

JEONG ET AL.--- Feeding by *Luciella masanensis*

**Feeding by the *Pfiesteria*-like Heterotrophic Dinoflagellate *Luciella masanensis***

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**ABSTRACT:** To explore the feeding ecology of the *Pfiesteria*-like dinoflagellate *Luciella masanensis* (GenBank Accession number = AM050344, previously Lucy), we investigated the feeding behavior and the kinds of prey species that *L. masanensis* fed on and determined its growth and ingestion rates of *L. masanensis* when it fed on the dinoflagellate *Amphidinium carterae* and an unidentified cryptophyte species (equivalent spherical diameter, ESD = 5.6  $\mu\text{m}$ ), which were the dominant phototrophic species when *L. masanensis* and similar small heterotrophic dinoflagellates were abundant in Masan Bay, Korea in 2005. Additionally, these parameters were also measured for *L. masanensis* fed on blood cells of the perch *Lateolabrax japonicus* and the raphidophyte *Heterosigma akashiwo* in the laboratory. *L. masanensis* fed on prey cells by using a peduncle after anchoring the prey with tow filament, and was able to feed on diverse prey such as cryptophytes, raphidophytes, diatoms, mixotrophic dinoflagellates, and the blood cells of fish and humans. Among the prey species tested in the present study, perch blood cells were observed to be the optimal prey for *L. masanensis*. Specific growth rates of *L. masanensis* feeding on perch blood cells, *A. carterae*, *H. akashiwo*, and the cryptophyte, either increased continuously or became saturated with increasing the mean prey concentration. The maximum specific growth rate of *L. masanensis* feeding on perch blood cells ( $1.46 \text{ d}^{-1}$ ) was much greater than that of *A. carterae* ( $0.59 \text{ d}^{-1}$ ), the cryptophyte ( $0.24 \text{ d}^{-1}$ ), or *H. akashiwo* ( $0.20 \text{ d}^{-1}$ ). The maximum ingestion rate of *L. masanensis* on perch blood cells ( $2.6 \text{ ng C grazer}^{-1} \text{ d}^{-1}$ ) was also much higher than that of *A. carterae* ( $0.32 \text{ ng C grazer}^{-1} \text{ d}^{-1}$ ), the cryptophyte

(0.44 ng C grazer<sup>-1</sup> d<sup>-1</sup>), or *H. akashiwo* (0.16 ng C grazer<sup>-1</sup> d<sup>-1</sup>). The kinds of prey species which *L. masanensis* is able to feed on were the same as those of *Pfiesteria piscicida*, but very different from those of another *Pfiesteria*-like dinoflagellate *Stoeckeria alpicida*. However, the maximum growth and ingestion rates of *L. masanensis* on perch blood cells, *A. carterae*, *H. akashiwo*, and the cryptophyte were considerably lower than those of *P. piscicida*. Therefore, these three dinoflagellates may occupy different ecological niches in marine planktonic communities, even though they have a similar size and shape and the same feeding mechanisms.

**Key Words.** Food web, Growth, Harmful Algal Bloom, Ingestion, Peduncle, Protist, Red tide

Heterotrophic dinoflagellates are one of the major groups of heterotrophic protists in marine environments (Jacobson and Anderson 1986; Jeong 1995; Lessard 1984, 1991). Heterotrophic dinoflagellates play the following diverse roles in marine plankton communities (Lessard 1991; Jeong 1999): (1) they prey on bacteria (Lessard and Swift 1985; Strom 1991), phototrophic planktons (Buskey, Coulter, and Brown 1994; Hansen 1992; Jacobson and Anderson 1986; Jeong and Latz 1994; Jeong et al. 2001a, 2001b, 2003a, 2003b, 2004c; Kim and Jeong 2004; Naustvoll 1998; Strom and Buskey 1993; Tillmann 2004), heterotrophic protists (Hansen 1991; Jeong et al. 2007), and the eggs and naupliar stages of metazoans (Jeong 1994b); (2) they are important prey for some metazoans (Gifford and Dagg 1991; Jeong

1994a, 1999, 2001a; Klein Breteler 1980) and heterotrophic protists (Jeong et al. 2004a); and (3) some dinoflagellates are predators of and simultaneously prey for other dinoflagellates (Jeong et al. 1997). Therefore, exploring the interactions between heterotrophic dinoflagellates and their co-occurring planktons (i.e. their prey or predators) is very important in understanding the cycling of materials, energy flow, and population dynamics in marine planktonic food webs.

The harmful heterotrophic dinoflagellate *Pfiesteria piscicida* was first reported in the early 1990's, and several *Pfiesteria*-like dinoflagellate (PLD) species were reported later (Burkholder and Glasgow 2001; Jeong et al. 2005b; Litaker et al. 2005, Mason et al. 2007; Steidinger et al. 1996). Both scientists and the public have paid attention to these dinoflagellates because some of the species are known to be harmful to fish (Burkholder et al. 1992; Glasgow et al. 2001) and shellfish (e.g. Springer, Burkholder, and Shumway 1996). They feed on their prey using a peduncle (a feeding tube) after anchoring the prey by a tow filament (Burkholder and Glasgow 1995; Jeong et al. 2005a). While there have been many studies on the ecology, physiology, and toxicity of *P. piscicida* and *Pseudopfiesteria shumwayae* (Burkholder and Glasgow 1997; Feinstein et al. 2002; Gordon and Dyer 2005; Lewitus, Glasgow, and Burkholder 1999; Moeller et al. 2007; Seaborn et al. 1999; Setälä, Autio, and Kuosa 2005; Stoecker and Gustafson 2002), there have been fewer studies on those of PLDs thus far (Jeong et al. 2005a; Parrow and Burkholder 2004).

*Luciella masanensis* (previously Lucy) is a PLD that was first observed in the water samples collected from the St. Lucie River Estuary, Florida, USA (Litaker et al. 2005; Mason et al. 2007; Steidinger et al. 2001). The presence of this dinoflagellate has not yet been reported outside the USA and no studies of its ecology have been reported until now. Now one important question arises; is the ecology of *L. masanensis* similar to that of *P. piscicida* or other PLDs? We have recently found *L. masanensis* in Masan Bay, located off the southern coast of Korea. *P. piscicida* and another PLD *Stoeckeria algicida* were also found in Masan Bay (Jeong et al. 2005a, 2005b, 2006). If *L. masanensis*, *P. piscicida*, and *S. algicida* respond differently to co-occurring potential prey, their relative abundances may be quite different even when they are present together.

We established clonal cultures of the Korean strains of *L. masanensis* that were collected from the surface of Masan Bay. To understand the basic ecology of *L. masanensis*, we examined its feeding behavior and the kinds of prey it fed on, and conducted experiments to examine its numerical and functional responses while feeding on the dinoflagellate *Amphidinium carterae*, the raphidophyte *Heterosigma akashiwo*, an unidentified cryptophyte species, and perch blood cells in the laboratory. *Amphidinium* spp. and cryptophytes were the dominant phototrophic species when *L. masanensis* and similar small heterotrophic dinoflagellates were abundant in Masan Bay, Korea in 2005. Also, *H. akashiwo* and perch blood cells are known as the optimal prey for *S. algicida* and *P. piscicida*, respectively (Jeong et al. 2005a, 2006).

The feeding behavior and the kinds of prey species that *L. masanensis* fed on and the numerical and functional responses of *L. masanensis* to several prey species were compared to those of *P. piscicida*, and *S. alpicida*. Also, the maximum growth and grazing rates of *L. masanensis* feeding on the algal prey, obtained in the present study, were compared to those of other heterotrophic/mixotrophic protists on the same prey species, reported in the literature. The results of the present study provide a basis for understanding the interactions between *L. masanensis* and its prey species and also the differences in the feeding ecology among *L. masanensis*, *P. piscicida*, and *S. alpicida*, which are clearly divergent in the phylogeny based on the small subunit rDNA sequences (Jeong et al. 2005b).

## MATERIALS AND METHODS

**Isolation and culture of *Luciella masanensis*.** Using water samplers, plankton samples were collected at a pier in Masan Bay, Korea, in April 2005 when the water temperature and salinity were 16.0 °C and 28.0 practical salinity units (psu), respectively. The samples were screened gently through a 154- $\mu\text{m}$  Nitex mesh and placed in 1-L polycarbonate (PC) bottles. A mixture comprising an unidentified cryptophyte (ESD = 5.6  $\mu\text{m}$ ) and perch blood cells were added as food. The bottles were placed on plankton wheels rotating at 0.9 rpm and was incubated at 20 °C under an illumination of 20  $\mu\text{E m}^{-2} \text{s}^{-1}$  provided by cool white fluorescent light on a 14:10 h light-dark cycle. Three days later, aliquots of the enriched water were transferred to 6-well tissue culture plates and a clonal culture of *L. masanensis* was established

by two serial single cell isolations. As the concentration of *L. masanensis* feeding on the prey mixture increased, the grazers were subsequently transferred to 32, 80, 270, and 500 ml PC bottles of fresh blood cells. The bottles were again filled to capacity with freshly filtered seawater, capped, and placed on a rotating wheel, as described above. Once dense cultures of *L. masanensis* (7,000--8,000 cells ml<sup>-1</sup>) were obtained, they were transferred to 500-ml PC bottles containing *Amphidinium carterae* (ca. 30,000--40,000 cells ml<sup>-1</sup>) or perch blood cells (ca. 300,000 cells ml<sup>-1</sup>) everyday. Experiments were conducted once large volumes of *L. masanensis* culture were available. The carbon content of *L. masanensis* was estimated from the cell volume (see next subsection) according to the method of Menden-Deuer & Lessard (2000). The morphology and DNA sequence of this *L. masanensis* strain are provided in Mason et al. (2007).

**Preparation of prey.** Phototrophic cells were grown in enriched f/2 seawater media (Guillard and Ryther 1962) without silicate at 20°C with continuous illumination of 20 μE m<sup>-2</sup> s<sup>-1</sup> provided by cool white fluorescent lights. Only cultures in the exponential growth phase were used for the feeding experiments.

Perch blood cells, obtained by cutting the fin of the tail of live adults (ca. 50 cm), were maintained at 4 °C. The experiments on the perch blood cells started within 2-3 hours after they were obtained.

The carbon content for the perch blood cells (0.009 ng C per cell,  $n > 2,000$ ) and *A. carterae* (0.07 ng C per cell) was measured using a CHN analyzer (CM 5012 CO<sub>2</sub> Coulometer, UIC Inc, Joliet, IL, USA). Also, the carbon contents of *Heterosigma akashiwo* (0.1 ng C per cell) and an unidentified cryptophyte (0.017 ng C per cell) were used as in Jeong et al. (2005a) and Jeong et al. (2004b), respectively.

**Feeding process.** A culture of *L. masanensis* starved for 24 h was transferred to a 6 well-plate chamber containing a dense culture of perch blood cells, *A. carterae*, *H. akashiwo*, and a cryptophyte. The feeding behavior of  $> 30$  unfed *L. masanensis* cells on each of the target species was then observed under a dissecting microscope at a magnification of 50x--90x. A dense culture of *L. masanensis* starved for 24 h was added into a 1-ml Sedgwick-Rafter counting chamber (hereafter SRC) containing a target prey species, and a series of pictures of *L. masanensis* at several different stages of the feeding process was then taken using a digital camera mounted on a Carl Zeiss inverted microscope (Axiovert 200M, Carl Zeiss, Germany) at a magnification of 100x--630x.

After each of perch blood cells, *A. carterae*, *H. akashiwo* and a cryptophyte was provided to *L. masanensis* as prey, the time lag ( $n = 5$  for each prey) between the deployment of a tow filament and a peduncle of *L. masanensis* and the time ( $n = 5$  for each prey) for a prey cell to be completely ingested by a *L. masanensis* cell after the predator had deployed its peduncle to the prey cell were measured.

**Prey species.** Expt 1 was designed to investigate whether or not *L. masanensis* was able to feed on each of the target prey species (Table 1). The initial concentrations of each prey species offered were similar in terms of their carbon biomass. To confirm that no ingestion by *L. masanensis* on some prey species had occurred, additional higher prey concentrations were provided.

