



## Feeding by common heterotrophic dinoflagellates and a ciliate on the red-tide ciliate *Mesodinium rubrum*

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*Mesodinium rubrum* is a cosmopolitan ciliate that often causes red tides. Predation by heterotrophic protists is a critical factor that affects the population dynamics of red tide species. However, there have been few studies on protistan predators feeding on *M. rubrum*. To investigate heterotrophic protists grazing on *M. rubrum*, we tested whether the heterotrophic dinoflagellates *Gyrodiniellum shiwhaense*, *Gyrodinium dominans*, *Gyrodinium spirale*, *Luciella masanensis*, *Oblea rotunda*, *Oxyrrhis marina*, *Pfiesteria piscicida*, *Polykrikos kofoidii*, *Protoperidinium bipes*, and *Stoeckeria algicida*, and the ciliate *Strombidium* sp. preyed on *M. rubrum*. *G. dominans*, *L. masanensis*, *O. rotunda*, *P. kofoidii*, and *Strombidium* sp. preyed on *M. rubrum*. However, only *G. dominans* had a positive growth feeding on *M. rubrum*. The growth and ingestion rates of *G. dominans* on *M. rubrum* increased rapidly with increasing mean prey concentration <math><321\text{ ng C mL}^{-1}</math>, but became saturated or slowly at higher concentrations. The maximum growth rate of *G. dominans* on *M. rubrum* was G. dominans on populations of *M. rubrum* were up to G. dominans may sometimes have a considerable grazing impact on populations of *M. rubrum*.

**Key Words:** ciliate; growth; harmful algal bloom; ingestion; predation

### INTRODUCTION

*Mesodinium rubrum* is a globally distributed ciliate (Lindholm 1985, Crawford 1989, Williams 1996, Gibson et al. 1997) that sometimes causes red tides in coastal waters (Johnson et al. 2004, Yih et al. 2004, Hansen and Fenchel 2006, Hansen et al. 2013, Johnson et al. 2013, Kang et al. 2013). *M. rubrum* is capable of both photosynthesis and prey ingestion (Gustafson et al. 2000, Yih et al. 2004, 2013). In addition, this species is an important prey for some dinoflagellate predators (i.e., *Amylax tria-*

*cantha*, *Alexandrium pseudogonyaulax*, *Dinophysis* spp., *Neoceratium furca*, and *Oxyphysis oxytoxoides*) and an effective grazer of cryptophytes (Yih et al. 2004, Park et al. 2006, 2011, 2013b, Blossom et al. 2012, Hansen et al. 2013, Johnson et al. 2013).

The predation of *M. rubrum* by heterotrophic protists is one of the critical factors that affect the population dynamics of red tide species. Heterotrophic protists play an important role in marine food webs, as they connect pho-



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trophic plankton to higher trophic levels (Stoecker and Capuzzo 1990, Sherr and Sherr 2002, Myung et al. 2011, Garzio and Steinberg 2013). However, there have been few studies on the feeding patterns of common heterotrophic protists that frequently co-occur with *M. rubrum*. *O. oxytoxoides* is the only heterotrophic dinoflagellate that is known to feed on *M. rubrum* (Park et al. 2011). However, the growth and ingestion rates and / or the impact of heterotrophic protist grazing on *M. rubrum* have not been reported.

*Gyrodiniellum shiwhaense*, *Gyrodinium dominans*, *Gyrodinium spirale*, *Luciella masanensis*, *Oblea rotunda*, *Oxyrrhis marina*, *Pfiesteria piscicida*, *Polykrikos kofoidii*, *Protoperidinium bipes*, and *Stoeckeria algicida*, and naked ciliates having sizes of 30-50  $\mu\text{m}$  have been reported to be present in many waters (Strom and Buskey 1993, Jeong et al. 2004, 2005, 2006, 2007, 2011a, 2011b, Kim and Jeong 2004, Yoo et al. 2010, 2013a, Seuthe et al. 2011, Kang et al. 2013). Furthermore, they often co-occur with *M. rubrum* (Hansen et al. 1995, Bouley and Kimmerer 2006, Kang et al. 2013). Thus it is worthwhile to explore interactions between *M. rubrum* and these heterotrophic protists.

The results of the present study would provide a basis for understanding the interactions between *M. rubrum* and heterotrophic protists.

## MATERIALS AND METHODS

### Preparation of experimental organisms

*M. rubrum* (MR-MAL01) was isolated from water samples collected from Gomso Bay, Korea (35°40' N, 126°40' E) in May 2001 at a water temperature and salinity of 18°C and 31.5, respectively. A clonal culture of *M. rubrum* was established as in Yih et al. (2004). The culture was maintained with *Teleaulax* sp. (previously described as a cryptophyte) in 500-mL bottles on a shelf at 20°C under an illumination of 20  $\mu\text{E m}^{-2} \text{s}^{-1}$  of cool white fluorescent light on a 14 h : 10 h light-dark cycle (Yih et al. 2004).

For the isolation and culture of the heterotrophic dinoflagellates *G. shiwhaense*, *G. dominans*, *G. spirale*, *L. masanensis*, *O. rotunda*, *O. marina*, *P. piscicida*, *P. kofoidii*, *P. bipes*, *S. algicida*, and the naked ciliate *Strombidium* sp. plankton samples were collected from the waters of coastal area in Korea in 2001-2013, and a clonal culture of each species was established by two serial single-cell isolations (Table 1).

