

1 **Grazing impact of heterotrophic dinoflagellates and ciliates on common red-tide**
2 **euglenophyte *Eutreptiella gymnastica* in Masan Bay, Korea**

3
4 **Hae Jin Jeong^{a,*}, Tae Hoon Kim^b, Yeong Du Yoo^a, Eun Young Yoon^a**

5 **Jae Seong Kim^c, Kyeong Ah Seong^d, Kwang Young Kim^e, Jae Yeon Park^f**

6
7 ^a*School of Earth and Environmental Sciences, College of Natural Sciences, Seoul National*
8 *University, Seoul 151-747, Republic of Korea*

9 ^b*Research Institute of Oceanography, Seoul National University, Seoul 151-747, Republic of*
10 *Korea*

11 ^c*Red Tide Research Center, Kunsan National University, Kunsan 573-701, Republic of Korea*

12 ^d*Saemankeum Environmental Research Center, Kunsan National University, Kunsan 573-701,*
13 *Republic of Korea*

14 ^e*Department of Oceanography, Chonnam National University, Gwangju, 500-757, Republic of*
15 *Korea*

16 ^f*Environment, Energy, Resource Institute, Advanced Institutes of Convergence Technology,*
17 *Seoul National University-Gyeonggi Province, Suwon 443-270, Republic of Korea*
18

19 * Corresponding Author.

20 Tel: +82-2-880-6746

21 Fax: +82-2-874-9695

22 E-mail: hjjeong@snu.ac.kr

23 **Abstract.** The euglenophyte *Eutreptiella gymnastica* is a common red tide causative species.
24 However, there have been no studies on the grazing impact of heterotrophic protists on this
25 species. To investigate the grazing impact of heterotrophic protists on *E. gymnastica*, we
26 measured daily the abundances of *E. gymnastica* and co-occurring potential heterotrophic
27 protistan grazers in Masan Bay, Korea, in August 2004 when an *E. gymnastica* red tide occurred.
28 In addition, we tested whether the common heterotrophic dinoflagellates *Gyrodinium dominans*,
29 *Oxyrrhis marina*, *Pfiesteria piscicida*, *Polykrikos kofoidii*, *Protoperidinium bipes*, and *Stoeckeria*
30 *algicida* and the naked ciliates *Strobilidium* sp. (30-40 μm in cell length) and *Strombidinopsis* sp.
31 (70-100 μm in cell length) were able to feed on *E. gymnastica*. We also measured their growth
32 and ingestion rates on *E. gymnastica* as a function of prey concentration. Finally, we calculated
33 the grazing coefficients by combining field data on the abundance of the heterotrophic
34 dinoflagellate and ciliate grazers and co-occurring *E. gymnastica* with laboratory data on
35 ingestion rates obtained in this study. The maximum abundance of *E. gymnastica* in Masan Bay
36 in August, 2004 was 7,575 cells ml^{-1} , while those of *Gyrodinium* spp., *P. kofoidii*, *P. bipes*, the
37 naked ciliates (≤ 50 μm in cell length), and naked ciliates (> 50 μm in cell length) were 50, 9, 58,
38 32, and 3 cells ml^{-1} , respectively. The maximum growth rate of *G. dominans* on *E. gymnastica*
39 (1.13 d^{-1}) was higher than that of *O. marina* (0.81 d^{-1}) or *P. bipes* (0.77 d^{-1}). However, *E.*
40 *gymnastica* did not support positive growth of *P. kofoidii*, *Strobilidium* sp., and *Strombidinopsis*
41 sp. ($-0.04 \sim -2.8 \text{ d}^{-1}$). The maximum ingestion rates of *G. dominans*, *P. kofoidii*, *P. bipes*, *O.*
42 *marina*, and *Strobilidium* sp. on *E. gymnastica* ($2.1\text{-}2.7 \text{ ng C predator}^{-1}\text{d}^{-1}$) were similar, but they
43 were much lower than that of *Strombidinopsis* sp. ($156 \text{ ng C predator}^{-1}\text{d}^{-1}$). The calculated

44 grazing coefficients for *P. bipes*, small heterotrophic *Gyrodinium* spp. (25-35 μm in cell length),
45 naked ciliates (≤ 50 μm in cell length), *P. kofoidii*, and naked ciliates (> 50 μm in cell length) on
46 *E. gymnastica* were up to 0.77, 0.61, 0.22, 0.07 and 0.03 d^{-1} , respectively (i.e., up to 54, 46, 20, 7,
47 and 3% of *E. gymnastica* populations were removed by the population of each of these
48 heterotrophic protistan grazers in 1 d, respectively). The results of the present study suggest that
49 *P. bipes*, small heterotrophic *Gyrodinium* spp., and naked ciliates (≤ 50 μm in cell length)
50 sometimes have considerable potential grazing impact on the populations of *E. gymnastica*.

51 *Keywords:* Feeding, Growth, Harmful Algal Bloom, Ingestion, Protist, Red Tide

52

53 **1. Introduction**

54

55 The euglenophyte *Eutreptiella gymnastica* is a commonly reported causative species of red
56 tides in temperate waters (e.g., Olli et al., 1996). The occurrence of red tides of *E. gymnastica*
57 has been reported in many countries (e.g., Yamochi, 1984; Stonik, 2007). To predict the
58 outbreak, persistence, and decline of red tides, both growth (k) and mortality rate (g) of the red-
59 tide causative species should be measured. There have been many studies on the growth of *E.*
60 *gymnastica* (e.g., Lundholm et al., 2005). Studies have reported that *E. gymnastica* tolerate a
61 wide range of temperatures and salinities (Thronsen, 1973) and some *Eutreptiella* spp. are
62 extreme r-strategists with high growth potential in environments having elevated nutrient levels
63 and decreasing turbulence (Olli et al., 1996; Lundholm et al., 2005). However, there have been
64 very few studies on the grazing impact of zooplankton on *E. gymnastica* (Uye and Takamatsu,

65 1990; Olli et al., 1996). To make matters worse, there has been no study on the grazing impact of
66 heterotrophic protists, even though many studies have suggested that grazing by heterotrophic
67 protists often affects the dynamics of red tides or causes a change in causative species (Watras et
68 al., 1985; Jeong, 1995; Kamiyama and Matsuyama, 2005; Turner, 2006; Buskey, 2008; Stoecker
69 et al., 2008). The abundance of heterotrophic dinoflagellates or ciliates is usually 100-10,000
70 times greater than that of copepods, whereas the ingestion rates of the former grazers on red tide
71 algae are usually 10-100 times lower than those of the latter grazers (summarized by Jeong et al.,
72 2010). Thus, in general, the grazing impact of heterotrophic dinoflagellates or ciliates on red-tide
73 algae is much higher than that of copepods (Calbet et al., 2003; Calbet and Landry, 2004; Kim
74 and Jeong, 2004; Turner and Borkman, 2005). Thus, to understand the population dynamics of *E.*
75 *gymnastica*, it is worthwhile to investigate predator-prey relationships between *E. gymnastica*
76 and co-occurring potential heterotrophic protistan grazers and assess grazing pressure by the
77 grazers on *E. gymnastica*.

78 To investigate the grazing impact of heterotrophic protists on *E. gymnastica*, before,
79 during, and after a red tide dominated by *E. gymnastica* in Masan Bay, Korea, in August 2004,
80 we monitored the abundance of this alga and co-occurring heterotrophic protists. During this red
81 tide, several heterotrophic dinoflagellate and ciliate species co-occurred; therefore, it is a
82 possibility that these heterotrophic dinoflagellates and ciliates feed on *E. gymnastica*. Thus, the
83 present study investigated feeding by the dominant heterotrophic dinoflagellates *Gyrodinium*
84 *dominans* and *Protooperidinium bipes* and also the common heterotrophic dinoflagellates
85 *Oxyrrhis marina*, *Polykrikos kofoidii*, *Pfiesteria piscicida*, *Stoeckeria algicida*, and the naked

86 ciliates *Strobilidium* sp. (30-40 μm in cell length) and *Strombidinopsis* sp. (70-100 μm in cell
87 length) on *E. gymnastica*. (1) We tested whether these 8 heterotrophic protist species were able
88 to feed on *E. gymnastica*. (2) We also measured the growth and/or ingestion rates of *G.*
89 *dominans*, *O. marina*, *P. kofoidii*, *P. bipes*, *Strobilidium* sp., and *Strombidinopsis* sp., which were
90 revealed to feed on the algal prey, on *E. gymnastica* as a function of prey concentration. (3) In
91 addition, we also calculated grazing coefficients by combining field data on the abundances of
92 small heterotrophic *Gyrodinium* spp. (25-35 μm in cell length), *P. kofoidii*, *P. bipes*, naked
93 ciliates (≤ 50 μm in cell length), and naked ciliates (> 50 μm in cell length) and co-occurring *E.*
94 *gymnastica* with laboratory data on ingestion rates. (4) We also compared the growth and and/or
95 ingestion rates of these heterotrophic protistan grazers on *E. gymnastica* to those on the other
96 red-tide algae reported in the literature.

97 The results of the present study provide a basis for understanding the interactions
98 between *E. gymnastica* and heterotrophic protists and bloom dynamics.

99

100 **2. Materials and Methods**

101

102 *2.1. Abundances in Masan Bay, Korea*

103

104 Water samples were taken from the surface at a pier in Masan Bay using water samplers
105 before, during, and after a red tide dominated by *Eutreptiella gymnastica* in August, 2004.
106 Plankton samples for counting were poured into 500-ml polyethylene bottles and preserved with
107 acidic Lugol's solution, Bouin's solution, and glutaraldehyde. The fixed samples were

108 concentrated to 1/5-1/10 using the 2-d settlement method. After being well mixed, all or > 300
109 *Eutreptiella gymnastica* and co-occurring heterotrophic protist cells in three to five 1-ml
110 Sedgwick-Rafter counting chambers (hereafter SRCs) were counted under a light microscope
111 with standard transmitted illumination.

112 Water temperatures and salinities in the surface waters were measured using a YSI 30
113 (YSI, LA, USA) and pH and DO were measured using pH-11 (Schott Handy – Lab, Mainz,
114 Germany) and Oxi 197i (WTW, Weilheim, Germany), respectively.

115

116 2.2. Preparation of experimental organisms.

117

118 For isolation and culture of *Eutreptiella gymnastica* (GenBank accession number =
119 FJ719618), plankton samples collected using water samplers were taken from the water in Masan
120 Bay, Korea, during June 2005 when the water temperature and salinity were 23.8 °C and 28.7,
121 respectively (Table 1). These samples were screened gently through a 154- μ m Nitex mesh and
122 placed in 6-well tissue culture plates. A clonal culture of *E. gymnastica* was established by two
123 serial single cell isolations. As the concentration of *E. gymnastica* increased, the *E. gymnastica*
124 samples were subsequently transferred to 50, 120, 250, and 500 mL polycarbonate (PC) bottles
125 of fresh f/2 seawater media. The bottles were filled to capacity with freshly filtered seawater,
126 capped, and placed on a shelf at 20 °C under an illumination of 20 μ E m⁻² s⁻¹ of cool white
127 fluorescent light on a 14 h:10 h light–dark cycle.

128 For the isolation and culture of the heterotrophic dinoflagellate predators *Gyrodinium*
129 *dominans*, *Oxyrrhis marina*, *Polykrikos kofoidii*, *Pfiesteria piscicida*, *Stoeckeria algicida*, and
130 *Protoperidinium bipes*, plankton samples collected using water samplers were taken from the
131 coastal waters off Keum Estuary, Masan, Incheon, or Shiwha, Korea in 2001-2010, and a clonal
132 culture of each species was established by two serial single-cell isolations (Table 1).

133 For the isolation and culture of the ciliate *Strobilidium* sp. (30-40 μm in cell length),
134 plankton samples collected using a water sampler were taken from a water in Shiwha Bay,
135 Korea, during September 2010 when the water temperature and salinity were 20.0 $^{\circ}\text{C}$ and 11.2,
136 respectively (Table 1). For the isolation and culture of the ciliate *Strombidinopsis* sp. (70-100 μm
137 in cell length), plankton samples collected using water samplers were taken from a pier in Masan
138 Bay, Korea, during May 2009 when the water temperature and salinity were 20.2 $^{\circ}\text{C}$ and 30.1,
139 respectively (Table 1). A clonal culture of each of *Strobilidium* sp. and *Strombidinopsis* sp. was
140 also established by two serial single cell isolations.

141 The carbon contents for *E. gymnastica* (0.14 ng C per cell, n=50), the heterotrophic
142 dinoflagellates, and the ciliate were estimated from cell volume according to Menden-Deuer and
143 Lessard (2000). The cell volume of the predators was estimated using the method of Kim and
144 Jeong (2004) for *G. dominans*, Jeong et al. (2008a) for *O. marina*, Jeong et al. (2007a) for *P.*
145 *piscicida* and *S.algicida*, Jeong et al. (2004a) for *P. bipes*, Jeong et al. (2001b) for *P. kofoidii*, and
146 Jeong et al. (2008b) for *Strobilidium* sp. and *Strombidinopsis* sp..

147

148 2.3. Feeding occurrence.

149

150 Expt 1 was designed to test whether each of *G. dominans*, *O. marina*, *P. piscicida*, *P.*
151 *kofoidii*, *P. bipes*, *S. algicida*, *Strobilidium* sp., and *Strombidinopsis* sp. was able to feed on *E.*
152 *gymnastica* (Table 2).

153 Approximately 8×10^5 *E. gymnastica* cells were added to each of the two 80 ml PC bottles
154 containing each of the heterotrophic dinoflagellates (3,200-400,000) and the ciliate (160-400)
155 (final *E. gymnastica* prey concentration = ca. 10,000 cells ml⁻¹). One control bottle (without
156 prey) was set up for each experiment. The bottles were placed on a plankton wheel rotating at 0.9
157 rpm and incubated at 20 °C under an illumination of 20 $\mu\text{E m}^{-2} \text{s}^{-1}$ on a 14 h: 10h light-dark
158 cycle.

159 Five milliliter aliquots were removed from each bottle after 1, 2, 6, and 24 h incubation
160 and then transferred into 6-well plate chambers (or slide glasses). Approximately 200 cells in the
161 plate chamber (or slide glasses) were observed under a dissecting microscope (or inverted
162 microscope) at a magnification of 20-90x (or 100-630x) to determine whether the predators were
163 able to feed on *E. gymnastica*.

164

165 2.4. Growth and ingestion rates.

