascade occurred in the pelagic community.

DISCUSSION

Coastal eutrophication results in degraded water quality and blooms of noxious algal species, which can lead to disruptions in food webs (Flaherty and Landsberg, 2011), generation of toxic chemicals (Glasgow et al., 2001), and anoxic conditions leading to rapid loss of habitat on both small (Bologna, Gibbons-Ohr, and Downes-Gastrich, 2007) and large spatial scales (Howarth et al., 2011). Barnegat Bay, in particular, has seen significant land-use changes through increasing coastal development rates (Conway and Lathrop, 2005) and has been classified as highly eutrophic (Kennish et al., 2007). Meanwhile, overharvesting and loss of essential fish habitat have substantially changed food webs by the easing of top-down pressures (Casini et al., 2009). The synergistic impact of these factors has opened

Table 1. *Extended.*

FRE	DCW	DCE	HCW	HCE	WW	WE	TCW	TCE
1.25 b	0.82 b	2.08 b	4.33 b	1.37 b	41.0 a	3.63 b	5.86b	2.23 b
0.83 e	1.72 de	2.44 abcde	5.07 abcd	2.44 abcde	5.41 abc	2.26 cde	5.91 a	5.82 ab
1.35 b	1.14 b	1.18 b	1.26 b	0.67 b	1.45 b	0.59 b	2.69 a	1.36 b
1.90 abcd	1.10 bcdef	2.19 ab	1.95 abc	1.64 abcde	1.39 abcdef	2.29 a	2.12 ab	2.01 ab
1.25 bcd	1.30 bc	0.95 bcde	1.11 bcde	0.96 bcde	0.87 bcde	0.98 bcde	2.41 a	1.75 ab
0.06 c	0.09 bc	0.16 bc	0.59 a	0.63 a	0.25 bc	0.46 ab	0.09 bc	0.13 bc
0.27 abc	0.33 abc	0.56 a	0.22 abc	0.11 bc	0.31 abc	0.44 ab	0.24 abc	0.40 abc
0.09 bcd	0.16 abcd	0.07 bcd	0.40 ab	0.16 abcd	0.29 abcd	0.15 abcd	0.48 a	0.39 abc
0.38 abc	0.25 abcde	0.50 a	0.13 bcde	0.09 dce	0.08 de	0.41 ab	0.14 bcde	0.35 abcd
0.15 b	0.04 b	0.52 a	0.17 b	0.07 b	0.05 b	0.28 ab	0.10 b	0.11 b
0.16 ab	0.04 ab	0.26 ab	0.09 ab	0.05 ab	0.20 ab	0.32 a	0.24 ab	0.24 ab
0.02 b	0.00 b	0.30 a	0.04 b	0.02 b	0.07 b	0.01 b	0.00 b	0.14 ab
0.12 ab	0.09 ab	0.11 ab	0.09 ab	0.07 ab	0.03 b	0.17 a	0.04 ab	0.04 ab
0.00 c	0.00 c	0.00 c	0.02 c	0.02 c	0.00 c	0.03 c	0.01 c	0.02 c
0.02 ab	0.02 ab	0.00 b	0.04 ab	0.00 b	0.00 b	0.10 a	0.00 b	0.05 ab
0.02 ab	0.04 ab	0.02 ab	0.10 a	0.02 ab	0.03 ab	0.02 ab	0.00 b	0.08 ab

the door for gelatinous zooplankton to play a major role in structuring pelagic communities (see Oguz and Gilbert, 2007), especially when they become established. Our findings provide the first quantification of *C. quinquecirrha* population distribution in this region and document the successful release of ephyrae, verifying the now self-sustaining population (Figure 4c). Their new prevalence in the system has the potential to restructure pelagic food webs and community structure by assuming an apex predator status in the bay.