The carbon contents for *M. rubrum* (0.43 ng C cell<sup>-1</sup>, n = 40), the heterotrophic dinoflagellates, and the ciliates were estimated from cell volume according to Menden-Deuer and Lessard (2000). The cell volume of the preserved predators after each feeding experiment was

**Table 1.** Conditions for the isolation and maintenance of the experimental organisms, and feeding occurrence by diverse heterotrophic protistan predators

	Type	FM	Strain isolation information				Prey species for maintenance	Feeding
			Location	Time	Temperature (°C)	Salinity		
<b>Predator</b>								
<i>Gyrodiniellum shiwhaense</i>	HTD	PD	Shiwha	May 2010	19.0	27.7	<i>Amphidnium carterae</i>	N
<i>Gyrodinium dominans</i>	HTD	EG	Masan	Nov 2011	19.7	31.0	<i>Amphidnium carterae</i>	Y
<i>Gyrodinium spirale</i>	HTD	EG	Masan	May 2009	19.7	31.0	<i>Prorocentrum minimum</i>	N
<i>Luciella masanensis</i>	HTD	PD	Shiwha	Dec 2012	2.0	28.0	<i>Teleaulax</i> sp.	Y
<i>Oblea rotunda</i>	HTD	PA	Shiwha	Aug 2010	26.8	23.7	<i>Prorocentrum minimum</i>	Y
<i>Oxyrrhis marina</i>	HTD	EG	Kunsan	May 2001	16.0	27.7	<i>Amphidnium carterae</i>	N
<i>Pfiesteria piscicida</i>	HTD	PD	Jinhae	Feb 2010	6.3	30.6	<i>Amphidnium carterae</i>	N
<i>Polykrikos kofoidii</i>	HTD	EG	Shiwha	Mar 2010	9.3	23.4	<i>Lingulodinium polyedrum</i>	Y
<i>Protoperidinium bipes</i>	HTD	PA	Shiwha	Mar 2012	6.4	27.8	<i>Skeletonema costatum</i>	N
<i>Stoeckeria algicida</i>	HTD	PD	Masan	Aug 2007	24.5	29.7	<i>Heterosigma akashiwo</i>	N
<i>Strombidium</i> sp.	NC	FF	Pohang	Jan 2013	5.0	13.0	<i>Heterocapsa rotundata</i>	Y
<b>Prey</b>								
<i>Mesodinium rubrum</i>	MNC	EG	Gomso Bay	May 2001	18	31.5	<i>Teleaulax</i> sp.	

FM, feeding mechanism; HTD, heterotrophic dinoflagellate; PD, peduncle feeder; N, the predator observed not to feed on a living *M. rubrum* cell; EG, engulfment feeder; Y, the predator observed to feed on a living *M. rubrum* cell; PA, pallium feeder; NC, naked ciliate; FF, filter feeder; MNC, Mixotrophic naked ciliate.

conducted was estimated using the methods of Kim and Jeong (2004) for *G. dominans* and *G. spirale*, the protocol of Jeong et al. (2008) for *O. marina*, and the methods of Jeong et al. (2001) for *P. kofoidii*. The cell volume of *O. rotunda* was calculated with an assumption that its geometry is an ellipsoid.

## Feeding occurrence

Experiment 1 was designed to test whether *G. shiwhaense*, *G. dominans*, *G. spirale*, *L. masanensis*, *O. rotunda*, *O. marina*, *P. piscicida*, *P. kofoidii*, *P. bipes*, and *S. algicida*, and the naked ciliate *Strombidium* sp. were able to feed on *M. rubrum* (Table 1).

Approximately 10,000 *M. rubrum* cells were added to each of the two 42-mL polycarbonate (PC) bottles containing each of the heterotrophic dinoflagellates (2,000–10,000 cells) and the ciliates (10–80 cells) (final *M. rubrum* prey concentration = ca. 1,000–5,000 cells mL<sup>-1</sup>). One control bottle (without prey) was set up for each experiment. The bottles were placed on a plankton wheel rotating at 0.9 rpm and incubated at 20°C under an illumination of 20  $\mu\text{E m}^{-2}\text{s}^{-1}$  on a 14 h : 10 h light-dark cycle.

Five milliliter aliquots were removed from each bottle after 1, 2, 6, and 24 h incubation and then transferred into 6-well plate. Approximately 200 cells in the plate chamber were observed under a dissecting microscope at a magnification of 10–63 $\times$  (SZX10; Olympus, Tokyo, Japan) to determine whether the predators were able to feed on *M. rubrum*. Predator cells containing prey cells were transferred onto glass slides and then their photographs were taken at a magnification of 400–1,000 $\times$  with a camera mounted on an inverted microscope (Zeiss-Axiovert 200M; Carl Zeiss Ltd., Göttingen, Germany).

## Prey concentration effects on growth and ingestion rates

Experiment 2 was designed to measure the growth and ingestion rates of *G. dominans* as a function of *M. rubrum* concentration.