A dense culture of *L. masanensis* growing on *A. carterae* was transferred to a 1-L PC bottle containing freshly filtered seawater. Three 1-ml aliquots were then removed from the bottle and examined using a compound microscope to determine the concentration of *L. masanensis*.

In this experiment, the initial concentrations of *L. masanensis* and each target prey species were established using an autopipette to deliver a predetermined volume of culture of a known cell density to the experimental bottles. Duplicate 80-ml PC bottles (containing mixtures of *L. masanensis* and a target prey) and duplicate predator control bottles (containing *L. masanensis* only) were set up for each target prey species. The bottles were filled to capacity with freshly filtered seawater, capped, and then placed on a shelf and incubated at 20 °C under the continuous illumination of  $20 \mu\text{E m}^{-2} \text{s}^{-1}$  of cool white fluorescent light. After 6 h incubation, a 5-ml aliquot was removed from each bottle and transferred into a 6 well-plate chamber. For each target species, the feeding behavior of  $> 10$  *L. masanensis* cells capturing prey cells and  $> 30$  unfed *L. masanensis* cells was then observed under a dissecting microscope

at a magnification of 50-90 X to determine whether or not *L. masanensis* was able to feed on the target prey species.

For comparison, whether or not *Stoeckeria algicida* was able to feed on each of the target prey species was also investigated, in the manner described above (Table 1).

**Growth and ingestion rates.** Expt 2 was designed to measure the growth, ingestion, and clearance rates of *L. masanensis*, as a function of the prey concentration, when feeding on *Amphidinium carterae*, *Heterosigma akashiwo*, a cryptophyte, and perch blood cells. We chose these algae as the prey species because they were the dominant algal species when *L. masanensis* and similar small heterotrophic dinoflagellates were abundant in Masan Bay in 2005. We also chose perch blood cells because they were the optimal prey for *Pfiesteria piscicida* (Jeong et al. 2006) and were observed to support the maximum growth of *L. masanensis* in a preliminary test. *H. akashiwo* was chosen because it was the optimal prey for *Stoeckeria algicida* (Jeong et al. 2005a).

For pre-incubation, one day before the experiment with perch blood cells was conducted, a dense culture (7,000--8,000 cells ml<sup>-1</sup>) of *L. masanensis* growing on perch blood cells (ca. 300,000 cells ml<sup>-1</sup>) was transferred into two 500 ml PC bottles; one of these bottles had a low prey concentration (15,000 cells ml<sup>-1</sup>), and the other had a medium prey concentration (50,000 cells ml<sup>-1</sup>). Similarly, the pre-incubation time, prey concentration for maintenance, and low and medium prey concentrations for *A. carterae* prey were 1.5 days, 30,000--40,000 cells ml<sup>-1</sup>,

and 500 and 7,000 cells ml<sup>-1</sup>, for *H. akashiwo* prey 2 days, 30,000--40,000 cells ml<sup>-1</sup>, and 500 and 5,000 cells ml<sup>-1</sup>, for a cryptophyte prey 2 days, 50,000--70,000 cells ml<sup>-1</sup>, and 500 and 5,000 cells ml<sup>-1</sup>. The pre-incubation period for each target prey species was different (1--2 d) because all the experiments were begun when the prey cells were not detectable in ambient waters. The abundances of *L. masanensis* and its prey were determined by enumerating the cells present in three 1-ml SRCs.

The initial concentrations of *L. masanensis* and each target prey were established using an autopipette to deliver predetermined volumes of known cell concentrations to the bottles. Triplicate 42-ml PC experiment bottles (containing mixtures of predator and prey) and triplicate control bottles (containing prey only) were set up for each predator-prey combination. Triplicate control bottles containing only *L. masanensis* were also established at one predator concentration. To make the water conditions similar, the water of a predator culture was filtered through a 0.7 µm GF/F filter and then added into the prey control bottles in the same amount as the volume of the predator culture added into the predator control bottles and the experimental bottles for each predator-prey combination. Also, the water of a prey culture was filtered in the same manner and then added into the predator control bottles in the same amount as the volume of the prey culture added into the prey control bottles and the experimental bottles. Ten ml of f/2 medium were added to all the bottles, which were then filled to capacity with freshly filtered seawater and capped. To determine the actual predator and prey concentrations at the beginning of the experiment and after 24 h incubation for perch

blood cells and 48h for the algal prey, a 5-ml aliquot was removed from each bottle and fixed with 5% Lugol's solution, and all or > 200 predator and prey cells in three 1-ml SRCs were enumerated. The ranges of the mean actual prey [and predator] concentrations ( $\pm$  standard error, n=3) in the experimental bottles at the beginning of the experiment were 90 (4) -- 616,200 (8,920) cells ml<sup>-1</sup> [and 7 (0.3) -- 1,380 (25) cells ml<sup>-1</sup>] for perch blood cells, 60 (3) -- 20,100 (790) cells ml<sup>-1</sup> [and 20 (1) -- 1,540 (40)] for *A. carterae*, 40 (1) -- 95,590 (640) cells ml<sup>-1</sup> [and 10 (1) -- 1,170 (110)] for a cryptophyte, and 50 (3) -- 17,650 (340) cells ml<sup>-1</sup> [and 6 (1) -- 960 (50)] for *H. akashiwo*. The mean actual predator concentrations ( $\pm$  SE, n=3) in the control bottles containing only *L. masanensis* for all these experiments were 890 (4) --1,670 (50) cells ml<sup>-1</sup>. Prior to taking subsamples, the condition of *L. masanensis* and its prey was assessed using a dissecting microscope. The bottles were filled again to capacity with freshly filtered seawater, capped, and placed on a rotating wheel at 0.9 RPM at 20 °C under an illumination of 20  $\mu\text{E m}^{-2} \text{s}^{-1}$  of cool white fluorescent light on a 14:10 hr light-dark cycle. The dilution of the cultures associated with refilling the bottles was taken into consideration in calculating growth and ingestion rates.

The specific growth rate of *L. masanensis*,  $\mu$  (d<sup>-1</sup>), was calculated as follows:

$$\mu = \frac{\text{Ln}(L_t/L_0)}{t} \quad (1)$$

where  $L_0$  is the initial concentration of *L. masanensis* and  $L_t$  is the final concentration after time  $t$ . The times were 24 h for perch blood cells and 48 h for the algal prey. Approximately 20% of the blood cells were observed to shrink after 24 h.

Data for the growth rate of *L. masanensis* were fitted to a Michaelis-Menten equation as in Montagnes and Lessard (1999):

$$\mu = \frac{\mu_{\max} (x - x')}{K_{GR} + (x - x')} \quad (2)$$

where  $\mu_{\max}$  = the maximum growth rate ( $d^{-1}$ ),  $x$  = prey concentration (cells  $ml^{-1}$  or ng C  $ml^{-1}$ ),  $x'$  = the threshold prey concentration (the prey concentration where  $\mu = 0$ ), and  $K_{GR}$  = the prey concentration sustaining  $\frac{1}{2} \mu_{\max}$ . The data were iteratively fitted to the model using DeltaGraph® (Delta Point).

The ingestion and clearance rates were calculated using the equations of Frost (1972) and Heinbokel (1978). The incubation times for calculating ingestion and clearance rates were the same as for estimating growth rate. Ingestion rate data for *L. masanensis* were fitted to a Michaelis-Menten equation:

$$IR = \frac{I_{\max} (x)}{K_{IR} + (x)} \quad (3)$$

where  $I_{\max}$  = the maximum ingestion rate (cells grazer $^{-1}d^{-1}$  or ng C grazer $^{-1}d^{-1}$ );  $x$  = prey concentration (cells  $ml^{-1}$  or ng C  $ml^{-1}$ ),  $K_{IR}$  = the prey concentration sustaining  $\frac{1}{2} I_{\max}$ .

**Cell volume of *Luciella masanensis*.** After incubation, the cell length and maximum width of *L. masanensis* preserved in 5 % acid Lugol's solution (n=30 for each prey concentration) were measured using an image analysis system on images collected with a compound microscope (Image-Pro Plus 4.5, Media cybernetics, Silver spring, USA). The shape of *L. masanensis* was estimated to be a prolate spheroid. The cell volume of preserved *L. masanensis* was calculated according to the following equation:  $\text{volume} = 4/3 \pi [(\text{cell length} + \text{cell width})/4]^3$ .

**Gross growth efficiency.** Gross growth efficiency (GGE), defined as the grazer biomass produced (+) or lost (-) per prey biomass ingested, was calculated from estimates of carbon content per cell based on the cell volume for each mean prey concentration.

## RESULTS

**Prey species.** *Luciella masanensis* was able to feed on the diverse prey items offered in the present study (the diatoms *Skeletonema costatum* and *Thalassiosira rotula*; the naked mixotrophic dinoflagellates *Amphidinium carterae*, *Akashiwo sanguinea*, *Cochlodinium polykrikoides*, and *Gymnodinium catenatum*, and the smallest thecate mixotrophic dinoflagellate *Heterocapsa rotundata*; the raphidophytes *Chattonella ovata* and *Heterosigma akashiwo*; the cryptophytes *Rhodomonas salina* and an unidentified cryptophyte species; the blood cells of the perch *Lateolabrax japonica* and the flounder *Pleuronichthys cornutus*; and human red blood cells), while it did not feed on the large thecate mixotrophic dinoflagellates

*Prorocentrum minimum*, *Gonyaulax polygramma*, and *Lingulodinium polyedrum* that had ESD's  $\geq 12 \mu\text{m}$  (Table 1). Among the prey species that *L. masanensis* was able to ingest, all the prey species supported positive growth in *L. masanensis*, except *A. sanguinea*.

**Feeding process.** *L. masanensis* fed on its prey using a peduncle after anchoring the prey by a tow filament (Fig. 1--14). The distances between the predator cell and the prey cell were 5--10  $\mu\text{m}$  when the predator attached the tow filament to the prey cell; however, the distance reduced to a value similar to the prey cell length before the peduncle was deployed. The time lag (mean  $\pm$  standard error,  $n = 5$  for each prey) between the deployment of a tow filament and a peduncle was  $14.2 \pm 2.8$  sec for perch blood cells,  $20.2 \pm 3.5$  sec for *H. akashiwo*,  $36.2 \pm 2.5$  sec for a cryptophyte, and  $60.6 \pm 6.0$  sec for *A. carterae*. The prey materials were transferred inside the predator cell through the peduncle. The time (mean  $\pm$  standard error,  $n = 5$  for each prey) for a prey cell to be completely fed on by a *L. masanensis* cell after the predator deployed its peduncle to the prey cell was  $12.8 \pm 3.3$  sec for perch blood cells,  $82.1 \pm 1.6$  sec for a cryptophyte,  $118.2 \pm 25.8$  sec for *H. akashiwo*, and  $203.3 \pm 8.1$  sec for *A. carterae*. Up to 2-3 *L. masanensis* cells were observed deploying their peduncles simultaneously to a prey cell.

**Growth rates.** With increasing mean prey concentration, the specific growth rate of *L. masanensis* on perch blood cells increased rapidly at prey concentrations  $< \text{ca. } 400 \text{ ng C ml}^{-1}$  ( $44,400 \text{ cells ml}^{-1}$ ), but it increased only slowly at higher prey concentrations (Fig. 15). When the data were fitted to Eq. (2), the maximum specific growth rate of *L. masanensis* on perch

blood cells was  $1.455 \text{ d}^{-1}$ . The threshold prey concentration (where net growth = 0) for *L. masanensis* was  $69 \text{ ng C ml}^{-1}$  ( $7,670 \text{ cells ml}^{-1}$ ).

With increasing mean prey concentration the specific growth rate of *L. masanensis* on *A. carterae* increased continuously at the prey concentrations offered in the present study (Fig. 16). When the data were fitted to Eq. (2), the maximum specific growth rate of *L. masanensis* on *A. carterae* was  $0.587 \text{ d}^{-1}$ . The threshold prey concentration for *L. masanensis* was  $67 \text{ ng C ml}^{-1}$  ( $962 \text{ cells ml}^{-1}$ ).

