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Potential Abatement of Bay Nettle (Chrysaora chesapeakei) Blooms Through Polyp Removal Within Lagoon Communities in Barnegat Bay, NJ

Anthony Luca Tamberelli

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Potential Abatement of Bay Nettle (*Chrysaora chesapeakei***) Blooms through Polyp Removal within Lagoon Communities in Barnegat Bay, NJ**

Abstract

Jellyfish blooms have gained increased attention in recent decades due to their negative impacts on ecosystems and human activities. Urban development, pollution, and overfishing are some of many possible impacts that can bolster the frequency, duration, and intensity of jellyfish blooms. In Barnegat Bay, NJ, USA, the invasive bay nettle *Chrysaora chesapeakei* exerts topdown predation pressure on zooplankton, including ctenophores, hydrozoans, crustaceans, and ichthyoplankton. Bay nettle populations rely on hard substrates for larval settlement and polyp clonal growth. To determine whether abatement efforts targeted at bay nettle polyps can disrupt the life cycle and limit medusae populations, a three-year sampling project was conducted between June 2021 and August 2023. Scrubbing efforts to remove bay nettle polyps were conducted at two sites, while a third site was used as a control without scrubbing. One year after polyp removal efforts began, there were significantly fewer ephyrae present in the scrubbed lagoons when compared to the control, as well as a significant reduction in ephyrae density from pre-scrubbing to post-scrubbing. No significant decreases of adult medusae were observed at any site, likely due to the mobility of medusae generated from polyps located throughout these interconnected lagoon communities, despite the local reductions in ephyrae. As such, to fully mitigate medusae blooms of *C. chesapeakei* in lagoon developments, a community effort is needed to disrupt the polyp life-history stage and achieve mitigative goals. Nonetheless, the significant decreases observed in ephyrae densities demonstrate the efficacy of dock and bulkhead scrubbing in reducing *C. chesapeakei* populations.

MONTCLAIR STATE UNIVERSITY

Potential Abatement of Bay Nettle (Chrysaora chesapeakei) Blooms through Polyp Removal

within Lagoon Communities in Barnegat Bay, NJ

By

Anthony Luca Tamberelli

A Master's Thesis Submitted to the Faculty of

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College: College of Science and Mathematics Department: Biology

Thesis Committee:

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POTENTIAL ABATEMENT OF BAY NETTLE (*CHRYSAORA CHESAPEAKEI***) BLOOMS THROUGH POLYP REMOVAL WITHIN LAGOON COMMUNITIES IN BARNEGAT BAY, NJ**

A THESIS

Submitted in partial fulfillment of requirements For the degree of Master of Science, Biology

By

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Introduction

 Gelatinous zooplankton are recognized as common and abundant marine organisms with global distributions (Condon et al., 2012; Duarte et al., 2013). The ecology of these organisms can place them at different trophic levels, whether it be apex predators or mesopredators that have some degree of control over lower trophic levels, including other gelatinous zooplankton (Nagata et al., 2015). Since "gelatinous zooplankton" include scyphozoan and hydrozoan cnidarians, ctenophores, siphonophores, and other gelatinous taxa, the role individual species play varies widely among systems.

In recent years, gelatinous zooplankton populations have been observed to generate extensive blooms at both local and global scales. For example, certain regions such as Japan and Korea have suffered intense blooms of the moon jelly *Aurelia aurita* and *A. coerulea*, respectively (Purcell et al., 2007; Yoon et al., 2018), while global observations of jelly populations suggest overall density increases for various species (Condon et al., 2012). There is speculation on whether blooms are on the rise globally due to a paucity of definitive evidence (see Condon et al., 2012), yet an increasing frequency of local blooms for some species is welldocumented (Yoon et al., 2018).

The recurrent jellyfish blooms have led to more scientific investigation, for example with Lynam *et al.* (2006) and Duarte *et al.* (2013), because of their potential consequences on affected ecosystems and food webs, fisheries, recreational activities, and public health. A great deal of motivation towards studying recent blooms of gelatinous zooplankton stems from human interaction with impacted systems. This not only includes considerations for how jelly blooms can influence anthropogenic activities, but also how humans have influenced and possibly catalyzed these blooms.

Over the past two centuries, coastal development has increased in estuarine environments, largely due to a rise in human population. Increasing populations in coastal areas has led to degradation of salt marshes and wetlands, increased urbanization and industrialization, and increased prevalence of artificial structures such as bulkheads, docks, and seawalls (Purcell et al., 2007). Overfishing may also result from growing human populations in developed coastal

areas, thereby impacting local ecosystems with reduced crustacean and fish populations (Purcell et al., 2007; Nagata et al., 2015). Increased construction activity near coastal areas facilitates nutrient loading from soil erosion, which reduces water quality (Paul & Meyer, 2001). Eutrophication from runoff can also worsen water quality as algal blooms generate large quantities of algal cells, forming a layer on the water surface and removing oxygen from the water during decomposition (Howarth et al., 2000). Greater sewage inputs will further sully waters with increased pathogen densities (Paul & Meyer, 2001) and require additional oxygen for decomposition, potentially leading to hypoxia (Mihelcic $& Zimmerman, 2014$).

Eutrophication and coastal development also negatively impact vascular plant communities (e.g., salt marshes, seagrass beds, etc.), resulting in reduced primary production and physical habitat for organisms. These natural habitats are usually replaced by artificial structures such as docks, waterside properties, and lagoon channels, requiring that marsh or wetland halophytes are removed and sediments are excavated (Pang et al., 2017; Bologna et al., 2018). Stressors from coastal development can impact trophic interactions within food webs, yet certain taxa may be differentially affected depending on conditions (Bilkovic & Roggero, 2008; Karpowicz et al., 2020). For instance, prey items may be weakened by stressors and become more vulnerable to predation or predators instead may be too hindered to effectively catch prey (Breitburg et al., 1997). Moreover, trophic cascades can occur if enough stress is applied to food webs, whether it be from pollution or invasive species (Purcell et al., 2007). Despite worsening conditions, certain taxa are able to tolerate degraded conditions. Gelatinous zooplankton, including scyphozoans, hydrozoans, ctenophores, and related organisms are prominent examples due to the publicized concerns of intensive blooms in select regions around the world (Condon et al., 2012; Yoon et al., 2018), as well as their ability to survive in low-oxygen conditions typical of areas with high coastal development (Breitburg et al., 1997; Bologna et al., 2017).