Mnemiopsis leidyi and *C. quinquecirrha* are both voracious predators with significant top-down potential (Breitburg and Burrell, 2014). Purcell *et al.* (2001) reviewed distribution and predator–prey interactions of *M. leidyi* in native systems and compared impacts with regions that have seen recent introductions. They identified that unrestricted *M. leidyi* populations have the potential to severely reduce zooplankton abundance by their rapid and relatively indeterminate consumption. Mountford (1980) demonstrated that the initial bloom of *M. leidyi* in late spring in Barnegat Bay led to a collapse of copepod populations and a substantial reduction in overall zooplankton biomass and our results concur. He further surmised that unrestrained *M. leidyi* populations would increase until food resources are depleted and clearly, the significant top-down relationship we established between *M. leidyi* and their potential prey

demonstrates their potential to structure the pelagic community (Figure 6b). It is this prolific reproduction potential coupled with high feeding rates that have led to significant changes in planktonic communities in regions that have seen invasions of *M. leidyi* (Finenko *et al.*, 2013; Oguz *et al.*, 2012; Roohi *et al.*, 2010), but changes in native communities have also occurred, fueled by development, eutrophication, and hypoxia (Breitburg *et al.*, 1997). Kimmel, Boynton, and Roman (2012) modeled the abundance of *Acartia tonsa* (Dana, 1849) in Chesapeake Bay. They proposed that the significant reduction in this copepod population is a result of *M. leidyi* predation and that this trophic change is having a secondary impact on fisheries, especially bay anchovy (*Anchoa mitchilli*, Valenciennes, 1848). The underlying causes of eutrophication and reductions in *M. leidyi* predators (*C. quinquecirrha*, in particular) has relieved them from top-down pressure, allowing their numbers to grow and elevating their impact on the system. In coastal Long Island, *M. leidyi* has increased in abundance and peak biomass is appearing earlier in the year. McNamara, Lonsdale, and Cerrato (2010) have shown that this temporal shift has the potential to be a significant mortality event for bivalve larvae as well as other zooplankton species. The results presented here demonstrate the predation potential of *M. leidyi*, as their distribution showed signifi-

Table 2. *Peracarida correlation analysis.*

	IB	GAM	CAP	PYC	ER	AOR	LJ	PX	AML	AMT
MEL	0.52***	0.33***	0.34***	0.21***	0.2***	0.37***	0.3***	0.45***	0.19***	0.17**
IB		0.2***	0.26***	0.27***	0.3***	0.2***	0.1*	0.38***	0.15**	0.14**
GAM			0.06 ns	0.08 ns	0.03 ns	0.15**	0.08 ns	0.09 ns	0.09 ns	-0.01 ns
CAP				0.22***	0.11*	0.38***	0.34***	0.17***	0.42***	0.11*
PYC					0.01 ns	0.13*	0.16**	0.17**	0.25***	0.11*
ER						0.31***	0.06 ns	0.21***	-0.02 ns	0.16**
AOR							0.36***	0.36***	0.34***	0.33***
LJ								0.17***	0.18***	0.16**
PX									0.14**	0.32***
AML										0.19***

Values in table represent the Pearson's *r* with significance indicated by **p* < 0.05, ***p* < 0.01, ****p* < 0.001.

Taxonomic abbreviations as follows: MEL = Mellitidae, IB = Idotea baltica, GAM = Gammarus spp., CAP = Caprellidae, PYC = Pycnogonidae, ER = Erichsonella spp., AOR = Aoridae, LJ = Lilljeborgiidae, PX = Phoxocephalidae, AML = Ampelisca spp., AMT = Ampithodae.

Table 3. Contributing taxa defining the planktonic community associated with plankton-tow samples on the basis of SIMPER analysis. Similarity percentages and species contributions provided for each site.