With increasing mean prey concentration the specific growth rate of *L. masanensis* on a cryptophyte increased rapidly at the prey concentrations  $< \text{ca. } 60 \text{ ng C ml}^{-1}$  ( $3,500 \text{ cells ml}^{-1}$ ), but it increased slowly at the higher prey concentrations (Fig. 17). When the data were fitted to Eq. (2), the maximum specific growth rate of *L. masanensis* on the cryptophyte was  $0.238 \text{ d}^{-1}$ . A threshold prey concentration (where net growth = 0) for *L. masanensis* was  $140 \text{ ng C ml}^{-1}$  ( $8,240 \text{ cells ml}^{-1}$ ).

With increasing mean prey concentration the specific growth rate of *L. masanensis* on *H. akashiwo* increased rapidly at the prey concentrations  $< \text{ca. } 400 \text{ ng C ml}^{-1}$  ( $4,000 \text{ cells ml}^{-1}$ ), but it increased slowly at the higher prey concentrations (Fig. 18). When the data were fitted to Eq. (2), the maximum specific growth rate of *L. masanensis* on *H. akashiwo* was  $0.199 \text{ d}^{-1}$ . The threshold prey concentration for *L. masanensis* was  $330 \text{ ng C ml}^{-1}$  ( $3,300 \text{ cells ml}^{-1}$ ).

**Ingestion and clearance rates.** The ingestion rates of *L. masanensis* on perch blood cells increased rapidly at the prey concentrations  $< \text{ca. } 400 \text{ ng C ml}^{-1}$  ( $44,400 \text{ cells ml}^{-1}$ ), but it increased slowly at the higher prey concentrations (Fig. 19). When the data were fitted to Eq. (3), the maximum ingestion rate of *L. masanensis* on perch blood cells was  $2.6 \text{ ng C grazer}^{-1} \text{ d}^{-1}$  ( $290 \text{ cells grazer}^{-1} \text{ d}^{-1}$ ). The maximum clearance rate of *L. masanensis* on perch blood cells was  $0.83 \text{ } \mu\text{l grazer}^{-1} \text{ h}^{-1}$  at the mean prey concentration of  $1.6 \text{ ng C ml}^{-1}$  ( $180 \text{ cells ml}^{-1}$ ) and the maximum volume-specific clearance rate of *L. masanensis* was  $3.0 \times 10^6 \text{ h}^{-1}$ .

The ingestion rates of *L. masanensis* on *A. carterae* increased continuously with increasing mean prey concentration (Fig. 20). When the data were fitted to Eq. (3), the maximum ingestion rate of *L. masanensis* on *A. carterae* was  $0.32 \text{ ng C grazer}^{-1} \text{ d}^{-1}$  ( $4.5 \text{ cells grazer}^{-1} \text{ d}^{-1}$ ). The maximum clearance rate on *A. carterae* was  $0.06 \text{ } \mu\text{l grazer}^{-1} \text{ h}^{-1}$  at the mean prey concentration of  $15 \text{ ng C ml}^{-1}$  ( $210 \text{ cells ml}^{-1}$ ) and the maximum volume-specific clearance rate of *L. masanensis* was  $2.5 \times 10^5 \text{ h}^{-1}$ .

The ingestion rates of *L. masanensis* on a cryptophyte increased continuously with increasing mean prey concentration (Fig. 21). When the data were fitted to Eq. (3), the maximum ingestion rate of *L. masanensis* on a cryptophyte was  $0.44 \text{ ng C grazer}^{-1} \text{ d}^{-1}$  ( $26 \text{ cells grazer}^{-1} \text{ d}^{-1}$ ). The maximum clearance rate on a cryptophyte was  $0.13 \text{ } \mu\text{l grazer}^{-1} \text{ h}^{-1}$  at a mean prey concentration of  $3.0 \text{ ng C ml}^{-1}$  ( $176 \text{ cells ml}^{-1}$ ) and the maximum volume-specific clearance rate of *L. masanensis* was  $5.9 \times 10^5 \text{ h}^{-1}$ .

The ingestion rates of *L. masanensis* on *H. akashiwo* increased with increasing mean prey concentration before becoming saturated at the mean prey concentration of ca. 150 ng C ml<sup>-1</sup> (1,500 cells ml<sup>-1</sup>) (Fig. 22). When the data were fitted to Eq. (3), the maximum ingestion rate of *L. masanensis* on *H. akashiwo* was 0.16 ng C grazer<sup>-1</sup> d<sup>-1</sup> (16 cells grazer<sup>-1</sup> d<sup>-1</sup>). The maximum clearance rate on *H. akashiwo* was 0.14 µl grazer<sup>-1</sup> h<sup>-1</sup> at the mean prey concentration of 6.4 ng C ml<sup>-1</sup> (64 cells ml<sup>-1</sup>) and the maximum volume-specific clearance rate of *L. masanensis* was 6.0 x 10<sup>5</sup> h<sup>-1</sup>.

**Cell volume.** After 24 h incubation, the mean cell volume of *L. masanensis* fed perch blood cells at the mean prey concentrations of 0--13.8 ng C ml<sup>-1</sup> (260--300 µm<sup>3</sup>) were not significantly different ( $p > 0.1$ , 1-way ANOVA; Fig. 23A). However, at higher prey concentrations, the cell volume increased continuously from 350 to 660 µm<sup>3</sup> at the mean prey concentrations  $\leq 635$  ng C ml<sup>-1</sup> (70,560 cells ml<sup>-1</sup>), but decreased to 370 µm<sup>3</sup> at the higher prey concentrations. In this experiment, the greatest cell volume of *L. masanensis* fed perch blood cells (1,200 µm<sup>3</sup>) was approximately 14 times greater than the least cell volume (85 µm<sup>3</sup>). The cell volume of *L. masanensis* fed perch blood cells where the maximum volume-specific clearance rate was obtained was 280 µm<sup>3</sup>.

After 48 h incubation, the mean cell volume of *L. masanensis* fed *Amphidinium carterae* at the low mean prey concentration of 6.6 ng C ml<sup>-1</sup> (190 µm<sup>3</sup>) was not significantly different from that of *L. masanensis* without any added prey (180 µm<sup>3</sup>) ( $p > 0.1$ , one-tailed t test; Fig.

23B). At higher prey concentrations, the cell volume increased continuously from 200 to 670  $\mu\text{m}^3$  at the mean prey concentrations  $\leq 970 \text{ ng C ml}^{-1}$  (9,700 cells  $\text{ml}^{-1}$ ), but decreased to 560  $\mu\text{m}^3$  at the higher prey concentrations. The greatest cell volume of *L. masanensis* fed *A. carterae* measured in these experiments (1,180  $\mu\text{m}^3$ ) was approximately 9 times greater than the least cell volume (130  $\mu\text{m}^3$ ). The cell volume of *L. masanensis* fed *A. carterae* where the maximum volume-specific clearance rate was obtained was 240  $\mu\text{m}^3$ .

After 48 h incubation, the mean cell volume of *L. masanensis* fed a cryptophyte at the low mean prey concentration of 0.9 ng C  $\text{ml}^{-1}$  (205  $\mu\text{m}^3$ ) was not significantly different from that of *L. masanensis* without added prey (186  $\mu\text{m}^3$ ) ( $p > 0.05$ , one-tailed t test; Fig. 23C). At higher prey concentrations the cell volume increased from 220 to 470  $\mu\text{m}^3$ . The greatest cell volume of *L. masanensis* fed a cryptophyte measured in these experiments (1140  $\mu\text{m}^3$ ) was approximately 8 times greater than the least cell volume (140  $\mu\text{m}^3$ ). The cell volume of *L. masanensis* fed a cryptophyte where the maximum volume-specific clearance rate was obtained was 220  $\mu\text{m}^3$ .

After 48 h incubation, the mean cell volumes of *L. masanensis* fed *H. akashiwo* at all mean prey concentrations (380--460  $\mu\text{m}^3$ ) were not significantly different ( $p > 0.1$ , 1-way ANOVA; Fig. 23D). The greatest cell volume of *L. masanensis* fed *H. akashiwo* measured in these experiments (830  $\mu\text{m}^3$ ) was approximately 4 times greater than the least cell volume (200  $\mu\text{m}^3$ ). The cell volume of *L. masanensis* fed *H. akashiwo* where the maximum volume-specific clearance rate was obtained was 430  $\mu\text{m}^3$ .

**Gross growth efficiency.** Gross growth efficiencies (GGEs) of *L. masanensis* fed perch blood cells were negative at the mean prey concentrations of  $\leq 42 \text{ ng C ml}^{-1}$  (4,670 cells  $\text{ml}^{-1}$ ); however, these efficiencies increased up to 8 % at the mean prey concentration of 635 ng C  $\text{ml}^{-1}$  (70,560 cells  $\text{ml}^{-1}$ ) and then decreased slightly at higher prey concentrations with increasing mean prey concentration. GGEs of *L. masanensis* fed *Amphidinium carterae* were negative at the mean prey concentrations of  $\leq 83 \text{ ng C ml}^{-1}$  (830 cells  $\text{ml}^{-1}$ ), but these efficiencies were 17--25 % at higher mean prey concentrations. GGEs of *L. masanensis* fed a cryptophyte were negative at the mean prey concentrations of  $\leq 182 \text{ ng C ml}^{-1}$  (10,710 cells  $\text{ml}^{-1}$ ), but these efficiencies increased up to 9 % at higher mean prey concentrations. GGEs of *L. masanensis* fed *H. akashiwo* were negative at the mean prey concentrations of  $\leq 147 \text{ ng C ml}^{-1}$  (1,470 cells  $\text{ml}^{-1}$ ), but these efficiencies were 3--5 % at higher mean prey concentrations.

## DISCUSSION

**Feeding behavior and prey species of *Luciella masanensis*.** In a manner similar to *Pfiesteria piscicida*, *Pseudopfiesteria shumwayae*, and *Stoeckeria algicida* (Burkholder and Glasgow 1995; Jeong et al. 2005a), *Luciella masanensis* fed on its prey using a peduncle after anchoring the prey by a tow filament. Three major feeding mechanisms of the planktonic heterotrophic dinoflagellates have been discovered (Burkholder and Glasgow 1995; Hansen

1992; Jeong and Latz 1994); engulfment feeding, pallium feeding, and peduncle feeding. The results of the present study provide a basis for understanding the advantages and disadvantages of the peduncle feeding heterotrophic dinoflagellates over the other heterotrophic dinoflagellates which have different feeding mechanisms. For example, the peduncle feeding *L. masanensis* is even able to feed on prey much larger than itself (i.e. the naked dinoflagellates *Akashiwo sanguinea*, *Cochlodinium polykrikoides*, *Gymnodinium catenatum*, and the raphidophyte *Chattonella ovata*). Thus *L. masanensis* may have an advantage in feeding on large prey over the engulfment-feeding heterotrophic dinoflagellates which generally feed on prey smaller than themselves (Hansen 1992; Jeong et al. 2001b). However, *L. masanensis* is not able feed on the thecate mixotrophic dinoflagellates that had ESD's  $\geq 12$   $\mu\text{m}$ . *L. masanensis* may have difficulty in piercing the theca of the mixotrophic dinoflagellates using the peduncle. Unlike *L. masanensis*, engulfment feeding (i.e. *Oxyrrhis marina*) or pallium feeding small heterotrophic dinoflagellates (i.e. *Oblea rotunda*, *Diplopsalis lenticula*), are able to feed on the mixotrophic dinoflagellate *Prorocentrum minimum* that had an ESD of 12.1  $\mu\text{m}$  (Jeong et al. 2001a; Naustvoll 1998; Strom and Buskey 1993). Thus, different feeding mechanisms, and thus the types of prey species, may give rise to different ecological niches for the heterotrophic dinoflagellates and allow several heterotrophic dinoflagellates to co-exist in a given marine environment. In general, the time lag between the deployment of a tow filament and a peduncle of *L. masanensis* (14--61 sec) and the time for a prey cell to be completely fed on by a *L. masanensis* cell after the deployment of its peduncle to the prey cell (13--203 sec)

are likely to be primarily affected by the prey size. *L. masanensis* spends more energy in feeding on larger prey, but it may gain more energy from a larger prey cell compared to a smaller prey cell.