Cnidarians exhibit both sexual and asexual reproduction through medusa and polyp life stages, respectively (**Figure 1**). Adult medusae produce planula larvae that eventually settle and form benthic polyps, which then clone themselves via several asexual pathways. Some scyphozoans also generate asexual podocysts that remain dormant during harsher conditions in the winter (**Figure 1**; Arai, 2009; Thein et al., 2012). With enough energy, polyps undergo strobilation and generate ephyrae that eventually mature into adult medusae. The polyp life-stage is often recognized as a driver of jellyfish populations due to their high reproductive output

under ideal conditions, as well as their ability to remain dormant outside of growing seasons and resupply their populations with a new generation the following year (Thein et al., 2012; Treible & Condon, 2019). Coastal development further bolsters polyp success with a greater availability of ample recruitment space on artificial structures such as bulkheads and docks (Soranno, 2016). In addition, coastally developed habitats experience worsening water quality, which facilitates predation for gelatinous predators due to weakened fitness in potential prey and competitors (Breitburg et al., 1997). Moreover, rising water temperatures due to climate change may influence the timing and intensity of asexual reproduction in polyps, with some species generating more polyps and ephyrae at earlier times of the year (Treible & Condon, 2019).

Figure 1: Depiction of possible life stages for scyphozoan jellyfish; diagram from Thein, Ikeda, and Uye (2012) for *Aurelia aurita* in Hiroshima Bay, Japan.

Scyphozoans have specifically been of concern because many species can exert top-down predatory pressure on zooplankton communities (Nagata et al., 2015; Bologna et al., 2017) and can even instigate collapses to ecosystems and fisheries (Lynam et al., 2006; Yoon et al., 2018). While numerous species of scyphozoans are recognized as native to New Jersey, USA, the establishment of the bay nettle *Chrysaora chesapeakei* to New Jersey is a relatively recent introduction. It is unknown when bay nettles were introduced into the back-bay regions of New Jersey, but they are now well-established as an apex generalist predator (Meredith et al., 2016; Bologna et al., 2017). The ctenophore *Mnemiopsis leidyi* also resides as an apex zooplankton

predator in the system, but they, too, are prey for the invasive *C. chesapeakei*, resulting in their seasonal top-down control by bay nettles (Bologna et al., 2017, 2018).

Similar to other cnidarians in systems experiencing coastal development (e.g., Yoon et al., 2018), bay nettles experience greater fitness in Barnegat Bay's residential lagoon habitats, as hypoxic conditions facilitate prey capture and artificial structures provide additional surface area for polyp recruitment (Soranno, 2016). In turn, bay nettles have proliferated and expanded to multiple areas within Barnegat Bay, especially in the more-developed, lower-salinity northern portions of the bay (Bologna et al., 2017).

 Despite their dominance in the system, bay nettle populations declined following the intense weather event of Hurricane Sandy in late 2012 (Bologna et al., 2018). Both natural and anthropogenic environments suffered extensive damage across New England, including Barnegat Bay, NJ, which experienced an island breach that flooded coastal residential areas and destroyed structures such as bulkheads and docks. Comparing data from before and after the hurricane, Bologna *et al.* (2018) demonstrated a significant decline in bay nettles, likely due to the loss of viable polyp habitat (i.e., bulkheads, docks). With the reduction in bay nettles, a stochastic ecological succession occurred with many previously suppressed hydrozoan populations increasing to noticeable densities (Bologna et al., 2018).

Recognizing the potential to decrease bay nettle populations, research efforts have focused on combating the issues related to their invasion by devising strategies to reduce reproductive output of these gelatinous organisms. Local efforts in Barnegat Bay echo those around the world, such as those in Korea to mitigate extensive *Aurelia coerulea* populations (Yoon et al., 2018). By employing strategies to disrupt the asexual polyp stages of scyphozoans, future adult medusae generations will be reduced. This project aims to test the efficacy of polyp removal and life history disruption through physical removal via dock scrubbing and power washing in lagoon developments. We hypothesize that disrupting the life cycle of *Chrysaora chesapeakei* at the polyp stage will cause future reductions in ephyrae, and thus reduce adult medusae in successive years following abatement efforts. In response, prey taxa in the system such as crustaceans, fish larvae, and other less-dominant gelatinous species may be expected to potentially recover; or, alternatively, other predatory jellies such as *M. leidyi* may experience blooms as they are relieved from bay nettle predation or competition (Purcell & Decker, 2005), thereby yielding no possible recovery in prey taxa.

Materials and Methods

Site Descriptions

 Three sites within developed lagoon communities in Barnegat Bay, NJ, USA were selected to evaluate the efficacy of polyp removal on subsequent jellyfish and zooplankton communities (**Figure 2**). Within the Berkeley Shores housing development, two sites were chosen to evaluate the impact of polyp removal on zooplankton: Berkeley Shores Lagoon (hereafter referred to as "Berkeley Shores") (39.91174°N, 74.13239°W) and BK Lagoon (39.91508°N, 74.12551°W). Forked River Lagoon (39.82310°N, 74.17621°W) was chosen as an external control site where polyp removal did not occur for comparative evaluation of the efficacy of polyp removal. These sites were chosen because the partner organizations Save Barnegat Bay and Berkeley Township Underwater Search and Rescue (BTUSAR) were involved in dock scrubbing at select sites with hopes to mitigate bay nettle production. BTUSAR scrubbed 69 properties at Berkeley Shores between March and June 2022; and 34 properties at BK Lagoon in November 2021, March 2022, and May 2022. In total, approximately 6.072 m^2 of surface area was scrubbed.

Figure 2: Top: Satellite image of the three visited sites, each labeled and depicted with a yellow marker. Bottom: Scrubbed properties in BK Lagoon (Section 1) and Berkeley Shores (Sections $2 - 6$).

