



Mesozooplankton Community Dynamics and Grazing Potential Across Algal Bloom Cycles in a Subtropical Estuary

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L. Holly Sweat^{1*}, Hunter Alexander^{1†}, Edward J. Philips² and Kevin B. Johnson¹

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Hongbin Liu,
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China
Edward Buskey,
The University of Texas at Austin,
United States

*Correspondence:

L. Holly Sweat
sweatl@si.edu

† Present address:

L. Holly Sweat,
Smithsonian Marine Station, National
Museum of Natural History,
Smithsonian Institution, Fort Pierce,
FL, United States
Hunter Alexander,
Data Collection Bureau, Southwest
Florida Water Management District,
Brooksville, FL, United States

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¹ Biological Oceanography Laboratory, Department of Ocean Engineering and Marine Sciences, Florida Institute of Technology, Melbourne, FL, United States, ² Fisheries and Aquatic Sciences Program, School of Forest, Fisheries, and Geomatics Sciences, Institute of Food and Agricultural Sciences, University of Florida, Gainesville, FL, United States

Mesozooplankton, as abundant grazers of microalgae in coastal systems, have the potential to prevent or mitigate harmful algal blooms (HABs) and their effects. The Indian River Lagoon (IRL) is a subtropical estuary in eastern Florida (United States) where repeated blooms, dominated by the toxic dinoflagellate *Pyrodinium bahamense*, the brown tide species *Aureoumbra lagunensis*, pico/nano planktonic cyanobacteria and other nano-eukaryotes, have highlighted the need to better understand fluctuations in the grazing potential of mesozooplankton populations across bloom cycles. Mesozooplankton and abiotic environmental data were collected at five sites in the northern IRL system at 6-week intervals from November 2013 through June 2016. A total of 107 taxa from 14 phyla were detected. Communities varied across sites, dates and between bloom and non-bloom periods, with densities up to 338 individuals L⁻¹. Eight taxa comprising 85–94% of the total population at each site were identified as primary potential grazers, including barnacle nauplii, cladocerans, adult copepods, gastropod veligers, larvaceans, and polychaete metatrochophores. Although abundant, the estimated grazing potential of the primary taxa, calculated from their measured densities and previously published grazing rates, suggest that mesozooplankton lack the capacity to suppress phytoplankton once they reach bloom levels. These findings illustrate the utility of monitoring data and underscore the importance of systematically evaluating algal bloom controls with a consideration for the dynamic conditions of each unique ecosystem.

Keywords: bloom controls, estuary, Florida, grazing potential, harmful algal blooms, Indian River Lagoon, mesozooplankton, phytoplankton

INTRODUCTION

Mesozooplankton are important grazers of phytoplankton in a wide variety of marine systems. Comprised of holoplankton such as copepods and meroplanktonic larvae ranging from 200 μm to 2 mm, mesozooplanktonic grazers ingest an estimated 12–18% of global oceanic primary production annually (Calbet, 2001; Calbet and Saiz, 2005). Ingestion rates are typically greatest in highly productive coastal systems (Calbet, 2001) such as estuaries, where eutrophication and

other anthropogenic alterations support the formation of phytoplankton blooms (Sunda et al., 2006; Anderson et al., 2008; Heisler et al., 2008; Raven et al., 2020).

The Indian River Lagoon (IRL) estuary is a biodiverse barrier island lagoon stretching from warm temperate to subtropical climate zones across 251 km of Florida's east coast (United States). The estuary system consists of three connected regions: the Mosquito Lagoon, the Indian River Lagoon and the Banana River Lagoon. Phytoplankton blooms have long been observed in the IRL, but they experienced a dramatic increase in intensity and change in composition in 2011 (Phlips et al., 2021). Prior to 2011, relatively large dinoflagellates and diatoms were the dominant bloom species (Phlips et al., 2015). However, widespread seagrass losses in 2009–2010, and extraordinarily cold winter water temperatures in 2010, were followed by blooms of small-celled species (<5 μm in diameter). In 2011, picocyanobacteria and Pedinophyceae species bloomed throughout the northern IRL, followed by repeated intense blooms of the brown tide pelagophyte *Aureoumbra lagunensis*, and other small-celled taxa (Phlips et al., 2021). None of these taxa were documented at such levels in the estuary prior to 2011 but have occurred repeatedly in the years since (Phlips et al., 2015, 2020; Schaefer et al., 2019). The blooms have decreased light penetration and dissolved oxygen concentrations, leading to large-scale losses of habitat and changes in biological communities (Phlips et al., 2015; Lapointe et al., 2020; Lewis et al., 2020, 2021; Lazensky et al., 2021) that have defined the IRL for decades.

Harmful algal blooms (HABs) are not isolated to the IRL or similar systems. In the United States alone, such blooms occur in all 50 states, caused by over 100 taxa (Anderson et al., 2021) that impact human and ecosystem health, tourism, and commercial fishing and aquaculture industries with a combined value of \$7 billion in 2018/2019 (National Marine Fisheries Service, 2021). Climate change and other anthropogenically-driven environmental effects are expanding ranges and increasing bloom frequencies of many phytoplankton taxa (Gobler, 2020). It is therefore crucial to better understand bloom impacts on ecosystems, and to evaluate potential top-down controls such as grazing by a variety of organisms.

Microzooplankton (20–200 μm) are recognized for their potential to graze blooms of small-celled phytoplankton (e.g., Sautour et al., 2000; Sherr and Sherr, 2007; Calbet, 2008; Schmoker et al., 2013) like those occurring in the IRL system. In contrast, mesozooplankton have received less attention as top-down bloom controls because they are typically deemed inefficient consumers of small cells (Calbet and Landry, 1999; Calbet et al., 2003; Davis et al., 2012; Morison et al., 2020). However, some studies have documented the ability of mesozooplankton to consume particles <5 μm (Calbet et al., 2000; Davis et al., 2012). Furthermore, these larger zooplankton are major components of the IRL system (Youngbluth et al., 1976; Rey et al., 1991; Dix and Hanisak, 2015), are a critical link between phytoplankton and higher trophic levels (Sommer and Stibor, 2002; Lobry et al., 2008; David et al., 2016), and should be considered in the big picture as bloom impacts and potential control mechanisms are explored. This study

investigated mesozooplankton in the IRL system with the following objectives:

- (1) Evaluate the spatial and temporal variability of mesozooplankton communities at bloom hotspots.
- (2) Estimate the grazing potential of mesozooplankton populations on natural levels of phytoplankton biomass.
- (3) Identify key mesozooplankton grazers as potential candidates for bloom control.