166

167 Expt 2-7 were designed to measure the growth and ingestion rates of *Gyrodinium*
168 *dominans*, *Oxyrrhis marina*, *Polykrikos kofoidii*, *Protooperidinium bipes*, *Strobilidium* sp., and

169 *Strombidinopsis* sp. as a function of the prey concentration when fed on *Eutreptiella gymnastica*
170 (Table 2).

171 One week before these experiments were conducted, dense cultures of *G. dominans* (or
172 the other heterotrophic predators except for *P. kofoidii*, *Strobilidium* sp., and *Strombidinopsis*
173 sp.) growing on algal prey listed in Table 1 were transferred into 500-mL PC bottles containing
174 *E. gymnastica* (20,000 cells ml⁻¹). These predator cultures were transferred to 500-ml PC bottles
175 of fresh prey (ca. 20,000 cells ml⁻¹) every two days. The bottles were filled to capacity with
176 freshly filtered seawater, capped, and placed on plankton wheels rotating at 0.9 rpm and
177 incubated at 20^o C under an illumination of 20 μE m⁻² s⁻¹ on a 14 h:10 h light-dark cycle. To
178 monitor the conditions and interaction between the predator and prey species, the cultures were
179 periodically removed from the rotating wheels, examined by observation through the surface of
180 the capped bottles by using a dissecting microscope, and then returned to the rotating wheels.
181 One or two days before this pre-incubation process had been completed, the *E. gymnastica* prey
182 cells in ambient water were no longer detectable, but some prey cells were still observed inside
183 the protoplasts of the predators. Thus, these predators were starved for 1-2 days. This was
184 carried out to minimize possible residual growth resulting from the ingestion of prey during
185 batch culture. After this pre-incubation period, three 1 ml aliquots from each bottle were counted
186 using a light microscope to determine cell concentrations of *G. dominans* (or the other
187 heterotrophic dinoflagellate predators), and the cultures were then used to conduct these
188 experiments.

189 *P. kofoidii*, *Strobilidium* sp., and *Strombidinopsis* sp. actively ingested prey cells, but did
190 not grow when *E. gymnastica* was provided as prey. Thus, 2 days before this experiment was
191 conducted, dense cultures of each of *P. kofoidii*, *Strobilidium* sp., and *Strombidinopsis* sp.
192 growing on *Scrippsiella trochoidea*, *Heterocapsa rotundata*, and *Prorocentrum minimum*,
193 respectively were transferred into 250-mL PC bottles containing *E. gymnastica* (5,000 cells).
194 Once *E. gymnastica* prey cells in ambient water were no longer detectable, three 1 ml aliquots
195 from each bottle were counted to determine cell concentrations of each of *P. kofoidii*,
196 *Strobilidium* sp., and *Strombidinopsis* sp..

197 For each experiment, the initial concentrations of *G. dominans* (or other predators) and *E.*
198 *gymnastica* were established using an autopipette to deliver predetermined volumes of known
199 cell concentrations to the bottles. Triplicate 42-ml PC experiment bottles (mixtures of predator
200 and prey) and triplicate control bottles (prey only) were set up at each predator-prey
201 combination. Triplicate control bottles containing only *G. dominans* (or other predators) were
202 also established at one predator concentration. To obtain similar water conditions, the water of a
203 predator culture was filtered through a 0.7- μm GF/F filter and then added to the prey control
204 bottles in the same amount as the volume of the predator culture added to the experiment bottles
205 for each predator-prey combination. All the bottles were then filled to capacity with freshly
206 filtered seawater and capped. To determine the actual predator and prey densities at the
207 beginning of the experiment, a 5-ml aliquot was removed from each bottle, fixed with 5%
208 Lugol's solution, and examined using a light microscope to determine predator and prey
209 abundance by enumerating the cells in three to four 1-ml SRCs. The bottles were refilled to

210 capacity with freshly filtered seawater, capped, and placed on rotating wheels under the
 211 conditions described above. Dilution of the cultures associated with refilling the bottles was
 212 considered when calculating growth and ingestion rates. A 10-ml aliquot was taken from each
 213 bottle after 48-h incubation (24-h incubation for the ciliates) and fixed with 5% Lugol's solution,
 214 and the abundance of *G. dominans* (or other predators) and the prey were determined by
 215 counting all or >300 cells in three to five 1-ml SRCs. Prior to taking the subsamples, the
 216 condition of *G. dominans* (or other predators) and its prey was assessed using a dissecting
 217 microscope as described above.

218 The specific growth rate of *G. dominans* (or other predators), μ (d^{-1}), was calculated as:

$$219 \quad \mu (d) = [\text{Ln} (P_t/P_0)] / t \quad (1)$$

220

221 where P_0 and P_t = the concentration of *G. dominans* (or other predators) at 0 h and 48 h (or 24 h
 222 for the ciliates), respectively.

223 Data for *G. dominans* (or other predators) growth rates were fitted to a Michaelis-Menten
 224 equation:

$$225 \quad \mu = \frac{\mu_{\max} (x - x')}{K_{GR} + (x - x')} \quad (2)$$

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

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

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

233
234 where I_{max} = the maximum ingestion rate (cells predator⁻¹d⁻¹ or ng C predator⁻¹d⁻¹); x = prey
235 concentration (cells ml⁻¹ or ng C ml⁻¹), and K_{IR} = the prey concentration sustaining $\frac{1}{2} I_{\text{max}}$.

236

237 2.5. Gross growth efficiency.

238

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

242

243 2.6. Grazing impact.

244

245 We estimated grazing coefficients (g) attributable to small heterotrophic *Gyrodinium* spp.
246 (25-35 μm in cell length) [*Protoberidinium bipes*, *Polykrikos kofoidii*, naked ciliates ($\leq 50 \mu\text{m}$ in
247 cell length), or naked ciliates ($> 50 \mu\text{m}$ in cell length)] on *Eutreptiella gymnastica* by combining
248 field data on abundances of small *Gyrodinium* spp. (or the other taxa) and prey with ingestion

249 rates of the predators on the prey obtained in the present study. We assumed that the ingestion
250 rates of the other small heterotrophic *Gyrodinium* spp. [naked ciliates ($\leq 50 \mu\text{m}$ in cell length) or
251 naked ciliates ($> 50 \mu\text{m}$ in cell length)] on *E. gymnastica* are the same as that of *G. dominans*
252 (*Strobilidium* sp. or *Strombidinopsis* sp.). *Gyrodinium* spp. were mostly *G. dominans* but rarely
253 were unidentified *Gyrodinium* sp. whose size was similar to *G. dominans* and difficult to
254 distinguish from *G. dominans* in fixed samples. The data on the abundances of *E. gymnastica* and
255 co-occurring small heterotrophic *Gyrodinium* spp. (the other taxa) used in this estimation were
256 obtained from water samples collected in August, 2004 from the waters in Masan Bay, Korea in
257 the present study.

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

$$259 \quad g = \text{CR} \times \text{GC} \times 24 \quad (4)$$

260 where CR is the clearance rate ($\text{ml predator}^{-1}\text{h}^{-1}$) of a predator on *E. gymnastica* at a given
261 prey concentration and GC is the predator concentration (cells ml^{-1}). CR values were calculated
262 as

$$263 \quad \text{CR} = \text{IR}/X \quad (5)$$

264 where IR is the ingestion rate ($\text{cells eaten predator}^{-1}\text{h}^{-1}$) of the predator on the prey and X
265 is the prey concentration (cells ml^{-1}). CR values were corrected using $Q_{10} = 2.8$ (Hansen et al.
266 1997) because in situ water temperatures and the temperature used in the laboratory for this
267 experiment ($20 \text{ }^{\circ}\text{C}$) were sometimes different.

268

269 **3. Results**

270

271 *3.1. Hydrography and abundances in Masan Bay.*

272

273 Water temperatures and salinities in the surface waters in Masan Bay from August 1 to
274 21, 2004 were 23.5-28.6 °C and 11.5-29.8, respectively (Fig. 1A, B). There was a red tide
275 dominated by *Eutreptiella gymnastica* ($> 1,000$ cells ml^{-1}) in Masan Bay from August 4 to 8,
276 2004 (Fig. 1C). Water temperatures and salinities in the surface waters in the red tide period
277 were 25.0-28.6 °C and 28.5-29.8, respectively (Fig. 1A, B). The pH values and dissolved oxygen
278 (DO) concentrations in the surface waters in the red tide period were 7.8-8.4 and 1.9-11.5 mg/l,
279 respectively.

280 The maximum abundance of *E. gymnastica* in the red tide period was 7,575 cells ml^{-1} ,
281 while that in the non-red-tide periods was 600 cells ml^{-1} . The peaks of the abundances of the
282 dominant heterotrophic dinoflagellates *Protoperidinium bipes* and small *Gyrodinium* spp. (25-35
283 μm in cell length), 58 and 50 cells ml^{-1} , respectively, almost concurred with that of *E.*
284 *gymnastica* (Fig. 1D, E). However, the maximum abundance of *Polykrikos kofoidii* (8.6 cells ml^{-1})
285 was found before the red tide dominated by *E. gymnastica*, while those of the naked ciliates
286 (≤ 50 μm in cell length) (32 cells ml^{-1}) and the naked ciliates (> 50 μm in cell length) (2.5 cells
287 ml^{-1}) were obtained after the red tide (Fig. 1F, G, H). However, the abundances of *P. kofoidii*, the

288 naked ciliates ($\leq 50 \mu\text{m}$), and the naked ciliates ($> 50 \mu\text{m}$) during the red tide were 0, 9.3, and 0.7
289 cells ml^{-1} , respectively. The abundances of both *P. bipes* and small *Gyrodinium* spp. in August,
290 2004 were significantly positively correlated with that of *E. gymnastica* ($p < 0.01$, linear
291 regression ANOVA; Fig. 2A, B), while that of *P. kofoidii*, the naked ciliates ($\leq 50 \mu\text{m}$ in cell
292 length), or the naked ciliates ($> 50 \mu\text{m}$ in cell length) were not correlated ($p > 0.1$, linear regression
293 ANOVA). This evidence suggests potential predator-prey relationships between *E. gymnastica*
294 and these dominant heterotrophic dinoflagellates.

295

296 3.2. Feeding occurrence and growth rate.

297

298 *Gyrodinium dominans*, *Oxyrrhis marina*, *Polykrikos kofoidii*, *Pfiesteria piscicida*,
299 *Protoperidinium bipes*, *Strobilidium* sp., and *Strombidinopsis* sp. were able to feed on
300 *Eutreptiella gymnastica*, while *Stoeckeria algicida* was not (Table 1).

301 The specific growth rates of *G. dominans* on *E. gymnastica* increased rapidly with
302 increasing mean prey concentration $< \text{ca. } 1,320 \text{ ng C ml}^{-1}$ ($9,460 \text{ cells ml}^{-1}$), but became saturated
303 at higher concentrations (Fig. 3). When the data were fitted to Eq. (2), the maximum specific
304 growth rate (μ_{max}) of *G. dominans* on *E. gymnastica* was 1.13 d^{-1} (Table 3). The feeding
305 threshold prey concentration for the growth of *G. dominans* (i.e. no growth) was 106 ng C ml^{-1}
306 ($760 \text{ cells ml}^{-1}$).

307 The specific growth rates of *O. marina* on *E. gymnastica* increased rapidly with
308 increasing mean prey concentration < ca. 113 ng C ml⁻¹ (810 cells ml⁻¹), but became saturated at
309 higher concentrations (Fig. 4). When the data were fitted to Eq. (2), the μ_{\max} of *O. marina* on *E.*
310 *gymnastica* was 0.81 d⁻¹ (Table 3). The feeding threshold prey concentration for the growth of *O.*
311 *marina* was 0.8 ng C ml⁻¹ (6 cells ml⁻¹).

312 The specific growth rates of *P. bipes* on *E. gymnastica* increased rapidly with increasing
313 mean prey concentration < ca. 2,220 ng C ml⁻¹ (15,830 cells ml⁻¹), but became saturated at higher
314 concentrations (Fig. 5). When the data were fitted to Eq. (2), the μ_{\max} of *P. bipes* on *E.*
315 *gymnastica* was 0.77 d⁻¹ (Table 3). The feeding threshold prey concentration for the growth of *P.*
316 *bipes* was 18 ng C ml⁻¹ (130 cells ml⁻¹).

317 The specific growth rates of *P. kofoidii* on *E. gymnastica* increased with increasing mean
318 prey concentration < ca. 6,550 ng C ml⁻¹ (920 cells ml⁻¹), but became saturated at higher
319 concentrations (Fig. 6). However, all growth rates of *P. kofoidii* on *E. gymnastica* were negative
320 (Table 3). The highest value among the growth rates was -0.04 d⁻¹.

321 At given prey concentrations, all specific growth rates of *Strobilidium* sp. on *E.*
322 *gymnastica* were negative (Fig. 7). The highest value among the growth rates was -0.94 d⁻¹
323 achieved at the highest prey concentration (Table 3).

324 The specific growth rates of *Strombidinopsis* sp. on *E. gymnastica* increased rapidly with
325 increasing mean prey concentration < ca. 240 ng C ml⁻¹ (1,740 cells ml⁻¹), but increased slowly at
326 higher concentrations (Fig. 8). However, at given prey concentrations, all growth rates were

327 negative with a maximum value of -0.14 d^{-1} at the highest prey concentration (Table 3). Thus, *E.*
328 *gymnastica* did not support positive growth of this large naked ciliate at the mean prey
329 concentrations $< \text{ca. } 11,840 \text{ ng C ml}^{-1}$ ($84,570 \text{ cells ml}^{-1}$).

330

331 3.3. Ingestion and clearance rates.

332

333 The ingestion rates of *Gyrodinium dominans* on *Eutreptiella gymnastica* increased
334 rapidly with increasing mean prey concentration $< \text{ca. } 1,320 \text{ ng C ml}^{-1}$ ($9,460 \text{ cells ml}^{-1}$), but
335 became saturated at higher concentrations (Fig. 9). When the data were fitted to Eq. (3), the
336 maximum ingestion rate (I_{max}) of *G. dominans* on *E. gymnastica* was $2.7 \text{ ng C predator}^{-1} \text{ d}^{-1}$ (19
337 $\text{cells predator}^{-1} \text{ d}^{-1}$) (Table 3). The maximum clearance rate of *G. dominans* on *E. gymnastica* was
338 $1.5 \mu\text{l predator}^{-1} \text{ h}^{-1}$. Gross growth efficiencies (GGEs) of *G. dominans* on *E. gymnastica* at the
339 prey concentrations where the ingestion rates were saturated were 24-31%.