Dense cultures of *G. dominans* growing on the algal prey listed in Table 1 were transferred to 500-mL PC bottles containing filtered seawater. The bottles were filled to capacity with freshly filtered seawater, capped, and placed on plankton wheels rotating at 0.9 rpm and incubated at 20°C under an illumination of 20  $\mu\text{E m}^{-2}\text{s}^{-1}$  on a 14 h : 10 h light-dark cycle. To monitor the conditions and interaction between the predator and prey species, the cultures were periodically removed from the rotating wheels, ex-

amined through the surface of the capped bottles using a dissecting microscope, and then returned to the rotating wheels. At timepoints at which prey cells were no longer present in ambient water, they were still observed inside the protoplasm of the predators. We therefore decided to starve the predators for 1 day in order to minimize possible residual growth resulting from the ingestion of prey during batch culture. After this incubation period, cell concentrations of *G. dominans* were determined in three 1-mL aliquots from each bottle using a light microscope, and the cultures were then used to conduct experiments.

For each experiment, the initial concentrations of *G. dominans* and *M. rubrum* were established using an autopipette to deliver predetermined volumes of known cell concentrations to the bottles. Triplicate 42-mL PC experiment bottles (mixtures of predator and prey) and triplicate control bottles (prey only) were set up at each predator-prey combination. Triplicate control bottles containing only *G. dominans* were also established at one predator concentration. To obtain similar water conditions, the water of predator cultures was filtered through a 0.7- $\mu\text{m}$  GF/F filter and then added to the prey control bottles in the same amount as the predator culture for each predator-prey combination. All bottles were then filled to capacity with freshly filtered seawater and capped. To determine the actual predator and prey densities at the beginning of the experiment, a 5-mL aliquot was removed from each bottle, fixed with 5% Lugol's solution, and examined using a light microscope to enumerate the cells in three 1-mL Sedgwick-Rafter chambers (SRCs). The bottles were refilled to capacity with freshly filtered seawater, capped, and placed on rotating wheels under the conditions described above. Dilution of the cultures associated with refilling the bottles was considered when calculating growth and ingestion rates. A 10-mL aliquot was taken from each bottle after 48-h incubation and fixed with 5% Lugol's solution, and the abundance of *G. dominans* and prey were determined by counting all or >300 cells in three 1-mL SRCs. Before taking the subsamples, the conditions of *G. dominans* and their prey were assessed using a dissecting microscope as described above.

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

$$\mu = [\text{Ln} (P_t / P_0)] / t \quad (1)$$

, where  $P_0$  and  $P_t$  = the concentration of *G. dominans* at 0 d and 2 d, respectively.

Data for *G. dominans* growth rates were fitted to a Michaelis-Menten equation:

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

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

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

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

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

Additionally, the growth and ingestion rates of *L. masanensis*, *O. rotunda*, and *Strombidium* sp. on *M. rubrum* prey at a single prey concentration at which both growth and ingestion rates of *G. dominans* on *M. rubrum* were saturated were measured as described above.

### Cell volume of *Gyrodinium dominans*

After the 2-d incubation, the cell length and maximum width of *G. dominans* preserved in 5% acid Lugol's solution ( $n = 20-30$  for each prey concentration) were measured using an image analysis system on images collected with an inverted microscope (AxioVision 4.5; Carl Zeiss Ltd.). The shape of *G. dominans* was estimated to 2 cones joined at the cell equator (= maximum width of the cell). The carbon content was estimated from cell volume according to Menden-Deuer and Lessard (2000).

### Grazing impact

We estimated grazing coefficients attributable to small heterotrophic *Gyrodinium* spp. (25-35  $\mu m$  in cell length) on *Mesodinium* by combining field data on abundances of small *Gyrodinium* spp. and prey with ingestion rates of the predators on the prey obtained in the present study. We assumed that the ingestion rates of the other small heterotrophic *Gyrodinium* spp. on *M. rubrum* are the same as that of *G. dominans*. The data on the abundances

of *M. rubrum* and co-occurring small heterotrophic *Gyrodinium* spp. used in this estimation were obtained from water samples collected in 2004-2005 from Masan Bay and in 2008-2009 from Shiwha Bay.

The grazing coefficients ( $g, h^{-1}$ ) were calculated as:

$$g = CR \times GC \quad (4)$$

, where CR is the clearance rate ( $mL predator^{-1} h^{-1}$ ) of a predator on *M. rubrum* at a given prey concentration and GC is the predator concentration (cells  $mL^{-1}$ ). CR's were calculated as:

$$CR = IR(h) / x \quad (5)$$

, where IR ( $h$ ) is the ingestion rate (cells eaten predator $^{-1} h^{-1}$ ) of the predator on the prey and  $x$  is the prey concentration (cells  $mL^{-1}$ ). CR's were corrected using  $Q_{10} = 2.8$  (Hansen et al. 1997) because in situ water temperatures and the temperature used in the laboratory for this experiment ( $20^{\circ}C$ ) were sometimes different.