*L. masanensis* was able to feed on diverse prey items including diatoms, mixotrophic dinoflagellates, raphidophytes, and fish blood cells. Due to the ability of *L. masanensis* to feed on diverse prey species, this heterotrophic dinoflagellate is likely to be present in the coastal waters off many countries and it is worthwhile to explore the presence of *L. masanensis* in the countries other than Korea and the USA. In particular, *L. masanensis* may be easily observed during red tides dominated by the naked mixotrophic dinoflagellates or raphidophytes, while it may be more difficult to observe during red tides dominated by large thecate mixotrophic dinoflagellates. The kinds of prey species which *L. masanensis* feeds on are the same as those of *P. piscicida*, but very different from those of *S. algalica*, which is known to be able to feed only on *Heterosigma akashiwo* and the blood cells (Table 1), even though these three dinoflagellates are similar to one another in size, shape, and feeding mechanisms. Interestingly, in the phylogeny of dinoflagellates based on the small subunit rDNA sequences, *L. masanensis* is close to *P. piscicida*, but these two dinoflagellates are divergent with *S. algalica* (Jeong et al. 2005b). *L. masanensis* and *P. piscicida*, which are able to feed on diverse prey species, may be evolved from *S. algalica* which has few prey species. In prey recognition and/or digestion of heterotrophic dinoflagellates, enzymes are involved (Wootton et al. 2007). *L. masanensis* and *P. piscicida* may have more enzymes involving in prey recognition and/or

digestion compared with *S. algicida*. However, for a better understanding of the relationships between the kinds of prey species and the phylogeny of these three heterotrophic dinoflagellates, it is worthwhile investigating their proteomics. In natural environments, *L. masanensis* may frequently co-occur with *P. piscicida*, but not with *S. algicida* except when *H. akashiwo* and fish blood cells are abundant. Also, *L. masanensis* may compete with *P. piscicida* for diverse common prey species and *L. masanensis*, *P. piscicida*, and *S. algicida* may compete for *H. akashiwo* prey.

**Growth and ingestion.** The maximum growth rate (MGR) of *L. masanensis* determined in the present study ( $1.46 \text{ d}^{-1}$ ) was lower by 13-16 % than that of *P. piscicida* ( $1.74 \text{ d}^{-1}$ ) and *S. algicida* ( $1.62 \text{ d}^{-1}$ ), while the maximum ingestion rates (MIR) of *L. masanensis* ( $2.6 \text{ ng C grazer}^{-1} \text{ d}^{-1}$ ) were lower by 40 % than those of *P. piscicida* ( $4.3 \text{ ng C grazer}^{-1} \text{ d}^{-1}$ ), but it was approximately 3 times higher than that of *S. algicida* ( $0.8 \text{ ng C grazer}^{-1} \text{ d}^{-1}$ ; Table 2). The MGR and MIR of *L. masanensis* were obtained when fed on perch blood cells like *P. piscicida* (Jeong et al. 2006), but those of *S. algicida* were obtained when fed on *H. akashiwo* (Jeong et al. 2005a). Therefore, *L. masanensis* has the same optimal prey as *P. piscicida* (i.e. fish blood), but a different one from *S. algicida* (i.e. alga). The MIRs of *L. masanensis* on *Amphidinium carterae* (the optimal algal prey for *L. masanensis*) and *H. akashiwo* ( $0.17\text{--}0.32 \text{ ng C grazer}^{-1} \text{ d}^{-1}$ ) were much lower than that of *S. algicida* on *H. akashiwo*. This evidence suggests that *L. masanensis* optimally ingests blood cells compared to algal prey. However, the MIR of *S.*

*algicida* on perch blood cells was ca. 0.3 ng C grazer<sup>-1</sup> d<sup>-1</sup> (our unpublished data). The ability of *L. masanensis* to feed efficiently on fish blood cells explains the higher maximum ingestion rates compared to *S. algicida*, which rarely ingests perch blood cells.

The MIRs of *L. masanensis* feeding on perch blood cells (2.61 ng C grazer<sup>-1</sup> d<sup>-1</sup>) were considerably greater than those on the algal prey *A. carterae*, *H. akashiwo*, and cryptophytes (0.17--0.32 ng C grazer<sup>-1</sup> d<sup>-1</sup>). The time lag between the deployment of a tow filament and a peduncle by *L. masanensis* feeding on perch blood cells and the time for the prey cell to be completely devoured by a *L. masanensis* cell after the predator deployed a peduncle to the prey cell (14 sec and 13 sec, respectively) were much shorter than those of the algal prey (20--61 sec and 82--203 sec, respectively). The motionless and easily digestible perch blood cells may be more easily handled and ingested by *L. masanensis* than the actively swimming and less digestible algal prey. *L. masanensis* and *P. piscicida* may increase its population by feeding on the blood cells of fishes after entering into the gashes of fishes together.

Whereas the difference between the MGRs or MIRs of *L. masanensis* and *P. piscicida* on perch blood cells was not big, the MGRs and MIRs of *L. masanensis* on the algal prey *A. carterae*, *H. akashiwo*, and the cryptophyte (0.19--0.59 d<sup>-1</sup> and 0.17--0.32 ng C grazer<sup>-1</sup> d<sup>-1</sup>, respectively) were much lower than those of *P. piscicida* on the same prey (1.10--1.22 d<sup>-1</sup> and 0.75--1.1 ng C grazer<sup>-1</sup> d<sup>-1</sup>, respectively; Table 2); the ratios of the MIRs of *P. piscicida* to those of *L. masanensis* when fed on *A. carterae*, *H. akashiwo*, and the cryptophyte were 3.7,

5.4, and 6.5. The size of *L. masanensis* is similar to that of *P. piscicida*. Therefore, unknown factors other than cell size, such as digestive enzyme activity, may be responsible for this difference in their MGRs and MIRs and it is worthwhile exploring this difference in respect to the genetic and biochemical properties of these two dinoflagellate predators. When *A. carterae* and/or the cryptophyte are abundant, the sequence in the abundances of *P. piscicida* and PLDs is expected to be as follows; *P. piscicida* > *L. masanensis* > *S. algicida*. However, when *H. akashiwo* is abundant, the sequence is expected to be as follows; *S. algicida* > *P. piscicida* > *L. masanensis*. The MIRs of *L. masanensis* on *A. carterae* and *H. akashiwo* in the present study (0.2--0.3 cells grazer<sup>-1</sup> d<sup>-1</sup>) were much lower than that of the heterotrophic dinoflagellate *Oxyrrhis marina* on the same prey (1.3--2.8 cells grazer<sup>-1</sup> d<sup>-1</sup>; Table 2). The difference in feeding mechanisms between *L. masanensis* (deploying a tow filament and then sucking prey materials through a peduncle) and *O. marina* (deploying a tow filament and then engulfing a prey cell) may be not responsible for this difference because the MIR of *P. piscicida* on *A. carterae* and *H. akashiwo* were similar to those of *O. marina*. The smaller cell volumes of *L. masanensis* than that of *O. marina* may be responsible for its lower MIR.

The maximum clearance rate (MCR) of *L. masanensis* on *A. carterae* (0.06 µl grazer<sup>-1</sup> h<sup>-1</sup>) was comparable to that of the ciliate *Tiarina fusus* on the same prey (0.1 µl grazer<sup>-1</sup> h<sup>-1</sup>), while the MCR of *L. masanensis* on a cryptophyte (0.13 µl grazer<sup>-1</sup> h<sup>-1</sup>) was comparable to that of the mixotrophic dinoflagellate *Gonyaulax polygramma* on the same prey (0.18 µl

grazer<sup>-1</sup> h<sup>-1</sup>; Table 2). Despite the similarity in MCRs on certain prey, the cell volume of *T. fusus* or *G. polygramma* are much greater than that of *L. masanensis*. Peduncle feeding dinoflagellates, such as *L. masanensis* may capture and ingest prey with similar efficiency at low prey concentrations compared to larger predators that feed by engulfing their prey, such as *T. fusus* and *G. polygramma*. The maximum volume-specific clearance rate of *L. masanensis* on perch blood cells ( $3.0 \times 10^6$  h<sup>-1</sup>) was lower than that of *S. algicida* on *H. akashiwo* ( $9.7 \times 10^6$  h<sup>-1</sup>) or of the heterotrophic dinoflagellate *Protoperdinium bipes* on the diatom *Skeletonema costatum* ( $5.4 \times 10^6$  h<sup>-1</sup>), the highest and second highest values of heterotrophic dinoflagellates reported (Jeong et al. 2004c, 2005a). The MCRs of *S. algicida* on *H. akashiwo* ( $3.7 \mu\text{l grazer}^{-1}\text{h}^{-1}$ ) and *P. bipes* on *S. costatum* ( $1.0 \mu\text{l grazer}^{-1}\text{h}^{-1}$ ) were approximately 4.6 and 1.2 times higher than that of *L. masanensis* on perch blood cells ( $0.8 \mu\text{l grazer}^{-1}\text{h}^{-1}$ ). The lower MCR of *L. masanensis* compared to that of *S. algicida* may be responsible for its lower maximum volume-specific clearance rate because the cell volume of *S. algicida* ( $380 \mu\text{m}^3$ ) when the maximum volume-specific clearance rate was obtained was only 1.4 times greater than that of *L. masanensis* ( $276 \mu\text{m}^3$ ).

The maximum GGE of *L. masanensis* (25 %, fed on *A. carterae*) was observed to be similar to those of common heterotrophic dinoflagellates on algae (Naustvall 1998; Kim and Jeong 2004). However, the maximum GGE of *L. masanensis* on *H. akashiwo* (5%) was much lower than that of *S. algicida* (79 %) or *Pfiesteria piscicida* (62 %) on the same prey. A mixotrophic growth using kleptoplastids obtained from *H. akashiwo* has been suggested as

being partially responsible for these high GGEs of *S. algicida* or *P. piscicida* (Jeong et al. 2005a, 2006). The evidence from the present study suggests that unlike *S. algicida* or *P. piscicida*, *L. masanensis* may not grow mixotrophically using kleptoplastids driven from the algal prey. After red tides dominated by *H. akashiwo*, *P. piscicida* has an advantage in maintaining its population over *S. algicida* or *L. masanensis* because *P. piscicida* is able to feed on diverse prey species and/or grow mixotrophically using kleptoplastids driven from *H. akashiwo*. However, *L. masanensis* cannot grow mixotrophically and *S. algicida* rarely has alternative prey. The maximum GGE of *L. masanensis* on perch blood cells was considerably low (8 %); Perch blood cells might not be a nutritious prey for *L. masanensis*, even though as many as 290 blood cells were ingested by a *L. masanensis* cell in a single day; or the carbon content of a *L. masanensis* cell might have been underestimated.

The grazing impact by *L. masanensis* on the algal prey is difficult to assess due to difficulty in distinguishing *L. masanensis* from similar small heterotrophic dinoflagellates (*P. piscicida*, *S. algicida* etc.) in fixed samples. DNA probes for identifying *L. masanensis* or *S. algicida* have not been developed yet. The MGRs of *L. masanensis* on *A. carterae*, *H. Akashiwo*, and the cryptophyte were much lower than those of *P. piscicida*. Therefore, the abundance of *L. masanensis* is likely to be lower than that of *P. piscicida* when *A. carterae*, *H. akashiwo*, and/or the cryptophyte are abundant. Also, the ratios of the MIRs of *L. masanensis* to those of *P. piscicida* were 0.15-0.27 when they fed on the algal prey. Therefore, if it is assumed that all similar small heterotrophic dinoflagellates are *L. masanensis*, the calculated

grazing impact by *L. masanensis* on the algal prey may be greatly overestimated. It would be worthwhile developing a method of exactly quantifying the abundance of *L. masanensis* in nature (i.e. DNA probes) to further our understanding of the grazing impact of *L. masanensis* on prey populations.

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Table 1. Taxa, sizes, and concentration of prey species offered as food to *Luciella masanensis* (*Lm*) and *Stoeckeria algicida* (*Sa*) in Expt 1. To confirm no ingestion by *L. masanensis* on some prey species, additional higher prey concentrations were provided. Mean equivalent spherical diameter (ESD,  $\mu\text{m}$ )  $\pm$  standard deviation of the mean was measured by an electronic particle counter (Coulter Multisizer II, Coulter Corporation, Miami, Florida, USA).  $n > 2000$  for each species. Feeding occurrence of *Pfiesteria piscicida* (*Pp*) is also provided. Y – A predator was observed to feed on a food cell; N – A predator was observed not to feed on a food cell. Data on *P. piscicida* were obtained from Jeong et al. (2006).