340 The ingestion rates of *Oxyrrhis marina* on *E. gymnastica* increased rapidly with
341 increasing mean prey concentration $< \text{ca. } 1,100 \text{ ng C ml}^{-1}$ ($7,860 \text{ cells ml}^{-1}$), but became saturated
342 at higher concentrations (Fig. 10). When the data were fitted to Eq. (3), the I_{max} of *O. marina* on
343 *E. gymnastica* was $2.7 \text{ ng C predator}^{-1} \text{ d}^{-1}$ ($19 \text{ cells predator}^{-1} \text{ d}^{-1}$) (Table 3). The maximum
344 clearance rate of *O. marina* on *E. gymnastica* was $3.8 \mu\text{l predator}^{-1} \text{ h}^{-1}$. GGEs of *O. marina* on *E.*
345 *gymnastica* at the prey concentrations where the ingestion rates were saturated were 13-26%.

346 The ingestion rates of *Protoperidinium bipes* on *E. gymnastica* increased rapidly with
347 increasing mean prey concentration < ca. 240 ng C ml⁻¹ (1,720 cells ml⁻¹), but became saturated
348 at higher concentrations (Fig. 11). When the data were fitted to Eq. (3), the I_{max} of *P. bipes* on *E.*
349 *gymnastica* was 2.0 ng C predator⁻¹ d⁻¹ (14 cells predator⁻¹ d⁻¹) (Table 3). The maximum clearance
350 rate of *P. bipes* on *E. gymnastica* was 0.9 μl predator⁻¹h⁻¹. GGEs of *P. bipes* on *E. gymnastica* at
351 the prey concentrations where the ingestion rates were saturated were 10-15%.

352 The ingestion rates of *Polykrikos kofoidii* on *E. gymnastica* increased rapidly with
353 increasing mean prey concentration < ca. 2840 ng C ml⁻¹ (20,280 cells ml⁻¹), but became
354 saturated at higher concentrations (Fig. 12). When the data were fitted to Eq. (3), the I_{max} of *P.*
355 *kofoidii* on *E. gymnastica* was 2.7 ng C predator⁻¹ d⁻¹ (19 cells predator⁻¹ d⁻¹) (Table 3). The
356 maximum clearance rate of *P. kofoidii* on *E. gymnastica* was 2.0 μl predator⁻¹h⁻¹.

357 The ingestion rates of *Strobilidium* sp. on *E. gymnastica* increased rapidly and then
358 increased relatively slowly with increasing mean prey concentration (Fig. 13). When the data
359 were fitted to Eq. (3), the I_{max} of *Strobilidium* sp. on *E. gymnastica* was 2.2 ng C predator⁻¹ d⁻¹ (16
360 cells predator⁻¹ d⁻¹) (Table 3). The maximum clearance rate of *Strobilidium* sp. on *E. gymnastica*
361 was 0.7 μl predator⁻¹h⁻¹.

362 The ingestion rates of *Strombidinopsis* sp. on *E. gymnastica* increased rapidly and then
363 increased relatively slowly with increasing mean prey concentration (Fig. 14). When the data
364 were fitted to Eq. (3), the I_{max} of *Strombidinopsis* sp. on *E. gymnastica* was 156 ng C predator⁻¹ d⁻¹.

365 ¹ (1,110 cells predator⁻¹ d⁻¹) (Table 3). The maximum clearance rate of *Strombidinopsis* sp. on *E.*
366 *gymnastica* was 9.9 μl predator⁻¹h⁻¹.

367

368 3.4. Grazing impact.

369

370 In Masan Bay in August, 2004, the calculated grazing coefficients attributable to small
371 heterotrophic *Gyrodinium* spp. (25-35 μm in cell length) on co-occurring *Eutreptiella*
372 *gymnastica* were 0.001 – 0.61 d⁻¹ (mean ± SE = 0.11 ± 0.03 d⁻¹, n=21) (Fig. 15A). In the red tide
373 period, the grazing coefficients attributable to small heterotrophic *Gyrodinium* spp. were 0.009 –
374 0.33 d⁻¹ (mean ± SE = 0.17 ± 0.06 d⁻¹, n=5), while that in the non-red-tide periods were 0.000 –
375 0.61 d⁻¹ (mean ± SE = 0.08 ± 0.04 d⁻¹, n=16).

376 In Masan Bay in August, 2004, the calculated grazing coefficients attributable to
377 *Protoperidinium bipes* on co-occurring *E. gymnastica* were 0.001 – 0.60 d⁻¹ (mean ± SE = 0.21 ±
378 0.04 d⁻¹, n=21) (Fig. 15B). In the red tide period, the grazing coefficients attributable to *P. bipes*
379 were 0.00 – 0.39 d⁻¹ (mean ± SE = 0.18 ± 0.08 d⁻¹, n=5), while that in the non-red-tide periods
380 were 0.00 – 0.60 d⁻¹ (mean ± SE = 0.21 ± 0.05 d⁻¹, n=16).

381 In Masan Bay in August, 2004, the calculated grazing coefficients attributable to
382 *Polykrikos kofoidii* on co-occurring *E. gymnastica* were 0.00 – 0.07 d⁻¹ (mean ± SE = 0.004 ±
383 0.003 d⁻¹, n=21) (Fig. 15C). In the red tide period, the grazing coefficients attributable to *P.*
384 *kofoidii* were zero.

385 In Masan Bay in August, 2004, the calculated grazing coefficients attributable to naked
386 ciliates ($\leq 50 \mu\text{m}$ in cell length) on co-occurring *E. gymnastica* were $0.000 - 0.22 \text{ d}^{-1}$ (mean \pm SE
387 $= 0.05 \pm 0.01 \text{ d}^{-1}$, $n=21$) (Fig. 15D). In the red tide period, the grazing coefficients attributable to
388 the naked ciliates $\leq 50 \mu\text{m}$ were $0.01 - 0.08 \text{ d}^{-1}$ (mean \pm SE $= 0.05 \pm 0.01 \text{ d}^{-1}$, $n=5$), while that in
389 the non-red-tide periods were $0.00 - 0.22 \text{ d}^{-1}$ (mean \pm SE $= 0.05 \pm 0.02 \text{ d}^{-1}$, $n=16$).

390 In Masan Bay in August, 2004, the calculated grazing coefficients attributable to the
391 naked ciliates ($> 50 \mu\text{m}$ in cell length) on co-occurring *E. gymnastica* were $0.00 - 0.13 \text{ d}^{-1}$ (mean
392 \pm SE $= 0.02 \pm 0.01 \text{ d}^{-1}$, $n=21$) (Fig. 15E). In the red tide period, the grazing coefficients
393 attributable to the naked ciliates $> 50 \mu\text{m}$ were $0.001 - 0.03 \text{ d}^{-1}$ (mean \pm SE $= 0.01 \pm 0.01 \text{ d}^{-1}$,
394 $n=5$), while that in the non-red-tide periods were $0.00 - 0.13 \text{ d}^{-1}$ (mean \pm SE $= 0.02 \pm 0.01 \text{ d}^{-1}$,
395 $n=16$).

396 In Masan Bay in August, 2004, the combined calculated grazing coefficients attributable
397 to small heterotrophic *Gyrodinium* spp., *P. bipes*, *P. kofoidii*, and the naked ciliates on co-
398 occurring *E. gymnastica* were $0.00 - 1.14 \text{ d}^{-1}$ (mean \pm SE $= 0.32 \pm 0.06 \text{ d}^{-1}$, $n=21$) (Fig. 15F). In
399 the red tide period, the combined grazing coefficients were $0.14 - 0.79 \text{ d}^{-1}$ (mean \pm SE $= 0.42 \pm$
400 0.13 d^{-1} , $n=5$), while that in the non-red-tide periods were $0.00 - 1.14 \text{ d}^{-1}$ (mean \pm SE $= 0.37 \pm$
401 0.09 d^{-1} , $n=16$).

402

403 4. Discussion

404

405 4.1. Predators

406
407
408 This study is the first report on feeding by heterotrophic protists on the common red tide
409 alga *Eutreptiella gymnastica*. Besides the dominant heterotrophic dinoflagellates *Gyrodinium*
410 *dominans* and *Protoperidinium bipes* in the study period in Masan Bay, other heterotrophic
411 dinoflagellates *Polykrikos kofoidii*, *Oxyrrhis marina*, and *Pfiesteria piscicida* and the ciliates
412 *Strobilidium* sp. and *Strombidinopsis* sp. were able to feed on *E. gymnastica*. Thus, in addition to
413 mesozooplankton (Uye and Takamatsu, 1990; Olli et al., 1996), heterotrophic dinoflagellates and
414 ciliates should be considered to be grazers on *E. gymnastica*.

415 Another heterotrophic dinoflagellate *Stoeckeria algicida* did not feed on *E. gymnastica*.
416 Thus, among the prey tested so far, the raphidophyte *Heterosigma akashiwo* is still the only prey
417 for *S. algicida* (Jeong et al., 2005a). The feeding mechanism of *S. algicida* (peduncle feeder) is
418 very similar to that of *P. piscicida* (Burkholder and Glasgow, 2001; Jeong et al., 2006), and the
419 size of *S. algicida* is also similar to that of *P. bipes* and *P. piscicida* (Jeong et al., 2004a, 2005a,
420 2006). Therefore, the feeding mechanism and size of the predators may not affect feeding
421 occurrence by heterotrophic protists on *E. gymnastica*. In the phylogenetic trees based on the
422 small subunit (SSU) rDNA of dinoflagellates, *S. algicida* is an ancestor of *P. piscicida* (Jeong et
423 al., 2005b, 2006). Thus, *S. algicida* may not have detecting and digestive enzymes strong enough
424 for detecting, capturing, piercing, and digesting *E. gymnastica*, while *P. piscicida* does.

425

426 4.2. Growth and ingestion rates.

427

428 The μ_{\max} of *G. dominans* on *E. gymnastica* was highest among the predators tested in the
429 present study. However, the prey concentration sustaining $\frac{1}{2} \mu_{\max}$ [K_{GR} , 499 ng C ml⁻¹ (3,565
430 cells ml⁻¹)] and threshold prey concentration for growth of *G. dominans* on *E. gymnastica* [x' ,
431 106 ng C ml⁻¹ (760 cells ml⁻¹)] were also much greater than those of *O. marina* or *P. bipes*. From
432 August 9 to 18 in the study period, when the concentrations of *E. gymnastica* were ca. 100-600
433 cells ml⁻¹, the abundance of *P. bipes* was greater than that of the small heterotrophic *Gyrodinium*
434 spp. (25-35 μ m in cell length; mostly *G. dominans*) in each day measurement. However, when
435 the concentrations of *E. gymnastica* were > 1200 cells ml⁻¹, the abundance of the small
436 heterotrophic *Gyrodinium* spp. and *P. bipes* were comparable. Thus, ca. 20% higher μ_{\max} , but 5-6
437 times higher K_{GR} and x' of *G. dominans* than *P. bipes* may cause this pattern in the relative
438 abundances of these 2 heterotrophic dinoflagellates in Masan Bay.

439 At the given prey concentrations in the present study, all growth rates of *Strombidinopsis*
440 sp., *Polykrikos kofoidii*, and *Strobilidium* sp. on *E. gymnastica* were negative. The I_{\max} of
441 *Strombidinopsis* sp. on *E. gymnastica* was ca. 150 ng C ciliate⁻¹d⁻¹ and the carbon content of a
442 cell of *Strombidinopsis* sp. was ca. 100 ng C. Thus, *Strombidinopsis* sp. acquired 150% of its
443 body carbon from *E. gymnastica* in a day. All prey except the heterotrophic dinoflagellate
444 *Luciella masanensis* in the literature supported positive growth (0.5-1.8 d⁻¹; Table 4), even
445 though the I_{\max} values of *Strombidinopsis* sp. on the mixotrophic dinoflagellates *Gymnodinium*
446 *aureolum* and *Protodinium simplex* (previously *Gymnodinium simplex*) or the heterotrophic
447 dinoflagellates *P. piscicida*, *S. algalicida*, *O. marina*, and *G. dominans* (70-110 ng C) were lower
448 than that on *E. gymnastica*. Thus, the I_{\max} of *Strombidinopsis* sp. on *E. gymnastica* may not be

449 the only factor causing the negative growth rate of *Strombidinopsis* sp.. *E. gymnastica* may not
450 be nutritional prey for *Strombidinopsis* sp.. Among the prey species tested in the present study
451 and literature, the ratio of μ_{\max} to I_{\max} (RMGI) of *Strombidinopsis* sp. was lowest when fed on *E.*
452 *gymnastica* (Fig. 16A-C). Thus, conversion of ingested *E. gymnastica* carbon to grazer's body
453 carbon may be low and/or *Strombidinopsis* sp. spends more energy on capturing, handling, and
454 digesting *E. gymnastica* cells than the other algal prey species. The RMGI values of *O. marina*,
455 *P. bipes*, and *P. kofoidii* were also lowest when they fed on *E. gymnastica* (Fig. 16D-L).
456 Euglenophytes are known to be poor food items for mesozooplankton because their reserve
457 product, paramylon, which is a carbohydrate similar to starch, is rarely digestible for the grazers
458 (Hirayama et al., 1979; Walne and Kivic, 1990; Olli, 1996). Although the cells may have been
459 grazed by mesozooplankton, the paramylon grains passed undigested through the gut, thus
460 diminishing the nutritional gain. *E. gymnastica* also has numerous paramylon grains, scattered in
461 the cytoplasm (Stonik, 2007). Therefore, these paramylon grains may be partially responsible for
462 the lowest RMGI for *Strombidinopsis* sp., *O. marina*, *P. bipes*, and *P. kofoidii*. In addition, the
463 RMGI of *G. dominans* on *E. gymnastica* was intermediate, even though both the μ_{\max} and I_{\max} of
464 *G. dominans* on *E. gymnastica* was highest among the algal prey tested (Fig. 16M-O). The MGR
465 of *G. dominans* on *E. gymnastica* was the same as that on the mixotrophic dinoflagellate
466 *Prorocentrum minimum*. Interestingly, the sizes of *P. minimum* (12.1 μm in the equivalent
467 spherical diameter) and *E. gymnastica* (12.6 μm in the equivalent spherical diameter) are very
468 similar. Thus, this evidence suggests that these prey sizes may be optimal prey sizes for *G.*
469 *dominans*. However, the RMGI of *G. dominans* on *E. gymnastica* was also approximately half

470 the RMGI on *P. minimum*. Thus, *E. gymnastica* may be a less nutritious prey for *G. dominans*
471 than *P. minimum*.

