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Predatory Activity of Myxobacteria *Corallococcus exiguus* against Soil Inhabiting Bacteria

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Abstract

Prokaryotic micropredators, including myxobacteria, shape the structure of the community in the soil as they prey on other microorganisms. Their unique behavior in nature has raised the interest in exploiting these bacterial groups to combat the threatening antibiotic resistance. The objective of this study is to assay the antibacterial activity of *Corallococcus exiguus*, a member of myxobacteria, based on their predation ability against soil inhabiting bacteria. A total of 17 soil bacteria from different taxa were preyed upon three *C. exiguus* isolates on TPM buffer agar medium. Based on the predation assay, all the three isolates actively killed all the Gram-negative Alphaproteobacteria and Betaproteobacteria members used in this study. Protease producing assay using casein as substrate revealed that these isolates were able to break down the protein with lytic index up to 1.33 ± 0.10. Their ethyl acetate extracts slightly inhibited the growth of one selected Gram-positive bacterium. Hydrolytic enzyme and secondary metabolite produced by *C. exiguus* are considered to play an important role in their predation activity.

Keywords: Antibacterial, *Corallococcus*, Myxobacteria, Predator, Prey, Soil

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Introduction

Predation plays a vital role in the survival of microorganisms in nature. However, unlike in macroorganisms, predation in microorganisms is often overlooked and underexplored. Predation in microorganisms shapes the structure of the microbial community in the environment. It can significantly reduce the relative abundance of microbial community members and shift the species composition (Feng *et al.*, 2017). A number of bacteria belong to *Deltaproteobacteria* are reported to be predators for other microorganisms. Their members such as *Bdellovibrio bacteriovorus* has thoroughly been studied for their predation activity specialized on Gram negative bacteria. Based on this capability, they are projected to control some of infamous pathogens causing acute hepatopancreatic necrosis disease in shrimps (Kongrueng *et al.*, 2017) and acquired infection in cystic fibrosis patients (Iebba *et al.*, 2014).

Myxobacteria group also known to prey on a wide range of microorganisms, from prokaryotic to eukaryotic cells. They are belong to a newly classified Phylum *Myxococcota* (Waite et al., 2020) (previously a member of Class *Deltaproteobacteria* in the Phylum *Proteobacteria*). Myxobacteria are mostly inhabit soil and other terrestrial habitat throughout the world. They are able to form fruiting bodies when starving, move on a solid surface, and produce chemical compounds capable of killing their prey microorganisms. Some of the recently found chemical compunds from myxobacteria are myxadazoles (Li *et al.*, 2021) and myxochelins (Wang *et al.*, 2021). With the increasing need for the new antibiotics due to antimicrobial resistance, exploring predatory microorganisms as a source of novel antibiotics has become an alternative endeavor to tackle this problem.

In addition to provide antibiotic materials, these predatory myxobacteria can potentially be employed as biocontrol agents against soil-borne pathogens in cultivated

plants. Myxobacteria *Corallococcus exiguus* was reported to inhibit *Fusarium odoratissimum* causing Panama disease in banana (Meliah *et al.,* 2020) while *Myxococcus xanthus* was reported to suppress *Ralstonia solanacearum* causing bacterial wilt disease in tomato (Dong *et al.,* 2022). Both studies reported the possible use of enzymes produced by myxobacteria to combat the pathogens. It is important to understand preferred preys of these predatory myxobacteria and their characteristics to effectively use them in both pharmaceutical and agricultural industries. Therefore, this study was conducted to assay the antibacterial activity of myxobacteria, especially *Corallococcus exiguus* based on their predation ability against soil inhabiting bacteria.

Research Methods

Bacterial strains

Three myxobacterial isolates *C. exiguus* SLU 3.3, KR39b.5 (Meliah *et al.,* 2020) and TE08-TB8 (Meliah *et al*., 2022) were used as predators in this study. They were collected from soil and karst samples in Sumatra separately in 2017-2018. Seventeen soil bacteria from different taxa were used as preys. These bacteria were obtained from the Indonesian Culture Collection (InaCC) as listed in Table 1.

