Grazing by the Copepod *Parvocalanus crassirostris* on *Picochlorum* sp. at Harmful Bloom Densities and the Role of Particle Size

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Harmful blooms of nanophytoplankton (2–20 µm) are increasingly common and sometimes severe, but requirements and controls of such blooms (e.g., water quality constraints, requirements for nutrients, and the presence of different guilds of grazers) are poorly understood. Laboratory grazing experiments were conducted to evaluate the potential for top-down control by the copepod *Parvocalanus crassirostris* on a small harmful algal species (an unidentified chlorophyte *Picochlorum*, 1–4 µm) and to test the effects of cell sizes on grazing rates. The *Picochlorum* sp. is a strain isolated from a long-lasting harmful algal bloom in the Indian River Lagoon that reached high densities (>1 × 10⁶ cells ml⁻¹). Experiments contrasted grazing on *Picochlorum* sp. with grazing on the palatable prymnesiophyte *Isochrysis galbana* (4–6 µm) in monocultures and mixed cultures. When presented in monocultures, grazing rates on *Picochlorum* sp. were lower than grazing rates on the palatable alternative. When *Picochlorum* sp. were presented alongside *I. galbana*, copepods essentially ceased feeding on the former. In additional experiments, *P. crassirostris* were fed plastic beads with diameters of 2.0–17.9 µm to control for differences in taste, toxicity, production of mucilage and shape of potential food. *Paracalanus crassirostris* fed most efficiently on beads with diameters of 7.0–7.9 µm. Results revealed that *P. crassirostris* can consume *Picochlorum* sp., but small size and the presence of palatable cells reduces the likelihood of top-down control of blooms of *Picochlorum* sp.

**Keywords:** top-down control, size selection, background plankton, nanoplankton, Indian River Lagoon

INTRODUCTION

Harmful Algal Blooms (HABs) are an increasing problem in estuaries around the world (Berry et al., 2015; Phlips et al., 2015; Cao et al., 2017). This increase in the frequency of blooms has been attributed to eutrophication and the effects of climate change (Smayda, 2008). Recent studies have highlighted the influence of such drivers on the structure and dynamics of phytoplanktonic assemblages (Zingone et al., 2010; O’Neil et al., 2012; Phlips et al., 2015). One example of such
Picochlorum grazing rates of a common herbivorous copepod, known to thus, limiting the potential for top-down control. In this study, grazers to capture, sort, and ingest a dominant phytoplankter, (Sweat et al., unpublished data). It is a small (<2 mm long), holoplanktonic, calanoid copepod that dwells in the upper 6–20 m of tropical and subtropical estuarine, coastal, and oceanic waters (Milstien, 1979; Turner and Dagg, 1983; Wong et al., 1993; Tang et al., 1994; Almeida et al., 2012; Sun et al., 2012; Liu et al., 2013). It is common for this species and other calanoid copepods to reside permanently in the mid- to upper water column (Ma and Johnson, 2017), where they feed on microalgae and nanoplankton. These cosmopolitan copepods have been shown to tolerate a wide range of temperatures (15–31°C), salinities (20–37), and eutrophic or turbid conditions (Milstien, 1979; Wong et al., 1993; Almeida et al., 2012). *Paracalanus crassirostris* mainly grazes on nanophytoplankton (Calbet et al., 2000) and is a globally important mesozooplanktonic grazer.

Both copepods (*P. crassirostris*) and algae (*Picochlorum sp.* and *I. galbana*) were cultured by Algagen, LLC (Vero Beach, FL 32961, United States). Copepods were originally isolated from net tows in the IRL. Starter cultures of the algae were isolated from IRL by the E. Phlips at the University of Florida. Cultures were maintained in whole seawater filtered through a 0.45-µm filter, with the addition of Guillard’s F/2 marine enrichment solution. All algae were cultured in 2-l glass jars held at 26°C, with continuous aeration and 1,100 lux of light provided continuously by fluorescent bulbs. Both *I. galbana* and *Picochlorum sp.* were cultured at a salinity of 25. Copepods were cultured at 26°C and a salinity of 25 in 2-l glass jars that were aerated gently, and they were fed *I. galbana* at 15,000 cells ml⁻¹ daily. For 24 h immediately preceding experiments, copepods were maintained without food in gently aerated, 2-l glass jars under a 12/12 light/dark cycle.