472 All of the μ_{\max} , I_{\max} , and RMGI values of *G. dominans*, *O. marina*, *P. bipes*, or
473 *Strombidinopsis* sp. for all prey species listed in Table 4 were not correlated with prey size ($p > 0.$
474 1 , linear regression ANOVA). Different taxonomic groups (diatoms, chlorophyte, cryptophytes,
475 mixotrophic dinoflagellates, heterotrophic dinoflagellates, raphidophytes, and/or heterotrophic
476 nanoflagellates) may have different nutritional values for each predator. Even in the mixotrophic
477 dinoflagellate prey group, μ_{\max} , I_{\max} , and RMGI of *G. dominans* and *Strombidinopsis* sp. on the
478 prey species were not correlated with prey size ($p > 0.1$, linear regression ANOVA). Thus, prey
479 species in the same taxonomic group may also have a different nutritional value.

480 On the basis of the results in Table 4, it is suggested that when *P. minimum* is abundant in
481 natural environments, both *G. dominans* and *Strombidinopsis* sp. are abundant. However, when
482 *E. gymnastica* is abundant, *G. dominans* is expected to be abundant, while *Strombidinopsis* sp. is
483 not. In the present study period, during red tides dominated by *E. gymnastica*, *G. dominans* was
484 abundant, but *Strombidinopsis* sp. was rarely observed. In addition, during red tides dominated
485 by either *P. minimum* or by *E. gymnastica*, *Polykrikos kofoidii* is expected to be rare. The data on
486 the abundances of *E. gymnastica* and *P. kofoidii* obtained in the present study support this
487 expectation.

488 Both μ_{\max} and I_{\max} of *Protoperidinium bipes* on *E. gymnastica* were 30-40% lower than
489 those on the diatom *Skeletonema costatum* (Table 4). However, a μ_{\max} of 0.77 d^{-1} is still high
490 (i.e., more than one division in a day). Thus, *P. bipes* is expected to be abundant when *E.*

491 *gymnastica* is abundant. The field data obtained in the present study confirmed this expectation.

492

493 4.3. Grazing impact.

494

495 The grazing coefficients attributable to heterotrophic protistan grazers on co-occurring
496 *Eutreptiella gymnastica* in Masan Bay in August 2004 were affected by the grazer species and
497 red tide or non-red tide periods.

498 The grazing coefficients attributable to small heterotrophic *Gyrodinium* spp. on co-
499 occurring *E. gymnastica* in Masan Bay in August, 2004 were $0.001 - 0.61 \text{ d}^{-1}$ (i.e., up to 46% of
500 *E. gymnastica* populations were removed by small *Gyrodinium* populations in 1 d). The highest
501 grazing coefficient in the non-red tide period (0.61 d^{-1}) was greater than that in the red tide
502 period (0.33 d^{-1} , i.e., up to 28% of *E. gymnastica* populations were removed by small
503 *Gyrodinium* populations in 1 d). However, removal of 28% of *E. gymnastica* populations in one
504 day is still considerable. Thus, small heterotrophic *Gyrodinium* spp. sometimes have
505 considerable grazing impact on the populations of *E. gymnastica* in both *E. gymnastica* red tide
506 and non-red tide periods.

507 In addition, the grazing coefficients attributable to *Protoperdinium bipes* on co-occurring
508 *E. gymnastica* in Masan Bay in August, 2004 were $0.001 - 0.60 \text{ d}^{-1}$ (i.e., up to 45% of *E.*
509 *gymnastica* populations were removed by *P. bipes* populations in 1 d). In the red tide period, the
510 grazing coefficients attributable to *P. bipes* were $0.00 - 0.39 \text{ d}^{-1}$ (i.e., up to 33% of *E. gymnastica*
511 populations were removed by *P. bipes* populations in 1 d), while those in the non-red-tide

512 periods were $0.00 - 0.60 \text{ d}^{-1}$. This evidence suggests that *P. bipes* also sometimes have
513 considerable grazing impact on the populations of *E. gymnastica* both in its red tide and non-red
514 tide periods.

515 However, the grazing coefficients attributable to *Polykrikos kofoidii* on co-occurring *E.*
516 *gymnastica* in Masan Bay in August, 2004 were only up to 0.07 d^{-1} (i.e., up to 7% of *E.*
517 *gymnastica* populations were removed by *P. kofoidii* populations in 1 d). In particular, in the red
518 tide period, the grazing coefficients attributable to *P. kofoidii* were zero. Thus, *P. kofoidii* usually
519 does not have considerable grazing impact on the populations of *E. gymnastica* in both its red
520 tide and non-red tide periods.

521 The grazing coefficients attributable to the naked ciliates ($\leq 50 \mu\text{m}$ in cell length) on co-
522 occurring *E. gymnastica* in Masan Bay in August, 2004 were $0.00 - 0.22 \text{ d}^{-1}$ (i.e., up to 20% of
523 *E. gymnastica* populations were removed by the naked ciliates $\leq 50 \mu\text{m}$ populations in 1 d). In the
524 red tide period, the grazing coefficients attributable to the naked ciliates $\leq 50 \mu\text{m}$ were up to only
525 0.08 d^{-1} (i.e., up to 8% of *E. gymnastica* populations were removed by the naked ciliates $\leq 50 \mu\text{m}$
526 populations in 1 d). This evidence suggests that the naked ciliates $\leq 50 \mu\text{m}$ sometimes have
527 considerable grazing impact on the populations of *E. gymnastica*, but not in the red tide period.

528 The grazing coefficients attributable to the naked ciliates ($> 50 \mu\text{m}$ in cell length) on co-
529 occurring *E. gymnastica* in Masan Bay in August, 2004 were $0.00 - 0.13 \text{ d}^{-1}$ (i.e., up to 12% of
530 *E. gymnastica* populations were removed by the naked ciliates $> 50 \mu\text{m}$ populations in 1 d). In the
531 red tide period, the grazing coefficients attributable to the naked ciliates $> 50 \mu\text{m}$ were up to only

532 0.03 d⁻¹ (i.e., up to 3.1% of *E. gymnastica* populations were removed by the naked ciliates >50
533 μm populations in 1 d). This evidence suggests that the naked ciliates >50 μm usually do not
534 have considerable grazing impact on the populations of *E. gymnastica* in its red tide periods.

535 The combined grazing coefficients attributable to small heterotrophic *Gyrodinium* spp.,
536 *P. bipes*, *P. kofoidii*, and the naked ciliates on co-occurring *E. gymnastica* in the study period
537 were 0.00 – 1.14 d⁻¹ (i.e., up to 68% of *E. gymnastica* populations were removed by these
538 heterotrophic protistan grazer populations in 1 d). In the red tide period, the combined grazing
539 coefficients were 0.14 – 0.79 d⁻¹ (i.e., 13-55% of *E. gymnastica* populations were removed by the
540 populations of these heterotrophic protistan grazers in 1 d). The maximum growth rates of *E.*
541 *gymnastica* obtained from lab experiments (batch culture) and a mesocosm study (nutrient
542 enriched) are 1.02 d⁻¹ and 0.72 d⁻¹, respectively (Olli et al., 1996; Lundholm et al., 2005).
543 Therefore, these heterotrophic protistan grazers may sometimes control the populations of *E.*
544 *gymnastica* even when *E. gymnastica* grows at the maximum rate. The grazing impact of
545 mesozooplankton has also been reported to sometime be considerable (ca. 0.6 d⁻¹, Olli et al.,
546 1996). Therefore, to predict the population dynamics of *E. gymnastica*, the grazing impact of
547 both heterotrophic protists and mesozooplankton should be assessed.

548

549 **Acknowledgements**

550 We thank Dr. Jae Yoon Song, Nam Seon Kang and Kyung Ha Lee for technical
551 supports. This paper was supported by the National Research Foundation of Korea Grant funded
552

553 by the Korea Government/MEST (NRF-C1ABA001-2010-0020700) and Ecological
554 Disturbance Program of KIMST award to HJ Jeong.

555

556 **References**

557

558 Burkholder, J.A.M., Glasgow, H.B.Jr., 2001. History of toxic *Pfiesteria* in North Carolina
559 estuaries from 1991 to the present. *Bioscience* 51, 827-841.

560 Buskey, E.J., 2008. How does eutrophication affect the role of grazers in harmful algal bloom
561 dynamics? *Harmful Algae* 8, 152-157.

562 Buskey, E.J., Hyatt, C.J., 1995. Effects of the Texas (USA) 'brown tide' alga on planktonic
563 grazers. *Mar. Ecol. Prog. Ser.* 126, 285-292.

564 Calbet, A., Landry, M., 2004. Phytoplankton growth, microzooplankton grazing, and carbon
565 cycling in marine ecosystems. *Limnol. Oceanogr.* 49, 51-57.

566 Calbet, A., Vaqué, D., Felipe, J., Vila, M., Sala, M.M., Alcaraz, M., Estrada, M., 2003. Relative
567 grazing impact of microzooplankton and mesozooplankton on a bloom of the toxic
568 dinoflagellate *Alexandrium minutum*. *Mar. Ecol. Prog. Ser.* 259, 303-309.

569 Frost, B.W., 1972. Effects of size and concentration of food particles on the feeding behavior of
570 the marine planktonic copepod *Calanus pacificus*. *Limnol. Oceanogr.* 17, 805-815.

571 Goldman, J.C., Dennett, M.R., Gordin, H., 1989. Dynamics of herbivorous grazing by the
572 heterotrophic dinoflagellate *Oxyrrhis marina*. *J. Plankton. Res.* 11, 391-407.

- 573 Hansen, P.J., Bjornsen, P.K., Hansen, B.W., 1997. Zooplankton grazing and growth: scaling
574 within the 2-2,000- μm body size range. *Limnol. Oceanogr.* 42, 687-704.
- 575 Heinbokel, J.F., 1978. Studies on the functional role of tintinnids in the Southern California
576 Bight. I. Grazing and growth rates in laboratory cultures. *Mar. Biol.* 47, 177-189.
- 577 Hirayama, K., Tagagi, K., Kimura, H., 1979. Nutritional effect of eight species of marine
578 phytoplankton on population growth of the rotifer, *Brachionus plicatilis*. *Bull. Jap. Soc. Sci.*
579 *Fish.* 45, 11-16.
- 580 Jeong, H.J., 1995. The interactions between microzooplanktonic grazers and dinoflagellates
581 causing red tides in the open coastal waters off southern California. Dissertation. University of
582 California, San Diego. 139 p. Available on microfilm from University of Michigan,
583 Accession Number 223882.
- 584 Jeong, H.J., Shim, J.H., Lee, C.W., Kim, J.S., Koh, S.M., 1999. Growth and grazing rates of the
585 marine planktonic ciliate *Strombidinopsis* sp. on red-tide and toxic dinoflagellates. *J. Euk.*
586 *Microb.* 46, 69-76.
- 587 Jeong, H.J., Kang, H.J., Shim, J.S., Park, J.Y., Kim, J.S., Song, J.Y., Choi, H.J., 2001a.
588 Interactions among the toxic dinoflagellate *Amphidinium carterae*, the heterotrophic
589 dinoflagellate *Oxyrrhis marina*, and the calanoid copepods *Acartia* spp.. *Mar. Ecol. Prog. Ser.*
590 218, 77-86.

- 591 Jeong, H.J., Kim, S.K., Kim, J.S., Kim, S.T., Yoo, Y.D., Yoon, J.Y., 2001b. Growth and grazing
592 rates of the heterotrophic dinoflagellate *Polykrikos kofoidii* on red-tide and toxic
593 dinoflagellates. J. Eukaryot. Microbiol. 48, 298-308.
- 594 Jeong, H.J., Kim, J.S., Yoo, Y.D., Kim, S.T., Kim, T.H., Park, M.G., Lee, C.H., Seong, K.A.,
595 Kang, N.S., Shim, J.H., 2003. Feeding by the heterotrophic dinoflagellate *Oxyrrhis marina* on
596 the red-tide raphidophyte *Heterosigma akashiwo*: a potential biological method to control red
597 tides using mass-cultured grazers. J. Eukaryot. Microb., 50. 274-282.
- 598 Jeong, H.J., Yoo, Y.D., Kim, S.T., Kang, N.S., 2004a. Feeding by the heterotrophic
599 dinoflagellate *Protoperdinium bipes* on the diatom *Skeletonema costatum*. Aquat. Microb.
600 Ecol., 36, 171-179.
- 601 Jeong, H.J., Yoo, Y.D., Kim, J.S., Kang, N.S., Kim, T.H., Kim, J.H., 2004b Feeding by the
602 marine planktonic ciliate *Strombidinopsis jeokjo* on common heterotrophic dinoflagellates.
603 Aquat. Microb. Ecol. 36, 181-187.
- 604 Jeong, H.J., Kim, J.S., Kim, J.H., Kim, S.T., Seong, K.A., Kim, T.H., Song, J.Y., Kim, S.K.,
605 2005a. Feeding and grazing impact of the newly described heterotrophic dinoflagellate
606 *Stoeckeria algicida* on the harmful alga *Heterosigma akashiwo*. Mar. Ecol. Prog. Ser. 295,
607 69-78.
- 608 Jeong, H.J., Kim, J.S., Park, J.Y., Kim, J.H., Kim, S.H., Lee, I.H., Lee, S.H., Ha, J.H., Yih,
609 W.H., 2005b. *Stoeckeria algicida* n. gen., n. sp. (Dinophyceae) from the coastal waters off

- 610 southern korea: morphology and small subunit ribosomal DNA gene sequence. J. Eukaryot.
611 Microbiol. 52, 382–390.
- 612 Jeong, H.J., Ha, J.H., Park, J.Y., Kim, J.H., Kang, N.S., Kim, S., Kim, J.S., Yoo, Y.D., Yih,
613 W.H., 2006. Distribution of the heterotrophic dinoflagellate *Pfieteria piscicida* in Korean
614 waters and its consumption of mixotrophic dinoflagellates, raphidophytes, and fish blood
615 cells. Aquat. Microb. Ecol. 44, 263-278.
- 616 Jeong, H.J., Kim, J.S., Song, J.Y., Kim, J.H., Kim, T.H., Kim, S.K., Kang, N.S., 2007a. Feeding
617 by heterotrophic protists and copepods on the heterotrophic dinoflagellates *Pfiesteria*
618 *piscicida*, *Stoeckeria algicida*, and *Luciella masanensis*. Mar. Ecol. Prog. Ser. 349, 199-211.
- 619 Jeong, H.J., Song, J.E., Kang, N.S., Kim, S., Yoo, Y.D., Park, J.Y., 2007b. Feeding by
620 heterotrophic dinoflagellates on the common marine heterotrophic nanoflagellate *Cafeteria*
621 sp. Mar. Ecol. Prog. Ser. 333, 151-160.
- 622 Jeong, H.J., Seong, K.A., Yoo, Y.D., Kim, T.H., Kang, N.S., Kim, S., Park, J.Y., Kim, J.S., Kim,
623 G.H., Song, J.Y., 2008a. Feeding and grazing impact of the small marine heterotrophic
624 dinoflagellates on heterotrophic bacteria. J. Eukaryot. Microbiol. 55, 271-288.
- 625 Jeong, H.J., Kim, J.S., Yoo, Y.D., Kim, S.T., Song, J.Y., Kim, T.H., Seong, K.A., Kang, N.S.,
626 Kim, M.S., Kim, J.H., Kim, S., Ryu, J.N., Lee, H.M., Yih, W.H., 2008b. Control of the
627 harmful alga *Cochlodinium polykrikoides* by the naked ciliate *Strombidinopsis jeokjo* in
628 mesocosm enclosures. Harmful Algae 7, 368-377.