Table 1. Bacterial strains used as prey and their taxonomic classification

Taxonomic classification	Strain	Source of sample	Geographical origin
Gram negative, *α-Proteobacteria*	*Rhizobium nepotum* InaCC B1174	Soil	Mount Tambora, West Nusa Tenggara
	Novosphingobium barchaimii InaCC B1175	Soil	Mount Tambora, West Nusa Tenggara
	Ensifer adhaerens InaCC B1176	Soil	Mount Tambora, West Nusa Tenggara
	Sphingobium yanoikuyae InaCC B1183	Soil	Mount Tambora, West Nusa Tenggara
Gram negative, *β-Proteobacteria*	*Alcaligenes faecalis* InaCC B444	Soil	Batimurung, Sulawesi
	Achromobacter spanius InaCC B845	Soil	Maratua Island
	Burkholderia tropica InaCC B852	Soil	Berau
	Azoarcus evansii InaCC B926	Paddy field soil	Indramayu, West Java
	Azospira oryzea InaCC B931	Paddy field soil	Indramayu, West Java
Gram negative, *γ-Proteobacteria*	*Pseudomonas putida* InaCC B72	Soil	North Kolaka, Sulawesi
	Klebsiella variicola InaCC B827	Soil	Wain River, Balikpapan
	Pantoea rodasii InaCC B847	Soil	Maratua Island
	Enterobacter aerogenes InaCC B865	Soil	Bangkirai Hill, Balikpapan
	Acinetobacter nosocomialis InaCC B897	Soil	Mahakam river, Kalimantan
Gram positive, high G +C, *Firmicutes*	*Bacillus cereus* InaCC B62	Soil	North Kolaka, Sulawesi
	Lysinibacillus xylanilyticus InaCC B347	Soil	Papua
	Edaphobacillus lindanitolerans InaCC B1087	Soil	Rambut Island, Jakarta

Predation assay on soil inhabiting bacteria

Predation assay was performed as mentioned by Morgan *et al.* (2010) with some modifications in the medium used to prepare the prey cells and instrument employed to count the optical density of both myxobacteria and soil bacteria cells. Myxobacteria cells were grown in 50 mL Casitone Yeast Extract broth (3 g casitone, 1 g yeast extract, 1.36 g CaCl2, 1000 mL distilled water; pH 7.2) for 5 days on shaker incubator. The cells were harvested by centrifuging at 5000 rpm for 15 minutes and then resuspended with 300µL TPM buffer (10 mL 0.8M $MgSO_4.7H_2O$, 10 mL 1M Tris-HCl pH 7.6, 980 mL distilled water).

Prey bacteria were prepared by inoculating them into Nutrient broth medium overnight on a shaker incubator. The inoculant was centrifuged at 5000 rpm for 15 minutes. TPM buffer was added to the cells obtained to make the density of ± 10^9 cells/mL. The density of the cells was adjusted by McFarland 4 solution. As many as 200 µL of cells suspension was spread on TPM agar (TPM buffer solidified with 1.5% agar). Myxobacterial cells suspension was dropped at the center of the prey plate in the amount of 10 µL. The plates were incubated at room temperature for 5 days. The procedure was performed twice for each prey.

Myxobacteria cells suspension was dropped onto the center of Casitone-Tris agar (CTT; 10 g casitone, 10 mL 0.8M $MgSO_4.7H_2O$, 10 mL 1M Tris-HCl, 980 mL distilled water, 15 g agar) as positive control. The distance of myxobacterial predation was treated as radius. It was measured from the center spot to the outer part of the clear zone and repeated 5 times for different end.

The mean distance and standard deviation of the myxobacterial swarm on assayed plates were calculated using data analysis tool integrated into Microsoft Excel. The cluster heatmap of myxobacteria and prey was constructed using the ComplexHeatmap R package (Gu *et al.*, 2016) in R studio (RStudio, 2020). Mean distance of each prey was used as variable.