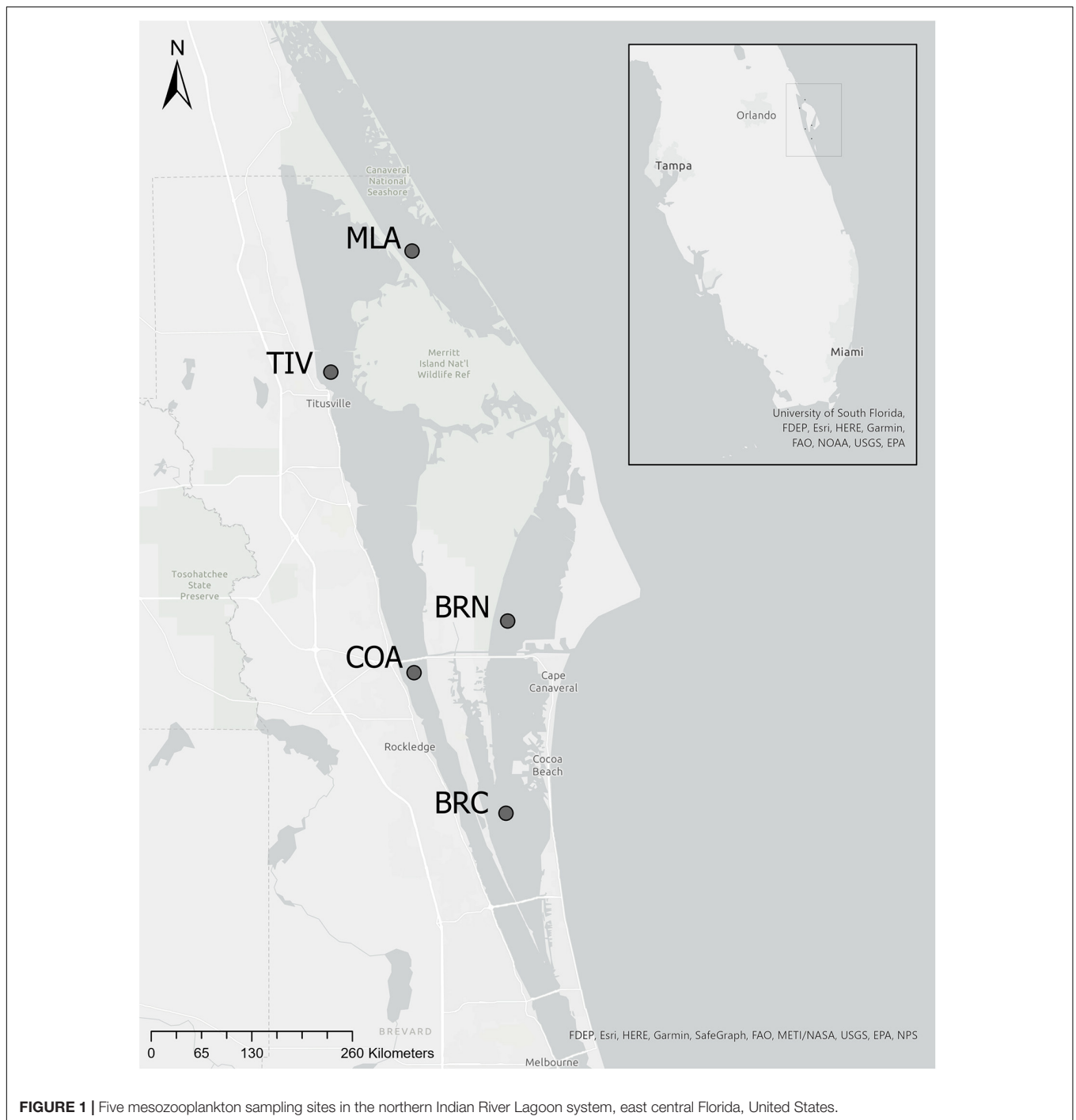
MATERIALS AND METHODS

Field Procedures

Mesozooplankton were sampled at five sites across the northern Indian River Lagoon (IRL) system (**Figure 1**) that were selected because of previous phytoplankton bloom activity (Phlips et al., 2015): the southern Mosquito Lagoon (MLA), the IRL at Titusville (TIV) and Cocoa (COA), Banana River North (BRN) and Banana River Central (BRC). MLA is 2 km southeast of the Haulover Canal, which serves as the only direct connection between the Mosquito Lagoon and the IRL. BRN is situated 2.8 km northwest of the Port Canaveral lock that links the Banana River Lagoon to the Atlantic Ocean. BRN and COA are each approximately 3 km from opposite sides of the Port Canaveral Barge Canal, which connects the IRL and Banana River Lagoon through the Sykes Creek drainage basin on Merritt Island. The average navigable distance between sites is 18.9 km. Mean depth ranged from 1.61 ± 0.03 to 3.13 ± 0.12 m for BRC and COA, respectively (**Table 1**).

Daytime plankton samples ($n = 4$) were collected with a ring net (153- μm mesh, 30-cm diameter) every 6 weeks from November 17, 2013 through June 27, 2016 for all sites except COA, which began on June 25, 2014. The net was towed horizontally within 1 m of the surface, effectively representing the entire shallow and generally well-mixed water column, which was supported by the presence of several benthic and demersal taxa (e.g., *Caprella* and *Cerapus* amphipods, *Sphaeroma* isopods, *Oxyurostylis* cumaceans, and several species of benthic foraminiferans and harpacticoid copepods) in the samples. Tow duration was 1 min and was reduced as needed to prevent clogging, which occurred when phytoplankton and zooplankton densities were at their highest and when byproducts (e.g., mucus and molts) were abundant. Tow volumes (0.02 – 35.63 m^3 , mean = 7.98 ± 0.41 m^3) were calculated from tow speeds and confirmed by in-net (Model 2030R, General Oceanics, Inc., Miami, FL, United States) and external (Model FP211, Global Water Instrumentation, Inc., Gold River, CA, United States) flowmeters. All resulting samples were immediately preserved in 5% formalin with sodium tetraborate buffer.

During each sampling event, total depth (m), water temperature ($^{\circ}\text{C}$) and salinity (ppt) were measured with a CastAway[®] CTD (SonTek, San Diego, CA, United States). Average water column temperatures and salinities were calculated using data from the profiles at standardized depths (0.15, 0.45, 0.75, and 1.05 m) within the range of a typical net tow. Surface dissolved oxygen (DO, mg L^{-1}) and pH were



measured with a YSI Model 85 handheld multiparameter meter (YSI, Inc., Yellow Springs, OH, United States). Water clarity was determined via Secchi disk depth (m) using a weighted, limnological disk (20-cm diameter).

Laboratory Procedures

After 1–2 weeks of fixation, samples were re-sieved (153 μm), transferred to 1- μm filtered seawater, and divided zero to eight times with a Motoda plankton splitter (Motoda, 1959)

to obtain aliquot densities at which all individuals could be easily differentiated in a 10 cm \times 10 cm gridded tray. Using stereomicroscopy (35 \times magnification), zooplankton from each grid were enumerated and identified to the lowest possible taxonomic level using several sources (e.g., Davis, 1949; Grice, 1960; Smith and Johnson, 1996; Johnson and Allen, 2012) until ≥ 300 individuals were recorded (Davidson and Clem, 2003; BS EN 14407:2004, 2004). Counts were normalized by volume for comparison across samples.

TABLE 1 | Key physical and biological characteristics of all five sampling sites.

		MLA	TIV	COA	BRN	BRC
Physical characteristics	Latitude	28.731	28.634	28.393	28.434	28.280
	Longitude	−80.732	−80.806	−80.731	−80.646	−80.648
	Depth (m)	1.72 ± 0.03	2.25 ± 0.12	3.13 ± 0.12	3.05 ± 0.12	1.61 ± 0.03
	Water temp (°C)	24.1 ± 0.6	24.1 ± 0.6	25.4 ± 0.7	25.0 ± 1.1	25.3 ± 1.0
	Salinity (ppt)	34.0 ± 0.5	31.6 ± 0.5	27.2 ± 0.6	31.9 ± 1.1	28.1 ± 0.8
	Surface DO (mg L ^{−1})	5.4 ± 0.3	5.5 ± 0.3	6.2 ± 0.3	5.5 ± 0.5	5.6 ± 0.8
	Surface pH	8.53 ± 0.03	8.43 ± 0.06	8.48 ± 0.06	8.54 ± 0.14	8.52 ± 0.12
	Secchi depth (m)	0.98 ± 0.06	1.46 ± 0.10	1.40 ± 0.09	1.21 ± 0.11	1.29 ± 0.11
Mesozooplankton community characteristics	Richness (# taxa)	15.1 ± 0.4	13.7 ± 0.3	12.3 ± 0.4	12.1 ± 0.4	13.8 ± 0.5
	Density (ind. L ^{−1})	12.0 ± 1.7	17.0 ± 3.9	35.7 ± 4.23	17.9 ± 2.6	34.1 ± 6.0
	Annelida (%)	0.4	0.2	3.1	0.5	0.6
	Arthropoda (%)	63.5	88.4	85.2	84.7	85.7
	Chordata (%)	5.7	6.9	8.8	7.2	7.6
	Mollusca (%)	27.0	2.1	1.3	3.0	4.4
Major algal taxa (% of total μg C mL ^{−1})	Other (%)	3.3	2.3	1.6	4.5	1.7
	<i>Aureoumbra lagunensis</i>	43.2	44.4	44.0	56.1	46.4
	Cyanobacteria	27.2	17.1	7.0	13.3	6.9
	Diatoms	1.3	2.6	10.4	4.4	20.5
	Dinoflagellates	6.1	10.9	24.4	10.2	19.6
	Other	22.2	25.0	14.1	16.0	6.6

Means are ± 1 SE.