- 629 Jeong, H.J., Yoo, Y.D., Kim, J.S., Seong, K.A., Kang, N.S., Kim, T.H., 2010. Growth, feeding,
630 and ecological roles of the mixotrophic and heterotrophic dinoflagellates in marine
631 planktonic food webs. *Ocean Sci. J.* 45, 65-91.
- 632 Kamiyama, T., Matsuyama, Y., 2005. Temporal changes in the ciliate assemblage and
633 consecutive estimates of their grazing effect during the course of a *Heterocapsa*
634 *circularisquama* bloom. *J. Plankton Res.* 27, 303-311.
- 635 Kim, J.S., Jeong, H.J., 2004. Feeding by the heterotrophic dinoflagellates *Gyrodinium dominans*
636 and *G. spirale* on the red-tide dinoflagellate *Prorocentrum minimum*. *Mar. Ecol. Prog. Ser.*
637 280, 85-94.
- 638 Lundholm, N., Hansen, P.J., Kotaki, Y., 2005. Lack of allelopathic effects of the domoic acid-
639 producing marine diatom *Pseudo-nitzschia multiseriata*. *Mar. Ecol. Prog. Ser.* 288, 21-33.
- 640 Menden-Deuer, S., Lessard, E., 2000. Carbon to volume relationships for dinoflagellates,
641 diatoms, and other protist plankton. *Limnol. Oceanogr.* 45, 569-579.
- 642 Montagnes, D.J.S., Berger, J.D., Taylor, F.J.R., 1996. Growth rate of the marine planktonic
643 ciliate *Strombidinopsis cheshiri* Snyder and Ohman as a function of food concentration and
644 interclonal variability. *J. Exp. Mar. Biol. Ecol.* 206, 121-132.
- 645 Montagnes, D.J.S., Lessard, E.J., 1999. Population dynamics of the marine planktonic ciliate
646 *Strombidinopsis multiaurata*: its potential to control phytoplankton blooms. *Aquat. Microb.*
647 *Ecol.* 20, 167-181.

- 648 Nakamura, Y., Yamazaki, Y., Hiromi, J., 1992 Growth and grazing of a heterotrophic
649 dinoflagellate, *Gyrodinium dominans*, feeding on a red tide flagellate, *Chattonella antiqua*.
650 Mar. Ecol. Prog. Ser. 82, 275-279.
- 651 Nakamura, Y., Suzuki, S.Y., Hiromi, J., 1995. Growth and grazing of a naked heterotrophic
652 dinoflagellate, *Gyrodinium dominans*. Aquat. Microb. Ecol. 9, 157-164.
- 653 Olli, K., 1996. Resting cyst formation of *Eutreptiella gymnastica* (Euglenophyceae) in the
654 northern coastal Baltic Sea. J. Phycol. 32, 535-542.
- 655 Olli, K., Heiskanen, A.S., Seppälä, J., 1996. Development and fate of *Eutreptiella gymnastica*
656 bloom in nutrient-enriched enclosures in the coastal Baltic Sea. J. Plankton Res. 18, 1587-
657 1604.
- 658 Stoecker, D.K., Thessen, A.E., Gustafson, D.E., 2008. “Windows of opportunity” for
659 dinoflagellate blooms: Reduced microzooplankton net growth coupled to eutrophication.
660 Harmful Algae 8, 158-166.
- 661 Stonik, I. V., 2007. Species of the genus *Eutreptiella* (Euglenophyceae) from Russian waters of
662 East/Japan Sea. Ocean. Sci. J. 42, 81-88.
- 663 Throndsen, J. 1973. Fine structure of *Eutreptiella gymnastica* (Euglenophyceae). Norw. J. Bot.
664 20, 271-280.
- 665 Tillmann, U., Reckermann, M., 2002. Dinoflagellate grazing on the raphidophyte *Fibrocapsa*
666 *japonica*. Aquat. Microb. Ecol. 26, 247-257.

- 667 Turner, J.T., 2006. Harmful algae interactions with marine planktonic grazers. In: Granéli E,
668 Turner JT (ed) Ecology of Harmful Algae. Springer-Verlag, Berlin, Germany, pp. 259-270.
- 669 Turner, J.T., Borkman, D.G., 2005. Impact of zooplankton grazing on *Alexandrium* blooms in the
670 offshore Gulf of Maine. Deep-Sea Res. II 52, 2801-2816.
- 671 Uye, S.I., Takamatsu, K., 1990. Feeding interactions between planktonic copepods and red-tide
672 flagellates from Japanese coastal waters. Mar. Ecol. Prog. Ser. 59, 97-107.
- 673 Walne, P.L., Kivic, P.A., 1990. Phylum Euglenida. In Margulis L, Corliss JO, Melkonian M,
674 Chapman DJ [Ed] *Handbook of Protoctista*, Jones and Bartlett Publishers, Boston, pp. 270-
675 287.
- 676 Watras, C.J., Garcon, V.C., Olson, R.J., Chishom, S.W., Anderson, D.M., 1985. The effect of
677 zooplankton grazing on estuarine blooms of the toxic dinoflagellate *Gonyaulax tamarensis*. J.
678 Plankton Res. 7, 891-908.
- 679 Yamochi, S., 1984. Nutritional factors involved in controlling the growth of red tide flagellates
680 *Prorocentrum micans*, *Eutreptiella* sp. and *Chattonella marina* in Osaka bay [Japan]. Bull.
681 Jap. Soc. Sci. Fish. 31, 97-106.
- 682 Yoo, Y.D., Jeong, H.J., Kang, N.S., Kim, J.S., Kim, T.H., Yoon, E.Y., 2010. Ecology of
683 *Gymnodinium aureolum*. II. Predation by common heterotrophic dinoflagellates and a ciliate.
684 Aquat. Microb. Ecol. 59, 257-272.

Table 1

Isolation and maintenance conditions of the experimental organisms. Sampling location and time, water temperature (T, °C), salinity (S, practical salinity units) for isolation, and prey species and concentrations (cells ml⁻¹) for maintenance.

HTD: Heterotrophic dinoflagellate. CIL: Ciliate. EU: Euglenophyte. Feeding occurrence: Y- Fed. N- Not feed.

Organism	Location	Time	T	S	Prey species	Concentration	Feeding
<i>Gyrodinium dominans</i> (HTD)	Masan Bay	April 2007	15.1	33.4	<i>Amphidinium carterea</i>	30,000 -40,000	Y
<i>Oxyrrhis marina</i> (HTD)	Keum Estuary	May 2001	16.0	27.7	<i>Amphidinium carterea</i>	30,000 -40,000	Y
<i>Pfiesteria piscicida</i> (HTD)	Off Incheon	July 2005	24.0	25.4	<i>Amphidinium carterea</i>	20,000 -30,000	Y
<i>Stoeckeria algicida</i> (HTD)	Masan Bay	May 2007	20.9	30.1	<i>Heterosigma akashiwo</i>	30,000	N
<i>Protoperidinium bipes</i> (HTD)	Shiwha Bay	Nov. 2008	13.0	28.5	<i>Skeletonema costatum</i>	50,000	Y
<i>Polykrikos kofoidii</i> (HTD)	Shiwha Bay	Mar. 2010	9.2	23.4	<i>Scrippsiella trochoidea</i>	10,000 -15,000	Y
<i>Strobilidium</i> sp. (CIL)	Shiwha Bay	Sep. 2010	20.0	11.2	<i>Heterocapsa rotundata</i>	50,000 -60,000	Y
<i>Strombidinopsis</i> sp. (CIL)	Masan Bay	May 2009	20.2	30.1	<i>Prorocentrum minimum</i>	20,000- 30,000	Y
<i>Eutreptiella gymnastica</i> (EU)	Masan Bay	June 2005	23.8	28.7			

Table 2

Design of experiments. The numbers in prey and predator columns are the actual initial densities (cells ml⁻¹) of prey and predator. Values in the parentheses in the predator column are the predator densities in the control bottles.

Expt No.	Prey		Predator	
	Species	Density	Species	Density
1	<i>Eutreptiella gymnastica</i>	10,000	<i>Gyrodinium dominans</i>	1,000
			<i>Oxyrrhis marina</i>	3,000
			<i>Protoperidinium bipes</i>	200
			<i>Pfiesteria piscicida</i>	5,000
			<i>Stoeckeria algicida</i>	5,000
			<i>Polykrikos kofoidii</i>	40
			<i>Strobilidium</i> sp.	50
			<i>Strombidinopsis</i> sp.	20
2	<i>E. gymnastica</i>	29, 109, 300, 1360, 3590, 11660, 32800, 115700	<i>G. dominans</i>	7, 11, 13, 21, 31, 56, 230, 570 (179)
3	<i>E. gymnastica</i>	27, 121, 290, 900, 2460, 8960, 24240, 88920	<i>O. marina</i>	4, 9, 10, 10, 24, 41, 85, 261 (276)
4	<i>E. gymnastica</i>	58, 204, 590, 2360, 5870, 16420, 31000, 57920	<i>P. bipes</i>	10, 12, 24, 39, 70, 80, 90, 240 (140)

5	<i>E. gymnastica</i>	21, 70, 220, 680, 2340, 6870, 20080, 34060	<i>P. kofoidii</i>	4, 9, 9, 18, 24,42, 43, 48 (41)
6	<i>E. gymnastica</i>	59, 620, 2630, 7490, 14510, 45160	<i>Strobilidium</i> sp.	10, 13, 13 27, 28, 36 (27)
7	<i>E. gymnastica</i>	40, 116, 253, 1000, 2760, 9660, 24610, 88810	<i>Strombidinopsis</i> sp.	3, 4, 8, 8, 16, 17, 18, 19 (16)

Table 3

Growth and grazing data for the heterotrophic dinoflagellates *Gyrodinium dominans*, *Oxyrrhis marina*, *Protoperidinium bipes*, *Polykrikos kofoidii*, and the naked ciliate *Strobilidium* sp. and the naked ciliate *Strombidinopsis* sp. on *Eutreptiella gymnastica*.

Predator	PDV	μ_{\max}	K_{GR}	x'	r^2	I_{\max}	K_{IR}	r^2	C_{\max}	MGGE
<i>Gyrodinium dominans</i>	2.9	1.13	499	106	0.97	2.7	229	0.97	1.5	31
<i>Oxyrrhis marina</i>	2.7	0.81	11	1	0.94	2.7	163	0.87	3.8	26
<i>Protoperidinium bipes</i>	1.5	0.77	70	18	0.87	2.0	109	0.77	0.9	15
<i>Polykrikos kofoidii</i>	96.0	-0.04*				2.7	472	0.79	2.0	-
<i>Strobilidium</i> sp.	7.2	-0.94*				2.2	722	0.74	0.7	-
<i>Strombidinopsis</i> sp.	186.0	-0.14*				156	6267	0.97	9.9	-

Parameters are for numerical and/or functional response from Eqs. (2) & (3) as presented in Fig. 3-14. * The maximum value among the mean growth and/or ingestion rates measured at the given prey concentrations. PDV: Predator's volume ($\times 10^3 \mu\text{m}^3$) when the maximum ingestion rate was achieved. μ_{\max} (maximum growth rate, d^{-1}), K_{GR} (prey concentration sustaining $0.5 \mu_{\max}$, ng C ml^{-1}), x' (threshold prey concentration, ng C ml^{-1}), I_{\max} (maximum ingestion rate, $\text{ng C predator}^{-1}\text{d}^{-1}$), K_{IR} (prey concentration sustaining $0.5 I_{\max}$, ng C ml^{-1}), C_{\max} (maximum clearance rate, $\mu\text{l predator}^{-1}\text{d}^{-1}$), and MGGE

(Maximum gross growth efficiency, %) of each predator on *E. gymnastica* at the prey concentrations where the ingestion rates were saturated or 2 highest ingestion rates were achieved.

Table 4

Comparison in growth and grazing data for *Gyrodinium dominans* (A), *Oxyrrhis marina* (B), *Protoperidinium bipes* (C), *Polykrikos kofoidii* (D), and *Strombidinopsis* spp. (E) on diverse prey. ESD (Equivalent Spherical Diameter, μm), μ_{max} (maximum growth rate, d^{-1}), I_{max} (maximum ingestion rate, $\text{ng C predator}^{-1}\text{d}^{-1}$), C_{max} (maximum clearance rate, $\mu\text{l predator}^{-1}\text{d}^{-1}$). RMGI: Ratio of μ_{max} to I_{max} . *The maximum value among the mean growth and/or ingestion rates measured at the given prey concentrations. Rates are corrected to 20°C using $Q_{10} = 2.8$ (Hansen et al. 1997). EU: Euglenophyte. MTD: Mixotrophic dinoflagellate. HTD: Heterotrophic dinoflagellate. DIA: Diatom. RA: Raphidophyte. PRY: Prymnesiophyte. CHL: Chlorophyte. HNF: Heterotrophic nanoflagellate. CRY: Cryptophyte.

A. *Gyrodinium dominans* predator

Prey species	ESD	μ_{max}	I_{max}	C_{max}	RMGI	&Reference
<i>Thalassiosira</i> sp. (DIA)	5.4	0.73				(1)
<i>Prorocentrum minimum</i> (MTD)	12.1	1.13	1.2	0.9	0.94	(2)
<i>Eutreptiella gymnastica</i> (EU)	12.6	1.13	2.7	1.5	0.42	(3)
<i>Heterocapsa triquetra</i> (MTD)	15.3	0.54	2.3		0.23	(1)
<i>Karenia mikimotoi</i> (MTD)	16.8	0.48				(1)
<i>Gymnodinium aureolum</i> (MTD)	19.5	0.92	2.0	0.1	0.46	(4)
<i>Chattonella antique</i> (RA)	35.3	0.50	2.3		0.22	(5)

&: 1. Nakamura et al. (1995); 2. Kim and Jeong (2004); 3. This study; 4. Yoo et al. 2010; 5. Nakamura et al. (1992).