Proteolytic assay

Agar plug containing myxobacteria cells was placed onto an agar medium containing skim milk casein (1 g glucose, 2.5 g yeast extract, 20 g agar and 10 g casein sterilized separately. The medium was dissolved in a total of 1000 mL distilled water) to assay their ability to lyse protein (Kiran *et al.*, 2015). They were incubated in 30^{o}C for 4 days. The lytic index was determined by measuring the ratio of the diameter of clear zone and diameter of the colony. This procedure was performed three times**.**

Antimicrobial assay of myxobacterial extracts

Myxobacterial extracts were prepared by inoculating 5 mL of seed culture to 100 mL CTT medium in 500 mL Erlenmeyer flask. After incubation for 4 days on shaker incubator, the culture was centrifuged at 10000 rpm, 4^{o}C. The supernatant obtained was added with 100 mL ethyl acetate and rotated overnight. The upper phase obtained was evaporated at 40^{o}C using rotary evaporator. The extract was then diluted with 1 mL ethyl acetate and stored in 4 ^{o}C (Meliah *et al*., 2020).

Antimicrobial assay was conducted using agar disc diffusion method (Balouiri *et al.*, 2016) on a double layer medium. A solid Mueller Hinton medium (MH; Oxoid) was used for the bottom layer. For the upper layer, a mixture of semi solid MH and *Lysinibacillus xylanilyticus* InaCC B347 cells with a density of 10^6 cells/mL was employed. This mixture was poured onto the bottom layer. Ethyl acetate extract of myxobacterium in a total of 40 µL was dropped on a 6 mm paper disc. The paper disc was air dried and subjected to 45 minutes of ultraviolet light exposure. This paper disc was put on a double layer medium prepared and then incubated at 4 ^{o}C for two hours. The incubation process was continued at a room temperature for 4 days.

Results and Discussion

Predation assay using 17 soil inhabiting bacteria revealed that myxobacteria *C. exiguus* SLU3.3, TE08-TB8, and KR39b.5 were able to prey on a total of four *Alphaproteobacteria* and five Betaproteobacteria members used in this study. These myxobacteria displayed higher predatory activity against *Betaproteobacteria Azospira oryzea*, makes it the most susceptible prey in this study. The predation activity was indicated by the length of myxobacterium trace from the initial spot to the remining visible prey

cells on agar plate. This predation activity decreased the area of prey lawn which created a seemingly clear zone, hence indicated the death of the prey cells.

A few differences in prey range of *C. exiguus* were showed against *Gammaproteobacteria* and *Firmicutes* members. *Pantoea rodasii* and *Acinetobacter nosocomialis* can be consumed by the three myxobacteria. On the other hand, *Klebsiella variicola* can only be consumed by *C. exiguus* TE08-TB8. In total, *C. exiguus* TE08-TB8 preyed on 14 soil bacteria. This makes the isolate as the most aggressive among tested myxobacteria in this study. Meanwhile, *Lysinibacillus xylanilyticus* InaCC B347, a member of *Firmicutes* was the only Gram positive that can be consumed by the three myxobacteria. Only *C. exiguus* KR39b.5 showed predation activity on *Edaphobacillus lindanitolerans*. These data were exhibited in Figure 1.

The assay also showed that the predation in *C. exiguus* is facultative as they were able to grow well on CTT medium consist of casitone and yeast extract as their nitrogen source in the absence of prey bacteria. These nutrients are easier to digest than prey bacteria based on the mean distance calculated from the assayed plates. The CTT data of KR39b.5 plates were excluded due to the presence of contaminant cells on the plates. Those cells might interfere the result of the assayed plates.