West				East			
Species	Avg. Abundance	Contribution, %	Cumulative %	Species	Avg. Abundance	Contribution, %	Cumulative %
Metedeconk River							
Caridea	0.95	26.32	26.32	Caridea	1.22	29.12	29.12
Calanoida	1.17	24.03	50.35	Brachyura	1.11	25.45	54.57
Fish Eggs	0.80	17.23	67.58	Calanoida	1.44	21.64	76.21
Brachyura	0.69	14.81	82.39	Fish Eggs	0.95	14.26	90.47
<i>Mnemiopsis leidyi</i>	0.47	12.44	94.84				
Silver Bay							
Fish Eggs	1.05	32.06	32.06	Caridea	0.82	23.96	23.96
Brachyura	0.78	22.92	54.99	Brachyura	0.88	22.10	46.06
Calanoida	0.77	18.32	73.31	Calanoida	1.02	16.63	62.69
Caridea	0.49	8.71	82.02	Fish Eggs	0.99	16.13	78.83
<i>Chrysaora quinquecirrha</i>	0.24	7.01	89.03	<i>C. quinquecirrha</i>	0.34	6.53	85.35
Fish Larvae	0.25	3.50	92.53	Polychaeta Larvae	0.32	3.96	89.32
				<i>Gammarus</i> spp.	0.27	2.83	92.15
Toms River							
Calanoida	1.24	47.79	47.79	Caridea	0.68	23.84	23.84
Brachyura	0.60	17.92	65.71	Brachyura	0.74	20.85	44.69
Fish Eggs	0.67	12.50	78.21	Calanoida	0.64	17.75	62.44
<i>M. leidyi</i>	0.47	10.25	88.46	Fish Eggs	0.82	17.74	80.17
Caridea	0.41	7.95	96.41	<i>M. leidyi</i>	0.49	11.06	91.24
Forked River							
Brachyura	1.18	26.94	26.94	Caridea	1.23	24.01	24.01
<i>M. leidyi</i>	0.85	20.70	47.65	Brachyura	1.03	22.61	46.63
Caridea	0.78	18.88	66.52	<i>M. leidyi</i>	0.87	15.00	61.63
Calanoida	0.87	18.55	85.07	Calanoida	0.75	12.99	74.62
Fish Eggs	0.74	10.17	95.25	Fish Eggs	0.82	9.35	83.97
				<i>Idotea baltica</i>	0.47	5.83	89.80
				Mellitidae	0.32	2.55	92.35
Double Creek							
<i>M. leidyi</i>	1.04	36.27	36.27	Brachyura	1.33	23.80	23.80
Caridea	0.90	21.06	57.34	Calanoida	1.30	17.07	40.86
Calanoida	1.04	20.10	77.44	Caridea	1.22	16.46	57.32
Brachyura	0.67	9.73	87.17	<i>M. leidyi</i>	0.82	13.14	70.46
Fish Eggs	0.63	5.16	92.32	Fish Eggs	0.87	9.79	80.25
				Ostrocoda	0.48	3.89	84.15
				<i>Idotea baltica</i>	0.45	3.44	87.59
				Mellitidae	0.49	3.26	90.85
Harvey Cedars							
Calanoida	2.01	26.70	26.70	Caridea	1.24	31.53	31.53
Brachyura	1.79	21.45	48.15	Brachyura	1.03	20.85	52.38
Caridea	1.31	20.22	68.37	Calanoida	1.19	15.10	67.48
Fish Eggs	0.93	10.67	79.04	Fish Eggs	0.72	14.55	82.03
<i>M. leidyi</i>	0.78	7.81	86.85	<i>M. leidyi</i>	0.70	10.15	92.18
Fish Larvae	0.46	3.70	90.55				
Westecunk Creek							
Brachyura	3.65	25.83	25.83	Brachyura	1.61	25.98	25.98
Calanoida	1.97	24.65	50.48	Caridea	1.39	25.08	51.06
<i>M. leidyi</i>	0.74	16.90	67.37	<i>M. leidyi</i>	0.77	12.38	63.44
Caridea	1.02	15.42	82.79	Calanoida	1.14	11.42	74.86
Fish Eggs	0.84	7.20	89.99	<i>Idotea baltica</i>	0.50	7.63	82.49
Fish Larvae	0.37	3.12	93.11	Fish Eggs	0.54	4.91	87.41
				Polychaeta larvae	0.33	2.73	90.14
Tuckerton Creek							
<i>M. leidyi</i>	1.33	32.25	32.25	Calanoida	1.90	24.76	24.76
Caridea	1.26	20.42	52.67	Caridea	1.23	18.90	43.66
Brachyura	1.82	18.12	70.79	Brachyura	1.22	16.10	59.76
Calanoida	1.78	16.09	86.88	<i>M. leidyi</i>	0.99	14.53	74.29
Fish Egg	1.03	5.94	92.82	Fish Egg	0.82	8.13	82.43
				Fish Larvae	0.44	4.12	86.55
				Mellitidae	0.43	4.05	90.60