B. *Oxyrrhis marina* predator

Prey species	ESD	μ_{\max}	I_{\max}	C_{\max}	RMGI	& Reference
<i>Phaeodactylum tricornutum</i> (DIA)	4.2	1.30	2.6	0.002	0.50	(1)
<i>Isochrysis galbana</i> (PRY)	4.8	0.79	7.0	0.02	0.11	(1)
<i>Dunaliella tertiolecta</i> (CHL)	7.3	0.79	1.4	0.01	0.56	(1)
<i>Amphidinium carterae</i> (MTD)	9.7	1.17	2.8	2.4	0.42	(2)
<i>Heterosigma akashiwo</i> (RA)	11.5	1.43	1.3	0.3	1.10	(3)
<i>Eutreptiella gymnastica</i> (EU)	12.6	0.82	3.3	4.0	0.25	(4)
<i>Gymnodinium aureolum</i> (MTD)	19.5	0.71	0.5	0.2	1.42	(5)
<i>Fibrocapsa japonica</i> (RA)	20.3	0.72	1.2		0.60	(6)
<i>Cafeteria</i> sp. (HNF)	3.5	0.19	0.3	0.5	0.63	(7)
<i>Pfiesteria piscicida</i> (HTD)	13.5	0.66	0.33	0.34	2.00	(8)
<i>Luciella masanensis</i> (HTD)	13.5	0.04*	0.07	0.02	0.57	(8)
<i>Stoeckeria algicida</i> (HTD)	13.9	0.22	0.13	0.61	1.69	(8)

&: 1. Goldman et al. (1989); 2. Jeong et al. (2001a); 3. Jeong et al. (2003); 4. This study; 5. Yoo et al. (2010); 6. Tillmann and Reckermann (2002); 7. Jeong et al. (2007b); 8. Jeong et al. (2007a).

C. Protoperidinium bipes predator

Prey species	ESD	μ_{\max}	I_{\max}	C_{\max}	RMGI	&Reference
<i>Skeletonema costatum</i> (DIA)	5.9	1.37	2.9	1.0	0.5	(1)
<i>Eutreptiella gymnastica</i> (EU)	12.6	0.77	2.0	0.9	0.4	(2)

&: 1. Jeong et al. (2004a); 2. This study.

D. *Polykrikos kofoidii* predator

Prey species	ESD	μ_{\max}	I_{\max}	C_{\max}	RMGI	&Reference
<i>Amphidinium carterae</i> (MTD)	9.7	0.101	7.6		0.01	(1)
<i>Prorocentrum minimum</i> (MTD)	12.1	-0.03	5.4		-0.01	(1)
<i>Eutreptiella gymnastica</i> (MTD)	12.6	-0.04	2.7	2.0	-0.01	(2)
<i>Gymnodinium impudicum</i> (MTD)	23.2	0.055	5.4	1.3	0.01	(1)
<i>Scrippsiella trochoidea</i> (MTD)	25.1	0.966	16.6	1.1	0.06	(1)
<i>Prorocentrum micans</i> (MTD)	26.0	0.062	4.6	2.3	0.01	(1)
<i>Ceratium furca</i> (MTD)	29.0	0.354	9.8	3.7	0.04	(1)
<i>Gymnodinium catenatum</i> (MTD)	34.0	1.12	17.1	4.6	0.07	(1)
<i>Lingulodinium polyedrum</i> (MTD)	37.9	0.826	24.4	5.9	0.03	(1)

&: 1. Jeong et al. (2001b); 2. This study.

E. *Strombidinopsis* predator

Prey species	ESD	μ_{\max}	I_{\max}	C_{\max}	RMGI	&Reference
<i>Thalassiosira pseudonana</i> (DIA)	3.7	1.49				(1)
<i>Pryenomonas salina</i> (CRY)	5.6	0.96				(2)
<i>Protodinium simplex</i> (MTD) (previously <i>Gymnodinium simplex</i>)	8.3	0.85	83		0.010	(3)
<i>Prorocentrum minimum</i> (MTD)	12.1	1.06	267	110	0.004	(4)
<i>Eutreptiella gymnastica</i> (EU)	12.6	-0.14	156	10	-0.001	(5)
<i>Gymnodinium aureolum</i> (MTD)	19.5	0.44	70	6	0.006	(6)
<i>Scrippsiella trochoidea</i> (MTD)	22.8	0.67	207	41	0.003	(4)
<i>Cochlodinium polykrikoides</i> (MTD)	25.9	1.38	353	50	0.004	(4)
<i>Akashiwo sanguinea</i> (MTD)	30.8	1.27	343	85	0.004	(4)
<i>Lingulodinium polyedrum</i> (MTD)	38.2	0.83	222	110	0.004	(4)
<i>Pfiesteria piscicida</i> (HTD)	13.5	1.77	44	15	0.041	(7)

<continued>

Table 4E. continued

Prey species	ESD	μ_{\max}	I_{\max}	C_{\max}	RMGI	^{&} Reference
<i>Luciella masanensis</i> (HTD)	13.5	-0.1	9.8	5.4	-0.010	(7)
<i>Stoeckeria algicida</i> (HTD)	13.9	1.61	49.3	6.5	0.033	(7)
<i>Oxyrrhis marina</i> (HTD)	15.6	0.59	87	13.4	0.007	(8)
<i>Gyrodinium dominans</i> (HTD)	20.0	0.54	108	14.5	0.005	(8)

[&] : 1. Montagnes et al. (1996); 2. Buskey & Hyatt (1995); 3. Montagnes & Lessard (1999); 4. Jeong et al. (1999); 5. This study; 6. Yoo et al. (2010); 7. Jeong et al. (2007a); 8. Jeong et al. (2004b).

Figure Legends

Fig. 1. Water temperature (T, A), Salinity (S, B), abundances of *Eutreptiella gymnastica* (C), small heterotrophic *Gyrodinium* spp. (25-35 μm in cell length, D), *Protoperidinium bipes* (E), *Polykrikos kofoidii*, (F), the naked ciliates (≤ 50 μm in cell length, G), and the naked ciliates (> 50 μm in cell length, H) at a pier in Masan Bay, Korea from August 1 to 21, 2004. A red tide dominated by *Eutreptiella gymnastica* occurred between August 4 and 8.

Fig. 2. The abundances of small heterotrophic *Gyrodinium* spp. (ASHG, 25-35 μm in cell length, A) and *Protoperidinium bipes* (APB, B) as a function of the abundance of *Eutreptiella gymnastica* (AEG) in Masan Bay, Korea from August 1 to 21, 2004. The p values in both (A) and (B) were <0.01 (linear regression ANOVA). Symbols represent single treatments. The equations of the linear regression were: (A) $\text{ASHG} = 0.005 (\text{AEG}) + 3.32, r^2=0.553$; (B) $\text{APB} = 0.004 (\text{AEG}) + 7.44, r^2=0.433$.

Fig. 3. Specific growth rates of the heterotrophic dinoflagellate *Gyrodinium dominans* on *Eutreptiella gymnastica* as a function of mean prey concentration (x). Symbols represent treatment means ± 1 SE. The curves are fitted by a Michaelis-Menten equation [Eq. (2)] using all treatments in the experiment. Growth rate (GR, d^{-1}) = $1.13 [(x-106)/(499 + (x-106))]$, $r^2=0.97$.

Fig. 4. Specific growth rates of the heterotrophic dinoflagellate *Oxyrrhis marina* on *Eutreptiella gymnastica* as a function of mean prey concentration (x). Symbols represent treatment means ± 1 SE. The curves are fitted by a Michaelis-Menten equation [Eq. (2)] using all treatments in the experiment. Growth rate (GR, d^{-1}) = $0.81 [(x-0.8)/(11 + (x-0.8))]$, $r^2=0.94$.

Fig. 5. Specific growth rates of the heterotrophic dinoflagellate *Protoperidinium bipes* on *Eutreptiella gymnastica* as a function of mean prey concentration (x). Symbols represent treatment means ± 1 SE. The curves are fitted by a Michaelis-Menten equation [Eq. (2)] using all treatments in the experiment. Growth rate (GR, d^{-1}) = $0.77 [(x-18)/(70 + (x-18))]$, $r^2=0.87$.

Fig. 6. Specific growth rates of the heterotrophic dinoflagellate *Polykrikos kofoidii* on *Eutreptiella gymnastica* as a function of mean prey concentration (x). Symbols represent treatment means ± 1 SE. At the given prey concentrations, the highest value among the growth rates was $-0.04 d^{-1}$.

Fig. 7. Specific growth rates of the naked ciliate *Strobilidium* sp. on *Eutreptiella gymnastica* as a function of mean prey concentration (x). Symbols represent treatment

means ± 1 SE. At the given prey concentrations, the highest value among the growth rates was -0.94 d^{-1} .

Fig. 8. Specific growth rates of the naked ciliate *Strombidinopsis* sp. on *Eutreptiella gymnastica* as a function of mean prey concentration (x). Symbols represent treatment means ± 1 SE. At the given prey concentrations, the highest value among the growth rates was -0.14 d^{-1} .

Fig. 9. Ingestion rates of the heterotrophic dinoflagellate *Gyrodinium dominans* on *Eutreptiella gymnastica* as a function of mean prey concentration (x). Symbols represent treatment means ± 1 SE. The curves are fitted by a Michaelis-Menten equation [Eq. (3)] using all treatments in the experiment. Ingestion rate (IR, $\text{ng C predator}^{-1}\text{d}^{-1}$) = $2.7 [x/(229+x)]$, $r^2=0.97$.

Fig. 10. Ingestion rates of the heterotrophic dinoflagellate *Oxyrrhis marina* on *Eutreptiella gymnastica* as a function of mean prey concentration (x). Symbols represent treatment means ± 1 SE. The curves are fitted by a Michaelis-Menten equation [Eq. (3)] using all treatments in the experiment. Ingestion rate (IR, $\text{ng C predator}^{-1}\text{d}^{-1}$) = $2.7 [x/(163+x)]$, $r^2=0.87$.

Fig. 11. Ingestion rates of the heterotrophic dinoflagellate *Protoperidinium bipes* on *Eutreptiella gymnastica* as a function of mean prey concentration (x). Symbols represent treatment means \pm 1 SE. The curves are fitted by a Michaelis-Menten equation [Eq. (3)] using all treatments in the experiment. Ingestion rate (IR, ng C predator⁻¹d⁻¹) = 2.0 [x/(109+x)], r²=0.77.

Fig. 12. Ingestion rates of the heterotrophic dinoflagellate *Polykrikos kofoidii* on *Eutreptiella gymnastica* as a function of mean prey concentration (x). Symbols represent treatment means \pm 1 SE. The curves are fitted by a Michaelis-Menten equation [Eq. (3)] using all treatments in the experiment. Ingestion rate (IR, ng C predator⁻¹d⁻¹) = 2.7 [x/(472+x)], r²=0.79.

Fig. 13. Ingestion rates of the naked ciliate *Strobilidium* sp. on *Eutreptiella gymnastica* as a function of mean prey concentration (x). Symbols represent treatment means \pm 1 SE. The curves are fitted by a Michaelis-Menten equation [Eq. (3)] using all treatments in the experiment. Ingestion rate (IR, ng C predator⁻¹d⁻¹) = 2.2 [x/(722+x)], r²=0.74.

Fig. 14. Ingestion rates of the naked ciliate *Strombidinopsis* sp. on *Eutreptiella gymnastica* as a function of mean prey concentration (x). Symbols represent treatment means \pm 1 SE.

The curves are fitted by a Michaelis-Menten equation [Eq. (3)] using all treatments in the experiment. Ingestion rate (IR, ng C predator⁻¹d⁻¹) = 156 [x/(6,267+x)], r²=0.97.

Fig. 15. Calculated grazing coefficients (g, d⁻¹) of small heterotrophic *Gyrodinium* spp. (25-35 μm in cell length, A), *Protoperidinium bipes* (B), *Polykrikos kofoidii* (C), the naked ciliates (≤ 50 μm in cell length, D), and the naked ciliates (> 50 μm in cell length, E) on co-occurring *Eutreptiella gymnastica*, and combined grazing coefficients (F) in Masan Bay from August 1st to 21st, 2004 (see text for calculation).

Fig. 16. Maximum growth (μ_{max}, A) and ingestion rates (I_{max}, B) of *Strombidinosis* spp. on *E. gymnastica* (Eg, Euglenophyte, EU) and the other prey species and the ratio of μ_{max} to I_{max} (RMGI) (C) as in Table 4. Tp: *Thalassiosira pseudonana* (Diatom, DIA); Ps: *Prynomonas salina* (Cryptophyte, CRY); Prs: *Protodinium simplex* (previously *Gymnodinium simplex*, Mixotrophic dinoflagellate, MTD), Pm: *Prorocentrum minimum*, Ga: *Gymnodinium aureolum*, St: *Scrippsiella trochoidea*. Cp: *Cochlodinium polykrikoides*, As: *Akashiwo sanguinea*, Lp: *Lingulodinium polyedrum*; Pp: *Pfiesteria piscicida* (Heterotrophic dinoflagellate, HTD), Lm: *Luciella masanensis*, Sa: *Stoeckeria algicida*, Om: *Oxyrrhis marina*, Gd: *Gyrodinium dominans*.

Maximum growth (μ_{max}, D) and ingestion rates (I_{max}, E) of *O. marina* on *E. gymnastica* (Eg, EU) and the other prey species and RMGI (F). Pt: *Phaeodactylum tricornutum* (DIA);

Ig: *Isochrysis galbana* (Prymnesiophyte, PRY); Dt: *Dunaliella tertiolecta* (Chlorophyte, CHL); Ha: *Heterosigma akashiwo* (Raphidophyte, RA), Fj: *Fibrocapsa japonica*; Ac: *Amphidinium carterae* (MTD), Ga: *G. aureolum*; Pp: *P. piscicida*, Lm: *L. masanensis*, Sa: *S. algicida*; Caf: *Cafeteria* sp. (Heterotrophic nanoflagellate, HNF);

Maximum growth (μ_{\max} , **G**) and ingestion rates (I_{\max} , **H**) of *Protoperidinium bipes* on *E. gymnastica* (EU) and *Skeletonema costatum* (Sk, DIA) and RMGI (**I**);

Maximum growth (μ_{\max} , **J**) and ingestion rates (I_{\max} , **K**) of *Polykrikos kofoidii* on *E. gymnastica* (Eg, EU) and the other prey species and RMGI (**L**). Ac: *Amphidinium carterae* (MTD), Pm: *P. minimum*, Gi: *Gymnodinium impudicum*, St: *S. trochoidea*, Pc: *Prorocentrum micans*, Cf: *Ceratium furca*, Gc: *Gymnodinium catenatum*, Lp: *L. polyedrum*.

