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 <321 ng C mL⁻¹, but became saturated or slowly at higher concentrations. The maximum growth rate of *G. dominans* on *M. rubrum* was 0.48 d⁻¹, while the maximum ingestion rate was 0.55 ng C predator⁻¹ d⁻¹. The grazing coefficients by *G. dominans* on populations of *M. rubrum* were up to 0.236 h⁻¹. Thus, *G. dominans* may sometimes have a considerable grazing impact on populations of *M. rubrum*.

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

**INTRODUCTION**


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

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

<table>
<thead>
<tr>
<th>Predator</th>
<th>Type</th>
<th>FM</th>
<th>Strain isolation information</th>
<th>Feeding</th>
<th>Prey species for maintenance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Location</td>
<td>Time</td>
<td>Temperature (°C)</td>
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<tr>
<td><em>Gyrodinium dominans</em></td>
<td>HTD</td>
<td>PD</td>
<td>Shiwha</td>
<td>May 2010</td>
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<tr>
<td><em>Gyrodinium spirale</em></td>
<td>HTD</td>
<td>EG</td>
<td>Masan</td>
<td>Nov 2011</td>
<td>19.7</td>
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<tr>
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<td>HTD</td>
<td>PD</td>
<td>Shiwha</td>
<td>Dec 2012</td>
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<tr>
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<td>HTD</td>
<td>PA</td>
<td>Shiwha</td>
<td>Aug 2010</td>
<td>26.8</td>
</tr>
<tr>
<td><em>Oxyrrhis marina</em></td>
<td>HTD</td>
<td>EG</td>
<td>Kunsan</td>
<td>May 2001</td>
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<tr>
<td><em>Pfiesteria piscicida</em></td>
<td>HTD</td>
<td>PD</td>
<td>Jinhae</td>
<td>Feb 2010</td>
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<td><em>Polykrikos kofoidii</em></td>
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<td>EG</td>
<td>Shiwha</td>
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<tr>
<td><em>Protoperidinium bipes</em></td>
<td>HTD</td>
<td>PA</td>
<td>Shiwha</td>
<td>Mar 2012</td>
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<tr>
<td><em>Stoeckeria algicida</em></td>
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<td>Masan</td>
<td>Aug 2007</td>
<td>24.5</td>
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<tr>
<td><em>Strombidium sp.</em></td>
<td>NC</td>
<td>FF</td>
<td>Pohang</td>
<td>Jan 2013</td>
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</tr>
</tbody>
</table>

**Prey**

<table>
<thead>
<tr>
<th>Type</th>
<th>FM</th>
<th>Strain isolation information</th>
<th>Feeding</th>
<th>Prey species for maintenance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Location</td>
<td>Time</td>
<td>Temperature (°C)</td>
</tr>
<tr>
<td><em>Mesodinium rubrum</em></td>
<td>MNC</td>
<td>EG</td>
<td>Gomso Bay</td>
<td>May 2001</td>
</tr>
</tbody>
</table>
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. rotundata was calculated with an assumption that its geometry is an ellipsoid.

**Feeding occurrence**

Experiment 1 was designed to test whether G. shiwaense, G. dominans, G. spirale, L. masanensis, O. rotundata, 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⁻¹). 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 µE m⁻² 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 400-1,000× 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 µE m⁻² 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, examined 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-µm 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⁻¹), was calculated as:

\[
\mu = \frac{[\ln (P_t / P_0)]}{t}
\]

(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:
\[ \mu = \frac{\mu_{\text{max}} (x - x')}{K_{\text{m}} + (x - x')} \]  

(2)

where \( \mu_{\text{max}} \) = 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 \( \mu = 0 \)), \( K_{\text{m}} \) = the prey concentration sustaining 1/2 \( \mu_{\text{max}} \). 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:

\[ IR = \frac{I_{\text{max}} (x)}{K_{IR} + (x)} \]  

(3)

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

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 µm 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 (\( g, h \)) were calculated as:

\[ g = CR \times GC \]  

(4)

\[ CR = IR (h) / x \]  

(5)

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:

\[ CR = IR (h) / x \]  

\[ g = CR \times GC \]  