## RESULTS

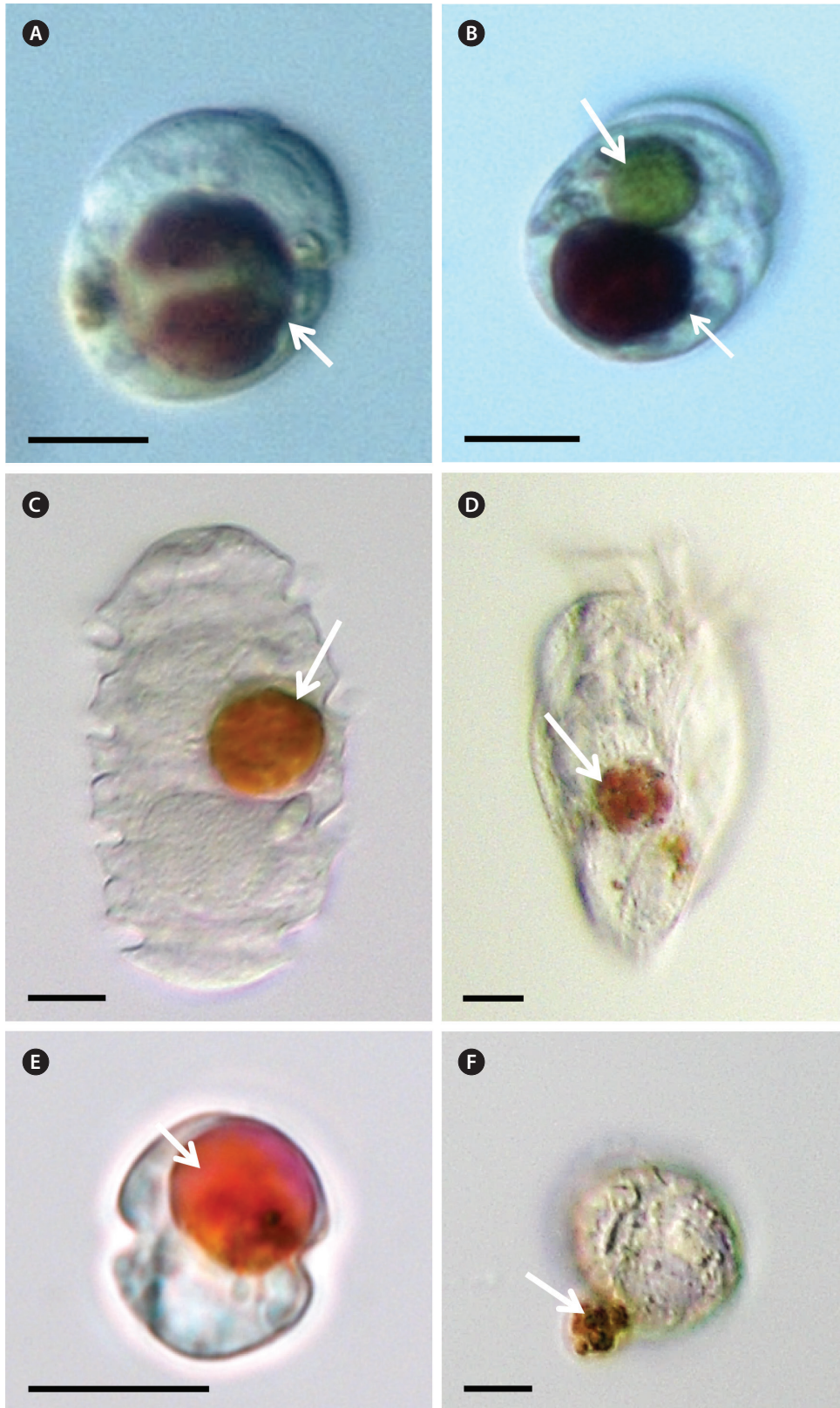
### Feeding occurrence

Among the predators tested in the present study, *G. dominans*, *L. masanensis*, *O. rotunda*, *P. kofoidii*, and *Strombidium* sp. preyed on *M. rubrum* (Table 1, Fig. 1). However, *G. shiwhaense*, *G. spirale*, *O. marina*, *P. piscicida*, *P. bipes*, and *S. algicida* did not attempt to attack, even when it encountered *M. rubrum*.

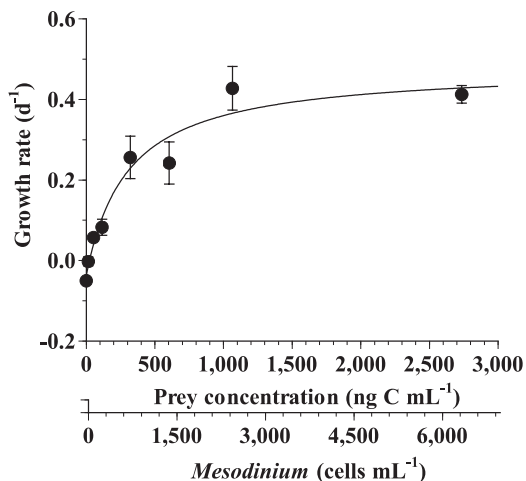
### Growth and ingestion rates

The specific growth rates of *G. dominans* on *M. rubrum* increased rapidly with increasing mean prey concentration up to ca. 321 ng C  $mL^{-1}$  (746 cells  $mL^{-1}$ ), but slowly at higher concentrations (Fig. 2). When the data were fitted to Eq. (2), the maximum specific growth rate ( $\mu_{\max}$ ) of *G. dominans* on *M. rubrum* was  $0.48 d^{-1}$ . The feeding threshold prey concentration for the growth of *G. dominans* (i.e., no growth) was 23.3 ng C  $mL^{-1}$  (54 cells  $mL^{-1}$ ).