Phytoplankton and Grazing Potential

Algal biomass data (*A. lagunensis*, cyanobacteria, diatoms, dinoflagellates, others) for the study period were obtained from weekly to biweekly monitoring by the Phlips Lab at the University of Florida. At each site, daytime phytoplankton samples ($n = 5$) were collected with an integrated water sampler (Sch 40 PVC pipe, 3.2 cm diameter) lowered vertically from the surface to within 0.1 m of the bottom. The five samples were pooled to reduce the effect of patchiness, and duplicate aliquots were preserved, one with Lugol's iodine solution and one with buffered glutaraldehyde (Phlips et al., 2010, 2020).

Phytoplankton composition was determined using the Utermöhl method (Utermöhl, 1958). Preserved samples were settled in 19-mm diameter cylindrical chambers. Phytoplankton cells were identified and counted at 400× and 100× magnification using inverted phase contrast microscopy (Leica Microsystems, Wetzlar, Germany). At 400×, 30–100 grids were examined until a minimum of 100 cells of a single taxon were counted. At 100×, a total bottom count was obtained for taxa >30 μm in size. Fluorescence microscopy was used on glutaraldehyde-preserved aliquots to enumerate picoplanktonic cyanobacteria (i.e., picocyanobacteria, which is mainly spherical *Synechococcus* spp. in the IRL) at 1,000× magnification (Phlips et al., 1999). Light microscopy was used to identify and enumerate *A. lagunensis* based on morphological features evident from previous work (Phlips and Badylak, 2013), which initially characterized *A. lagunensis* via light, scanning electron and transmission electron microscopy that was later supported by immunological assays and 18S rRNA gene sequencing conducted by colleagues at the Florida Fish and Wildlife Research Institute and Stony Brook University. To estimate cell biovolumes, subsamples of

seawater were filtered onto 0.2 μm Whatman® Nuclepore™ filters (GE Healthcare, Chicago, IL, United States) and mounted with immersion oil between a microscope slide and cover slip. Biovolumes were estimated by assigning combinations of geometric shapes to fit the cell characteristics of individual taxa (Smayda, 1978). Specific phytoplankton dimensions were measured for ≥100 randomly selected cells. Species of variable size (e.g., many diatom taxa) were placed into size categories. Phytoplankton carbon values (μg C mL^{−1}) were estimated by multiplying biovolume estimates (expressed as 10⁶ μm³ mL^{−1}) by conversion factors for different taxonomic groups: 0.061 for diatoms, 0.22 for cyanobacteria and small picoplanktonic eukaryotes (including *A. lagunensis*), and 0.16 for dinoflagellates and other taxa (Strathmann, 1967; Ahlgren, 1983; Sicko-Goad et al., 1984; Work et al., 2005).

The phytoplankton data were used to characterize sites, define bloom periods and compare with estimated grazing rates. Bloom periods at each site were defined as dates with an algal biomass >2 μg C mL^{−1} (Phlips et al., 2015, 2020) for at least one of the five phytoplankton categories. The phytoplankton monitoring schedule was more frequent and sometimes offset from that of the mesozooplankton monitoring. Therefore, a zooplankton sampling event was considered to occur during a phytoplankton bloom if bloom conditions were observed the same day that the zooplankton were collected, or both before and after (typically 1–7 days) they were collected. The same strategy was employed to define non-bloom periods. Relative chlorophyll (RFU) data from nearby continuous water quality monitoring stations (St. Johns River Water Management District Aquarius WebPortal¹)

¹<https://secure.sjrwmd.com/aqportal>

were used to support these designations. If the bloom status on a particular zooplankton sampling date remained unresolved, that date was defined as ‘unknown’ and was excluded from bloom/non-bloom comparisons.

Key potential grazers were identified as primarily herbivorous or omnivorous taxa reaching densities >10 ind. L^{-1} during the study period. Data on these taxa were used to demonstrate whether mesozooplankton may have the capacity to suppress algal blooms in this estuary through grazing. Ingestion rates (IR) were obtained from studies of the key grazers, or closely related taxa known to occur in the region, at the same or similar life stages, and examined at water temperatures within the range of this study (10.6–31.8°C). The minimum and maximum estimated grazing potentials (EGP_{min} and EGP_{max} , $\mu g C mL^{-1} d^{-1}$) for each taxon during each sampling event were obtained by multiplying their *in situ* densities (ind. mL^{-1}) by their IR_{min} and IR_{max} values ($\mu g C ind.^{-1} d^{-1}$), respectively. The EGP_{min} and EGP_{max} values were summed across the suite of eight key grazers to calculate the minimum and maximum Estimated Metagrazing Potential (EMP_{min} and EMP_{max} , $\mu g C mL^{-1} d^{-1}$) for the entire mesozooplankton community at each site over time. This EMP range provides an extremely rough but relatively inclusive estimate of mesozooplankton grazing potential at a site – ‘best’ and ‘worst-case’ scenarios that consider a variety of conditions and prey types.

Data Analysis

Univariate statistical analyses were conducted in The Real Statistics add-in package for Microsoft Excel². Following Levene’s tests for homoscedasticity, Welch’s analysis of variance (ANOVA, $\alpha = 0.05$) and Games–Howell *post hoc* tests were used to detect differences among sites for abiotic parameters, species richness (S) and zooplankton density (ind. L^{-1}). Welch’s *t*-tests were used to identify differences in key grazer densities from bloom and non-bloom periods within each site.

Multivariate community analyses were performed on square root transformed count data using the PRIMER v5 software package (PRIMER-E Ltd., Plymouth, United Kingdom). A two-way crossed analysis of similarities (ANOSIM, $\alpha = 0.05$, Bray–Curtis similarities) was used to find differences in zooplankton community composition among sites and dates. Within each site, differences in communities between bloom and non-bloom periods were detected with a one-way ANOSIM. Groups were considered different only when $R > 0.250$ and $p < 0.05$ (Clarke and Gorley, 2001). Taxa driving the differences were identified with similarity percentage (SIMPER) analyses.

RESULTS

Across all sites, a total of 439 samples were collected and 107 taxa from 14 phyla were identified. Per sample mesozooplankton richness and density ranged from 5 to 25 taxa and 0.1 to 338.1 ind. L^{-1} , respectively.

²real-statistics.com

Site Characteristics

Key physical and biological characteristics varied among the five sites during the study period (Table 1). Pairwise comparisons revealed that MLA was generally the most saline site (compared with TIV, BRC, and COA: $p \leq 0.026$) with the lowest water clarity (as Secchi depth, compared with TIV and COA: $p \leq 0.002$). No differences were detected among sites with regard to water column temperature, surface DO or surface pH ($p \geq 0.313$). MLA and TIV exhibited higher species richness than BRN and COA ($p \leq 0.038$), with BRC situated between the two groups. In contrast, MLA and TIV, along with BRN, hosted lower zooplankton densities than one or both of the other sites ($p \leq 0.012$).