Maximum growth (μ_{\max} , **M**) and ingestion rates (I_{\max} , **N**) of *G. dominans* on *E. gymnastica* (Eg, EU) and the other prey species and RMGI (**O**). Th: *Thalassiosira* sp. (DIA); Pm: *P. minimum* (MTD), Ht: *Heterocapsa triquetra*, Km: *Karenia mikimotoi*, Ga: *G. aureolum*; Ca: *C. antique* (RA).

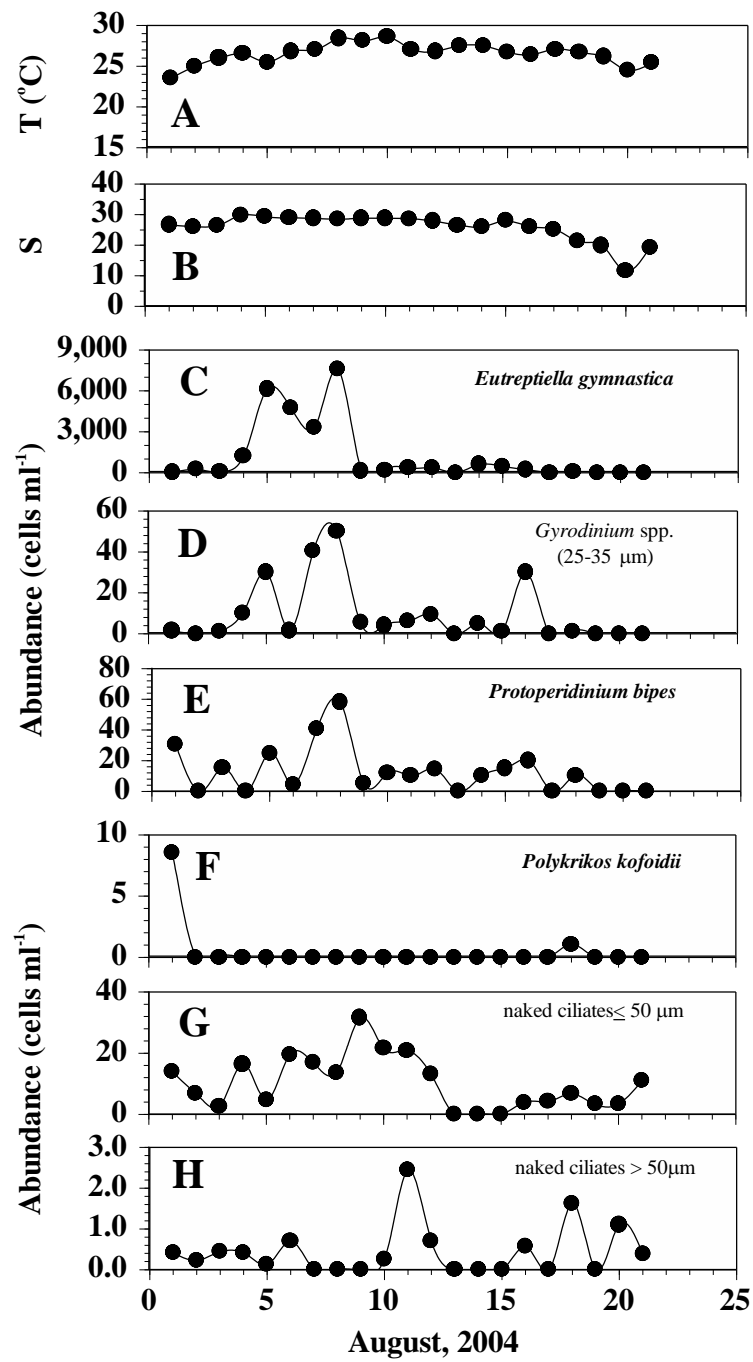


Fig. 1