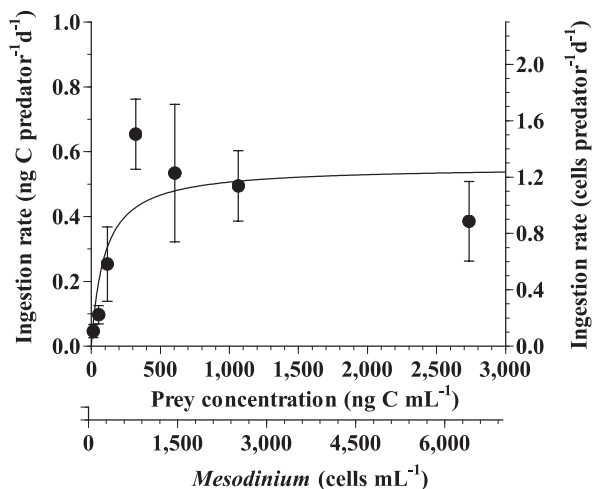
The ingestion rates of *G. dominans* on *M. rubrum* increased rapidly with increasing mean prey concentration up to ca. 321 ng C  $mL^{-1}$  (746 cells  $mL^{-1}$ ), but became saturated at higher concentrations (Fig. 3). When the data were fitted to Eq. (3), the maximum ingestion rate ( $I_{\max}$ ) of *G. dominans* on *M. rubrum* was  $0.55 ng C predator^{-1} d^{-1}$  (1.3 cells predator $^{-1} d^{-1}$ ). The maximum clearance rate of *G. dominans* on *M. rubrum* was  $0.14 \mu L predator^{-1} h^{-1}$ .



**Fig. 1.** Feeding by heterotrophic protistan predators on *Mesodinium rubrum*. (A & B) *Gyrodinium dominans* having 1-2 ingested *M. rubrum* cells. (C) *Polykrikos kofoidii*. (D) *Strombidium* sp. (E) *Luciella masanensis*. (F) *Oblea rotunda*. White arrows indicate prey (*M. rubrum*) materials. Scale bars represent: A-F, 10  $\mu$ m.



**Fig. 2.** Specific growth rate of the heterotrophic dinoflagellate *Gyrodinium dominans* on *Mesodinium rubrum* as a function of mean prey concentration ( $x$ ). Symbols represent treatment means  $\pm 1$  standard error. The curves are fitted by the Michaelis-Menten equation [Eq. (2)] using all treatments in the experiment. Growth rate ( $d^{-1}$ ) =  $0.48 [(x - 23.3) / (325.7 + [x - 23.3])]$ ,  $r^2 = 0.881$ .

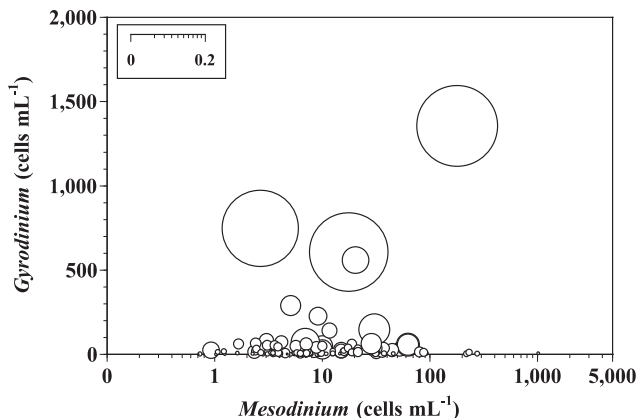


**Fig. 3.** Specific ingestion rates of the heterotrophic dinoflagellate *Gyrodinium dominans* on *Mesodinium rubrum* as a function of mean prey concentration ( $x$ ). Symbols represent treatment means  $\pm 1$  standard error. The curves are fitted by the Michaelis-Menten equation [Eq. (3)] using all treatments in the experiment. Ingestion rate ( $ng\ C\ predator^{-1}\ d^{-1}$ ) =  $0.55 [x / (94.6 + x)]$ ,  $r^2 = 0.453$ .

The growth rates of *L. masanensis*, *O. rotunda*, and *Strombidium* sp. on *M. rubrum* prey at single prey concentrations (995-1,130  $ng\ C\ mL^{-1}$ ) at which both growth and ingestion rates of *G. dominans* on *M. rubrum* were saturated were negative.

### Grazing impact

When the abundances of *M. rubrum* and small het-



**Fig. 4.** Calculated grazing coefficients of small heterotrophic *Gyrodinium* spp. ( $n = 121$ ) in relation to the concentration of co-occurring *Mesodinium rubrum* (see text for calculation). Clearance rates, measured under the conditions provided in the present study, were corrected using  $Q_{10} = 2.8$  (Hansen et al. 1997) because *in situ* water temperatures and the temperature used in the laboratory for this experiment ( $20^{\circ}C$ ) were sometimes different. The scales of the circles in the inset boxes are  $g\ (h^{-1})$ .

erotrophic *Gyrodinium* spp. (25-35  $\mu m$  in cell length) in Masan Bay in 2004-2005 and Shiwaha Bay in 2008-2009 ( $n = 121$ ) were  $1-1,014\ cells\ mL^{-1}$  and  $1-1,356\ cells\ mL^{-1}$ , respectively, grazing coefficients attributable to small heterotrophic *Gyrodinium* spp. on co-occurring *M. rubrum* were up to  $0.236\ h^{-1}$  (Fig. 4).

