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SHORT COMMUNICATION

Species specific differences in the ingestion of *Microcystis* cells by the calanoid copepods *Eurytemora affinis* and *Pseudodiaptomus forbesi*

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Copepod species showed large differences in the ingestion of *Microcystis* cells, but no difference among microcystin producing (MC+) or lacking (MC−) strains in a short feeding experiment. Differences in selective feeding may allow some copepods to better tolerate *Microcystis*.

KEYWORDS: microcystis; copepod; ingestion; zooplankton; cyanobacteria

Ingestion of *Microcystis* cells by zooplankton causes lethal and sub-lethal effects including toxicity, nutritional inadequacy and feeding suppression (Fulton and Paerl, 1987; DeMott and Moxter, 1991). Zooplankton can minimize these negative impacts by feeding adaptations to avoid ingestion or through tolerance to ingested toxins (Engstrom *et al*., 2000; Hansson *et al*., 2007). Hence, species-specific differences among ingestion rates on cyanobacteria can have major consequences for zooplankton community composition as well as the potential for managing blooms (Paerl, 1988; DeMott *et al*., 1991; Kirk and Gilbert, 1992; Wang *et al*., 2010).

Although copepods frequently dominate zooplankton and can co-exist with cyanobacteria blooms, studies on copepod-feeding behavior related to *Microcystis* are rare (Bouvy *et al*., 2001; Panosso *et al*., 2003; Work and Havens, 2003; Wilson *et al*., 2006). Tolerance for cyanobacteria varies among copepods, partly because species rely on different chemosensory cues for avoiding cyanobacterial food (Kurmayer and Juttner, 1999; Engstrom *et al*., 2000). *Microcystis* contains several toxic metabolites including microcystin (MC), microviridin, lipopolysaccharides and unidentified lipophylic compounds, which may act as cues for zooplankton to avoid ingestion (Kurmayer and Juttner, 1999; Rohrlack *et al*., 2004; Wiegand and Pflugmacher, 2005). Comparing ingestion rates on *Microcystis* strains of varying toxicity but similar morphology has been an effective method to show how some zooplankton tolerate *Microcystis* more than others (Rohrlack *et al*., 1999; Lurling, 2003; Ger *et al*., 2010).

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Copepods, especially *Eurytemora affinis* and *Pseudodiaptomus forbesi*, are the dominant zooplankton and the main food source for endangered fish in the freshwater portion of the San Francisco Estuary, where annual blooms of *Microcystis aeruginosa* raise concern for the food limited zooplankton (Muller-Solger *et al*., 2002; Sommer *et al*., 2007; Lehman *et al*., 2008). In a previous laboratory study, *Microcystis* (MC+ or MC−) was toxic to both *E. affinis* and *P. forbesi*, but the latter was able to co-exist especially with the MC+ strain, most likely because it minimized *Microcystis* ingestion (Ger *et al*., 2010). Our objective was to verify differences in the ingestion rates of *E. affinis* and *P. forbesi* on *Microcystis*, and to test the role of cellular MC as a possible copepod cue to avoid and thereby tolerate *Microcystis*. We hypothesized that in a mixed diet, *E. affinis* would ingest more *Microcystis* (MC+ or MC−) than *P. forbesi*, and that *P. forbesi* ingestion of MC+ *Microcystis* would be less than the MC− strain.