Field Sampling

Sampling was conducted during summer months (June, July, and August) of 2021, 2022, and 2023 to capture the peak progression of C. chesapeakei populations from strobilation to adulthood. Sites were assessed for water quality, including temperature (°C), salinity (ppt), and oxygen saturation (mg/L) using a multi-parameter probe (Professional Plus Series YSI®; Ohio, USA). Two sets of biological sampling occurred: (i) using 363-µm plankton nets (30 cm diameter, 0.0707 m² section area), and (ii) 3.2-mm mesh lift nets (0.84 x 0.84 m). Plankton net sampling was conducted off the stern of a 24' Carolina skiff operating at minimally engaged engine speed for one minute. During plankton tows, a General Oceanics, Inc. mechanical rotor flow meter was also deployed to calculate distance traveled; this measurement was coupled with

the cross-sectional area of the plankton tow net to standardize all sample volumes to m^3 . During 2021, triplicate plankton tow samples were collected at Berkeley Shores and Forked River Lagoon during each month ($N = 18$). In the subsequent years of 2022 and 2023, replication increased to four plankton tow samples per site visit, and the BK Lagoon site was added for sampling ($N = 72$; $N_{total} = 90$). Samples were brought on-board and processed in the field by identifying and counting all *M. leidyi* prior to preservation in 95% ethanol solution, as these organisms deteriorate rapidly when in preservatives. Samples were then transported to Montclair State University where they were stained with Rose Bengal, prior to laboratory identification and enumeration of individuals.

For lift nets, 10 samples were taken by dropping nets into the water, allowing them to sink to the benthos, and waiting 30 seconds after reaching the bottom before drawing them back up to the surface. Water depth was measured to the nearest 0.1 m using a weighted reel tape measure, which allowed for the standardization of sample volume in m³. All organisms from individual lift samples were removed from the net, identified, counted, and recorded *in-situ*. Bell diameter was measured for all *C. chesapeakei* collected, while *M. leidyi* were assessed based on a size ranking evaluation and binned into five size classes (0-10mm, 10-30mm, 30-50mm, 50- 70mm, and 70-90mm). *Mnemiopsis leidyi* individuals were sized based on the largest category they fit into. Other non-gelatinous organisms and aquatic plants caught in lift nets were recorded in notes for a given sample.

Laboratory Zooplankton Sample Processing

 Collected plankton tow samples were processed at Montclair State University. Preserved samples were washed across a 355-micron sieve and transferred into petri dishes for inspection under dissecting microscopes, where organisms were identified and enumerated to lowest practical taxonomic level and recorded. Completed samples were transferred to vials containing ethanol for future referencing of collected organisms.

Data Analysis

Completed plankton tow, lift net, and water quality data were compiled into individual files for data entry and standardization of individual samples. Data were entered as raw counts of individuals for both plankton tow and lift net samples. QAQC of sample data was conducted on

raw count data in the file before being standardized to "# individuals m⁻³" based on the volume of water sampled for each sample.

A mixed model 2-way ANCOVA was used to analyze density data with site and year as independent variables in the model and month of collection as the covariate (SAS®). Two sets of analyses were completed to account for differences in the sampling protocol. Specifically, since BK Lagoon was not sampled in 2021 (pre-scrubbing), the first analysis consisted of comparisons between Forked River Lagoon (control) and Berkley Shores (polyp removal) to determine the efficacy of scrubbing activities on planktonic organisms from 2021 (pre-scrubbing) through 2023 (post-scrubbing). This analysis is based on 65 plankton tow samples and 240 lift net samples across the three-year study period. The second analysis assessed differences in planktonic organisms post-scrubbing from the two sites that were scrubbed by 2022 (Berkeley Shores and BK Lagoon) and the control (Forked River Lagoon). These analyses used only data from 2022 and 2023 (post-scrubbing), as this was the first year BK Lagoon was sampled, resulting in 70 usable plankton tow samples and 180 usable lift net samples. The second set of analyses specifically looked to determine whether sites that were scrubbed to remove polyps differed from the non-scrubbed control site (Forked River Lagoon). Analyses were conducted on numerically dominant taxonomic groups, including *C. chesapeakei*, *M. leidyi*, *Turritopsis dohrnii*, calanoid copepods, fish eggs, *Menidia menidia* larvae, shrimp larvae, and crab larvae.

Additionally, a correlation analysis was conducted on the samples to ascertain whether any taxa demonstrated similarities in their relative abundance, as well as to test the hypothesis of top-down impacts by the two top predators in the system (*C. chesapeakei* and *M. leidyi*). Relationships between taxa were assessed directly, but top-down impacts were also evaluated using a sign-test of correlation coefficients (positive vs. negative) with potential prey to determine predator impacts on the community, as described in Bologna *et al.* (2017). Observed values were then tested against the null hypothesis distribution probability of 0.5 positive:0.5 negative, which follows a chi-squared distribution in sign test analyses.

Results

Water Quality

Salinity ranges often experienced slight mid-season declines in July, followed by a slight increase by August; however, in 2023, salinities were initially low before gradually increasing

throughout the summer (**Table 1**). On average, Forked River Lagoon had consistently higher salinities among sites, while Berkeley Shores had the lowest relative salinities. Regardless, all sites' salinities fluctuated synchronously with each other. Average salinities in 2021 were lowest on average across all sites, before salinities in 2022 increased by at least 2.5 ppt from the previous year. Salinities declined by 2023, yet were not as low as those seen in 2021.

Temperatures also demonstrated mid-season fluctuations at all sites in each sampling year, with temperatures spiking to some degree in July before dropping in August (**Table 1**). In 2022, however, all sites experienced considerably less variation in seasonal temperature relative to 2021 or 2023. Moreover, monthly temperatures were fairly synonymous across sites, especially in 2023. The only noticeable outliers to this observation were Forked River Lagoon in July 2021, which had a higher temperature spike than Berkeley Shores, and Berkeley Shores in 2022, which consistently yielded temperatures between 25° C and 26° C.

 Dissolved oxygen concentrations varied considerably by year, yet some sites either approached or crossed the 3.0 mg/L hypoxia threshold (as determined by Purcell et al., 2007) at least once during the sampling period (**Table 1**). Initially in 2021, sites experienced mid-season increases in DO concentrations to varying degrees. In fact, Forked River Lagoon's DO concentrations increased almost twofold by July before declining in August to near-hypoxic levels. DO concentrations increased on average by 2022, especially at Forked River Lagoon in August. However, sites instead experienced a decline by July before increasing into August, except for BK Lagoon which experienced the mid-season increase previously seen in 2021. By 2023, all sites experienced a drop in overall DO concentrations. Berkeley Shores approached the hypoxia threshold in June, Forked River Lagoon declined below the threshold in June, and BK Lagoon oscillated around the threshold in June and July before declining below it in August.