Zooplankton communities were dominated by arthropods (primarily copepods) at all sites, with MLA also containing a large percentage of molluscs (Table 1). *A. lagunensis* was the prevailing alga overall (43.2–56.1%), with percentages of other groups varying considerably by site. Bloom conditions occurred across all sites at a wide range of water temperatures during both wet and dry seasons (Figure 2), with blooms being detected from 5 to 26 days at BRN and MLA, respectively. Prior to June 2015, phytoplankton communities at all sites were assemblages of cyanobacteria, diatoms, dinoflagellates and others, which formed occasional blooms up to 12 $\mu g C L^{-1}$. During this period, *A. lagunensis* was a minor contributor to the system (Figure 2). In late 2015, total algal biomass dominated by *A. lagunensis* and ‘other’ taxa, rose at all sites and remained elevated for several months, peaking at 29.89 $\mu g C L^{-1}$ (85% *A. lagunensis*) at BRN on March 07, 2016. At the height of this bloom, the presence of other phytoplankton taxa was minimal.

Mesozooplankton Community Differences

Mesozooplankton communities varied across sites (global $R = 0.840$, $p = 0.001$; pairwise $R \geq 0.706$, $p = 0.001$) and dates (global $R = 0.910$, $p = 0.001$; pairwise $R \geq 0.599$, $p = 0.001$), and between bloom and non-bloom periods at BRN ($R = 0.440$, $p = 0.001$) and BRC ($R = 0.479$, $p = 0.001$). All differences were driven mainly by fluctuating densities of the three dominant copepods: the omnivorous *Acartia tonsa* and *Oithona colcarva*, and the primarily herbivorous *Parvocalanus crassirostris*. These copepods reached respective densities of 325, 156, and 116 ind. L^{-1} . At BRN and BRC, *P. crassirostris* was a major component of the communities only during non-bloom periods, while *A. tonsa* and *O. colcarva* were omnipresent.

Grazing Potential

Eight taxa comprising 85–94% of the total population at each site were identified as primary potential grazers: *Amphibalanus* spp. barnacle nauplii, *Evadne* sp. cladocerans, gastropod veligers (one species), *Oikopleura* sp. larvaceans, polychaete metatrichophores (one species), and the copepods *A. tonsa*, *O. colcarva*, and *P. crassirostris*. Of 40 density comparisons of these taxa between bloom and non-bloom periods, 23 were lower during bloom events ($p \leq 0.049$, Table 2). The greatest impacts were seen on

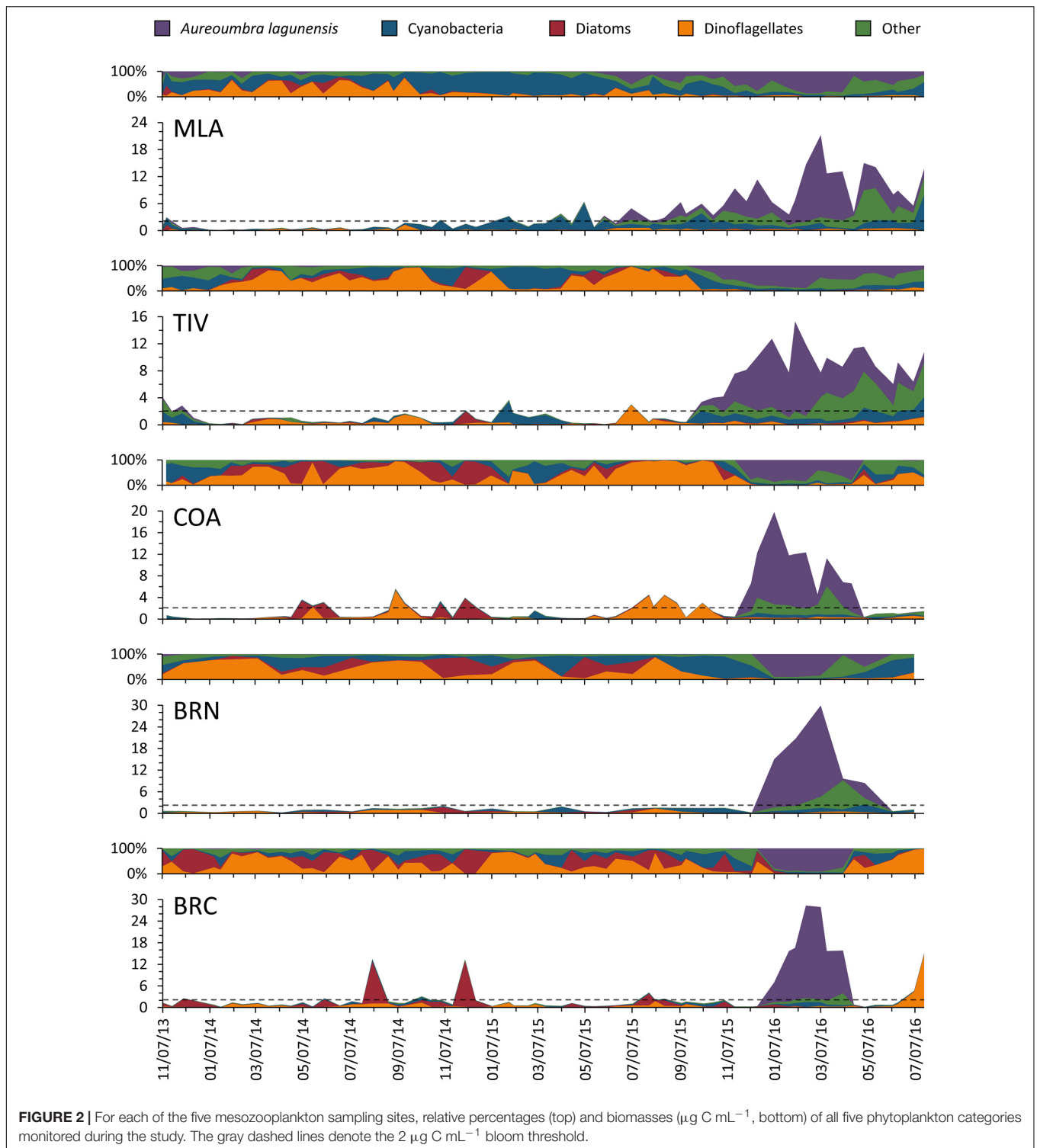


FIGURE 2 | For each of the five mesozooplankton sampling sites, relative percentages (top) and biomasses ($\mu\text{g C mL}^{-1}$, bottom) of all five phytoplankton categories monitored during the study. The gray dashed lines denote the $2 \mu\text{g C mL}^{-1}$ bloom threshold.

populations at BRN and BRC, where all eight and seven out of eight key grazers declined during blooms, respectively.

A review of the relevant literature on these taxa and their close relatives uncovered per-species ingestion rates (IRs) ranging from 0.001 to $13.1 \mu\text{g C ind}^{-1} \text{d}^{-1}$ for *Oithona* and *Oikopleura*, respectively (Table 3). The largest

community-wide Estimated Metagrazing Potential (EMP_{max}) of $1.22 \mu\text{g C mL}^{-1} \text{d}^{-1}$ was documented at TIV on October 1, 2015, resulting from high densities of all three copepod species. On several occasions, the EMP_{max} exceeded the minimum phytoplankton biomass documented at a particular site (Figure 3), signaling that mesozooplankton grazing can be

TABLE 2 | Key grazer densities (ind. m⁻³) at each site during known bloom (B) and non-bloom (NB) conditions.