Ingestion experiments used identical organisms, culturing conditions and treatment diets as in the survival experiments detailed in Ger *et al*. (Ger *et al*., 2010). Axenic batch cultures of MC+ (UTEX 2385) and MC− (UTEX 2386) *Microcystis* were maintained in the exponential growth phase in a modified ASM-1 medium. We assumed that the only difference between the two strains used was MC content, and that each strain had a comparable nutritional profile and digestibility. Both strains were previously verified by a conventional PCR targeting the *MIC* and *mcyB* genes to assure no cross contamination, and the MC production was measured using a commercially available ELISA (Envirologix, USA). The mean cell bound concentration of the MC+ strain during the experiment was 348 $\mu g\ L^{-1}$ ($\pm$49, $n = 8$) MC−LR, which corresponds to an estimated 4.87 $\mu g\ mg\ C^{-1}$ ($\pm$0.98, $n = 7$) of MC−LR per *Microcystis* biomass. Copepods were collected from ongoing cultures that have been under controlled laboratory conditions for over 1 year. An equal biovolume of *Nannochloropsis* (2 μm cell diameter, Eustigmatophyceae) and *Pavlova* (4 μm cell diameter, Chrysophyceae) (Instant Algae, USA), IA for short, was given as food at 400 and 500 $\mu g\ C\ L^{-1}\ day^{-1}$ for *E. affinis* and *P. forbesi*, respectively. Only CV-stage copepodites and adults were used in the ingestion experiment.

Each *Microcystis* strain (MC+ and MC−) was subsampled (150 mL) from exponentially growing cultures described above and transferred to 300 mL glass flasks, diluted with 100 mL culture medium and spiked with 2 mL of 24.39 μCi/mL $NaH^{14}CO_3$ (Oak Ridge National Laboratory, USA). Flasks were capped with sterile cotton balls, swirled three times a day and incubated for 48 h, which was previously determined as adequate for the uniform uptake of the radioactive label. Cell density and exponential growth were verified by changes in absorbance at 800 nm.

Ingestion of *Microcystis* was quantified by feeding copepods a mixed diet containing ^{14}C labeled *Microcystis* during a 30 min ingestion experiment. The treatment diets consisted of a *Microcystis*−IA mixture, with the proportion of *Microcystis* at 10, 25, 50 or 100% of total food (by carbon), using either the MC+ or MC− strain of *Microcystis*, plus IA, to a total food concentration of 400 (*E. affinis*) and 500 (*P. forbesi*) $\mu g\ C\ L^{-1}$, and given in triplicates. For each replicate, about 100 copepods were transferred from the batch cultures to a 2 L glass beaker, in clean culture medium, and starved for 4 h prior to addition of labeled food. This allows sufficient time to evacuate gut contents (W. Kimmerer, San Francisco, personal communication). All experiments took place at 22°C ($\pm$1) and other conditions were identical to batch cultures. Copepods were acclimated to this temperature 24 h prior to starvation.

Labeled treatment diets were added at appropriate amounts at the beginning of the experiment. Copepods were allowed to feed for 30 min, then collected on a 150 um mesh screen and anesthetized with carbonated water to prevent loss of fecal matter (DeMott and Moxter, 1991). Copepods were flushed and rinsed three times with carbonated water to wash off any external *Microcystis* cells, and placed in a petri dish with clean carbonated water for each replicate. From each petri dish, 10, 20 and 30 copepods were selected individually with pipettes, and filtered on a 25 mm HA filter (Millipore, USA) for radioactivity analysis measured via gas proportional counting using a Tennelec LB 5100 Series III system (Canberra Industries, USA) as described in Goldman (Goldman, 1961). Hence, each replicate consisted of 60 copepods divided on three filters.

The average per copepod ingestion rate (cells $copepod^{-1}\ h^{-1}$) was calculated by comparing the specific activity of copepods (μCi/animal) with that of *Microcystis* (μCi/cell *Microcystis*). Per copepod activity was measured by taking the average of three subsamples for each replicate. The activity of *Microcystis* was estimated by filtering 1 mL of culture (in replicates) on a 25 mm diameter HA filter (Millipore, USA) and comparing total filter activity to the *Microcystis* cell density during the experiment. The following formula was used to calculate ingestion rates:

$$\text{Ingestion} = (^{14}\text{C/copepod}) \times (^{14}\text{C/cell})^{-1} \times \text{h}^{-1}$$

Differences in ingestion rates between the treatments were analyzed using a two-way ANOVA (JMP 7.0). The effect of diet and copepod species on the ingestion rate was calculated. The diet, whose attributes were further broken down to strain (MC+ or MC−) and ratio of *Microcystis* (% *Microcystis*), was analyzed for differences in the effect of these parameters on ingestion. Only significant differences at the $P = 0.05$ level are mentioned. The specific ingestion rate was calculated by dividing the ingestion rate with the biomass per copepod, which was previously measured as 1.75 and 2.54 μg C for *E. affinis* and *P. forbesi*, respectively (Bouley and Kimmerer, 2006).