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 \( Q_{\text{m}} \) = 2.8 (Hansen et al. 1997) because in situ water temperatures and the temperature used in the laboratory for this experiment (20°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 (\( \mu_{\text{max}} \)) 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 (\( I_{\text{max}} \)) 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 µL 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 µm.
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 ± 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 ± 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 heterotrophic *Gyrodinium* spp. (25-35 µm in cell length) in Masan Bay in 2004-2005 and Shiwha 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 µm 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 µm 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 Amalx 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 d⁻¹) is lower than the mixotrophic growth rate of A. triacantha and D. acuminate on the same prey (0.68 and 0.91 d⁻¹, respectively) (Table 2). A lower ingestion rate of G. dominans on M. rubrum (0.55 ng C predator⁻¹ d⁻¹) when compared with A. triacantha (2.54 ng C predator⁻¹ d⁻¹) and D. acuminata (1.30 ng C predator⁻¹ 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. acuminate. 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 (µ_max) of G. dominans on M. rubrum (0.48 d⁻¹) is comparable to that on the mixotrophic dinoflagellates Heterocapsa triquetra and Karenia mikimotoi, and the raphidophyte Chattonella antiquae, but higher than that on the mixotrophic dinoflagellate Biechelia cincta, the cryptophyte Rhodomonas salina, and the chlorophyte Dunaliella teriolecta (Table 3). However, the µ_max of G. dominans on M. rubrum is lower than that observed with the mixotrophic dinoflagellates Gymnodinium aureolum, Procorcentrum minimum, and Symbiodinium voratum, the euglenophyte Eutreptiella gymnastica, and the diatom Thalassiosira (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. 2011, 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

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

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

ESD, equivalent spherical diameter (µm); GR, growth rate (d⁻¹); IR, ingestion rate (ng C predator⁻¹ d⁻¹); HTD, heterotrophic dinoflagellate; MTD, mixotrophic dinoflagellate.
Gymnastica or Gymnodinium aureolum at low prey concentrations. The $K_{GR}$ (the prey concentration sustaining 1/2 $\mu_{max}$) of Gymnastica on Mesodinium rubrum is greater than that on Gymnodinium aureolum, and Symbiodinium voratum, but lower than that on Eutreptiella gymnastica. Therefore, the growth of Gymnastica on Mesodinium rubrum is more sensitive to a change in prey concentration than the same parameter in Eutreptiella gymnastica, but less sensitive than Gymnodinium aureolum, and Symbiodinium voratum. The functional response of Gymnastica feeding on diverse algal prey species following the exception of Prorocentrum minimum. Therefore, Mesodinium rubrum is likely to be the most nutritious algal prey for Gymnastica, Prorocentrum minimum notwithstanding.

In the numerical response of Gymnastica to four algal prey species, the feeding threshold prey concentration for growth of Gymnastica on Mesodinium rubrum is lower than that of Eutreptiella gymnastica or Gymnodinium aureolum, but higher than that of Symbiodinium voratum (Table 3, Fig. 5A). Therefore, Gymnastica may preferentially grow on Mesodinium rubrum rather than on Eutreptiella gymnastica or Gymnodinium aureolum at low prey concentrations. The $K_{GR}$ (the prey concentration sustaining 1/2 $\mu_{max}$) of Gymnastica on Mesodinium rubrum is greater than that on Gymnodinium aureolum and Symbiodinium voratum, but lower than that on Eutreptiella gymnastica. Therefore, the growth of Gymnastica on Mesodinium rubrum is more sensitive to a change in prey concentration than the same parameter in Eutreptiella gymnastica, but less sensitive than Gymnodinium aureolum and Symbiodinium voratum. The functional response of Gymnastica feeding on diverse algal prey species followed by the exception of Prorocentrum minimum. Therefore, Mesodinium rubrum is likely to be the most nutritious algal prey for Gymnastica, Prorocentrum minimum notwithstanding.

### Table 3. Comparison of growth and grazing data for Gymnodinium aureolum on diverse prey species

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

ESD, equivalent spherical diameter ($\mu$m); MGR, maximum growth rate (d$^{-1}$); $K_{GR}$, the prey concentration sustaining 1/2 $\mu_{max}$ (ng C mL$^{-1}$); $x'$, threshold prey concentration (ng C mL$^{-1}$); MIR, maximum ingestion rate (ng C predator$^{-1}$ d$^{-1}$); $K_{IR}$, the prey concentration sustaining 1/2 $I_{max}$ (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.
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 Shiwha Bay in 2008-2009 show that up to 21% of M. rubrum populations can be removed by small Gyrodinium populations in approximately 1 day. 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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