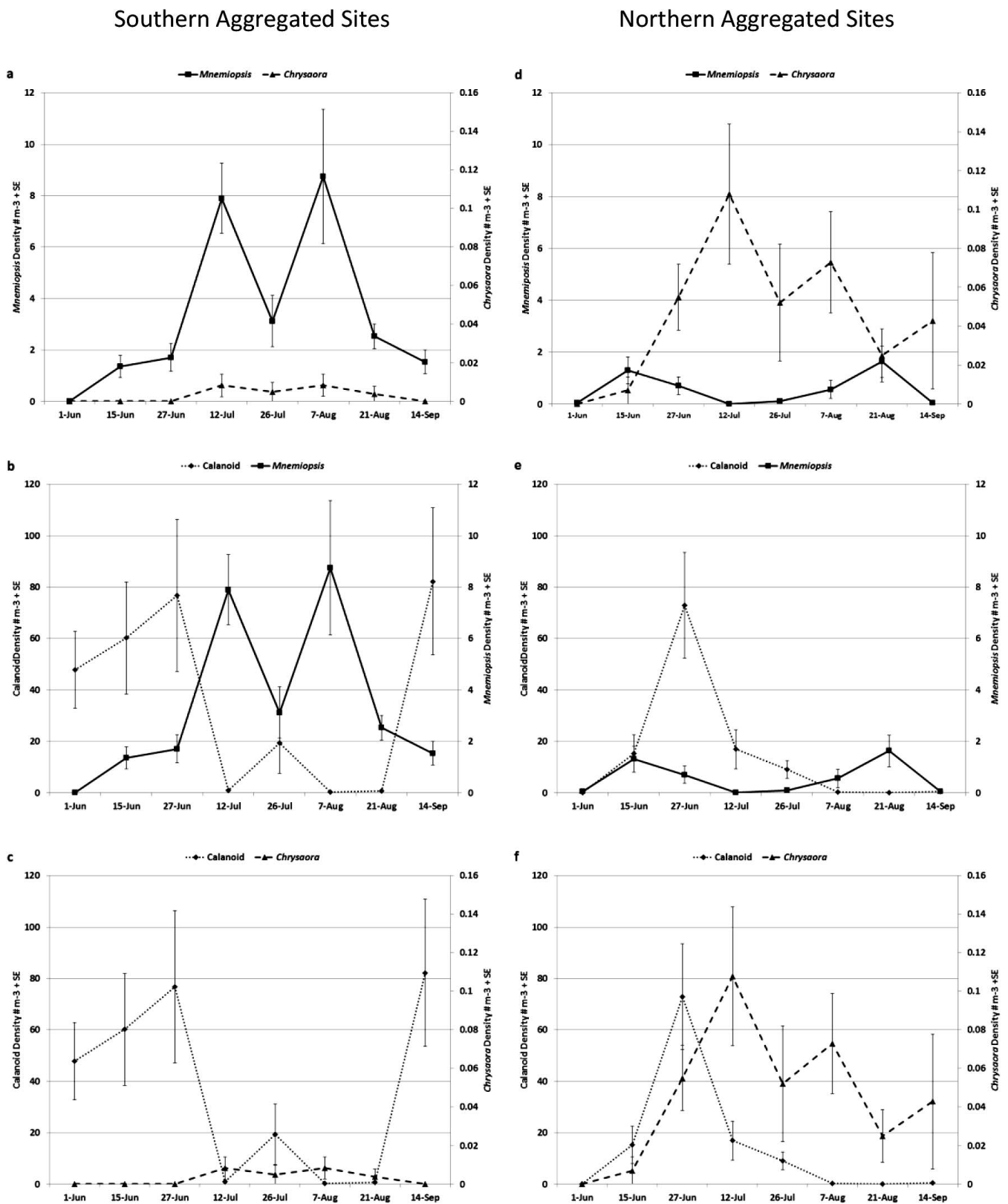


Figure 6. Seasonal distribution of *Mnemiopsis leidyi*, *Chrysaora quinquecirrha*, and calanoid copepods highlighting top-down interactions. Pattern distributions are designated from high salinity in the southern sites (a-c) and lower salinity in the northern regions (d-f). Results are presented as date average density \pm SE.

cant negative correlations with calanoid copepods, fish eggs, fish larvae, and cladocerans, and substantial copepod cropping in the southern part of the bay (Figure 6b). These findings concur with a nutrient–phytoplankton–zooplankton modeling of community dynamics that showed important structuring impacts of *M. leidyi* in Barnegat Bay (Crum *et al.*, 2014). Additionally, the disjunct distribution observed in our results indicates that *C. quinquecirrha* is having a significant top-down impact on *M. leidyi* (Figures 3, 5), but its restrictive distribution within the bay means that its impact is localized at this time (Table 3). Regardless, we have demonstrated the top-down control of *M. leidyi* by *C. quinquecirrha* and reject the null hypothesis of no effect.