Copepods ingested *Microcystis* in all treatments, though there were significant differences between species and their grazing rates on *Microcystis* (Fig. 1A). Ingestion rates varied between 500 and 4000 *Microcystis* cells copepod^{-1} h^{-1} for *E. affinis* and 170−720 *Microcystis* cells copepod^{-1} h^{-1} for *P. forbesi*, and were linearly proportional to the ratio of *Microcystis* in the diet ($r^2 = 0.66$ for *E. affinis* and 0.61 for *P. forbesi*, $P < 0.001$). There were strong differences between the two species grazing response to *Microcystis*. *Eurytemora affinis* ingestion was an order of magnitude higher compared with *P. forbesi*, for either strain and across all diets except the 10% *Microcystis* diet ($P < 0.001$). A 10-fold increase in the proportion of *Microcystis* resulted in a 3.47-fold increase for *P. forbesi* ingestion, compared to 5.76-fold increase in *E. affinis*. The slope for *E. affinis* ingestion was higher than that of *P. forbesi* (by a factor of 6.06, $P < 0.001$). Since the copepod species had comparable biomass, the specific ingestion rates showed similar trends, and the differences in ingestion rates were not due to differences in copepod size (Fig. 1B).

Results showed that the copepod species and the diet had a significant effect on the ingestion rate, independently and as an interaction term (Table Ia). Further, differences in the ratio of *Microcystis* and the way each species responded to this ratio (interaction) had a significant effect on ingestion (Table Ib). In contrast, both copepods grazed on either strain of *Microcystis* (MC+ or MC−) at similar rates (Table Ib).