Species	ESD ( $\pm$ SD)	Initial prey concentration (cells $\text{ml}^{-1}$ )	<i>Lm</i>	<i>Sa</i>	<i>Pp</i>
<b>Diatoms</b>					
<i>Skeletonema costatum</i>	5.9 (1.1)	100,000	Y	N	Y
<i>Thalassiosira rotula</i>	29.3 (2.2)	10,000	Y	N	Y
<b>Cryptophytes</b>					
Unidentified cryptophyte	5.6 (1.5)	30,000	Y	N	Y
<i>Rhodomonas salina</i>	7.0 (2.0)	25,000	Y	N	Y
<b>Rhaphidophytes</b>					
<i>Heterosigma akashiwo</i>	11.5 (1.9)	10,000	Y	Y	Y
<i>Chattonella ovata</i>	40.0 (1.6)	2,000	Y	N	Y

**Mixotrophic dinoflagellates**

<i>Heterocapsa rotundata</i>	5.8 (0.4)	30,000	Y	N	Y
<i>Amphidinium carterae</i>	9.7 (1.6)	20,000	Y	N	Y
<i>Prorocentrum minimum</i>	12.1 (2.5)	10,000--20,000	N	N	N
<i>Heterocapsa triquetra</i>	15.0 (4.3)	10,000--20,000	N	N	N
<i>Scrippsiella trochoidea</i>	22.8 (2.7)	10,000--20,000	N	N	N
<i>Cochlodinium polykrikoides</i>	25.9 (2.9)	3,000	Y	N	Y
<i>Prorocentrum micans</i>	26.6 (2.8)	3,000--5,000	N	N	N
<i>Akashiwo sanguinea</i>	30.8 (3.5)	1,000	Y	N	Y
<i>Gonyaulax polygramma</i>	32.5 (5.4)	1,000--3,000	N	N	N
<i>Alexandrium catenella</i>	32.6 (2.7)	1,000--3,000	N	N	N
<i>Gymnodinium catenatum</i>	33.9 (1.6)	1,500	Y	N	Y
<i>Lingulodinium polyedrum</i>	38.2 (3.6)	1,000--3,000	N	N	N
<b>Blood cells</b>					
Perch	6.1 (0.5)	200,000	Y	Y	Y
Flounder	6.0 (0.5)	200,000	Y	Y	Y

Human

4.8 (0.5)

200,000

Y

Y

Y

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Table 2. Comparison of growth, ingestion and clearance rates of *Luciella masanensis* and other protists on perch blood cells, *Amphidinium carterae*, *Heterosigma akashiwo*, and cryptophytes. Rates are corrected to 20° C using  $Q_{10} = 2.8$  (Hansen, Bjornsen, and Hansen, 1997). PV (Predators' volume as  $\times 10^3 \mu\text{m}^3$ );  $\mu_{\text{max}}$  (maximum growth rate in  $\text{d}^{-1}$ );  $I_{\text{max}}$  (maximum ingestion rate in  $\text{ng C predator}^{-1} \text{d}^{-1}$ );  $C_{\text{max}}$  (maximum clearance rate as  $\mu\text{l predator}^{-1} \text{h}^{-1}$ ); HD (heterotrophic dinoflagellate); MD (mixotrophic dinoflagellate); NC (naked ciliate). ud: undetectable.

Prey	Predator	PV	$\mu_{\text{max}}$	$I_{\text{max}}$	$C_{\text{max}}$	Reference
Perch blood cell	<i>Luciella masanensis</i> (HD)	1.3	1.46	2.6	0.8	This study
	<i>Pfiesteria piscicida</i> (HD)	1.3	1.74	4.3	2.5	Jeong et al. (2006)
<i>Amphidinium carterae</i>	<i>Luciella masanensis</i> (HD)	1.3	0.59	0.3	0.1	This study
	<i>Pfiesteria piscicida</i> (HD)	1.3	1.22	1.1	1.4	Jeong et al. (2006)
	<i>Oxyrrhis marina</i> (HD)	2.0	1.17	2.8	2.4	Jeong et al. (2001a)
	<i>Tiarina fusus</i> (NC)	25.4	(-)	2.7	0.1	Jeong et al. (2002)
	<i>Polykrikos kofoidii</i> (HD)	43.0	0.10	ud		Jeong et al. (2001b)
	<i>Strombidinopsis</i> sp. (NC)	560	(-)	ud		Jeong et al. (1999)

<i>Heterosigma akashiwo</i>	<i>Luciella masanensis</i> (HD)	1.1	0.20	0.2	0.4	This study
	<i>Pfiesteria piscicida</i> (HD)	1.2	1.10	0.8	0.1	This study
	<i>Stoeckeria algicida</i> (HD)	1.4	1.62	0.8	3.7	Jeong et al. 2005a
	<i>Gyrodinium dominans</i> (HD)	4.0	0.15			Nakamura et al. (1995)
	<i>Oxyrrhis marina</i> (HD)	2.0	1.43	1.3	0.3	Jeong et al. (2003)
	<i>Tiarina fusus</i> (NC)	25.4	0.12	6.5	0.7	Jeong et al. (2002)
Unidentified cryptophyte (ESD=5.6 $\mu$ m)	<i>Luciella masanensis</i> (HD)	0.3	0.23	0.44	0.1	This study
	<i>Pfiesteria piscicida</i> (PPMS)	1.2	1.10	1.11	0.1	Jeong et al. (2006)
	<i>Prorocentrum donghaiense</i> (MD)	1.2	0.51	0.03	0.04	Jeong et al. (2005c)
	<i>Heterocapsa triquetra</i> (MD)	1.8	0.28	0.04	0.1	Jeong et al. (2005c)
	<i>Cochlodinium polykrikodes</i> (MD)	9.0	0.32	0.16	0.3	Jeong et al. (2004b)
	<i>Prorocentrum micans</i> (MD)	9.9	0.20	0.04	0.1	Jeong et al. (2005c)
	<i>Gonyaulax polygramma</i> (MD)	18.0	0.28	0.18	0.2	Jeong et al. (2005d)

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## FIGURE LEGENDS

**Fig. 1--14.** Feeding by *Luciella masanensis* on a prey cell using a peduncle. **(1--5).** Perch blood cell prey. **1.** *L. masanensis* capturing a blood cell. **2--5.** The size of the blood cell decreased. **(6--10).** *Amphidinium carterae* prey. **6.** A *L. masanensis* cell feeding on an *A. carterae* cell. **7.** Another *L. masanensis* cell deployed a tow filament (arrow) to a prey cell eaten by the *L. masanensis* cell. **8--9.** Another *L. masanensis* cell deployed a peduncle (arrow) to a prey cell and sucked prey materials. The size of the prey cell decreased. **10.** Two *L. masanensis* cells contained the parts of prey materials after completion of feeding. **(11--14).** Cryptophyte prey. **11.** *L. masanensis* capturing a cryptophyte cell. **12--13.** *L. masanensis* sucking the prey materials (reddish colors) through a peduncle. **14.** *L. masanensis* containing prey materials. Arrows indicate prey materials. All prey and predator cells are the same cells in 1--5 except 2, in 6--10, and in 11--14. Scale bar = 5  $\mu\text{m}$ .

**Fig. 15.** Specific growth rates of *Luciella masanensis* on perch blood cells as a function of mean prey concentration ( $x$ ,  $\text{ng C ml}^{-1}$ ). Symbols represent treatment means  $\pm 1$  SE. The curve is fitted by a Michaelis-Menten equation [Eq. (2)] using all treatments in the experiment. Growth rate ( $\text{GR, d}^{-1}$ ) =  $1.455 [(x-68.6)/(609 + (x-68.6))]$ ,  $r^2=0.968$ .

**Fig. 16.** Specific growth rates of *Luciella masanensis* on the dinoflagellate *Amphidinium carterae* as a function of mean prey concentration ( $x$ ,  $\text{ng C ml}^{-1}$ ). Symbols represent treatment means  $\pm 1$  SE. The curve is fitted by a Michaelis-Menten equation [Eq. (2)] using all treatments in the experiment. Growth rate ( $\text{GR, d}^{-1}$ ) =  $0.587 [(x-67.4)/(1170 + (x-67.4))]$ ,  $r^2=0.690$ .

**Fig. 17.** Specific growth rates of *Luciella masanensis* on an unidentified cryptophyte species (equivalent spherical diameter, ESD = 5.6  $\mu\text{m}$ ) as a function of mean prey concentration ( $x$ ,  $\text{ng C ml}^{-1}$ ). Symbols represent treatment means  $\pm 1$  SE. The curve is fitted by a Michaelis-Menten equation [Eq. (2)] using all treatments in the experiment. Growth rate ( $\text{GR, d}^{-1}$ ) =  $0.238 [(x-142)/(285 + (x-142))]$ ,  $r^2=0.897$ .

**Fig. 18.** Specific growth rates of *Luciella masanensis* on the raphidophyte *Heterosigma akashiwo* as a function of mean prey concentration ( $x$ ,  $\text{ng C ml}^{-1}$ ). Symbols represent treatment means  $\pm 1$  SE. The curve is fitted by a Michaelis-Menten equation [Eq. (2)] using all treatments in the experiment. Growth rate ( $\text{GR, d}^{-1}$ ) =  $0.199 [(x-327)/(1020 + (x-327))]$ ,  $r^2=0.444$ .

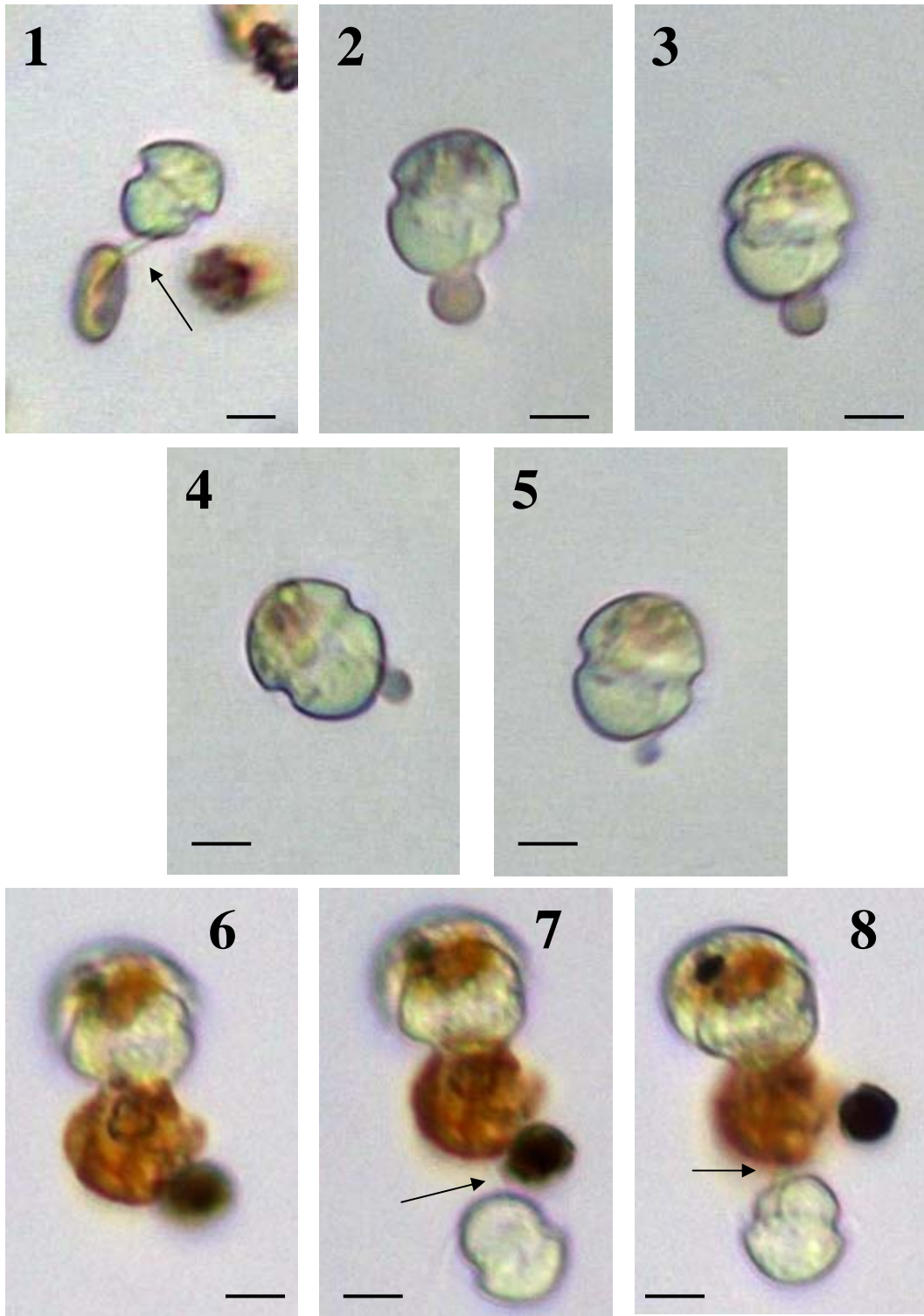
**Fig. 19.** Ingestion rates of *Luciella masanensis* on perch blood cells as a function of mean prey concentration ( $x$ ). Symbols represent treatment means  $\pm 1$  SE. The curve is fitted by a Michaelis-Menten equation [Eq. (3)] using all treatments in the experiment. Ingestion rate ( $\text{IR, ng C grazer}^{-1}\text{d}^{-1}$ ) =  $2.61 [x/(537+x)]$ ,  $r^2=0.977$ .