Salinity 2023

Plankton Tows

 44 taxa were identified from 88 plankton tow samples (**Appendix A**), since two samples were unusable, but only nine taxa were prioritized for analyses due to (i) the primary objective of the experiment, including *Chrysaora chesapeakei* medusae and ephyrae, or (ii) being numerically dominant in samples, including *M. leidyi*, *Turritopsis dohrnii*, calanoid copepods, fish eggs, *Menidia menidia* fish larvae, shrimp larvae, and crab larvae. Since two sets of analyses were conducted with regards to the sampling protocol (i.e., BK Lagoon was not sampled in

2021), individual taxa were evaluated with regards to differences among sites, years, and months through these analyses.

Across all three years, *C. chesapeakei* medusae densities were never greater than 0.80 individuals m⁻³. In 2021, medusae were only found in July, with greater densities at Berkeley Shores than Forked River Lagoon (**Figure 3A**). Sampling in 2022 yielded medusae at Forked River Lagoon and BK Lagoon, but none at Berkeley Shores (**Figure 3B**). Forked River initially harbored small populations in June, which increased fourfold by July, but none were collected in August. BK Lagoon's medusae densities were lower in comparison, but individuals were also only observed in July. By 2023, medusae densities reappeared at Berkeley Shores in all three months, gradually increasing as the summer progressed (**Figure 3C**), while BK Lagoon populations were only present in August. Forked River Lagoon yielded fewer overall medusae than seen in previous years and once again harbored individuals in July only. Regardless, *C. chesapeakei* medusae did not show statistically-significant differences among sites, years, or months for either analyses (3-year: $F_{6,58} = 0.85$, $P > 0.54$; 2-year: $F_{6,63} = 1.43$, $P > 0.2$). Furthermore, the sign-test of correlation for the three-year, two-site scenario demonstrated 25 of 33 negative correlations between *C. chesapeakei* and potential prey taxa, demonstrating a significant impact on prey taxa $(X^2 (N = 33) = 8.76, P < 0.003)$. A similar significant top-down pressure on prey was observed for the two-year, three-site post-scrubbing analysis $(X^2 (N = 36) =$ 9.00, $P < 0.001$).

Figure 3A-C. Monthly plankton tow densities for *Chrysaora chesapeakei* medusae between 2021 and 2023. Sites arranged left to right in south to north order. "N/A" signifies that BK Lagoon was not sampled in 2021.

 Bay nettle ephyrae were present at both Berkeley Shores and Forked River Lagoon in June of 2021, but declined as the summer progressed (**Figure 4A**). In 2022, post-scrubbing of Berkley Shores and BK Lagoon, ephyrae were only recorded at Forked River Lagoon, demonstrating the efficacy of scrubbing activities in reducing ephyrae (**Figure 4B**; 3-year: $F_{1,58}$ = 7.34, P < 0.009; 2-year: $F_{2,63} = 15.9$, P < 0.0001). In 2023, while a few ephyrae were observed in Berkeley Shores and BK Lagoon sites, significantly greater densities were seen at the nonscrubbed Forked River Lagoon site (**Figure 4C**; 3-year: $F_{1,58} = 7.34$, $P < 0.009$; 2-year: $F_{2,63} =$ 15.93, $P < 0.0001$).

Figure 4A-C. Monthly plankton tow densities for *Chrysaora chesapeakei* ephyrae between 2021 and 2023.

Mnemiopsis leidyi densities fluctuated among sites, months, and years. In 2021, all sites showed peak densities in June before declining throughout the summer, with Berkeley Shores having the highest densities (**Figure 5A**). For subsequent years, *M. leidyi* densities declined significantly among all sites evaluated (3-year: $F_{2,58} = 5.46$, $P < 0.007$; 2-year: $F_{1,63} = 7.29$, $P <$ 0.009), but were generally higher at both Berkley Shores and BK Lagoon in comparison to Forked River Lagoon (**Figure 5B-C**), with significantly greater densities at these sites in 2022 compared to 2023 (2-year: $F_{2,63} = 3.80$, P < 0.03). For the three-year, two-site analysis, 24 negative correlations were found between *M. leidyi* and other taxa (chi-squared: X^2 ($N = 32$) = 8.00, $P < 0.005$), and for the two-year, three-site post-scrubbing analysis, 27 negative correlations were found (chi-squared: X^2 ($N = 35$) = 10.31, P < 0.001); indicating *M. leidyi* is exerting top-down pressure on the zooplankton community as well.

Figure 5A-C. Monthly plankton tow densities for *Mnemiopsis leidyi* between 2021 and 2023.

Berkeley Shor June July August **BK Lagoon**

 2.0 0.0

Forked River Lagoon

 For the lesser non-target species which were abundant in plankton tows, calanoid copepods varied among sites and years. In 2021, copepods showed inverse density patterns between Berkeley Shores and Forked River Lagoon (**Figure 6**). Copepods in 2022 experienced significantly greater densities at Berkeley Shores than the other two sites (3-year: $F_{1,58} = 7.52$, P < 0.009 ; 2-year: F_{2,63} = 5.58, P < 0.006), while Forked River Lagoon densities were observably lower than the previous year. In 2023, copepod densities declined overall in comparison to the previous year (2-year: $F_{1,63} = 4.78$, $P < 0.033$), yet densities were observed to increase at BK Lagoon by August.

Figure 6. Yearly plankton tow densities for calanoid copepods between 2021 and 2023.

 Shrimp larvae densities demonstrated annual differences only (**Figure 7**), as 2023 contrasted significantly with pre-scrubbing $(3$ -year: $F_{2,58} = 3.96$, $P < 0.025$) and post-scrubbing conditions (2-year: $F_{1,63} = 4.63$, $P < 0.036$). Despite some overlap in timing for peak densities (e.g., Berkeley Shores and Forked River Lagoon yielding peaks in July 2022), no significant differences were found across sites, even when compared with post-scrubbing (3-year: $F_{6,58}$ = 1.54, P > 0.18; 2-year: $F_{6,63} = 1.85$, P > 0.10). No significant seasonal fluctuations were determined, although densities were not equal across months.

Figure 7. Yearly plankton tow densities for shrimp larvae between 2021 and 2023.