Grazing on Algae

Experiments were carried out in filtered seawater and held at 26°C for 20 h under 1,100 lux of artificial light. The experimental setup followed Abu-Rezq et al. (1997) which was an experiment involving relatively high densities of algae. Adult copepods (>200 µm long) were held in 3-ml containers, with algae at specified densities. Controls to estimate algal growth and non-grazing mortality had the same densities of algae and no copepods. Five replicates were prepared for each treatment and the control.

Size Selection

In order to minimize crowding and container effects, size selection experiments were carried out in a larger volume with a lower grazer density (ten adult copepods in 200 ml of filtered seawater). Preliminary experiments showed that copepods proactively grazed on beads for about 6 h, with grazing rates in the same range as that for some algae, and then grazing slowed. For this reason, size selection experiments were limited to a 6-h duration. Therefore, copepods were held for 6 h at temperatures of 25°C and salinities of 25 under 1,100 lux of artificial light. Beakers were gently aerated (one bubble per second) to keep beads suspended. Beads were flavored with water extracted from an *I. galbana* culture and filtered through a 0.45-µm membrane to encourage grazing.

Copepods were fed six different sizes of polystyrene beads (2.0–2.4, 3.0–3.4, 5.0–5.9, 7.0–7.9, 8.0–12.9, and 13.0–17.9 µm; Spherotech, Inc.). Copepods were fed each size range separately and in a mixture of all sizes. Concentrations were ~500 beads.
ml⁻¹ for all experiments. Controls had the same seawater volume and densities of beads but lacked copepods.

Statistical Analyses
The initial and final densities of microalgae or beads were measured via flow cytometry (BD Accuri C6), and copepod survival was scored via stereomicroscopy. Grazing rates (cells copepod⁻¹ h⁻¹) were determined using equations from Frost (1972), with the mean of replicate controls used for comparison (Frost, 1972). Statistically significant differences in grazing rates among different densities of algae were determined via analysis of variance (ANOVA) and post hoc Tukey pairwise comparisons (α = 0.05).

Methodological Considerations
In such laboratory grazing experiments, crowding and container effects are common concerns (Folt and Goldman, 1981; Peters, 1984; Helgen, 1987; Burns, 1995, 2000; Preuss et al., 2009; Lee et al., 2012), but the extreme densities of algae required to mimic conditions in the superbloom (at least 10⁶ cells ml⁻¹), dictated experimental volumes. The goal was to conduct replicated trials using monocultures and 50:50 mixtures of the two algal types in experimental volumes. The goal was to conduct replicated trials using monocultures and 50:50 mixtures of the two algal types at densities of 5.8 × 10⁴, 1.2 × 10⁵, 2.3 × 10⁵, 4.8 × 10⁵, 9.6 × 10⁵, and 1.9 × 10⁶ cells ml⁻¹, but cultures only yielded 9.5 × 10⁵ cells ml⁻¹ for the trials involving mixtures of the Picochlorum sp. and I. galbana. In addition, according to our preliminary experiments, grazer densities of 2.5 individuals ml⁻¹ were necessary in order to observe measurable effects in a reasonable timeframe. To our knowledge, copepod grazing rates have not been tested with cell densities on par with the superbloom. Exploring this unique phenomenon necessitated a compromise in the experimental design and it will, therefore, be important to interpret results with due regard for possible container artifacts.

Copepods used in the experiment were mostly adult females. P. crassirostris adult males are non-feeding due to their reduced feeding appendages, so they usually have short lifespan compared to females (Lawson and Grice, 1973). Copepods were kept in batch culture with densities from 1,000 to 2,000 individuals L⁻¹. At these densities, female and male ratio is over 7:1 (Alajmi and Zeng, 2014). Thus, 80–90% of the copepods were females. Female and male copepods are usually morphologically differentiated by fifth pereiopoda and genital somite (Prusova et al., 2012). The body size of P. crassirostris females (up to 450 µm) is larger than that of the males (up to 350 µm). In preparation for experiments, adult copepods were pre-selected using a 200 µm mesh. Then the largest copepods were gently selected using a Pasteur pipet under stereomicroscopy. Beyond these selection methods, sex of individual copepods remained unconfirmed because closer scrutiny of the fifth pereiopoda and genital somites might injure the copepods. Therefore, it is acknowledged that a low percentage of non-feeding males were likely included in these experiments. Replication (n = 5) was increased in an attempt to counteract the potential increased variability in grazing rates resulting from the limited inclusion of non-feeding males.