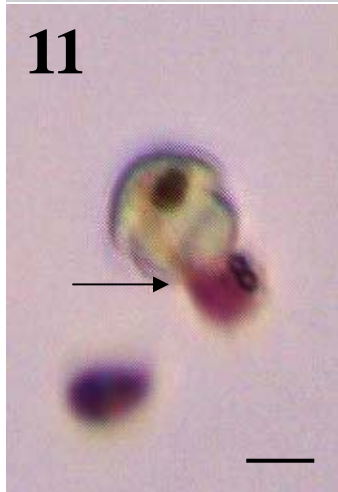
**Fig. 20.** Ingestion rates of *Luciella masanensis* on *Amphidinium carterae* as a function of mean prey concentration ( $x$ ). Symbols represent treatment means  $\pm 1$  SE. The curve is fitted by a Michaelis-Menten equation [Eq. (3)] using all treatments in the experiment. Ingestion rate ( $\text{IR, ng C grazer}^{-1}\text{d}^{-1}$ ) =  $0.32 [x/(2370+x)]$ ,  $r^2=0.843$ .

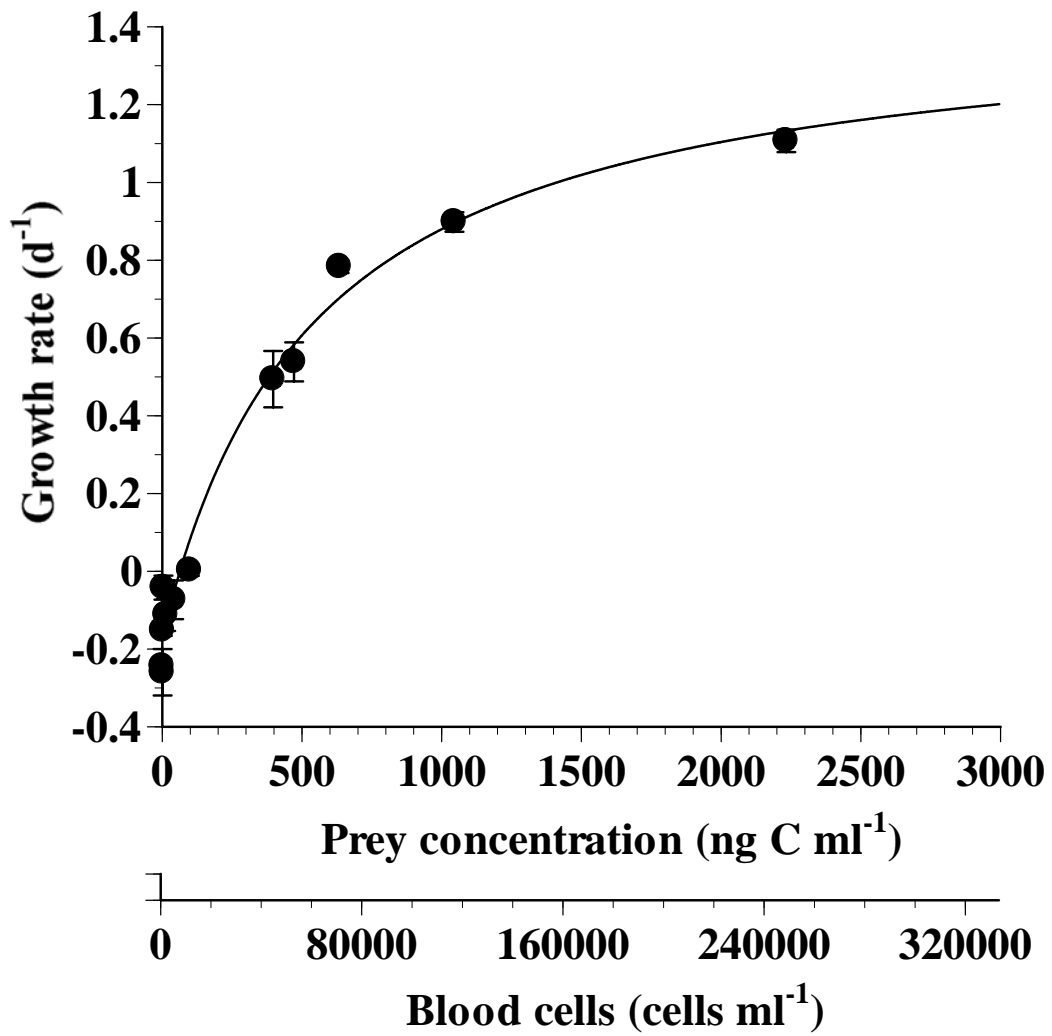
**Fig. 21.** Ingestion rates of *Luciella masanensis* on an unidentified cryptophyte species (ESD = 5.6  $\mu\text{m}$ ) as a function of mean prey concentration ( $x$ ). Symbols represent treatment means  $\pm 1$  SE. The curve is fitted by a Michaelis-Menten equation [Eq. (3)] using all treatments in the experiment. Ingestion rate ( $\text{IR, ng C grazer}^{-1}\text{d}^{-1}$ ) =  $0.44 [x/(2850+x)]$ ,  $r^2=0.872$ .

**Fig. 22.** Ingestion rates of *Luciella masanensis* on *Heterosigma akashiwo* as a function of mean prey concentration (x). Symbols represent treatment means  $\pm$  1 SE. The curve is fitted by a Michaelis-Menten equation [Eq. (3)] using all treatments in the experiment. Ingestion rate (IR, ng C grazer<sup>-1</sup>d<sup>-1</sup>) = 0.16 [x/(77+x)], r<sup>2</sup>=0.474.

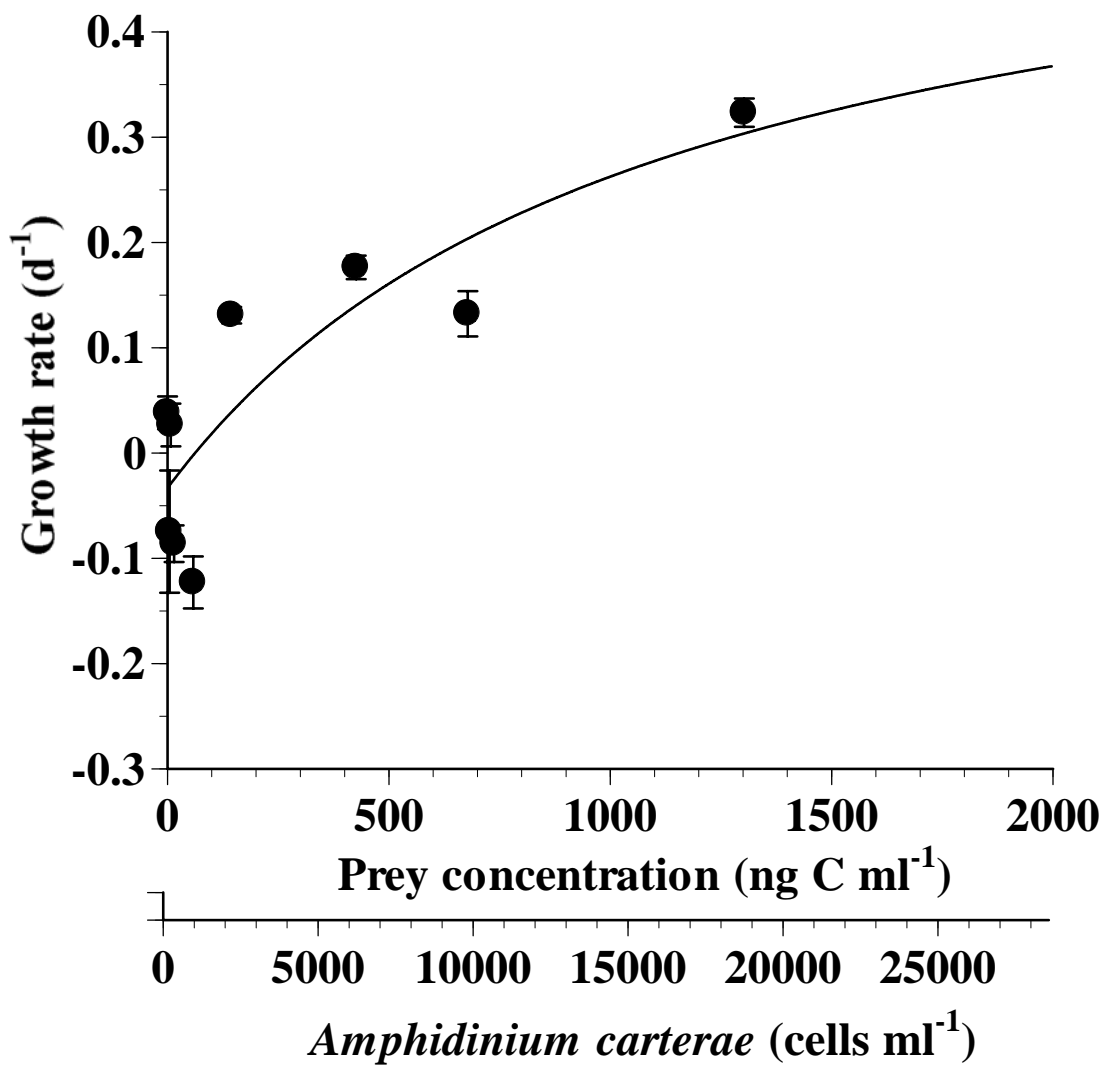
**Fig. 23.** The cell volume of *Luciella masanensis* on the blood of perch after 24 h incubation (A) and on *Amphidinium carterae* (B), a cryptophyte (C), and *Heterosigma akashiwo* (D) after 48 h incubation as a function of mean prey concentration. Symbols represent treatment means  $\pm$  1 SE.