		MLA	TIV	COA	BRN	BRC
<i>Acartia tonsa</i>	B	2347.6 ± 381.4	2662.8 ± 488.3	4535.9 ± 871.5	2560.4 ± 1008.5	326.5 ± 65.6
	NB	2582.8 ± 454.0	11320.8 ± 5496.4	20146.7 ± 6769.3*	4919.2 ± 515.9*	9235.2 ± 1172.4*
<i>Amphibalanus</i> spp. nauplii	B	96.0 ± 18.8*	224.5 ± 46.0	826.6 ± 250.5	51.0 ± 28.7	4.5 ± 1.9
	NB	43.2 ± 11.0	288.0 ± 83.0	1031.9 ± 431.9	123.0 ± 31.6*	144.9 ± 33.4*
<i>Evadne</i> sp.	B	2.7 ± 1.7	0.0	928.0 ± 341.5*	0.0	0.0
	NB	85.7 ± 48.1*	638.6 ± 240.0*	158.2 ± 77.3	723.0 ± 405.1*	5412.9 ± 3052.0*
Gastropod veliger sp. 1	B	431.3 ± 279.6	197.8 ± 64.9	468.9 ± 180.1	23.5 ± 15.0	65.9 ± 21.6
	NB	537.7 ± 108.2	443.1 ± 96.5*	411.5 ± 108.3	605.8 ± 243.7*	1573.9 ± 458.9*
<i>Oikopleura</i> sp.	B	225.0 ± 133.3	185.0 ± 76.6	5218.3 ± 2457.3*	0.2 ± 0.2	242.7 ± 117.1
	NB	348.9 ± 133.0	1495.8 ± 349.3*	883.7 ± 329.2	1367.4 ± 400.7*	3153.5 ± 2047.7
<i>Oithona colcarva</i>	B	1279.6 ± 275.4	2405.3 ± 466.2	3161.6 ± 661.2	773.8 ± 193.4	1922.7 ± 781.9
	NB	797.0 ± 133.4	2159.8 ± 274.1	10353.8 ± 1898.3*	4061.7 ± 609.4*	5966.8 ± 929.7*
<i>Parvocalanus crassirostris</i>	B	100.8 ± 28.0	41.2 ± 18.6	5040.5 ± 1473.3	2.0 ± 1.5	21.3 ± 10.0
	NB	1855.0 ± 259.0*	3195.8 ± 484.7*	5822.1 ± 1469.6	5723.6 ± 1730.3*	5903.8 ± 1422.1*
<i>Polychaete metatrophore</i> sp. 1	B	11.1 ± 4.1	13.8 ± 4.3	61.6 ± 34.5	32.9 ± 18.7	2.3 ± 1.2
	NB	23.6 ± 12.6	25.6 ± 6.5	97.8 ± 26.2	84.3 ± 17.4*	197.2 ± 69.8*

Means are ±1SE. Asterisks denote significantly greater values in bloom/non-bloom pairwise comparisons.

high enough to impact phytoplankton populations. However, EMP_{max} never exceeded the 2 µg C mL⁻¹ bloom threshold, suggesting that mesozooplankton lack the grazing capacity needed to suppress phytoplankton in this system once they reach bloom levels.

DISCUSSION

This investigation documents the spatial and temporal variation in mesozooplankton communities from a subtropical estuary affected by recurring phytoplankton blooms and provides a rough estimate of their grazing potential. It is important to acknowledge some limitations of this study. First, although the zooplankton tows sampled the majority of the well-mixed water column, only collecting during the day could have poorly estimated the abundances of some grazers due to diel vertical migration. Secondly, although grazing potential ranges were based on rates measured in a variety of conditions, they were still calculated indirectly from other studies. Grazing within a system is affected by a combination of factors, including those not examined by this study, such as phytoplankton quality and the abundance of alternative microzooplankton prey for omnivorous grazers. However, this study presents a method of utilizing datasets often readily available to scientists and resource managers working in bloom-impacted estuaries, providing an approximation of grazing potential to further monitoring and management efforts when direct grazing measurements are unavailable.

Results suggest that, while mesozooplankton grazing in the Indian River Lagoon system may exert some control on phytoplankton when abundances are low, it was not sufficient during the study period to suppress phytoplankton populations once they reached bloom levels. The largest Estimated Metagrazing Potential (EMP_{max}) calculated for the

mesozooplankton community was 1.22 µg C mL⁻¹ d⁻¹, lower than the 2 µg C mL⁻¹ threshold used herein to define bloom events. The brown tide pelagophyte *A. lagunensis* exhibited the largest algal biomass of all the phytoplankton groups surveyed during the study period. The prevalence of this alga and the composition of the zooplankton communities may help explain the apparent inability of mesozooplankton grazing to control blooms in the northern IRL system.

Two major factors affecting zooplankton grazing efficacy are prey cell size and the trophic modes of potential grazers. Many of the most abundant bloom-forming phytoplankton in the IRL and elsewhere are <5 µm, including *A. lagunensis*, pedinophytes, *Synechococcus* and other picocyanobacteria. Several studies have documented a tendency for mesozooplankton to graze on larger cells. Such findings are consistent with this study, which recorded the peak EMPs prior to the height of the *A. lagunensis* bloom, when algal biomasses were dominated by larger diatoms and dinoflagellates.

In addition, omnivorous mesozooplankton may also prey on microzooplankton that are often the more effective grazers of small autotrophs (Sautour et al., 2000; Calbet and Landry, 2004; Liu et al., 2005; Calbet, 2008; Davis et al., 2012). In this study, the copepods *A. tonsa* and *O. colcarva* were the most abundant mesozooplankton. Both genera are omnivorous and consume microzooplankton as a major and sometimes dominant part of their diets (Lonsdale et al., 1979, 2000; Castellani et al., 2005). Numerous studies have documented feeding in *Acartia* and *Oithona* under a variety of conditions. Jonsson and Tiselius (1990) observed the feeding behavior of *A. tonsa* on several ciliate taxa and on the alga *Cryptomonas baltica*. The authors noted that the copepods would devote time to suspension feeding on algal cells only when they were particularly abundant. At lower algal densities, *A. tonsa* would switch to raptorial feeding on ciliates. Rollwagen-Bollens and Penry (2003) investigated the feeding dynamics of *Acartia* spp. at two locations in San Francisco

TABLE 3 | Ingestion rates (IR, $\mu\text{g C ind}^{-1} \text{d}^{-1}$) from studies of key grazers, or closely related taxa known to occur in the region, at the same or similar life stages, and examined at water temperatures within the range of this study.