Although *M. leidyi* distribution has expanded globally through accidental introduction, *C. quinquecirrha* global distribution has remained relatively stable (Morandini and Marques, 2010), potentially because of its habitat preference of lower-salinity estuarine systems (Decker *et al.*, 2007). However, the significant increases in the Gulf of Mexico (Graham, 2001), persistent populations in the Chesapeake Bay (Decker *et al.*, 2007), and establishment in New Jersey (Bologna, 2011) indicate that these populations can and do have substantial food-web structuring capacities as top predators. Graham (2001) suggests that the increases in offshore populations, coupled with the summertime hypoxia in the Gulf of Mexico, could lead to substantial changes in pelagic systems. Both Breitberg and Burrell (2014) and Purcell (1992) indicated that *C. quinquecirrha* is an important predator in the Chesapeake Bay system, feeding heavily upon copepods, ctenophores, fish larvae, and fish eggs, and our results from Barnegat Bay agree.

As an emerging top predator in this system, the long-term impacts on community structure are difficult to predict. However, the significant top-down pressure exerted on *M. leidyi* did not result in a trophic cascade as expected (Figure 6e). Rather, the generalized control of numerous zooplankton, and specifically copepods, by *C. quinquecirrha* demonstrated a broad predatory influence in structuring the overall temporal planktonic community. As a result, within Barnegat Bay the individual and combined impacts of gelatinous zooplankton structure the temporal and spatial patterns of the pelagic community. If *C. quinquecirrha* continues to expand, it will likely exert significant top-down control, but may merely act as a replacement apex predator for *M. leidyi*.

CONCLUSION

Purcell, Uye, and Lo (2007) and Richardson *et al.* (2009) review the potential changes we may face in altered community structure dominated or restructured through gelatinous zooplankton increases. Although it is no easy task to predict the future structure of our oceans, human activities clearly set the stage for substantial shifts of communities on the planet (Hughes *et al.*, 2013). Increased coastal development has eliminated natural shorelines and replaced them with hardened structures such as houses, bulkheads, docks, and piers; whereas offshore energy production and waste disposal have increased hard substrates necessary for larval settlement and polyp production in many jellyfish (Duarte *et al.*, 2012). Loss of coastal wetlands has also limited their ability to sequester carbon and denitrify excess nutrients in

the system. Consequently, eutrophication has led to excessive primary production, which often results in hypoxic water masses and fuels alternate food webs on the basis of tolerance of environmental conditions (*e.g.*, dissolved oxygen) or survival under toxic blooms of noxious organisms. Last, overharvesting has had devastating impacts on exploited species and food webs. Therefore, the cumulative global human footprint is ever increasing and ocean change is inevitable. Although it is unknown whether corrective actions or better management will lead to stabilization, it is probable that eutrophied systems may become dominated by gelatinous zooplankton.

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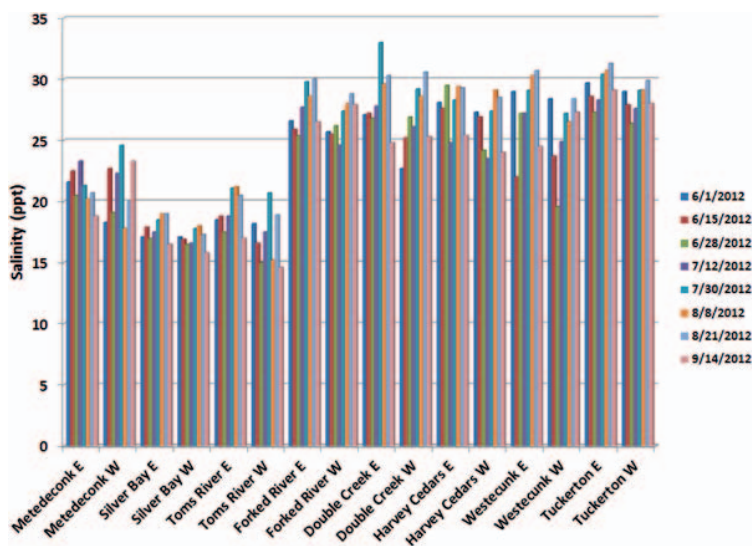


Figure A1. Salinity values for sampling sites during 2012 arranged north to south.