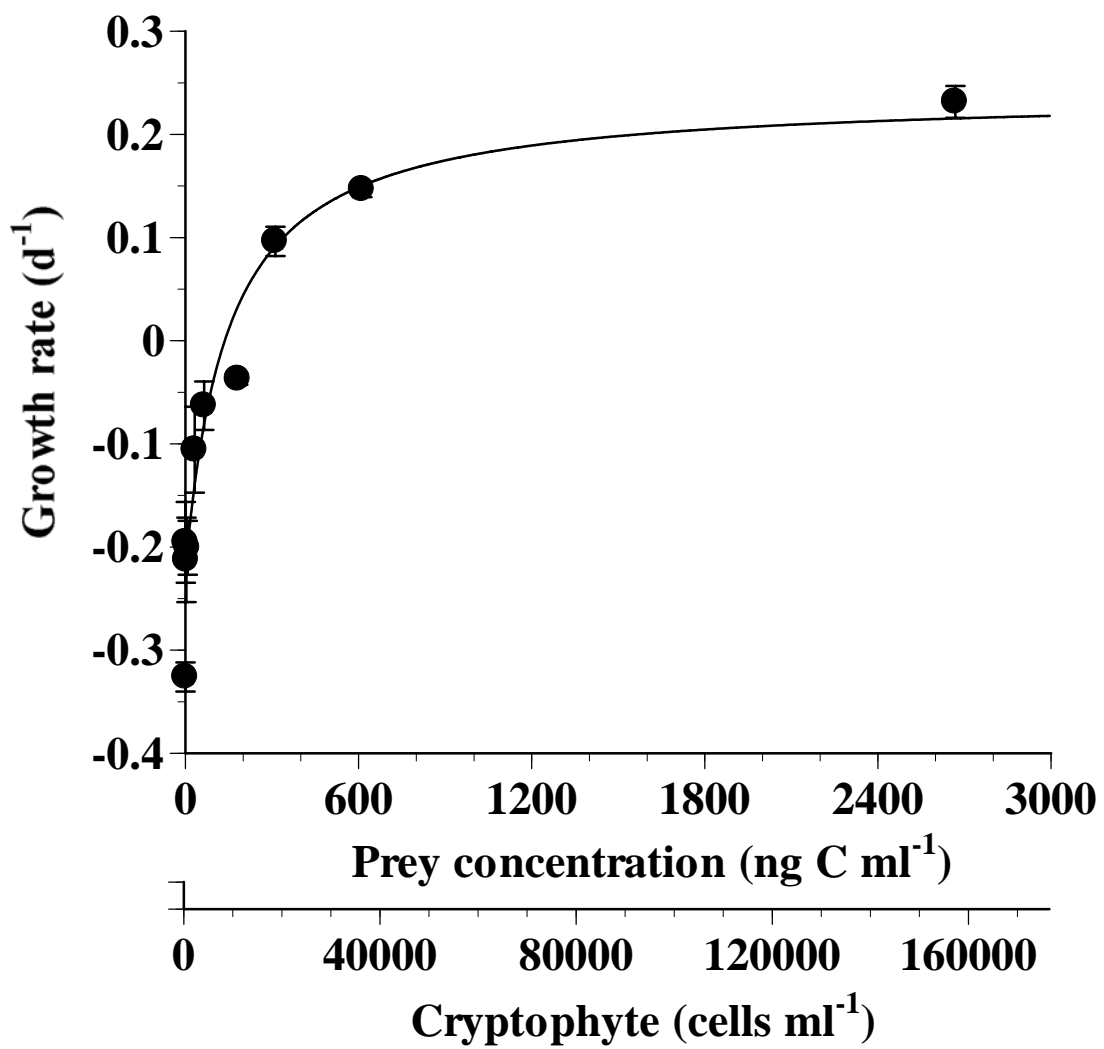




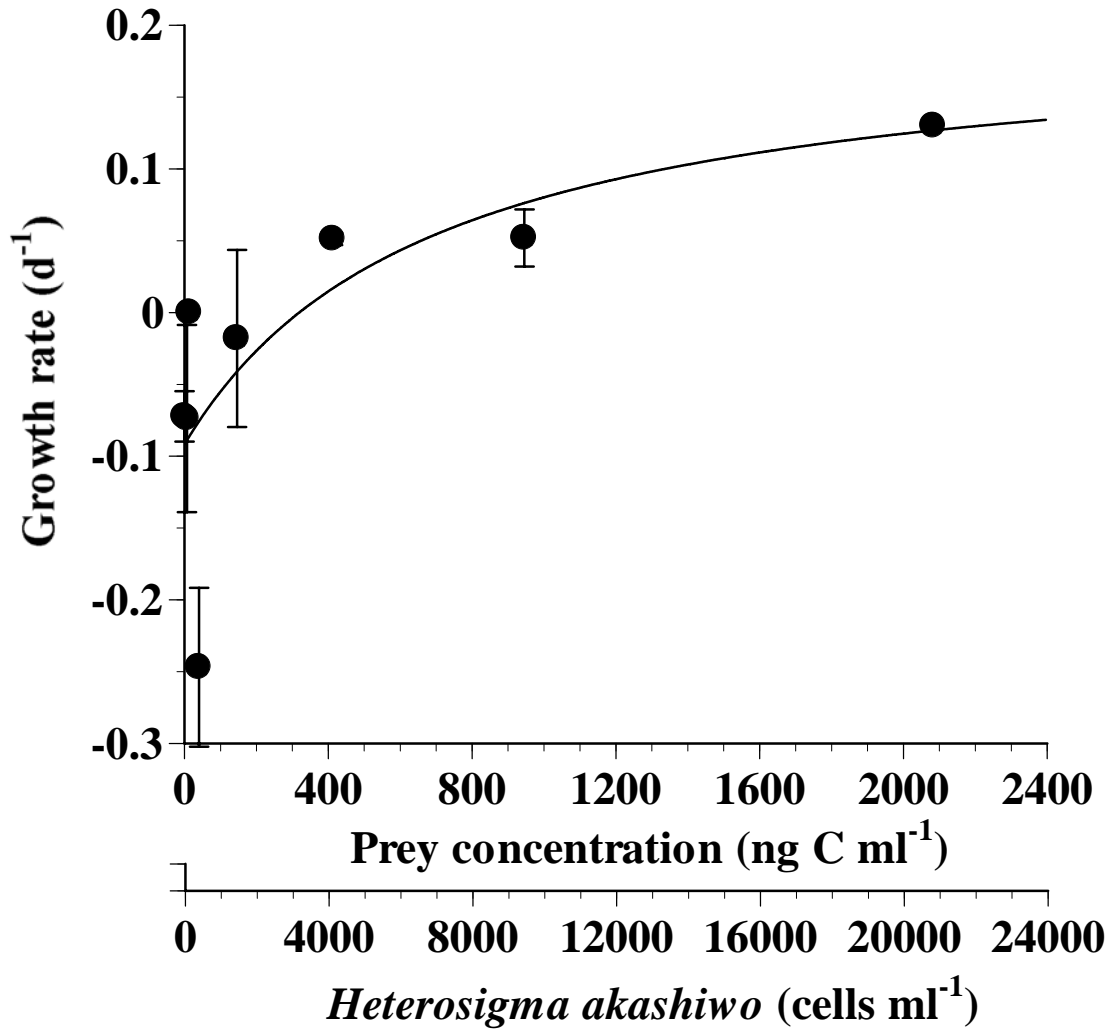
Jeong et al.  
Fig. 15



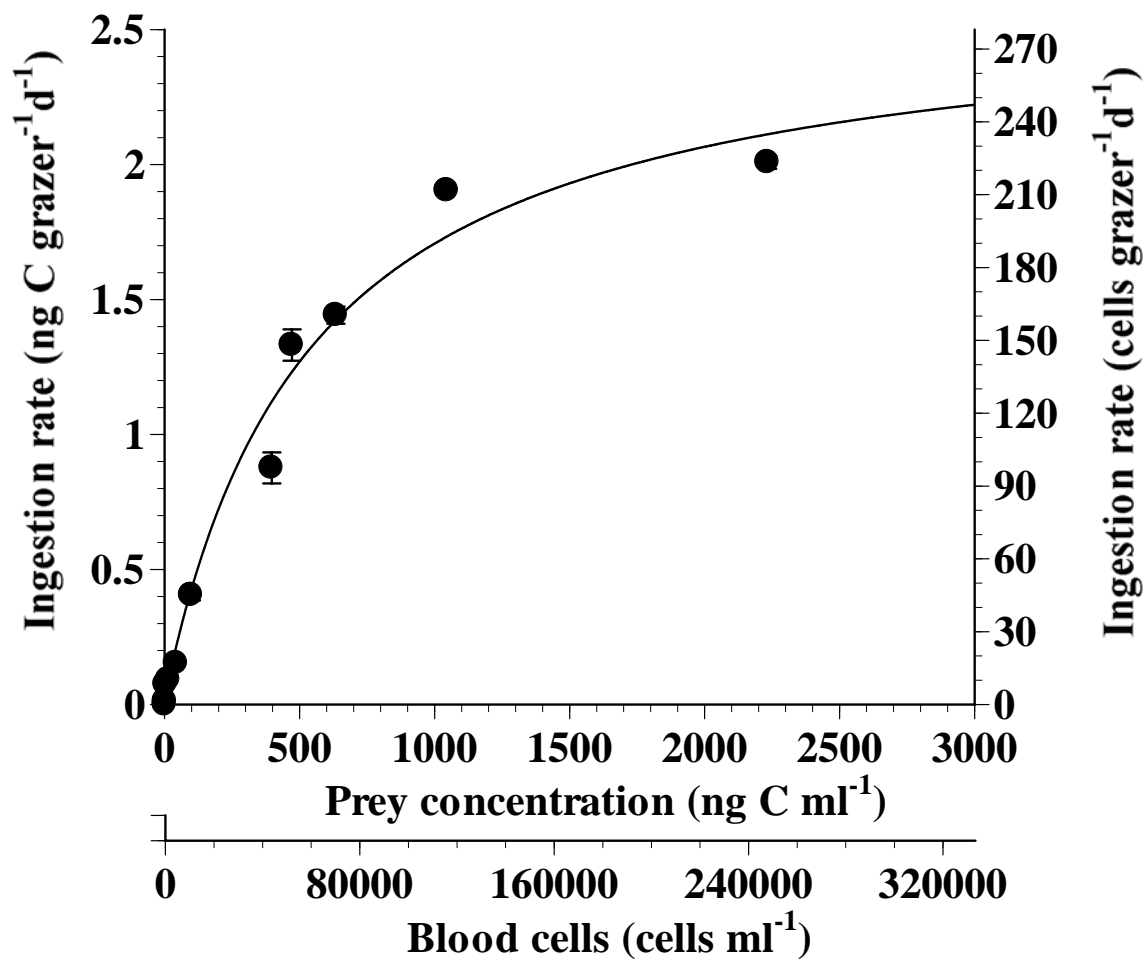
Jeong et al.  
Fig. 16



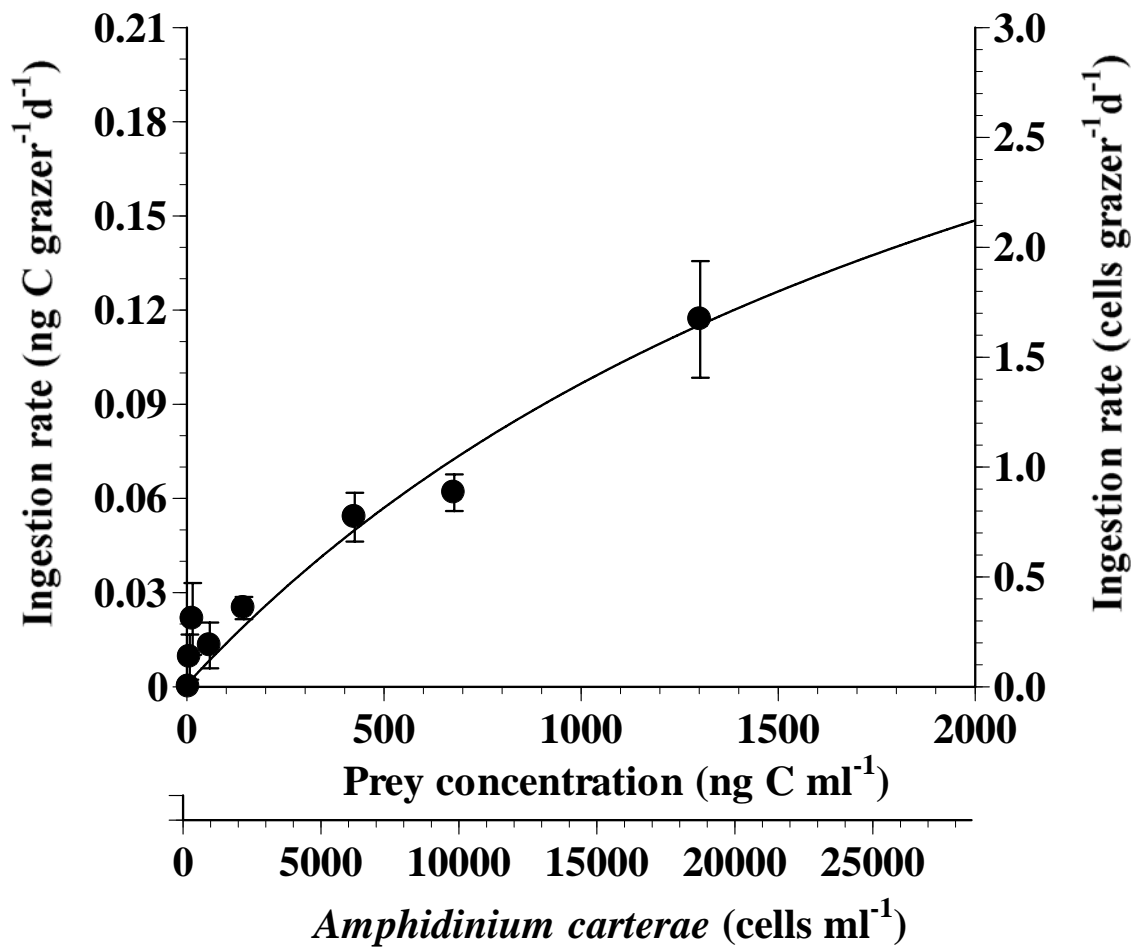
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Fig. 17