	IR	Taxon	Food source	Water °C	Citation
<i>Acartia tonsa</i>	11.447	<i>A. tonsa</i>	<i>Kryptoperidinium foliaceum</i>	*	Breier and Buskey, 2007
Adults	9.600	<i>A. tonsa</i>	nat. assemb.	20–30	Kleppel and Hazzard, 2000
	4.500	<i>A. tonsa</i>	nat. assemb.	20–30	Kleppel and Hazzard, 2000
	2.601	<i>A. tonsa</i>	<i>Amphidinium carterae</i>	20	Houde and Roman, 1987
	1.485	<i>A. tonsa</i>	nat. assemb.	15–26	White and Roman, 1992
	1.435	<i>A. tonsa</i>	<i>Thalassiosira weissflogii</i> [†]	20	Houde and Roman, 1987
	1.311	<i>A. tonsa</i>	<i>Chrysotila carterae</i>	20	Houde and Roman, 1987
	1.136	<i>A. tonsa</i>	<i>Amphidinium carterae</i>	20	Houde and Roman, 1987
	1.073	<i>A. tonsa</i>	<i>Thalassiosira weissflogii</i> [†]	20	Houde and Roman, 1987
	0.758	<i>A. tonsa</i>	<i>Cryptomonas baltica</i>	16	Ismar et al., 2018
	0.555	<i>A. tonsa</i>	<i>Thalassiosira weissflogii</i>	16	Ismar et al., 2018
	0.522	<i>A. tonsa</i>	<i>Karenia brevis</i>	*	Breier and Buskey, 2007
	0.060	<i>A. tonsa</i>	<i>Kryptoperidinium triquetrum</i> [§]	17	Jakobsen et al., 2005
	0.015	<i>A. tonsa</i>	<i>Isochrysis galbana</i>	16	Ismar et al., 2018
	0.004	<i>A. tonsa</i>	<i>Kryptoperidinium triquetrum</i> [§]	17	Jakobsen et al., 2005
<i>Amphibalanus</i> spp.	4.807	<i>A. amphitrite</i> [†]	<i>Chaetoceros gracilis</i>	28	Campanati et al., 2016
Nauplii	3.120	<i>A. improvisus</i> ⁺⁺⁺	<i>Skeletonema costatum</i>	15	Smart, 2003
	3.036	<i>A. amphitrite</i> [†]	<i>Chaetoceros calcitrans</i>	25	Desai and Prakash, 2009
	3.036	<i>A. amphitrite</i> [†]	<i>Chaetoceros gracilis</i>	28	Campanati et al., 2016
	2.714	<i>A. amphitrite</i> ⁺⁺⁺	<i>Chaetoceros muelleri</i>	25	Yu and Chan, 2020
	2.484	<i>A. amphitrite</i> [†]	<i>Chaetoceros gracilis</i>	28	Campanati et al., 2016
	2.438	<i>A. amphitrite</i> [†]	<i>Chaetoceros gracilis</i>	28	Campanati et al., 2016
	2.208	<i>A. amphitrite</i>	<i>Chaetoceros calcitrans</i>	25	Desai and Anil, 2004
	2.208	<i>A. amphitrite</i> [†]	<i>Chaetoceros calcitrans</i>	25	Desai and Prakash, 2009
	1.680	<i>A. amphitrite</i>	<i>Skeletonema costatum</i>	25	Desai and Anil, 2004
	1.490	<i>A. amphitrite</i> [†]	<i>Chaetoceros calcitrans</i>	25	Desai and Prakash, 2009
	1.104	<i>A. amphitrite</i>	<i>Chaetoceros calcitrans</i>	25	Desai and Anil, 2004
	0.960	<i>A. improvisu</i> [†]	<i>Skeletonema costatum</i>	15	Smart, 2003
	0.851	Unspecified barnacle	nat. assemb.	15–17	White and Roman, 1992
	0.835	<i>A. amphitrite</i> ⁺⁺	<i>Chaetoceros muelleri</i>	25	Yu and Chan, 2020
	0.192	<i>A. amphitrite</i>	<i>Skeletonema costatum</i>	25	Desai and Anil, 2004
	0.077	<i>A. amphitrite</i> [†]	<i>Synechococcus</i> spp.	23	Bemal and Anil, 2019
	0.045	<i>A. amphitrite</i> ⁺⁺	<i>Synechococcus</i> spp.	23	Bemal and Anil, 2019
	0.011	<i>A. amphitrite</i> [†]	<i>Synechococcus</i> spp.	23	Bemal and Anil, 2019
	0.007	<i>A. amphitrite</i> ⁺⁺	<i>Synechococcus</i> spp.	23	Bemal and Anil, 2019
<i>Evadne</i> sp.	1.300	<i>E. nordmanni</i>	nat. assemb.	17–18	Katechakis and Stibor, 2004
Adults	1.200	<i>Podon intermedius</i>	nat. assemb.	17–18	Katechakis and Stibor, 2004
	0.900	<i>Podon leuckartii</i>	nat. assemb. [‡]	18	Sánchez et al., 2011
	0.700	<i>Podon leuckartii</i>	nat. assemb. [‡]	16	Sánchez et al., 2011
	0.400	<i>E. nordmanni</i>	nat. assemb.	17–18	Katechakis and Stibor, 2004
	0.400	<i>Podon intermedius</i>	nat. assemb.	17–18	Katechakis and Stibor, 2004
	0.161	Unspecified cladocera	nat. assemb.	15–17	White and Roman, 1992
Gastropod sp. 1	4.021	<i>Ilyanassa obsoleta</i>	<i>Isochrysis galbana</i>	20	Pechenik, 1980
Veligers	3.888	<i>Ilyanassa obsoleta</i>	<i>Dunaliella tertiolecta</i>	20	Pechenik, 1980
	2.340	<i>Crepidula fornicata</i>	<i>Isochrysis galbana</i>	20	Pechenik, 1980
	2.199	<i>Ilyanassa obsoleta</i>	<i>Isochrysis galbana</i>	20	Pechenik, 1980
	1.731	<i>Ilyanassa obsoleta</i>	<i>Dunaliella tertiolecta</i>	20	Pechenik, 1980
	0.990	<i>Ilyanassa obsoleta</i>	<i>Isochrysis galbana</i>	20	Pechenik, 1980
	0.794	<i>Ilyanassa obsoleta</i>	<i>Isochrysis galbana</i>	20	Pechenik, 1980
	0.401	<i>Bittiolium alternatum</i>	<i>Isochrysis galbana</i>	20	Pechenik, 1980
	0.248	<i>Bittiolium alternatum</i>	<i>Isochrysis galbana</i>	20	Pechenik, 1980
<i>Oikopleura</i> sp.	13.100	<i>O. (Vexillaria) dioica</i>	<i>Isochrysis galbana</i>	15	Broms and Tiselius, 2003

(Continued)

TABLE 3 | (Continued)

	IR	Taxon	Food source	Water °C	Citation
Adults	11.952	<i>O. (Vexillaria) dioica</i>	<i>Tetraselmis suecica</i>	15	Acuña and Kiefer, 2000
	11.736	<i>O. (Vexillaria) dioica</i>	<i>Chlorella</i> sp.	15	Acuña and Kiefer, 2000
	11.000	<i>O. (Vexillaria) dioica</i>	<i>Thalassiosira pseudonana</i>	15	Lombard et al., 2009
	8.700	<i>O. (Vexillaria) dioica</i>	<i>Isochrysis galbana</i>	20	Broms and Tiselius, 2003
	4.800	<i>O. (Vexillaria) dioica</i>	<i>Thalassiosira pseudonana</i>	15	Lombard et al., 2009
	4.752	<i>O. (Vexillaria) dioica</i>	<i>Isochrysis galbana</i>	15	Acuña and Kiefer, 2000
	4.378	<i>O. (Coecaria) fusiformis</i>	nat. assemb. autotrophic eukaryotes	24	Scheinberg et al., 2005
	3.917	<i>O. (Coecaria) longicauda</i>	nat. assemb. autotrophic eukaryotes	24	Scheinberg et al., 2005
	2.353	<i>O. (Vexillaria) dioica</i>	<i>Isochrysis galbana</i>	20	Selander and Tiselius, 2003
<i>Oithona colcarva</i>	3.527	<i>O. brevicornis brevicornis</i>	<i>Prorocentrum shikokuense</i>	20	An et al., 2016
Adults	2.275	<i>O. brevicornis brevicornis</i>	<i>Prorocentrum shikokuense</i>	20	An et al., 2016
	0.510	<i>O. nana</i>	<i>Akashiwo sanguinea</i>	17–18	Svensen and Vernet, 2016
	0.375	<i>O. nana</i>	<i>Prorocentrum micans</i>	17–18	Svensen and Vernet, 2016
	0.159	<i>O. colcarva</i>	nat. assemb.	15–26	White and Roman, 1992
	0.100	<i>O. nana</i>	<i>Karlodinium</i> sp.	17–18	Svensen and Vernet, 2016
	0.003	<i>O. dissimilis</i>	nat. assemb. dinoflagellates	25	Zamora-Terol et al., 2014
	0.001	<i>O. dissimilis</i>	nat. assemb. dinoflagellates	25	Zamora-Terol et al., 2014
<i>Parvocalanus crassirostris</i>	4.000	<i>P. crassirostris</i>	<i>Dunaliella</i> sp.	24	Chen et al., 2013
Adults	3.011	<i>P. crassirostris</i>	<i>Isochrysis galbana</i>	26	Ma et al., 2021a
	2.941	<i>P. crassirostris</i>	<i>Isochrysis galbana</i>	26	Ma et al., unpublished
	1.253	<i>P. crassirostris</i>	<i>Thalassiosira weissflogii</i> ^l	24	Liu et al., 2016
	1.067	<i>P. crassirostris</i>	<i>Thalassiosira weissflogii</i> ^l	24	Liu et al., 2016
	0.775	<i>P. crassirostris</i>	<i>Tisochrysis lutea</i>	26	Alajmi et al., 2015
	0.691	<i>P. crassirostris</i>	nat. assemb.	26.0–27.5	Calbet et al., 2000
	0.503	<i>P. crassirostris</i>	<i>Thalassiosira weissflogii</i> ^g	24	Liu et al., 2016
	0.439	<i>P. crassirostris</i>	<i>Aureoumbra lagunensis</i>	26	Ma et al., unpublished
	0.387	<i>P. crassirostris</i>	<i>Thalassiosira weissflogii</i> ^g	24	Liu et al., 2016
	0.301	<i>P. crassirostris</i>	Prochlorophyte cyanobacterium	26	Ma et al., 2021b
	0.167	<i>P. crassirostris</i>	<i>Isochrysis galbana</i>	26	Ma et al., 2021a
	0.133	<i>P. crassirostris</i>	nat. assemb.	26.0–27.5	Calbet et al., 2000
	0.099	<i>P. crassirostris</i>	<i>Picochlorum</i> sp.	26	Ma et al., 2021a
	0.017	<i>P. crassirostris</i>	<i>Picochlorum</i> sp.	26	Ma et al., 2021a
	<i>Polychaete</i> sp. 1	1.310	<i>Polydora ciliata</i>	<i>Thalassiosira weissflogii</i>	16
Metatrophophores	0.989	<i>Polydora ciliata</i>	<i>Thalassiosira weissflogii</i>	16	Almeda et al., 2009
	0.868	<i>Polydora ciliata</i>	<i>Thalassiosira weissflogii</i>	16	Almeda et al., 2009
	0.537	Unspecified polychaete	nat. assemb.	15–23	White and Roman, 1992
	0.262	<i>Polydora ciliata</i>	<i>Thalassiosira weissflogii</i>	16	Hansen et al., 2010
	0.244	<i>Polydora ciliata</i>	<i>Thalassiosira weissflogii</i>	16	Almeda et al., 2009
	0.224	<i>Polydora ciliata</i>	nat. assemb., mainly <i>K. triquetrum</i>	16	Hansen et al., 2010
	0.220	<i>Polydora ciliata</i>	<i>Rhodomonas salina</i>	16	Almeda et al., 2009
	0.091	<i>Polydora ciliata</i>	<i>Rhodomonas salina</i>	16	Almeda et al., 2009