 Density extremes were prominent for crab larvae, which experienced booms throughout the summer post-scrubbing (**Figure 8**; 2-year: $F_{1,63} = 24.03$, $P \le 0.0001$). Density differences were also determined between pre-scrubbing and post-scrubbing years (3-year: $F_{2,58} = 8.61$, P < 0.001), as well as across sites in both analyses (3-year: $F_{1,58} = 13.85$, P < 0.001; 2-year: $F_{2,63} =$ 8.47, P < 0.001), as peak densities were seen particularly at Berkeley Shores in June 2022 and BK Lagoon in June 2023. However, significant confounding from site–year interactions was possible, regardless of the analysis used (3-year: $F_{2,58} = 9.47$, $P < 0.0005$; 2-year: $F_{2,63} = 10.40$, P < 0.0005).

Figure 8. Yearly plankton tow densities for crab larvae between 2021 and 2023.

Turritopsis dohrnii densities showed seasonal differences across months in both analyses (3-year: $F_{1,58} = 7.07$, $P < 0.011$; 2-year: $F_{1,63} = 8.52$, $P < 0.005$). Peak densities were seen at Forked River Lagoon in 2022 and 2023, but this density difference among sites was only seen in the three-year, two-site analysis ($F_{1,58} = 5.10$, $P < 0.03$), as no differences were determined in the post-scrubbing analysis ($F_{2,63}$ = 2.93, P > 0.06).

 Fish eggs did not demonstrated significant differences among sites, years, or months. This observation was made from both the three-year, two site analysis ($F_{6,58} = 1.32$, $P > 0.26$) and the two-year, three-site post-scrubbing analysis ($F_{6,63} = 0.48$, $P > 0.82$). Meanwhile, fish larvae for *Menidia menidia* showed monthly variation regardless of the analysis used (3-year: $F_{1,58} = 7.03$, $P < 0.011$; 2-year: $F_{1,63} = 7.57$, $P < 0.01$). Annual differences across all three years were not significant $(F_{2,58} = 3.01, P < 0.06)$, as well as for the two-year, three-site post-scrubbing analysis ($F_{1,63} = 3.37$, $P > 0.07$).

Lift Nets

 Two gelatinous zooplankton species were prevalent in lift net samples: *C. chesapeakei* and *M. leidyi*. Regarding *C. chesapeakei*, the highest densities occurred in 2021, with relatively fewer individuals collected in the following years for all sites (**Figure 9A-C**; 3-year: $F_{2, 173}$ = 12.58, P < 0.0001). Additionally, peak abundances varied among sites, with Forked River Lagoon showing the highest densities in June, while the other sites showed higher densities later into the summer. However, no significant differences were seen across sites when comparing all three years ($F_{1,173} = 0.04$, $P > 0.85$), even though differences were determined from the two-year, three site post-scrubbing analysis ($F_{2,173} = 7.68$, $P < 0.001$) with significantly fewer individuals collected from the unscrubbed site Forked River Lagoon (**Figure 9B-C**). Furthermore, seasonal differences were only deemed significant in the post-scrubbing analysis (3-year: $F_{1,173} = 0.44$, P > 0.50 ; 2-year: $F_{1,173} = 24.15$, $P < 0.0001$).

Figure 9A-C. Averaged *Chrysaora chesapeakei* medusa densities sampled from lift nets between 2021 and 2023.

Mnemiopsis leidyi densities were also highest in 2021, as peak densities were observed at Berkeley Shores in June, but significantly fewer individuals were collected in samples in proceeding years (**Figure 10A-C**; 3 -year: $F_{2,173} = 11.34$, $P < 0.0001$). Seasonality was deemed plausible by the three-year, two-site analysis ($F_{1,173} = 3.72$, $P > 0.055$), but not from the twoyear, three-site analysis ($F_{1,173} = 0.93$, $P > 0.33$). Post-scrubbing conditions also demonstrated differences in densities between 2022 and 2023 ($F_{1,173} = 20.26$, $P < 0.0001$), as well as differences across sites during this time $(F_{2,173} = 7.81, P \le 0.001)$; however, site–year interactions had possibly confounded these results $(F_{2,173} = 3.07, P \le 0.05)$.

Figure 10A-C. Averaged *Mnemiopsis leidyi* densities sampled from lift nets between 2021 and 2023.

Discussion

 After reviewing the three years of sampling data, scrubbing efforts at Berkeley Shores and BK Lagoon were successful for the abatement of *C. chesapeakei* ephyrae when compared to the non-scrubbed control site Forked River Lagoon (**Figure 4**). No ephyrae were collected in 2022 from the scrubbed sites and significantly fewer were collected in 2023 compared to the control. These results demonstrate polyp removal had an immediate effect in reducing ephyrae after one year of scrubbing and significant reductions continued to be observed two years after

scrubbing compared to the non-scrubbed control site. While these results showed the potential effectiveness of localized dock and bulkhead scrubbing, no significant differences in *C. chesapeakei* medusae densities were seen among sites or years for plankton tow samples (**Figure 3**). However, significantly more medusae were collected in lift net samples from the scrubbed sites compared to the control site (**Figure 9**). In fact, no medusae were collected from lift nets at Forked River Lagoon in 2022 and 2023, but they were present in plankton tows. Additionally, 2023 plankton tow medusae densities were higher at scrubbed sites than at Forked River Lagoon, albeit non-significant, potentially due to substantially higher densities of *C. chesapeakei* in the northern regions of Barnegat Bay (Bologna et al., 2017). This unexpected pattern may also reflect the mobility of adult medusae, which would suggest their ability to move within sites and between neighboring lagoon communities. Such dispersal may be instigated by depleted food sources in these lagoons compared to the open water regions of Barnegat Bay (Bologna et al., 2015), causing emigration of medusae to areas of higher prey abundance. Additionally, while these two regions were scrubbed to remove polyps, the larger lagoon system was not scrubbed. Consequently, these sites likely have established polyp populations in nearby unscrubbed lagoons that would supply medusae through dispersal. Artificial structures such as bulkheads, piers, and floating docks are observed at all sites and contribute to existing polyp populations and active settlement sites for planula larvae (Holst & Jarms, 2007; Duarte et al., 2013). Thus, increased support for bay nettle polyps would expectedly be found in these anthropogenic habitats which yield higher output of ephyrae. However, scrubbing activities significantly reduced ephyrae densities (**Figure 4**), thereby providing a practical tool for minimization of *C. chesapeakei* populations and bloom potential.

 While variation in bay nettle populations were impacted by scrubbing efforts, densities of the comb jelly *M. leidyi* showed significant declines in 2023 compared to the prior two years (**Figure 5 & 10**). It is possible that top-down impacts of bay nettles on *M. leidyi* were occurring, as there were negative, but non-significant, correlations between their densities for plankton tows. Bologna *et al.* (2017) demonstrated significant top-down pressure of *C. chesapeakei* on *M. leidyi* in the system, so the significant reduction seen in 2023 may be related to the increased abundance of *C. chesapeakei* observed in the wider Barnegat Bay system in 2023 (pers. obs.).