## DISCUSSION

### Predators

Among the heterotrophic dinoflagellates and a ciliate investigated in this study, *G. dominans*, *L. masanensis*, *O. rotunda*, *P. kofoidii*, and *Strombidium* sp. prey on *M. rubrum*. With respect to feeding mechanisms, *G. dominans*, *P. kofoidii*, and *Strombidium* sp. feed on prey by direct engulfment, but *L. masanensis* by a peduncle, and *O. rotunda* by a pallium (Strom and Buskey 1993, Kim and Jeong 2004, Jeong et al. 2007, Yoo et al. 2010). Since organisms with different feeding modalities were able to graze on *M. rubrum*, we conclude that feeding mechanisms do not generally determine the ability of heterotrophic protists to feed on *M. rubrum*. In addition, the size range of the predators that can feed on *M. rubrum* is also wide, and thus this factor is also not a critical determinant of protist feeding on *M. rubrum*. *G. shiwhaense*, *G. spirale*, *O. marina*, *P. piscicida*, *P. bipes*, and *S. algicida* did not even attack *M. rubrum* when they encountered the ciliate. Thus,

*G. dominans*, *L. masanensis*, *O. rotunda*, *P. kofoidii*, and *Strombidium* sp. may have an ability to detect *M. rubrum* cells by physical and / or chemical cues, while the other organisms may lack this feature.

*M. rubrum* usually stay motionless for a second, but swim or jump quickly. When it jumps, the maximum swimming speeds of *M. rubrum* are 2,217-12,000  $\mu\text{m s}^{-1}$ , which are comparable to or greater than that of *G. dominans*, *O. rotunda*, *P. kofoidii*, and *Strombidium* sp. (2,533, 420, 1,182, and 4,000  $\mu\text{m s}^{-1}$ , respectively) (Lee, unpublished data) (Barber and Smith 1981 cited by Smayda 2002, Crawford 1992, Buskey et al. 1993, Crawford and Lindholm 1997, Kim and Jeong 2004, Fenchel and Hansen 2006). Therefore, *G. dominans*, *O. rotunda*, *P. kofoidii*, and *Strombidium* sp. are likely to capture *M. rubrum* when they are motionless or when *M. rubrum* may bump into them and then stun them.

### Growth and ingestion rates

*G. dominans* was the only predator whose growth actually increased when grazing on *M. rubrum* in this study, even though *L. masanensis*, *O. rotunda*, *P. kofoidii*, and *Strombidium* sp. also fed on *M. rubrum*. In addition, the mixotrophic dinoflagellates *Amylax triacantha* and *Dinophysis acuminata* are known to grow on *M. rubrum* (Park et al. 2006, 2013b, Kim et al. 2008). Therefore, during red tides dominated by *M. rubrum*, *G. dominans*, *A. triacantha*, and *D. acuminata* are expected to be present. In contrast, *L. masanensis*, *O. rotunda*, *P. kofoidii*, and *Strombidium* sp. may be absent due to a lack of co-occurring alternative optimal prey species. The maximum growth rate of *G. dominans* on *M. rubrum* (0.48  $\text{d}^{-1}$ ) is lower than the mixotrophic growth rates of *A. triacantha* and *D. acuminata* on the same prey (0.68 and 0.91  $\text{d}^{-1}$ , respectively) (Table 2). A lower ingestion rate of *G. dominans* on *M. rubrum* (0.55  $\text{ng C predator}^{-1} \text{d}^{-1}$ ) when compared with *A. triacantha* (2.54  $\text{ng C predator}^{-1} \text{d}^{-1}$ ) and *D. acuminata* (1.30  $\text{ng C predator}^{-1} \text{d}^{-1}$ ) may be partially responsible for this lower growth rate. During *M. rubrum* red tides, *G. dominans* may be less abundant than *A. triacantha* and *D. acu-*

*minata*. However, *G. dominans* can grow on diverse algal prey species, while *A. triacantha* and *D. acuminata* can only grow on *M. rubrum* (Nakamura et al. 1992, 1995, Kim and Jeong 2004, Park et al. 2006, 2013b, Kim et al. 2008, Yoo et al. 2010, 2013b, Jeong et al. 2011a, 2014). Thus, the abundance of *G. dominans* in the period of red tides that are not associated with *M. rubrum* may be greater than those of *A. triacantha* and *D. acuminata*. We suggest that future studies should compare the relative abundances of these three predators, and their grazing impact on prey populations, during *M. rubrum*-associated red tides.