*Unspecified water temperature within 1–2°C of ambient in ship channel, Port Aransas, TX, United States; [†]senescent culture; [‡]growing culture; [§]mixed culture with ciliates; [¶]stage II nauplii; ^{**}stage III nauplii; ^{***}stage VI nauplii; ^gautotrophic nanoflagellates < 10 µm; ^llow silica; ^hhigh silica.

Bay (CA, United States) that hosted different assemblages of potential prey. The findings revealed that the copepods consumed different prey at the two sites but tended to target motile ciliates and flagellates >10 µm. Using *in situ* mesocosms containing natural densities of *A. lagunensis* and *Synechococcus* sp. from the upper Laguna Madre lagoon (Texas, United States), Buskey et al. (2003) tested whether *A. tonsa* indirectly affected phytoplankton densities by consuming herbivorous ciliates. Ciliate numbers increased in mesocosms where the copepods were removed, signaling that *A. tonsa* preyed on the microzooplankton.

However, the rise in ciliate grazers had different impacts on the two autotrophs, reducing *Synechococcus* sp. but leaving *A. lagunensis* populations unaffected. A laboratory study by Saiz et al. (2014) on *Oithona davisae* feeding revealed that adult females preyed most heavily on organisms >4 µm, including ciliates, heterotrophic flagellates and nauplii from other copepod species. The authors hypothesized that these preferences were the result of ambush feeding behavior that requires prey to be large and motile enough to trigger hydromechanical detection. Finally, in a study of the variability of mesozooplankton grazing

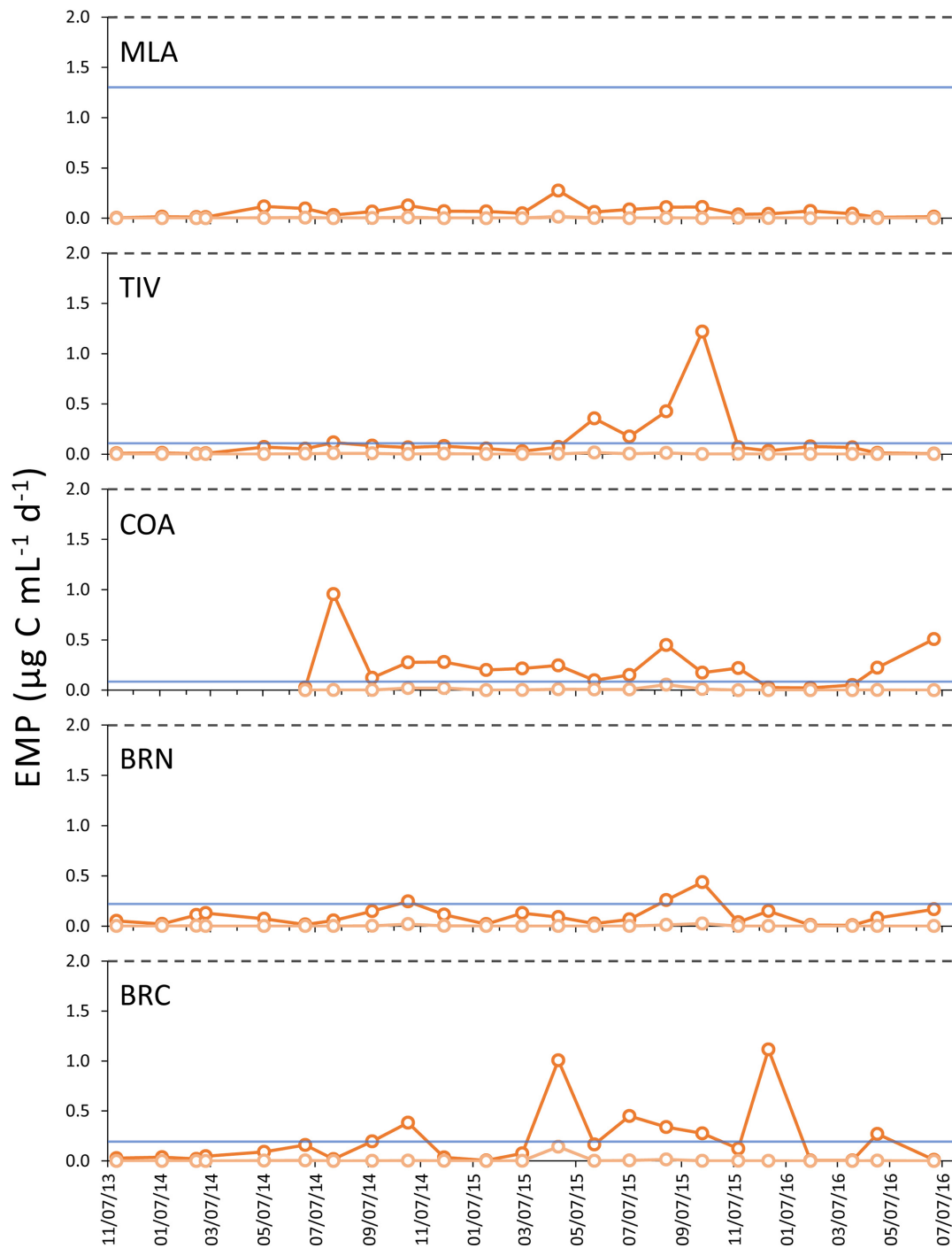


FIGURE 3 | Estimated Metagrazing Potential maxima (EMP_{max}, dark orange lines) and minima (EMP_{min}, pale orange lines) for the suite of key mesozooplankton grazers across all five monitoring sites. To aid comparisons between grazing potential and phytoplankton biomass, the phytoplankton bloom threshold ($2 \mu\text{g C mL}^{-1}$, gray dashed lines) and the minimum phytoplankton biomass recorded at each site (blue solid lines), are denoted.

on phytoplankton at two contrasting sites in Hong Kong, Chen et al. (2017) documented a high degree of carnivory in mesozooplankton populations comprised largely of *Acartia* and *Oithona*. The preference for microzooplankton prey reduced mean grazing impacts on phytoplankton to <4% at both sites.