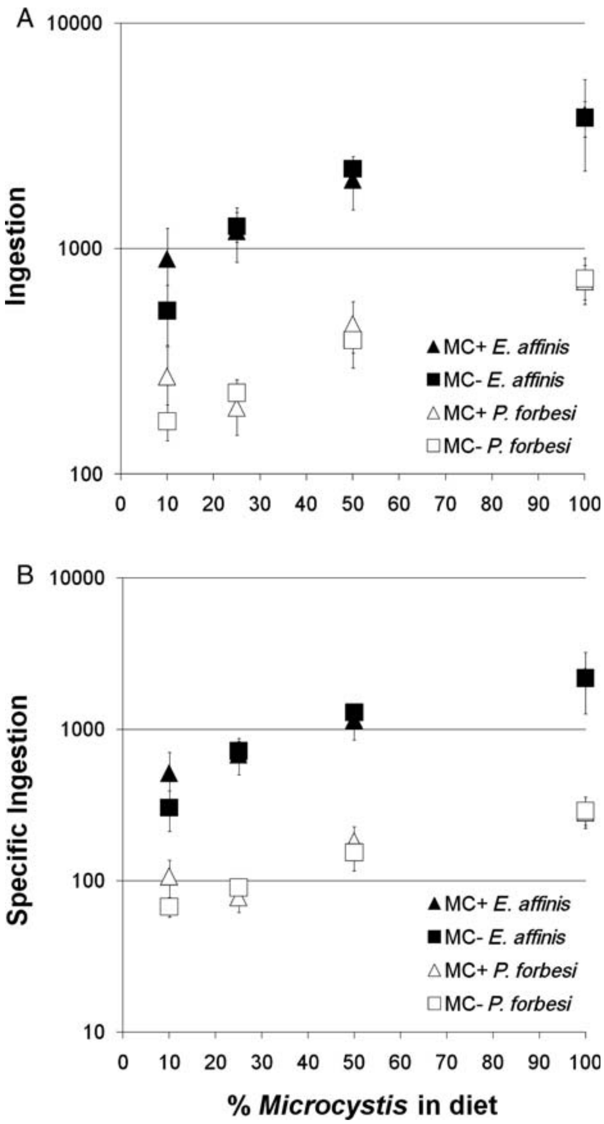

Fig. 1. (**A** and **B**) Ingestion rates of the copepods E. affinis and P. forbesi on Microcystis (MC+ or MC− strains) when provided as different proportions in a mixed diet containing Microcystis and IA. Comparing the ingestion rate per copepod [cell × (copepod h)−1] (A) with the specific ingestion rate relative to copepod biomass [cell × (μg C copepod h)−1] (B) corrects for the effect of copepod size on ingestion rates. Note the logarithmic scale on the y-axis. Bars indicate SE at the $P = 95\%$ level.

Table I: Summary results of a factorial analysis of variance on the Microcystis ingestion rate of copepods E. affinis and P. forbesi in relation to overall diet (a) and in relation to the strain (MC+ or MC−) and proportion of Microcystis in diet (%) (b)

Parameter	D.F.	*F*	*P*
(a)			
Species	1	44.246	<0.001
Diet	7	4.975	<0.001
Species × diet	7	2.950	0.036
(b)			
MC	1	0.024	0.876
%	3	11.511	<0.001
Species × MC	1	0.001	0.973
Species × %	3	5.752	0.003

Results show differences in the effect of copepod species, and specific attributes of the diet, such as presence of MC and the ratio of dietary Microcystis on copepod ingestion rates. The interaction term shows differences in how each copepod species responds to the dietary attributes.

Although *Microcystis* was ingested by both copepods, results indicate that *E. affinis* is less efficient at avoiding *Microcystis*, especially as its proportion in the diet increases. A similar comparison also found that *E. affinis* was relatively inefficient in avoiding *Nodularia* (cyanobacteria) when compared with a raptorial feeding copepod (Engstrom *et al.*, 2000). In our study, both copepods were filter-feeding calanoids, and lower *Microcystis* ingestion by *P. forbesi* is likely due to more effective selective feeding. *Microcystis* is typically the least preferred food for copepods and is ingested when alternative food becomes scarce (DeMott and Moxter, 1991; Burns and Hegarty, 1994; Kumar, 2003).

Zooplankton can co-exist with cyanobacteria through a species-specific combination of physiological tolerance to toxins and the rate of ingestion (Fulton and Paerl, 1987; Kurmayer and Juttner, 1999; Koski *et al.*, 2002). Selective feeding zooplankton that avoid cyanobacteria tend to have lower physiological tolerance to their toxins (Demott *et al.*, 1991; Kozlowski-Suzuki *et al.*, 2003; Gustaffson and Hansson, 2004; Sarnelle and Wilson, 2005). Compared to *E. affinis*, *P. forbesi* is less tolerant to dissolved MC, but more tolerant to the presence of *Microcystis* in the diet, suggesting that improved selective feeding (and not physiological tolerance) allows higher tolerance (Ger *et al.*, 2009, 2010).

Here, *P. forbesi* maintained a relatively low grazing rate even as the proportion of *Microcystis* increased in the diet. Considering also that this copepod survived over 11 days despite the presence of *Microcystis* (Ger *et al.*, 2010), such low *Microcystis* ingestion provides evidence that *P. forbesi* is indeed more efficient at avoiding harmful food. Since both copepods had similar optimal diet concentrations, it is likely that they ingest comparable levels of IA when *Microcystis* is not present. Yet, it is not possible to calculate the selective feeding efficiency without knowing the ingestion of the IA cells in addition to *Microcystis*. This information will be critical in future studies to compare selective feeding among copepods exposed to cyanobacteria. Thus, while the results do not prove it, they do provide further evidence that *P. forbesi* is more efficient at avoiding *Microcystis* compared with *E. affinis*.