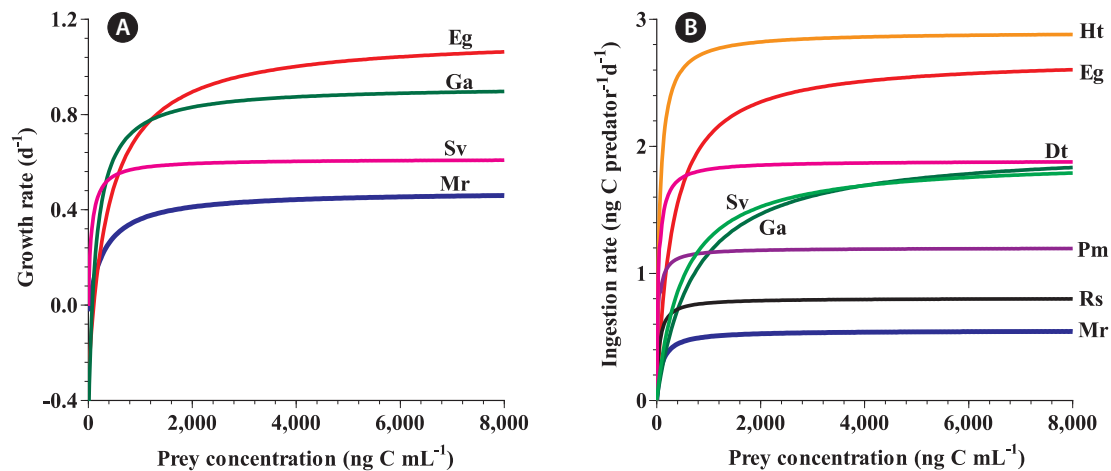
The maximum growth rate ( $\mu_{\text{max}}$ ) of *G. dominans* on *M. rubrum* (0.48  $\text{d}^{-1}$ ) is comparable to that on the mixotrophic dinoflagellates *Heterocapsa triquetra* and *Karenia mikimotoi*, and the raphidophyte *Chattonella antique*, but higher than that on the mixotrophic dinoflagellate *Biecheleria cincta*, the cryptophyte *Rhodomonas salina*, and the chlorophyte *Dunaliella teriolecta* (Table 3). However, the  $\mu_{\text{max}}$  of *G. dominans* on *M. rubrum* is lower than that observed with the mixotrophic dinoflagellates *Gymnodinium aureolum*, *Prorocentrum minimum*, and *Symbiodinium voratum*, the euglenophyte *Eutreptiella gymnastica*, and the diatom *Thalassiosira* sp. (Table 3). *M. rubrum*, these mixotrophic dinoflagellates, and the raphidophyte cause red tides in the waters of many countries (Crawford 1989, Heil et al. 2005, Jeong et al. 2011a, 2013, Park et al. 2013a, Yih et al. 2013). *G. dominans* is likely to be more abundant during *M. rubrum* red tides than during *B. cincta*, *R. salina*, or *D. teriolecta* red tides, but less abundant during *E. gymnastica*, *G. aureolum*, or *P. minimum* red tides.

The maximum rate at which *G. dominans* can ingest *M. rubrum* is one of the lowest among the algal prey species, with the exception of *B. cincta* and comparable to that on *R. salina* (Table 3). Interestingly, *M. rubrum* and *Rhodomonas* spp. exhibit jumping behaviors (Fenchel and Hansen 2006, Berge et al. 2008). These jumping behaviors of *M. rubrum* may act as an anti-predation behavior. However, the ratio of the maximum growth rate relative to the maximum ingestion rate of *G. dominans* on *M. rubrum* is greater than that on any other algal prey, with the

**Table 2.** Growth and ingestion rates of dinoflagellate predators when feeding on *Mesodinium rubrum*

Predators	ESD	Type	Feeding mechanism	GR	IR	Reference
<i>Gyrodinium dominans</i>	20.0	HTD	Engulfment	0.48	0.55	This study
<i>Amylax triacantha</i>	30.0	MTD	Engulfment	0.68	2.54	Park et al. (2013b)
<i>Dinophysis acuminata</i>	35.0	MTD	Peduncle	0.91	1.30	Kim et al. (2008)

ESD, equivalent spherical diameter ( $\mu\text{m}$ ); GR, growth rate ( $\text{d}^{-1}$ ); IR, ingestion rate ( $\text{ng C predator}^{-1} \text{d}^{-1}$ ); HTD, heterotrophic dinoflagellate; MTD, mixotrophic dinoflagellate.



**Fig. 5.** A comparison of the numerical (A) and functional (B) responses of the heterotrophic dinoflagellate *Gyrodinium dominans* feeding on diverse prey related to prey concentration. Rates are corrected to 20°C using  $Q_{10} = 2.8$  (Hansen et al. 1997). Eg, *Eutreptiella gymnastica*, euglenophyte; Ga, *Gymnodinium aureolum*, mixotrophic dinoflagellate; Sv, *Symbiodinium voratum*, mixotrophic dinoflagellate; Mr, *Mesodinium rubrum*, mixotrophic ciliate; Ht, *Heterocapsa triquetra*, mixotrophic dinoflagellate; Dt, *Dunaliella tertiolecta*, chlorophyte; Pm, *Prorocentrum minimum*, mixotrophic dinoflagellate; Rs, *Rhodomonas salina*, cryptophyte. All responses in (A) were fitted to Eq. 2, whereas those in (B) were fitted to Eq. 3.

exception of *P. minimum*. Therefore, *M. rubrum* is likely to be the most nutritious algal prey for *G. dominans*, *P. minimum* notwithstanding.