Another factor likely contributing to the persistence of *A. lagunensis* in the northern IRL system is a set of characteristics and behaviors exhibited by the species that reduces grazer fitness: (1) potential low nutritive value and toxicity, (2) allelopathy toward competitive phytoplankton, and (3) the secretion of

protective exopolymers. During the brown tide-rich blooms in late 2015 and 2016, mesozooplankton populations declined at all sites, presumably driven by deteriorating conditions from the rise in *A. lagunensis* biomass. After zooplankton declined in the Laguna Madre lagoon (Texas, United States) following an outbreak of *A. lagunensis*, Buskey and Hyatt (1995) investigated the condition of *A. tonsa* fed on cultures of the brown tide alga. Adult egg production rates and naupliar survival both decreased. The findings suggested that *A. lagunensis* was mortally toxic to nauplii and a poor food for adults, producing egg release rates similar to those of starved copepods. In a study that assessed the development of *A. tonsa* nauplii grazing on another brown tide organism, *Aureococcus anophagefferens*, Smith et al. (2008) found that naupliar development was delayed when larvae consumed the alga. Interestingly, the nauplii selectively fed on more palatable algae only when the cells were larger than *A. anophagefferens*.

Recent work has revealed that brown tides can also inhibit the growth of competing phytoplankton, potentially lowering the availability of other food sources for grazers. In an investigation of the allelopathic effects of *A. lagunensis* and *A. anophagefferens* on a wide variety of phytoplankton, Kang and Gobler (2018) documented reductions of up to 96% in the abundance of competing autotrophs. Filtrate of *Aureoombra* cultures also reduced the photosynthetic efficiency of *Synechococcus* and the diatom *Chaetoceros calcitrans* by 53 and 19%, respectively. A particularly concerning discovery was that strains of *Aureoombra* isolated from the IRL in 2012 and 2013 had a higher allelopathic potency compared to those obtained from Laguna Madre, Texas 20 years ago. The 2015–2016 blooms in the present study were usually dominated by *A. lagunensis* biomass, but frequently contained elevated levels of other phytoplankton as well. However, diatoms and dinoflagellates, two well-documented primary food sources for mesozooplankton, never exceeded $0.64 \mu\text{g C mL}^{-1}$ during this period. These results may reflect the use of allelopathic chemicals by *A. lagunensis* to reduce competitive phytoplankton populations.

The utilization of extracellular polymeric substances (EPS) may also give *A. lagunensis* a competitive edge. In laboratory experiments using cultures isolated from Texas, Liu and Buskey (2000a) found that the alga formed a mucus layer of secreted EPS. As populations progressed from growth to decline, per cell EPS production increased threefold, which was maximized under hypersaline conditions. The authors continued their investigation by feeding high and low EPS cultures of *A. lagunensis* to three protozoan species common in the bloom area (Liu and Buskey, 2000b). All taxa showed reduced growth rates in the high EPS treatment. A subsequent experiment with one of those taxa, the ciliate *Aspidisca* sp., revealed that the slower growth resulted from reduced grazing, possibly from mucus clogging its feeding apparatus or from impaired grazing caused by the altered swimming behavior observed in the high EPS treatment.

Two of the most promising candidates for grazing down brown tide and other phytoplankton during this study were the copepod *P. crassirostris* and the larvacean *Oikopleura* sp. Both taxa were major contributors to the EMP peaks documented at COA and BRC, and while *A. tonsa* exhibited the highest

densities overall, *P. crassirostris* was the most abundant primarily herbivorous grazer. However, densities of the copepod dropped by an average 81% during bloom periods. Researchers have also documented reduced feeding and increased mortality of *P. crassirostris* during grazing experiments on *A. lagunensis* and two other common IRL bloom taxa (Ma et al., 2021a,b and unpublished data), suggesting it is not a viable mitigator of many algal blooms in this estuary. In contrast, *Oikopleura* sp. was significantly more abundant during bloom periods at COA, although this was driven largely by its high densities during diatom and dinoflagellate-rich blooms in 2014 and summer 2015. However, the larvacean was still one of the most abundant taxa, with densities $>3 \text{ ind. L}^{-1}$, during the start of the 2015–2016 *A. lagunensis* blooms at MLA and TIV. Although we are unaware of any studies investigating the effects of *A. lagunensis* on *Oikopleura*, Badylak and Phlips (2008) tracked the abundances of *Oikopleura dioica* and the copepods *A. tonsa* and *O. colcarva* during a bloom of the toxic dinoflagellate *P. bahamense* in Tampa Bay (FL). While populations of both copepods declined, *O. dioica* abundances mimicked those of *P. bahamense*, suggesting it was more tolerant to the toxic alga. This resilience during some blooms, coupled with the ability to ingest copious small phytoplankton caught in mucous feeding nets (Acuña and Kiefer, 2000; Scheinberg et al., 2005; Troedsson et al., 2007), positions *Oikopleura* as the most likely mesozooplankton to suppress blooms of phytoplankton $<5 \mu\text{m}$ in the northern IRL system.

However, another layer of complexity exists for grazers able to consume *A. lagunensis*, in particular. The same EPS coating that deters some herbivores may keep the algal cells from being digested or even damaged when they are consumed. In a laboratory study testing the viability of *A. lagunensis* consumed by *A. tonsa*, Bersano et al. (2002) found undamaged cells that proceeded to inoculate new algal cultures after being sequestered inside copepod fecal pellets for 3 days. The authors postulated that the EPS layer helped protect cells from digestion, allowing them to re-enter the water column and persist as primary producers. This process has been documented for other algae as well. Porter (1976) detailed the grazing of the green alga *Sphaerocystis Schroeteri* by freshwater cladocerans from the genus *Daphnia*. Cells of this autotroph form colonies that are surrounded by a protective gelatinous sheath. Observations revealed that *S. Schroeteri* was fed on at a lower rate than unsheathed algal taxa and was resistant to digestion when consumed. In fact, $>90\%$ of ingested cells passed through the gut undamaged. The author noted that grazing did break up cell clusters and remove the protective sheath of many colonies, but this removal allowed for the uptake of nutrients by *S. Schroeteri* from within the guts of *Daphnia*, boosting algal growth that could compensate for the minor losses due to grazing.

These studies provide ample evidence that *A. lagunensis* can reduce grazing opportunities and foster malnourishment, starvation and population declines of mesozooplankton grazers. In the present study, dramatic reductions of primary grazers at all sites during the most intense blooms may have been caused by one or more of these ‘anti-grazer’ mechanisms, allowing the blooms to persist for several months. The IRL system is a complex and diverse estuary where phytoplankton communities

that were dominated by diatoms and dinoflagellates have been largely displaced over the past decade by smaller taxa that appear to evade grazing by mesozooplankton. The frequency of small-celled phytoplankton blooms is likely to increase as warming ocean temperatures favor these taxa over larger autotrophs (Flombaum et al., 2013; Phlips et al., 2015; Cloern, 2018). Recent research has revealed additional competitive advantages for some small species, such as the discovery of a protective resting stage for *A. lagunensis* that may facilitate future blooms and geographic expansion (Kang et al., 2017). This projected spread forewarns that more coastal systems will grapple with similar threats to economic, public and ecosystem health stemming from blooms of shared taxa. However, each estuary facing recurring phytoplankton blooms is unique with changing biological communities that provide different probabilities for top-down control. Therefore, it is important to systematically evaluate these potential controls with a consideration for the dynamic conditions of each ecosystem.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

KJ, LS, and HA conceived and designed the mesozooplankton monitoring plan. LS and HA collected and curated the

mesozooplankton and abiotic environmental data. EP supplied the phytoplankton data. LS analyzed the data and wrote the manuscript with support from KJ, HA, and EP. All authors contributed to the article and approved the submitted version.

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