It has been documented that prior experience with a food may influence consumption rates in downstream grazing experiments, such as with the ambush feeder Eucalanus pileatus (Price and Paffenhofer, 1984). However, filter-feeders display relatively indiscriminate grazing behavior compared to ambush feeders (Gismervik, 2006). As a filter-feeder (Santhosh et al., 2018), P. crassirostris may be less likely to be influenced by previous feeding experience. It is acknowledged, however, that the culturing of P. crassirostris adults on I. galbana prior to the start of the experiments could potentially increase grazing on that same species in short-term experiments (Ayukai, 1987). In order to minimize the influence of previous grazing experience, copepods were starved for 24 h prior to the onset of experiments. However, this common operation used in other studies sometimes inflated estimates of grazing rates (Frost, 1972; Toullac et al., 2019). It is acknowledged that some of the aforementioned methods could result in exaggerated ingestion rates under some conditions.

RESULTS
Parvocalanus crassirostris grazed on monocultures of I. galbana and the Picochlorum sp. without suffering any mortality. Grazing rates increased with increasing densities of both I. galbana (p < 0.001 between the treatments of 5.8 × 10⁴ and 1.9 × 10⁶ cells ml⁻¹) and the Picochlorum sp., although the rates were not statistically different among different Picochlorum sp. treatments (Figure 1A). At densities above 2.3 × 10⁵ cells ml⁻¹, grazing pressure on the Picochlorum sp. was significantly less than that exerted on the more palatable I. galbana (p < 0.05; Figure 1A).

There was no copepod mortality in experiments employing mixed cultures of I. galbana and the Picochlorum sp. In mixed treatments, grazing rates on I. galbana were lower than when they were presented as a monoculture, but the general pattern of increased grazing at higher densities was similar (Figure 1). In contrast, grazing on the Picochlorum sp. in the mixed culture decreased or ceased altogether, and grazing rates at densities of 1.2 × 10⁵, 4.8 × 10⁵, and 9.6 × 10⁵ cells ml⁻¹ are indistinguishable from zero (Figure 1B).

There was no copepod mortality observed in size selection experiments. Parvocalanus crassirostris grazed differentially on different size beads when fed only one size range (Figure 2A). Copepod grazing rates on 7.0–7.9 µm beads were significantly higher and less variable than consumption rates for the smallest beads (2.0–2.4 µm) and the largest beads (13.0–17.9 µm; p < 0.05; Figure 2A). When fed mixtures of bead sizes, differences in grazing rates disappeared, and the grazing rates on both the smallest beads (2.0–2.4 µm) and the largest beads (13.0–17.9 µm) increased, rendering the rates indistinguishable from rates on mid-sized beads (p > 0.05, Figure 2B).

DISCUSSION
Top-down control of algae via grazing varies with grazer characteristics, algal food type, and environmental conditions (Peters, 1984; Hansen et al., 1997; Atkinson, 1998;
Ma et al. Grazing Harmful Densities of Picochlorum

FIGURE 1 | Mean numbers of cells consumed per hour (±standard deviation, SD) by Parvocalanus crassirostris grazing on different densities of Isochrysis galbana and Picochlorum sp. presented as (A) monocultures and as (B) mixtures of 50% I. galbana and 50% Picochlorum sp. Different letters identify significantly different means based on analysis of variance and Tukey’s post hoc pairwise comparisons (α = 0.05).

Nejstgaard et al., 2007; Seuront and Vincent, 2008). Our experiments involved adults of one documented herbivore, which standardized many characteristics (body size, foraging speed, feeding efficiency, and life stage) for these experiments. This study focused on characteristics of phytoplanktonic food, in particular their densities and cell sizes.

Algal densities influenced P. crassirostris grazing rates, regardless of the species of algae being offered or whether they were offered as monocultures or mixed cultures containing HAB species. Mean grazing rates on the palatable I. galbana in monocultures ranged from $1.1 \times 10^3$ to $1.8 \times 10^4$ cells copepod$^{-1}$ h$^{-1}$, which were similar to rates reported for P. crassirostris feeding on nanoplankton (Calbet et al., 2000). P. crassirostris is a filter feeder, with no evidence of raptorial behavior (McKinnon and Klumpp, 1998; Santhosh et al., 2018). Such copepods have been observed to generate small-scale currents that entrain particles, which are subsequently captured by feeding appendages (Koehl and Strickler, 1981). It follows that encounters and resulting grazing rates will, to some degree, depend on algal densities, provided there are no other constraints. Given that many studies have shown positive density-dependent grazing patterns in copepods (Frost, 1972; Abu-Rezq et al., 1997; Anzueto-Sánchez et al., 2014), artifacts due to containment should not have affected HAB grazing substantially or differentially.