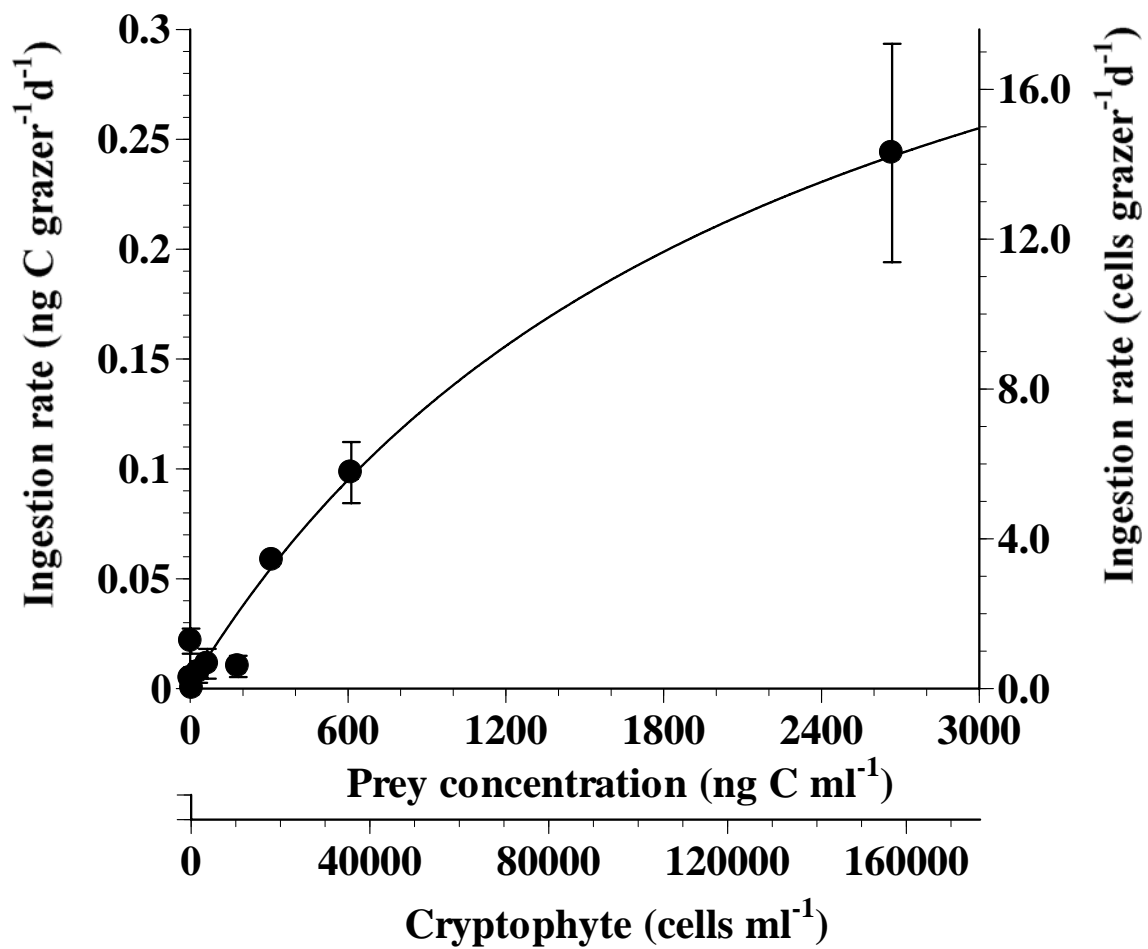
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Fig. 18



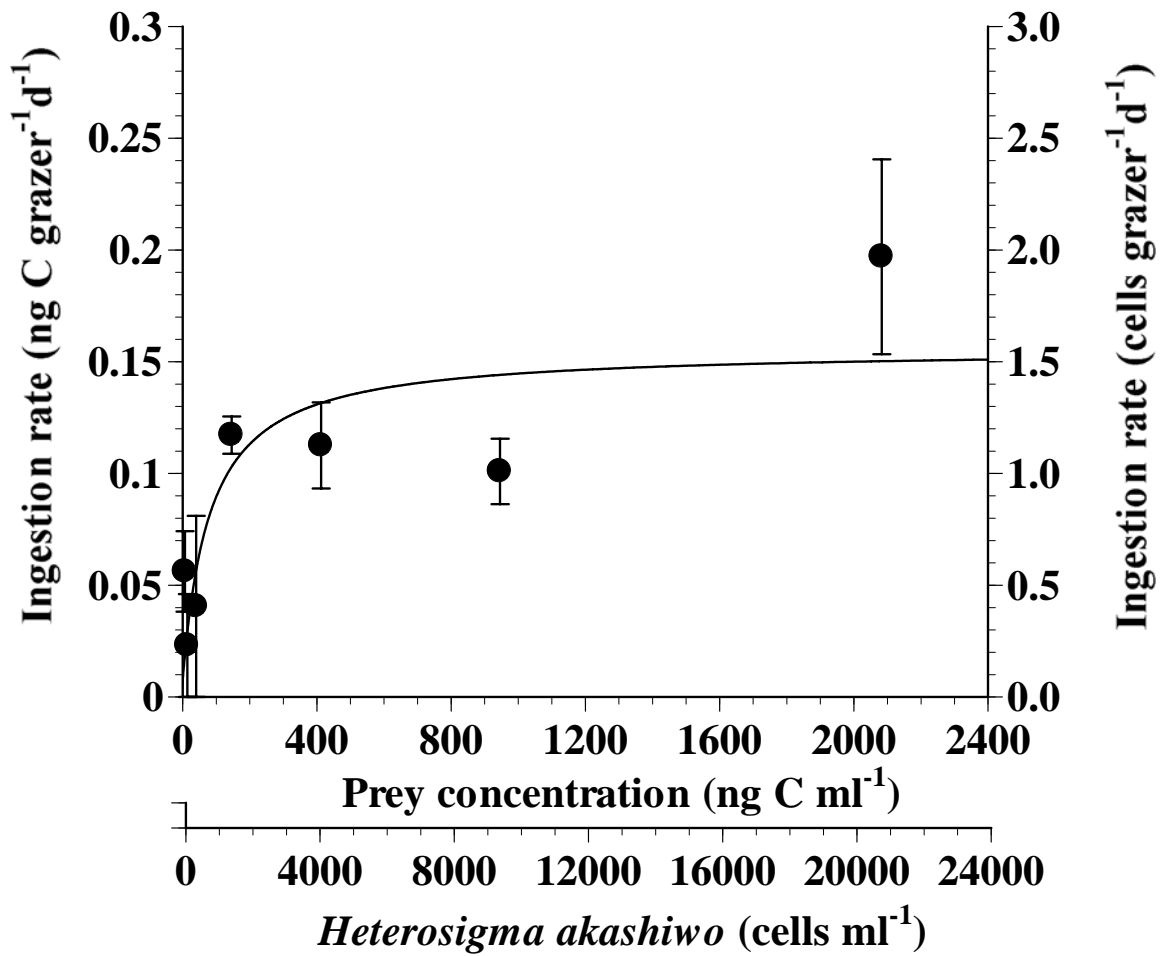
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Fig. 19



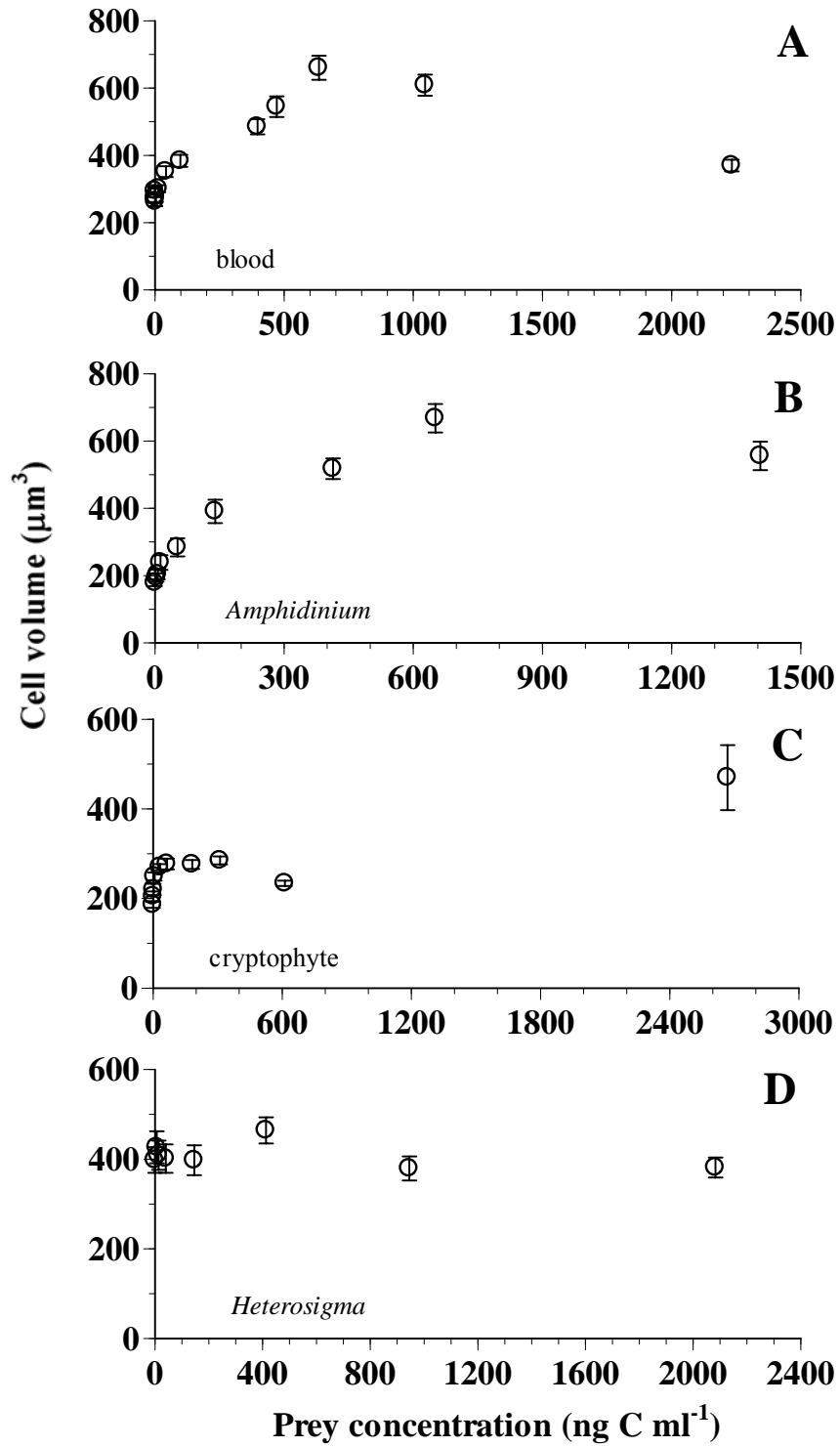
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Fig. 20



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Fig. 21



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Fig. 22



Jeong et al. Fig. 23