Prey items such as copepods, shrimp larvae, and crab larvae were seen to respond to changes in these predator populations, as well. For example, shrimp larvae and crab larvae

displayed differences between sampling years, with declines correlated with increasing comb jelly populations, albeit not significant. Such observations relate to *M. leidyi*'s efficient predatory abilities on zooplanktonic taxa including crustaceans, fish, and bivalves (Purcell et al., 2001). The top-down analysis showed a significant negative relationship between *M. leidyi* and other prey taxa in the plankton tows, especially in the absence of apex predators such as *C. chesapeakei*, which can regulate other gelatinous predators (Purcell et al., 2001; Breitburg & Fulford, 2006; Bologna et al. 2017, 2018). Copepod densities showed some degree of increase alongside comb jelly increases and bay nettle declines following scrubbing (**Figure 6**). Copepods may be favored prey items of bay nettles (Bologna et al., 2017); however, other literature suggests that the generalist diet of *C. chesapeakei* would target a wide variety of other taxa (e.g., fish, crustaceans, bivalves, other gelatinous species) without preference (Nagata et al., 2015; Meredith et al., 2016). Thus, the increase in copepods could partially be due to relieved predation pressures from bay nettles. Other minor taxa such as *Menidia menidia* and *T. dohrnii* did not reveal significant density differences among years in tandem with predator density fluctuations. *Menidia menidia* showed no major differences across sites as well, implying density changes were simply due to ontogeny (i.e., maturation out of larval stage between months). Meanwhile, *T. dohrnii* densities showed significant differences between sites in the three-year, two-site analysis, yet not in the two-year, three-site post-scrubbing analysis. *Turritopsis dohrnii* were observed to be highest at Forked River Lagoon, where they may be able to compete with bay nettle ephyrae for prey due to greater morphological development (P. A. X. Bologna, pers. comm.). The presence of ephyrae at this site also possibly reduced the development of comb jellies, inhibiting these populations from competing with *T. dohrnii*.

Regardless, trophic interactions between comb jellies and prey taxa in the absence of bay nettles demonstrated how predation from *M. leidyi* may be more intense than that from *C. chesapeakei* depending on the circumstances. Despite their own taxa-wide predation pressures, gelatinous predators such as *C. chesapeakei* could potentially regulate the predatory impacts from *M. leidyi* (Purcell et al., 2001; Breitburg & Fulford, 2006). Considering how *M. leidyi* predation can easily intensify under ideal conditions (Purcell et al., 2001), *C. chesapeakei*'s ability to check *M. leidyi* may serve to stabilize the trophic web in a new "alternate state" (Beisner et al., 2003) where intense predation from comb jellies on zooplankton is balanced by predation from bay nettles on comb jellies (Purcell & Decker, 2005). Similar scenarios were

observed between *M. leidyi* and the predatory comb jelly *Beroe ovata* in the Black Sea (Purcell et al., 2001) and between *M. leidyi* and *C. chesapeakei* in the Chesapeake Bay, USA (Purcell & Decker, 2005). In contrast, Bologna *et al.* (2017) did not observe trophic cascades under similar conditions within Barnegat Bay, suggesting the introduction of *C. chesapeakei* as an apex generalist predator (Meredith et al., 2016) broadly influenced all lower trophic levels.

Aside from trophic interactions, water quality was reviewed for potential influences on zooplankton densities. Overall, salinity, temperature, and dissolved oxygen did not vary drastically between sites, as well as between years. Sites demonstrated synchronous changes in temperature during the summer, and salinity showed no extreme changes during the sampling period. Dissolved oxygen did not demonstrate substantial changes, as well, yet concentrations declined in August 2023 across all sites. Lower oxygen concentrations can leave sensitive taxa more vulnerable to predation from unaffected gelatinous predators (Breitburg et al., 1997; Karpowicz et al., 2020). However, even though bay nettle blooms were observed in 2023 (pers. obs.) during periods of lower oxygen, these oxygen declines may not have been intense enough to strongly influence bay nettle populations.

Scrubbing efforts have been used previously in various regions around the world in an attempt to disrupt the development of nuisance jellyfish species. For example, Yoon *et al.* (2018) targeted Asian moon jellies *Aurelia coerulea*, which were generating recurrent blooms in Korea beginning in the 1980s. Coastal development and declining ecosystems bolstered the blooms, resulting in millions of dollars of fishery losses. After studying different abatement strategies, they determined power scrubbing of polyps was effective at hindering development of *A. coerulea* for roughly three years before populations began to recover (Yoon et al., 2018). Results from this research indicate that significant reductions in ephyrae were still observed two years post-scrubbing (**Figure 4**), meaning that this approach to jellyfish management and abatement might be actionable on a larger spatial scale to minimize the bloom potential of *C. chesapeakei*. Yoon *et al.* (2018) argued that scrubbing may be more successful if efforts are conducted over larger areas (e.g., more surface area) and repeated more frequently (e.g., every year). Since abatement efforts in 2021 and 2022 were limited to certain lagoon channels and did not eliminate every possible surface on which polyps could reside, increasing the breadth of scrubbing can remove a greater proportion of polyp populations. Regardless, significantly fewer ephyrae were collected in sampled sites that were scrubbed one and two years later (**Figure 4**). Even if polyps

do not colonize every possible surface, greater scrubbing areas throughout lagoons will ensure greater chances of finding and removing polyp populations. Such improvements may also consider different types of surfaces scrubbed in the future. Bay nettle polyps seem to favor artificial surfaces such as vinyl and polyethylene terephthalate (PET), but will also settle on the underside of surfaces for greater protection from UV light and facilitated strobilation and waste excretion (Holst & Jarms, 2007; Soranno, 2016). Focusing on these particular surfaces may increase the likelihood of successfully finding and removing polyp populations. Furthermore, Yoon *et al*. (2018) also observed relatively short-term recovery of jellyfish populations following scrubbing.