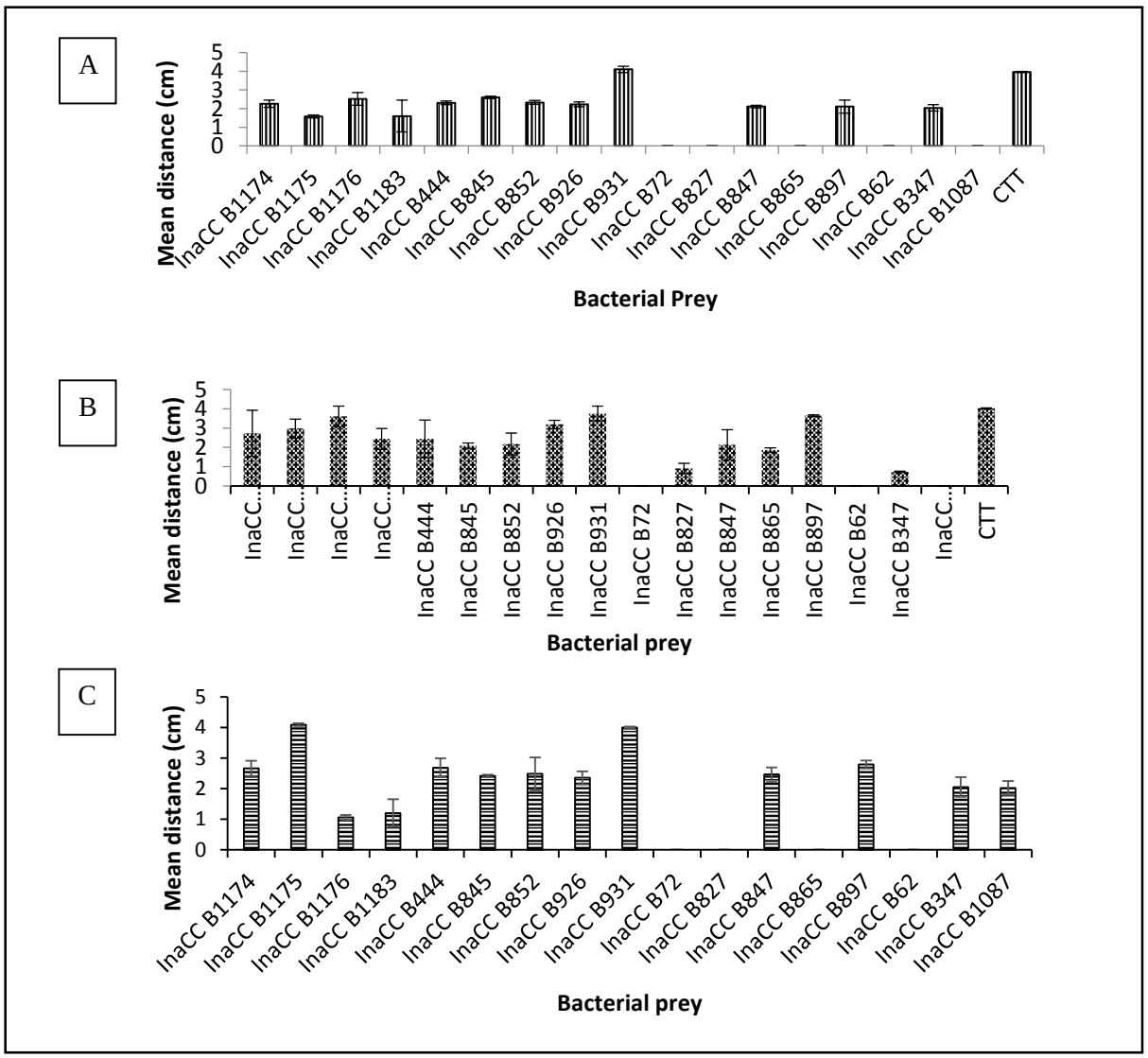

Figure 1. Mean distance of *C. exiguus* SLU3.3 (A), TE08-TB8 (B), and KR39b.5 (C) colonies from the center point during predation assay on various soil inhabiting bacteria. Tested soil bacteria were labeled by their InaCC collection number.

Most of predatory performance of myxobacteria was studied in the genus *Myxococcus*, particularly *Myxococcus xanthus* (Berleman *et al.*, 2006; Morgan *et al.*, 2010). They are known to have a broad range of prey from different taxa. However, it is also reported that *Corallococus* had a wide range of prey microorganisms, including *Escherichia coli*, *Pseudomonas aeruginosa*, *Bacillus subtilis*, *Staphylococcus aureus*, and *Candida albicans* (Livingstone *et al.*, 2020). Based on the predation assay, the three *Corallococus* were unable to prey on *P. putida* and *B. cereus*.