In the numerical response of *G. dominans* to four algal prey species, the feeding threshold prey concentration for growth of *G. dominans* on *M. rubrum* is lower than that of *E. gymnastica* or *G. aureolum*, but higher than that of *S. voratum* (Table 3, Fig. 5A). Therefore, *G. dominans* may preferentially grow on *M. rubrum* rather than on *E.*

*gymnastica* or *G. aureolum* at low prey concentrations. The  $K_{GR}$  (the prey concentration sustaining  $1/2 \mu_{max}$ ) of *G. dominans* on *M. rubrum* is greater than that on *G. aureolum*, and *S. voratum*, but lower than that on *E. gymnastica*. Therefore, the growth of *G. dominans* on *M. rubrum* is more sensitive to a change in prey concentration than the same parameter in *E. gymnastica*, but less sensitive than *G. aureolum*, and *S. voratum*. The functional response of *G. dominans* feeding on diverse algal prey species fol-

**Table 3.** Comparison of growth and grazing data for *Gyrodinium dominans* on diverse prey species

Prey species	Type	ESD	MGR	$K_{GR}$	$x'$	MIR	$K_{IR}$	RMGI	Reference
<i>Thalassiosira</i> sp.	DIA	5.4	0.73	-	-	-	-	-	Nakamura et al. (1995)
<i>Rhodomonas salina</i>	CR	6.5	0.21	-	-	0.8	49	0.21	Calbet et al. (2013)
<i>Dunaliella tertiolecta</i>	CH	6.5	0.28	-	-	1.9	37	0.12	Calbet et al. (2013)
<i>Symbiodinium voratum</i>	MTD	11.1	0.61	65	0.4	1.9	493	0.32	Jeong et al. (2014)
<i>Prorocentrum minimum</i>	MTD	12.1	1.13	-	-	1.2	31	0.94	Kim and Jeong (2004)
<i>Biecheleria cincta</i>	MTD	12.2	0.07	-	-	0.1	-	0.54	Yoo et al. (2013b)
<i>Eutreptiella gymnastica</i>	EU	12.6	1.13	499	106	2.7	299	0.42	Jeong et al. (2011a)
<i>Heterocapsa triquetra</i>	MTD	15.3	0.54	-	-	2.9	56	0.23	Nakamura et al. (1995)
<i>Karenia mikimotoi</i>	MTD	16.8	0.48	-	-	-	-	-	Nakamura et al. (1995)
<i>Gymnodinium aureolum</i>	MTD	19.5	0.92	207	76	2.0	727	0.46	Jeong et al. (2010)
<i>Mesodinium rubrum</i>	MNC	22.0	0.48	326	23	0.6	95	0.87	This study
<i>Chattonella antique</i>	RA	35.3	0.50	-	-	2.3	-	0.22	Nakamura et al. (1992)

ESD, equivalent spherical diameter ( $\mu\text{m}$ ); MGR, maximum growth rate ( $\text{d}^{-1}$ );  $K_{GR}$ , the prey concentration sustaining  $1/2 \mu_{max}$  ( $\text{ng C mL}^{-1}$ );  $x'$ , threshold prey concentration ( $\text{ng C mL}^{-1}$ ); MIR, maximum ingestion rate ( $\text{ng C predator}^{-1} \text{d}^{-1}$ );  $K_{IR}$ , the prey concentration sustaining  $1/2 I_{max}$  ( $\text{ng C mL}^{-1}$ ); RMGI, ratio of MGR relative to MIR. Rates are corrected to 20°C using  $Q_{10} = 2.8$  (Hansen et al. 1997); DIA, diatom; CR, cryptophyte; CH, chlorophyte; MTD, mixotrophic dinoflagellate; EU, euglenophyte; MNC, mixotrophic naked ciliate; RA, raphidophyte.



lows a Holling type II pattern (Holling 1959). With respect to the functional response of *G. dominans* to eight algal prey species, the  $K_{IR}$  (the prey concentration sustaining  $1/2 I_{max}$ ) when grown on *M. rubrum* is greater than that obtained with *R. salina*, *P. minimum*, *D. teriolecta*, and *H. triquetra*, but lower than that obtained with *E. gymnastica*, *G. aureolum*, and *S. voratum* (Fig. 5B). Therefore, the ingestion of *G. dominans* on *M. rubrum* is more sensitive to a change in prey concentration than *E. gymnastica*, *G. aureolum*, and *S. voratum*, but less sensitive than *R. salina*, *P. minimum*, *D. teriolecta*, and *H. triquetra*.

### Grazing impact

To our knowledge, prior to this study, there had been no reports on the impact of protist grazing on *Mesodinium* populations. Grazing coefficients derived from studies in Masan Bay in 2004-2005 and Shihwa Bay in 2008-2009 show that up to 21% of *M. rubrum* populations can be removed by small *Gyrodinium* populations in approximately 1 d. Therefore, small heterotrophic *Gyrodinium* spp. can have a considerable grazing impact on populations of *M. rubrum* under suitable conditions. *G. dominans* is one of the few protistan grazers that are able to feed on *M. rubrum*, and is the only protistan grazer with a documented grazing impact on *M. rubrum* abundance. This finding should be taken into consideration when developing models to explain the red tide dynamics of *M. rubrum*.

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