In this project, bay nettle medusae in 2023 were observed at higher abundances than in previous years, accounting for 63.8% of all medusae captured in plankton tows (unpubl. data), despite the absence of ephyrae at post-scrubbing sites (**Figure 4B**). This observation likely relates to ephyrae release from the wider lagoon systems in Barnegat Bay, as well as interannual variation in bloom conditions. Lilley *et al.* (2009) reviewed the distributional characteristics of the scyphozoan *Rhizostoma* spp. in European waters. They found that substantial differences in bloom developments occurred among years and regions, potentially related to climactic events and prey availability. However, they also identified regions where consistent blooms were present and the fact that the location of polyps for many, if not all, of the species within the genus *Rhizostoma* spp. were unknown (Lilley et al., 2009). The identification of primary polyp locations in Barnegat Bay (Soranno, 2016) and the effectiveness of scrubbing activities in reducing ephyrae densities (**Figure 4**) suggests that larger-scale scrubbing efforts in these artificial lagoons could be an effective measure to reduce *C. chesapeakei* populations. However, a potential limiting factor may be the degree of cooperation from homeowners within affected lagoonal communities, as scrubbing can only be conducted on bulkheads within consenting individuals' properties. Thus, a greater number of homeowners who volunteer support for the project will increase percentage of lagoon channels scrubbed.

Regardless of possible improvements, the long-term effects of these abatement efforts can only be predicted from the data generated from this research. Ideally, scrubbing and related intervention strategies should hinder the development and cloning rate of bay nettle polyps, reducing the number of predatory medusae in the system. However, it is unknown how long these reduction effects will last for, and whether other affected taxa will be able to recover

despite the freedom from bay nettle predation. Bologna *et al.* (2018) clearly demonstrated that after Superstorm Sandy hit this region in 2012, there was a significant reduction in *C. chesapeakei* densities potentially related to massive infrastructure destruction of polyp habitat (e.g., floating docks), leading to subsequent increase in the density and species richness of other gelatinous zooplankton. Taken together, measures to interrupt the life history of *C. chesapeakei* by reducing or eliminating polyps will likely result in reductions of medusae and the nuisance issues they present to the public and their impact as apex predators.

Conclusion

 Implications of bay nettle reductions remain unknown, especially with regards to whether comb jellies *M. leidyi* will return as the apex predator and enact top-down predation once they are relieved from bay nettle predation. In Chesapeake Bay where both species are native, lower annual *C. chesapeakei* abundance resulted in increased *M. leidyi* densities with an ensuing trophic cascade (Purcell & Decker, 2005). However, Bologna *et al.* (2017) demonstrated that no trophic cascade was present in Barnegat Bay, where there is no evidence that *C. chesapeakei* is a native species yet exerted substantial top-down pressure on all taxa. It is possible that a suite of gelatinous zooplankton species may emerge as important pelagic predators following reductions in *C. chesapeakei* densities, as was reported by Bologna *et al.* (2018), but none of those species command the predation potential of bay nettles. With these realities in mind, it is imperative to continue both scrubbing to reduce polyp populations and monitoring efforts in Barnegat Bay to document the successful reduction of *C. chesapeakei* populations. These efforts will also help determine the effects of polyp abatement on pelagic community structure and the density of important taxa like copepods, fish larvae, crab larvae, and shrimp larvae, which are critical to recreationally and commercially important fisheries species.

Literature Cited

- Arai, M. N. (2009). The potential importance of podocysts to the formation of scyphozoan blooms: A review. In *Jellyfish Blooms: Causes, Consequences, and Recent Advances: Proceedings of the Second International Jellyfish Blooms Symposium, held at the Gold Coast, Queensland, Australia, 24–27 June, 2007* (pp. 241-246). Netherlands: Springer.
- Beisner, B. E., Haydon, D. T., & Cuddington, K. (2003). Alternative stable states in ecology. *Frontiers in Ecology and the Environment, 1*(7), *376-382*. https://doi.org/10.1890/1540- 9295(2003)001[0376:ASSIE]2.0.CO;2
- Bilkovic, D. M., & Roggero, M. M. (2008). Effects of coastal development on nearshore estuarine nekton communities. *Marine Ecology Progress Series, 358, 27-39*. doi: 10.3354/meps07279
- Breitburg, D. L., Loher, T., Pacey, C. A., & Gerstein, A. (1997). Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web. *Ecological Monographs, 67*(4)*, 489-507*. https://doi.org/10.1890/0012- 9615(1997)067[0489:VEOLDO]2.0.CO;2
- Breitburg, D. L., & Fulford, R. S. (2006). Oyster-sea nettle interdependence and altered control within the Chesapeake Bay ecosystem. *Estuaries and Coasts, 29*(5)*, 776-784*. https://doi.org/10.1007/BF02786528
- Bologna, P., Gaynor, J., & Meredith, R. (2015). Impacts of invasive sea nettles (*Chrysaora quinquecirrha*) and ctenophores on planktonic community structure and bloom prediction of sea nettles using molecular techniques. In *NJDEP Final Project Report* (p. *137*).
- Bologna, P. A. X., Gaynor, J. J., Barry, C. L., & Restaino, D. J. (2017). Top-down impacts of sea nettles (*Chrysaora quinquecirrha*) on pelagic community structure in Barnegat Bay, New Jersey, U.S.A. *Journal of Coastal Research, 78*(10078), *193-204*. https://doi.org/10.2112/SI78-015.1
- Bologna, P., Gaynor, J. J., Meredith, R., Restaino, D., & Barry, C. (2018). Stochastic event alters gelatinous zooplankton community structure: Impacts of Hurricane Sandy in a Mid-Atlantic estuary. *Marine Ecology Progress, 591, 217-227*. doi:10.3354/meps12262
- Condon, R. H., Duarte, C. M., Pitt, K. A., Robinson, K. L., Lucas, C. H., Sutherland, K. R., Mianzan, H. W., Bogeberg, M., Purcell, J. E., Decker, M. B., Uye, S., Madin, L. P., Brodeur, R. D., Haddock, S. H. D., Malej, A., Parry, G. D., Eriksen, E., Quiñones, J.,

Acha, M., Harvey, M., Arthur, J. M., & Graham, W. M. (2012). Recurrent jellyfish blooms are a consequence of global oscillations. *Proceedings of the National Academy of Sciences, 110(3), 1000-1005*. https://doi.org/10.1073/pnas.1210920110