A study involving *P. putida* and *Cystobacter ferrugineus*, a member of myxobacteria, revealed that *P. putida* capable of surviving myxobacterial predation by increasing the expression of genes involved in ferric uptake (*furA*) and mucoid conversion (Akbar & Stevens, 2021). By increasing the iron uptake, their chance to access iron for their growth from the environment is greater than that of their predator. The mechanism of *Bacillus* cells to prevent annihilation by predatory myxobacteria differs among their species. *B. licheniformis* cells are reported to deactivate myxovirescin A via glucosylation employing the glycosyltransferase (GTase) YjiC in the process (Wang *et al.*, 2019). Myxovirescin A is a secondary metabolite produced by *M. xanthus* to kill prey microorganisms (Xiao *et al.*, 2011). Meanwhile, *B. subtilis* cells produce antibiotic bacillaene and spores to protect themselves from *M. xanthus* (Müller *et al.*, 2014). However, apparently the same mechanism is not applicable to other myxobacteria species as previously reported by Livingstone *et al.* (2020) against predatory *Corallococus* spp. These defense mechanisms show that as the predators develop several mechanisms to kill their preys, the preys also develop mechanisms to avoid predation. Hence, predation in nature is suggested to affect not only the population but also evolution of microorganisms involved (Kaitala *et al.*, 2020).

The dendrogram generated from the cluster heatmap showed that predator *C. exiguus* SLU3.3 and TE08-TB8 were similar to each other than KR39b.5. Based on the mean distance of swarming colonies on agar plates, the analysis separated prey into two major groups consisted of relatively susceptible and resistant to the predatory activity of *C. exiguus* (Figure 2). Prey bacteria labeled as InaCC B347, InaCC B1087, InaCC B865, InaCC B827, InaCC B72 and InaCC B62 belonged to the resistant group. The blue area displayed the short distance of predator colonies from their origin spot, hence indicating low predatory activities.

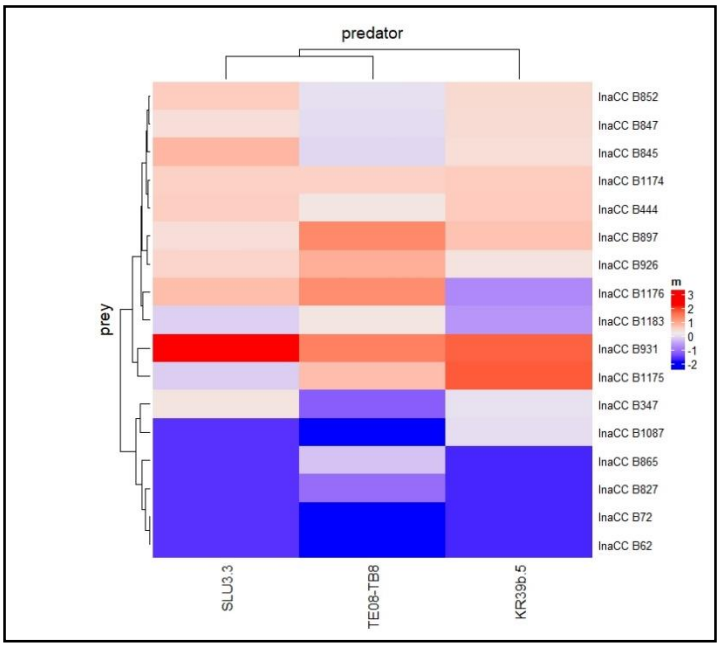

Figure 2. The clustering of predator and prey based on predatory mean distance. Blue indicates lower value and red indicates higher value of standardized mean distance of predator swarm.

Myxobacteria generally attack their target by utilizing their ability to produce chemical substances to degrade cell components of prey microorganisms and their ability to move on a solid surface known as gliding motility. This gliding motility helps myxobacteria in hunting their prey in a way that a group of wolves hunt and attack their prey (Berleman & Kirby, 2009). This motility consists of adventurous (A) and social (S) motility systems (Nan *et al.*, 2011). Mutation of their locomotion system, especially the adventurous motility system encoded by *cglB* showed a 35-55% predation ability decrease in *M. xanthus* (Pham *et al.*, 2005).