Previously, *P. forbesi* survival was higher on a MC+ diet, indicating lower ingestion on this strain (Ger *et al.*, 2010). Contrary to expectation, *P. forbesi* ingested both strains similarly, at least in the short term. Since some copepods avoid cyanobacteria species regardless of the strain and others ingest only strains that lack certain metabolites, it is possible that both copepods in this study responded to a general *Microcystis* metabolite rather than MC (Kurmayer and Juttner, 1999; Engstrom *et al.*, 2000). However, simply looking at the initial response to a 30 min *Microcystis* exposure may be misleading because previous exposure to *Microcystis* can improve zooplankton tolerance through changes in feeding behavior (Gustaffson and Hansson, 2004; Sarnelle and Wilson, 2005). Indeed, *P. forbesi* tolerance to *Microcystis* and the strain-specific effects (MC+ vs. MC−) emerged after 5 days of being exposed to the diet in the earlier survival experiment (Ger *et al.*, 2010).

When this is viewed in light of the current ingestion results, the negative relationship between ingestion and copepod survival as well as the importance of acclimation to *Microcystis* is highlighted. The results show that *P. forbesi* can avoid *Microcystis* better than *E. affinis* even during the initial response without any acclimation to the cyanobacteria. However, we know that *P. forbesi* tolerance to *Microcystis* increases after 5 days of exposure (Ger *et al.*, 2010). We also know that following this acclimation period, *P. forbesi* survival is higher when fed the MC+ *Microcystis*, most likely because it uses MC as a cue to avoid this strain (Ger *et al.*, 2010). Yet, *P. forbesi* ingested both strains (MC+ and MC−) of *Microcystis* at comparable rates in this short-term exposure. This is most likely because *P. forbesi* needs an acclimation period to further decrease the ingestion of *Microcystis*, and particularly the MC+ strain. As such, we predict that acclimation is a significant factor increasing the efficiency of *P. forbesi* feeding selectivity, and it may be a critical process for this copepod to detect different strains using MC as a potential cue to avoid ingestion. Accordingly, comparing survival with ingestion before and after exposure to *Microcystis* would clarify why some zooplankton can improve tolerance to cyanobacteria over the short term (within lifetime). This would also reveal if copepods and especially *P. forbesi* develop strain-specific responses to *Microcystis* after several days of exposure.

Laboratory-based studies can provide mechanisms that are useful but may not represent natural conditions. Using single-celled *Microcystis* to measure zooplankton ingestion is a common limitation that can overestimate what happens in nature (Wilson *et al.*, 2006). *Microcystis* typically exists as large colonies during blooms, which increases efficiency of feeding selectivity in copepods (Tackx *et al.*, 2003; Wilson *et al.*, 2006; Tillmans *et al.*, 2008). For this reason and because of the possible effects of previous exposure explained above, copepods are expected to ingest less *Microcystis* during natural blooms. Finally, the use of non-living IA as "good" food may have caused the copepods to ingest more *Microcystis* compared to a control diet with live algae, resulting in an overestimation of its ingestion. Thus, our results likely represent an upper limit for the ingestion of *Microcystis* by the copepods *E. affinis* and *P. forbesi*.

The results support conclusions of the previous survival experiment that *P. forbesi* can tolerate *Microcystis* better than *E. affinis* due to its superior ability to avoid *Microcystis* while most likely feeding selectively on alternative food sources. Selective grazing can promote *Microcystis* by eliminating phytoplankton competitors, and *Microcystis* can further shift the zooplankton community to the dominance of selective feeding or smaller zooplankton, creating a more stable plankton assemblage (Fulton and Paerl, 1987; Hansson *et al.*, 2007; Wang *et al.*, 2010). We found that copepods ingest *Microcystis* at different rates, which may have significant effects on both the phytoplankton and zooplankton community in the San Francisco Estuary. Specifically, *P. forbesi* is more likely to co-exist with and may promote blooms of *Microcystis* via highly selective feeding on competing phytoplankton species.

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