- Delpy, F., Pagano, M., Blanchot, J., Carlotti, F., & Thibault-Botha, T. (2012). Man-induced hydrological changes, metazooplankton communities and invasive species in the Berre Lagoon (Mediterranean Sea, France). *Marine Pollution Bulletin, 64*(9)*, 1921-1932*. https://doi.org/10.1016/j.marpolbul.2012.06.020
- Duarte, C. M., Pitt, K. A., Lucas, C. H., Purcell, J. E., Uye, S., Robinson, K., Brotz, L., Decker, M. B., Sutherland, K. R., Malej, A., Madin, L., Mianzan, H., Gili, J., Fuentes, V., Atienza, D., Pagés, F., Breitburg, D., Malek, J., Graham, W. M., & Condon, R. H. (2013). Is global ocean sprawl a cause of jellyfish blooms? *Frontiers in Ecology and the Environment, 11*(2), *91-97*. doi:10.1890/110246
- Holst, S., & Jarms, G. (2007). Substrate choice and settlement preferences of planula larvae of five Scyphozoa (Cnidaria) from German Bight, North Sea. *Marine Biology, 151, 863– 871*. https://doi.org/10.1007/s00227-006-0530-y
- Howarth, R. W., Anderson, D., Cloern, J., Elfring, C., Hopkinson, C., Lapointe, B., Malone, T., Marcus, N., McGlathery, K., Sharpley, A., & Walker, D. (2000). Nutrient pollution of coastal rivers, bays, and seas. *Issues in Ecology, 7, 1-14*. https://www.esa.org/wpcontent/uploads/2013/03/issue7.pdf
- Karpowicz, M., Ejsmont-Karabin, J., Kozłowska, J., Feniova, I., & Dzialowski, A. R. (2020). Zooplankton community responses to oxygen stress. *Water, 12*(3), *706*. https://www.mdpi.com/2073-4441/12/3/706/pdf
- Lilley, M. K. S., Houghton, J. D. R. & Hays, G. C. (2009). Distribution, extent of inter-annual variability and diet of the bloom-forming jellyfish *Rhizostoma* in European waters. *Journal of the Marine Biological Association of the United Kingdom*, *89*(1), *39-48*.
- Lynam, C. P., Gibbons, M. J., Axelsen, B. E., Sparks, C. A. J., Coetzee, J., Heywood, B. G., & Brierly, A. S. (2006). Jellyfish overtake fish in a heavily fished ecosystem. *Current Biology, 16*(19), *1976*. https://doi.org/10.1016/j.cub.2006.09.012
- Meredith, R. W., Gaynor, J. J., & Bologna, P. A. X. (2016). Diet assessment of the Atlantic Sea Nettle *Chrysaora quinquecirrha* in Barnegat Bay, New Jersey, using next-generation sequencing. *Molecular Ecology, 25*(24), *6248-6266*. https://doi.org/10.1111/mec.13918
- Mihelcic, J. R., & Zimmerman, J. B. (2014). *Environmental engineering: Fundamentals, sustainability, design: 2nd edition*. Hoboken, NJ: Wiley.
- Nagata, R. M., Moreira, M. Z., Pimentel, C. R., & Morandini, A. C. (2015). Food web characterization based on δ 15N and δ 13C reveals isotopic niche partitioning between fish and jellyfish in a relatively pristine ecosystem. *Marine Ecology Progress Series, 519, 13- 27*. doi: 10.3354/meps11071
- Pang, H., Ingelido, P., Hirst, B., Pflaumer, J., Witt, A., Zaman, A., & Aiello, J. (2017). Water quality condition and assessment within the Barnegat Bay watershed between 2011 and 2015. *Journal of Coastal Research, 78*(10078)*, 7-21*. https://doi.org/10.2112/SI78-002.1
- Paul, M. J., & Meyer, J. L. (2001). Streams in the urban landscape. *Annual Review of Ecology and Systematics, 32, 333-365*. https://doi.org/10.1146/annurev.ecolsys.32.081501.114040
- Purcell, J.E., & Decker, M.B. (2005). Effects of climate on relative predation by scyphomedusae and ctenophores on copepods in Chesapeake Bay during 1987‐2000. *Limnology and Oceanography, 50*(1)*, 376-387*.
- Purcell, J. E., Shiganova, T. A., Decker, M. B., & Houde, E. D. (2001). The ctenophore *Mnemiopsis* in native and exotic habitats: U.S. estuaries versus the Black Sea basin. *Hydrobiologia, 451, 145–176*. https://doi.org/10.1023/A:1011826618539
- Purcell, J. E., Uye, S., & Lo, W. (2007). Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology Progress Series, 350, 153- 174*. doi: 10.3354/meps07093
- Soranno, A. L. (2016). Settling patterns of *Chrysaora quinquecirrha* polyps on common vinyl construction material: Potential implications for jellyfish blooms and coastal development in Barnegat Bay New Jersey. *Montclair State University Digital Commons: Theses, Dissertations, and Culminating Projects, 616*.

https://digitalcommons.montclair.edu/cgi/viewcontent.cgi?article=1617&context=etd

- Thein, H., Ikeda, H., & Uye, S. I. (2012). The potential role of podocysts in perpetuation of the common jellyfish *Aurelia aurita* s.l. (Cnidaria: Scyphozoa) in anthropogenically perturbed coastal waters. *Hydrobiologia, 690, 157-167*.
- Treible, L. M., & Condon, R. H. (2019). Temperature-driven asexual reproduction and strobilation in three scyphozoan jellyfish polyps. *Journal of Experimental Marine Biology and Ecology, 520, 151204*. https://doi.org/10.1016/j.jembe.2019.151204

Yoon, W., Chase, J., Koh, B., & Han, C. (2018). Polyp removal of a bloom forming jellyfish, *Aurelia coerulea*, in Korean waters and its value evaluation. *Ocean Science Journal, 53, 499-507*. https://dx.doi.org/10.1007/s12601-018-0015-1

Appendices

Appendix A. List of identified taxa from plankton tows for each site sampled during the experiment. No samples were collected in 2021 for BK Lagoon, so such no listing occurs. Values in the appendix represent the average standardized density (# individuals m^{-3}) \pm 1SD.

BERKELEY SHORES (2022) MEAN+SD

BEAN-SD MEAN-SD

FORKED RIVER LAGOON

(2021) MEAN+SD

FORKED RIVER LAGOON (2022) MEAN+SD

FORKED RIVER LAGOON (2023) MEAN+SD TAXA JUNE JULY AUGUST *Mnemiopsis leidyi* 0+0 0.26 \pm 0.2 1.21 \pm 0.6