Based on protease assay, all the myxobacteria tested in this research are capable of degrading skim milk casein in the assay medium. Their lytic indices range from 1.18-1.33 (Table 2). The assay of their ethyl acetate extracts on the only Gram positive isolate killed by *C. exiguus* revealed that the extracts were slightly able to inhibit the prey bacteria. We tried to analyze their volatile compounds of the extracts using gas chromatography-mass spectrometry. However, none of them were detected. The fermentation medium, extraction method, and solvent chosen were suggested to cause this result. A study with the same myxobacterial group reported the use of VY/2 medium as the fermentation medium and solid phase microextraction fibers to collect volatile compounds from myxobacteria successfully detected important compounds useful against phytopathogens (Ye *et al.*, 2020).

Table 2. The ability of *C.exiguus* strains to produce protease and inhibit Gram Positive *L. xylanilyticus* InaCC B347 as measured by clear zone on agar plates

Isolate ID	Clear zone index	
	Skim milk casein	**Extract against *L. xylanilyticus* InaCC B347**
C. exiguus SLU3.3	1.33 ± 0.10	0.17 ± 0.0
C. exiguus TE08-TB8	1.28 + 0.21	0.22 ± 0.09
C. exiguus KR39b.5	1.18 ± 0.02	0.17 ± 0.0

Chemical substances produced by myxobacteria for their predation activity include hydrolytic enzymes and secondary metabolites. Hydrolytic enzymes that are suggested to influence their predation activity are proteases. Protease produced by predatory bacteria degrades the protein in the cell wall of their prey (Grenier, 1994). Protease encoded by *mepA* in myxobacteria *M. xanthus* is revealed to play significant role in killing prey cells (Berleman *et al.*, 2014). Several reports showed that Gram negative bacteria are prone to predation by myxobacteria and other predatory bacteria, such as *Bdellovibrio bacteriovorus* (Im *et al*., 2018). The property of their cell walls might influence their susceptibility. The thin peptidoglycan of Gram negative bacteria tend to get lysed easier than the thick peptidoglycan of Gram positive bacteria. In this study, at least 10 out of 13 Gram negative bacteria were lysed by *C. exiguus.* The genus of *Corallococcus* is known to produce acidic and neutral extracellular protease (Dahm *et al.*, 2015). A report predicted that 4.9-5.5% of *Corallococcus* genome encodes proteases that play an important role in their predation activity (Zhao *et al.*, 2021).

The same report also stated that the genus *Corallococcus* harbored a tremendous amount of biosynthetic gene clusters in their genome with an average of 57 clusters. Therefore, it is believed that the genus is capable of producing multiple secondary metabolites. The genus was reported to produce active compounds, such as corallorazines (Schmitz *et al.*, 2014), corallopyronins (Schäberle *et al.*, 2015), and coralmycins (Kim *et al.*, 2016) to inhibit other microorganisms. However, the extract of *C. exiguus* only slightly inhibited the growth of Gram positive *Lysinibacillus xylanilyticus* tested in this study. *L. xylanilyticus* is a xylan degrading Gram positive bacteria and first described from forest humus, Korea (Lee *et al.* 2010). Based on these results, both enzymatic and secondary metabolite were suggested to assist the predatory activity of *C. exiguus* against soil inhabiting bacteria.

Conclusion and Suggestion

Myxobacteria *C. exiguus* used in this study showed predatory activity against at least 12 soil inhabiting bacteria. They were mostly preying on Gram negative Alphaproteobacteria and Betaproteobacteria groups. On the other hand, only one Gram positive bacterium, namely *Lysinibacillus xylanilyticus* could be eaten by *C. exiguus*. Further analysis revealed that *L. xylanilyticus* was slightly inhibited by ethyl acetate extract of *C. exiguus*. All the three myxobacteria were capable of degrading protein. Their ability to produce protease and secondary metabolite are considered to play a role in predatory activity.

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