Copepods have exhibited size-selective feeding (Wilson, 1973; Berggreen et al., 1988). Parvocalanus crassirostris has been
Ma et al. Grazing Harmful Densities of Picochlorum

**FIGURE 2** | Mean numbers of beads consumed per hour (± standard deviation, SD) by Parvocalanus crassirostris grazing on (A) beads of a single size and (B) a mixture of different sized beads. Different letters identify significantly different means based on analysis of variance and Tukey’s post hoc pairwise comparisons ($\alpha = 0.05$).

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observed to graze on nanophytoplankton with diameters of 2–20 $\mu$m (Calbet et al., 2000), but this *Picochlorum* sp. and other algae at the lower edge of this range may be more difficult for *P. crassirostris* to detect, capture, or consume. The potential for a grazer to control a harmful bloom is likely influenced by whether the algae are of optimal size. The size of the *Picochlororum* sp. was 1–4 $\mu$m in diameter, which is outside of the optimal size range based upon patterns of feeding on beads (7.0–7.9 $\mu$m). Small particle size could contribute to the low grazing rates on *Picochlororum* sp. Other algal species comprising that same bloom were picocyanobacteria (<1 $\mu$m; IRL Consortium, 2015), and these harmful bloom species were smaller than the apparent optimal size of food for *P. crassirostris*, which may have made them difficult to detect, capture or consume. This copepod species was the dominant mesozooplanktonic herbivore in the IRL, and its inability to exert clear top-down control on this mixed bloom of small-celled algae may have exacerbated the chronic bloom. According to our 3-year (2014–2016) mesozooplankton survey, *P. crassirostris* populate the IRL year-round, with an average density of 5,452 ± 648 (mean ± SE
individuals m\(^{-3}\)), which comprised ~30% of total copepod abundance in the IRL (Sweat et al., unpublished data). Even if applying our highest grazing rates of 3,067 cells hour\(^{-1}\) individual\(^{-1}\), only 4.01E + 08 cells m\(^{-3}\) of *Picochlorum* sp. would be grazed per day. During the superbloom, *Picochlorum* sp. density was up to 7 million cells ml\(^{-1}\) (7E + 12 cells m\(^{-3}\)), which is 4 orders-of-magnitude higher than the estimated daily grazing capacity from *P. crassirostris*. Although abundance data were not available for mesozooplankton during the 2011 superbloom, a brown tide occurred during our mesozooplankton survey from late 2015 to early 2016. During the brown tide, numbers of *P. crassirostris* declined by 97% relative to the same months without a bloom in the preceding year (Sweat et al., unpublished data). Reductions in populations of copepods during algal blooms is a common phenomenon (Badyak and Philips, 2008). Thus, *P. crassirostris* may be a poor candidate for top-down control on algal blooms. Some studies have pointed out that nauplii and copepodites are often more abundant than the adult copepods and they can have a significant grazing impact on populations of their foods (Merrell and Stoecker, 2003). The size selection experiments also suggested this as a possible explanation. When a mixture of bead sizes was offered to *P. crassirostris*, differential grazing rates were less distinct (Figure 2B); the smallest and largest beads may have functioned as background plankton, obscuring the intermediate-sized beads or occupying the foraging time of the copepod.

In conclusion, grazing rates on *Picochlorum* sp. were much lower than grazing rates on *I. galbana*, and copepods appeared to show selective avoidance of *Picochlorum* sp. when offered the palatable alternative. Size selection experiments confirmed that *P. crassirostris* had lower grazing rates when feeding on smaller particles that were in the same size range as the unidentified *Picochlorum*. Thus, *P. crassirostris*, a dominant, cosmopolitan, herbivorous copepod present during the bloom of *Picochlorum* sp., was unlikely to exert effective top-down control on this harmful alga.

**DATA AVAILABILITY STATEMENT**

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

**AUTHOR CONTRIBUTIONS**

XM and KJ conceived the study. XM carried out data collection. XM and CJ analyzed data. All authors contributed to interpretation of the results and preparation and revision of the manuscript. All authors approved the submission.

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