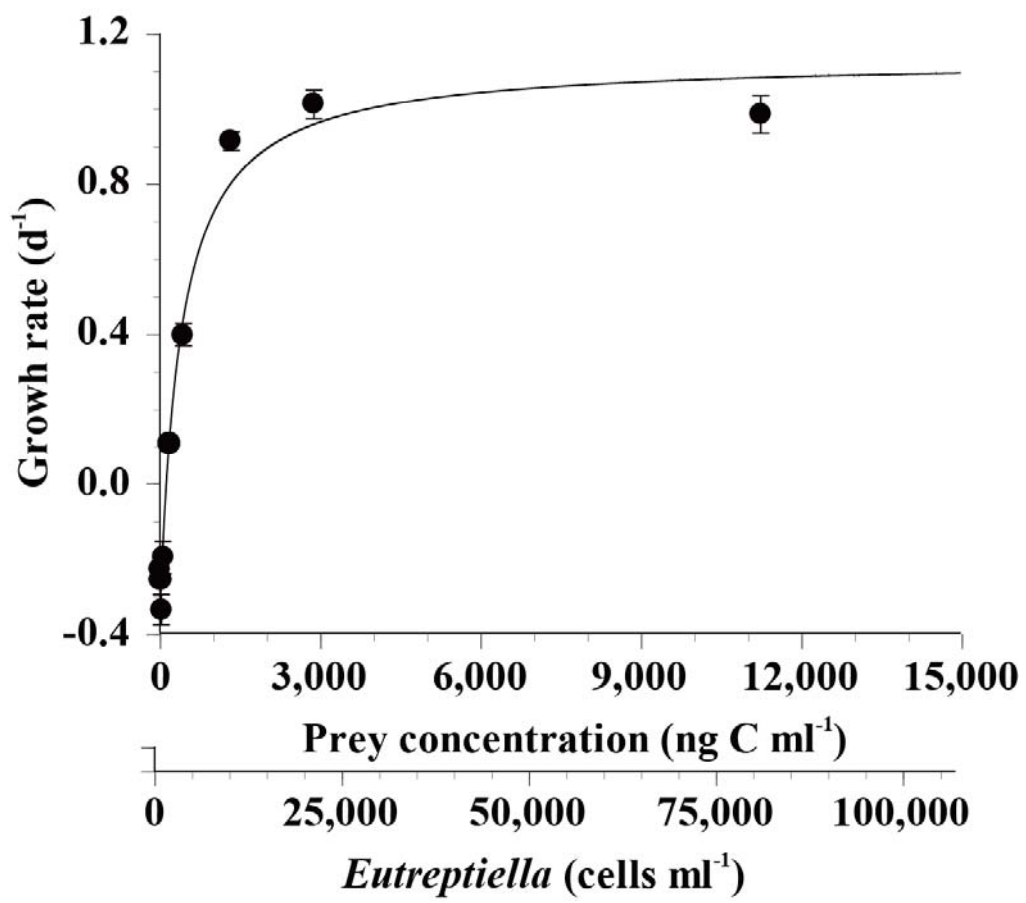


Fig. 3

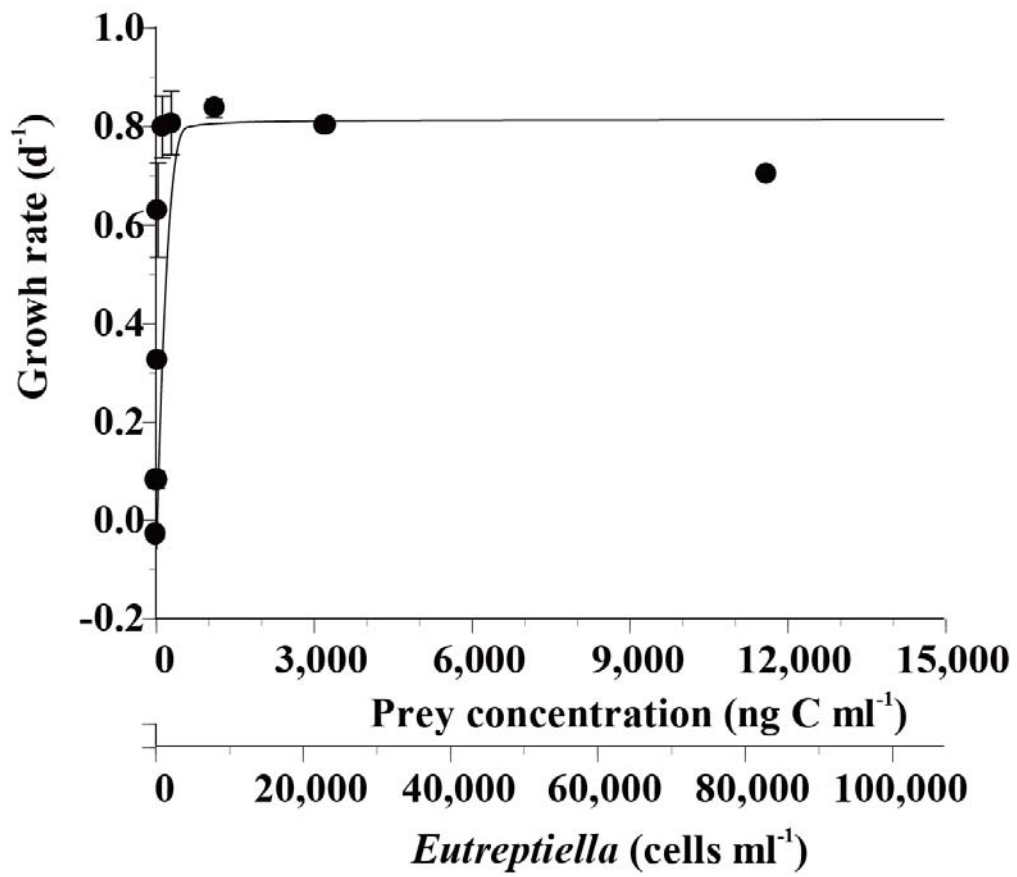


Fig. 4

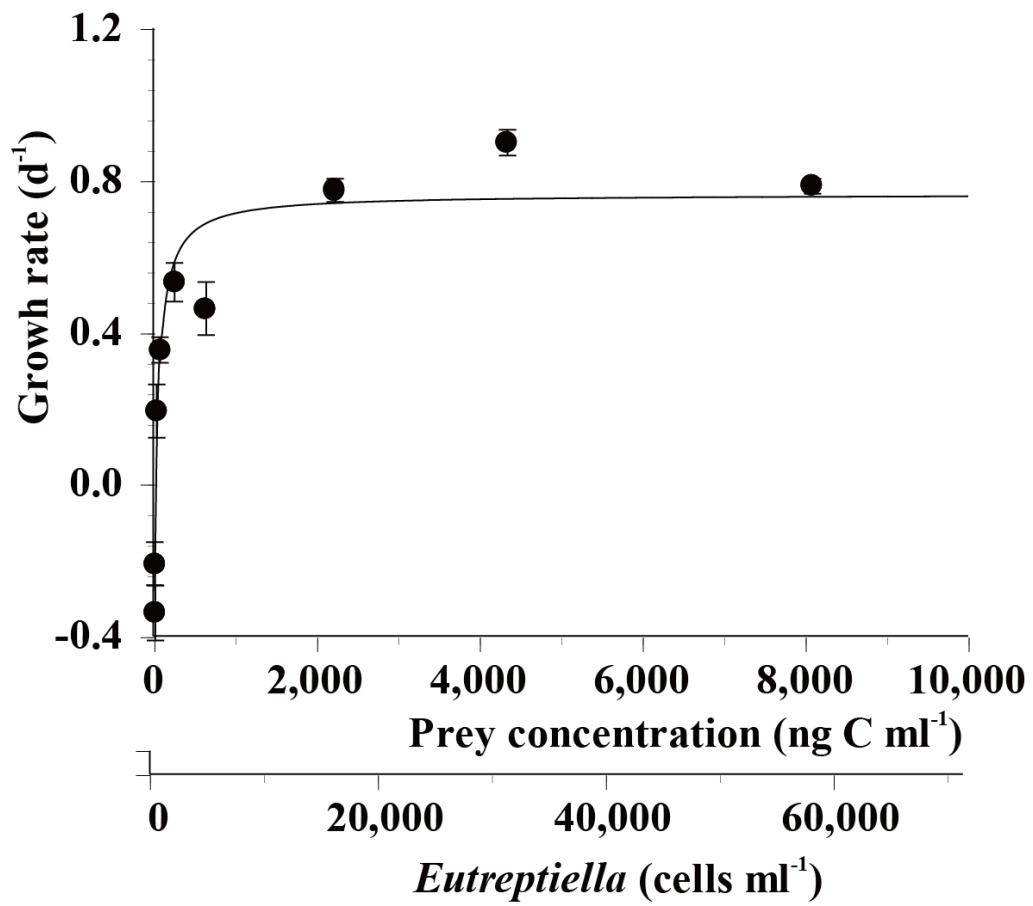


Fig. 5

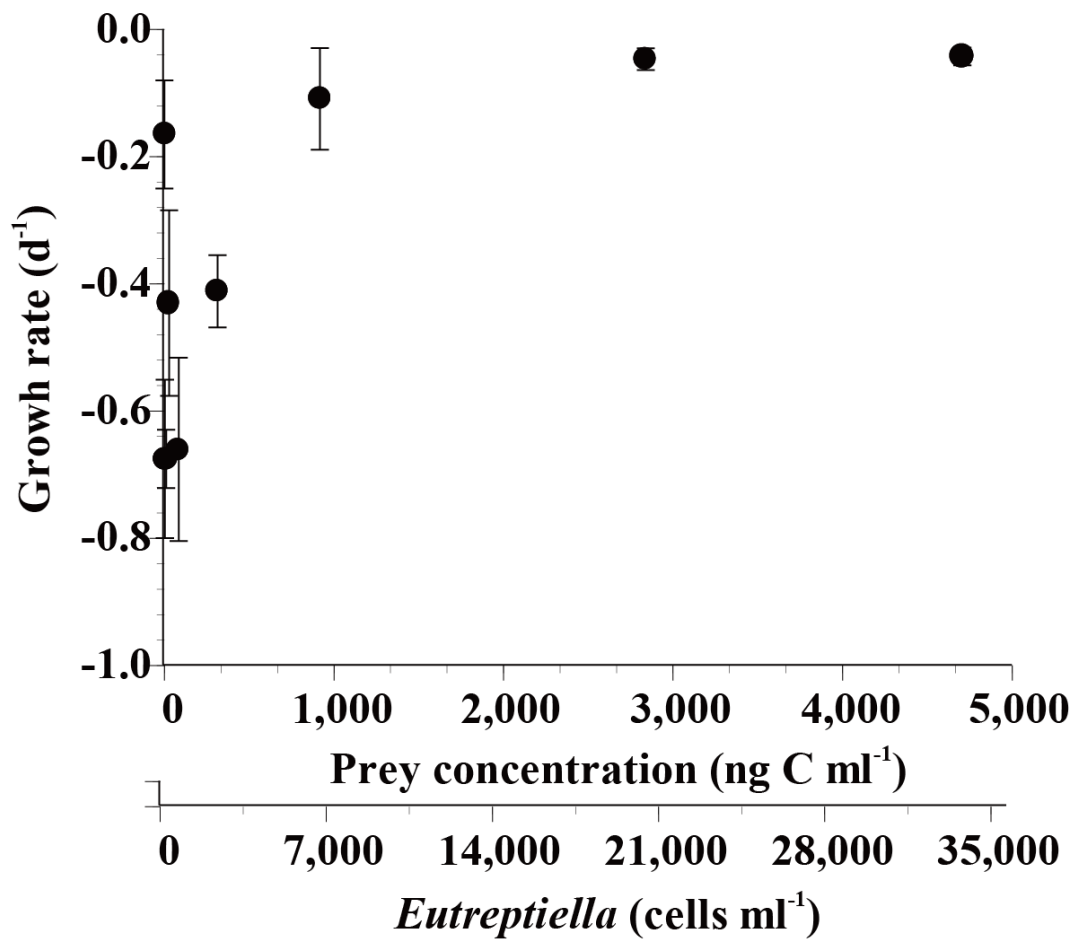


Fig. 6

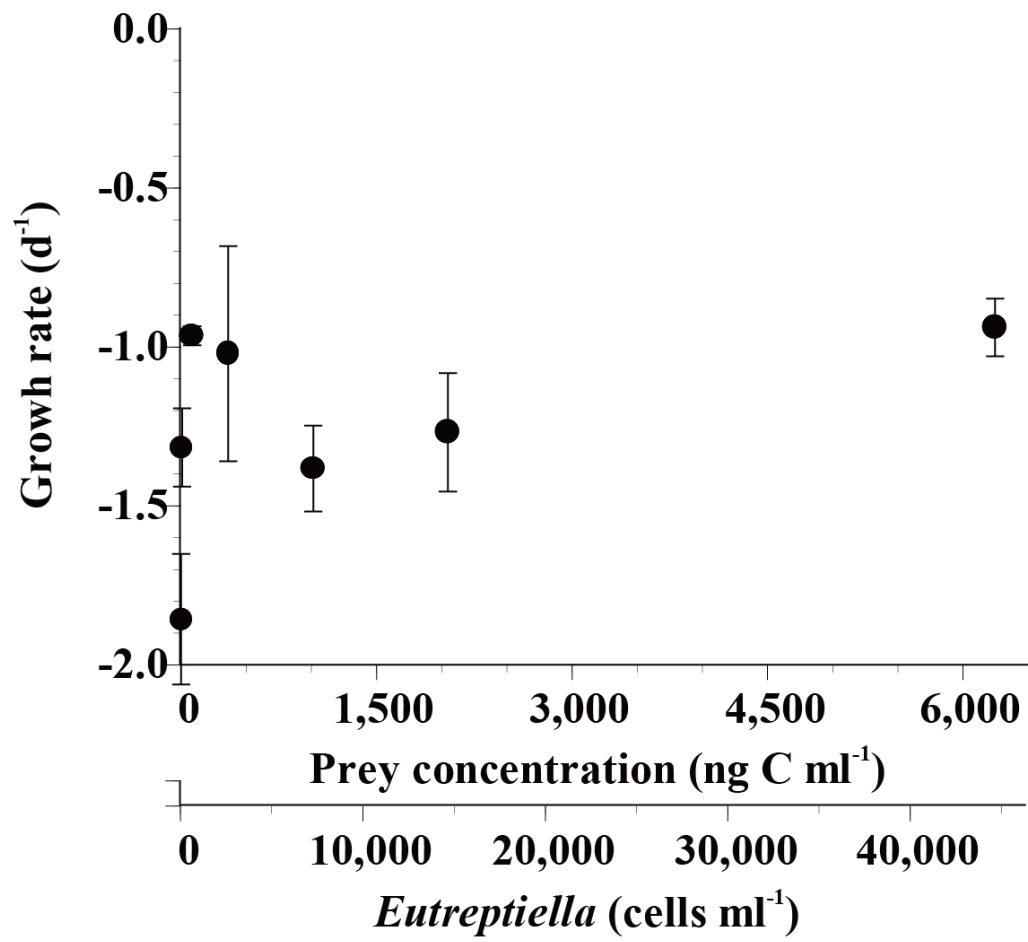


Fig. 7

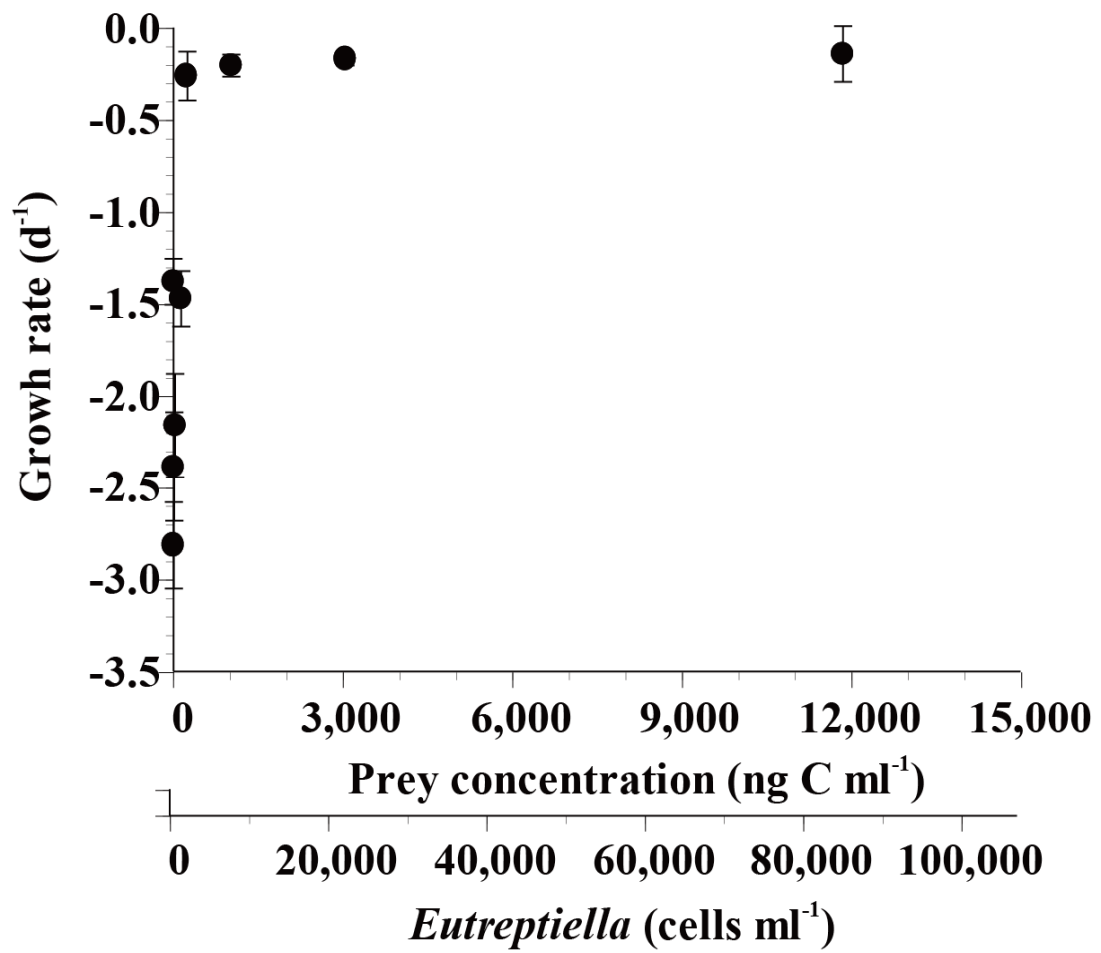


Fig. 8

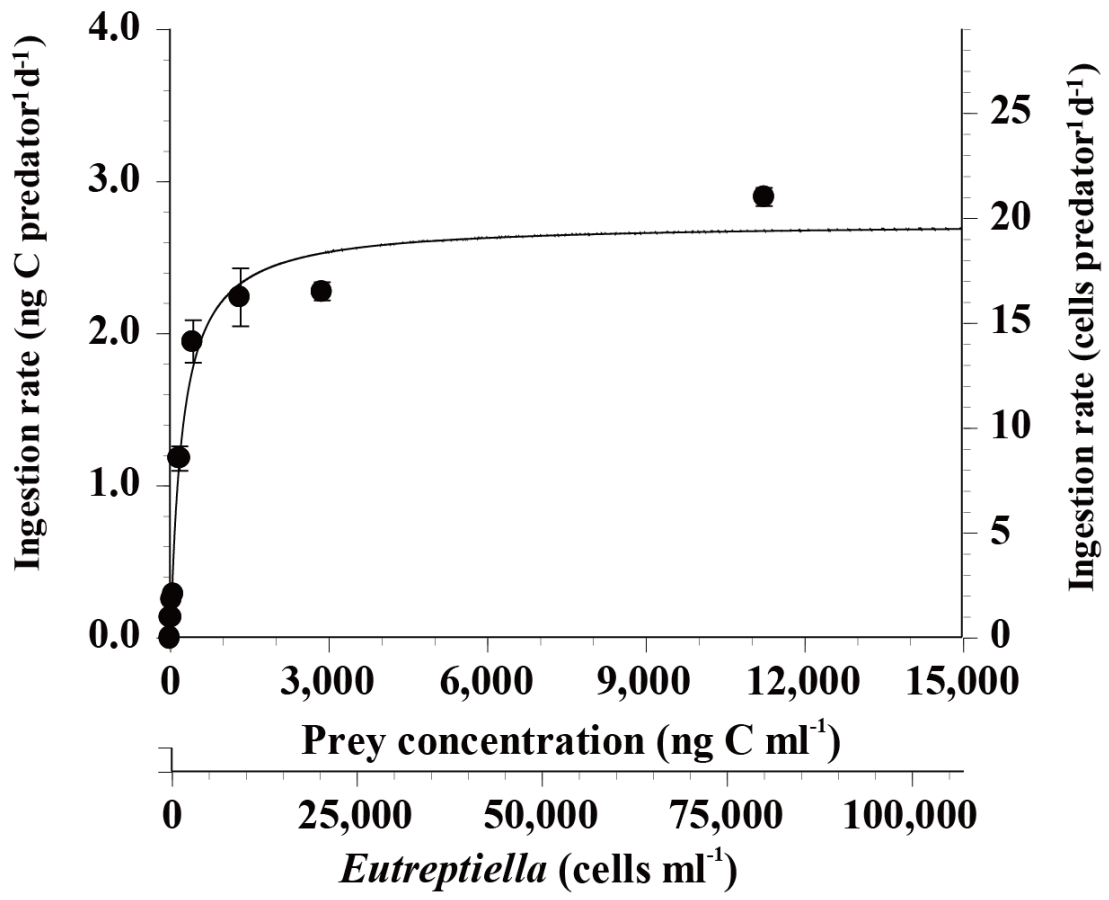


Fig. 9

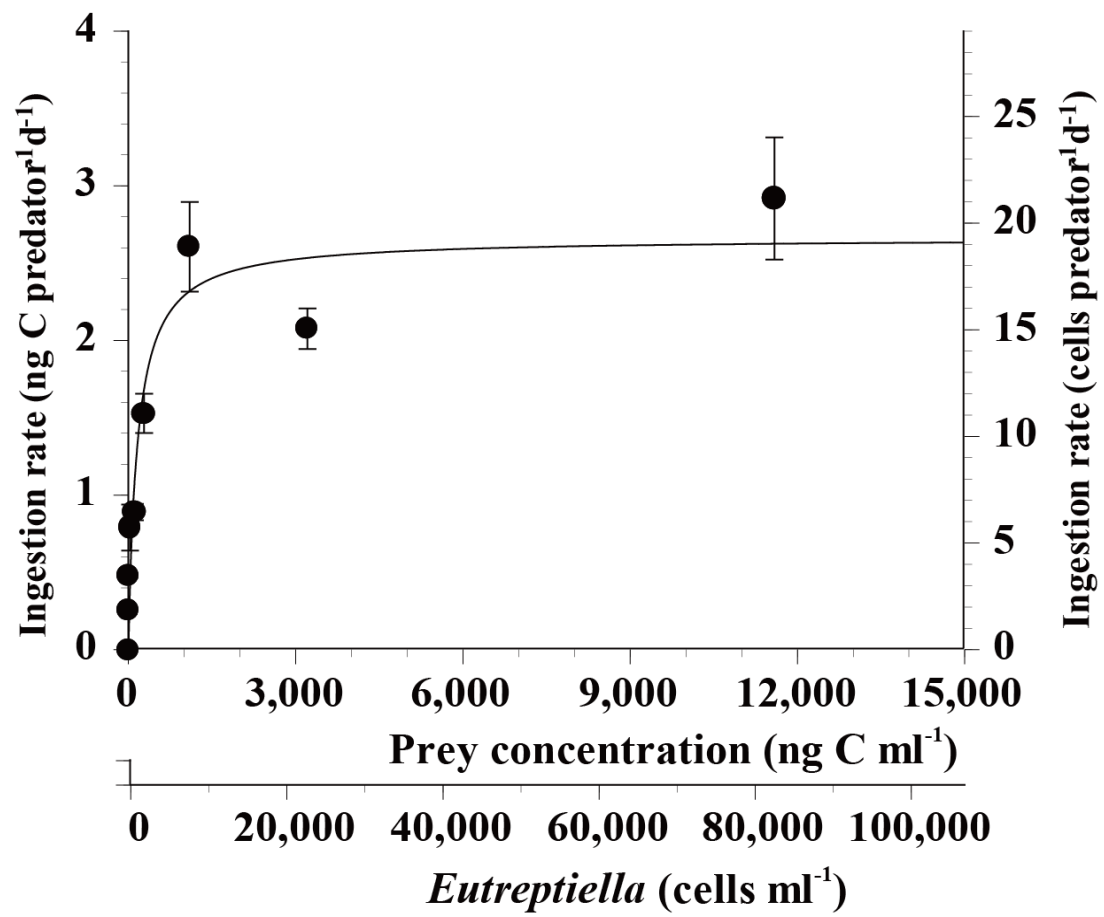


Fig. 10

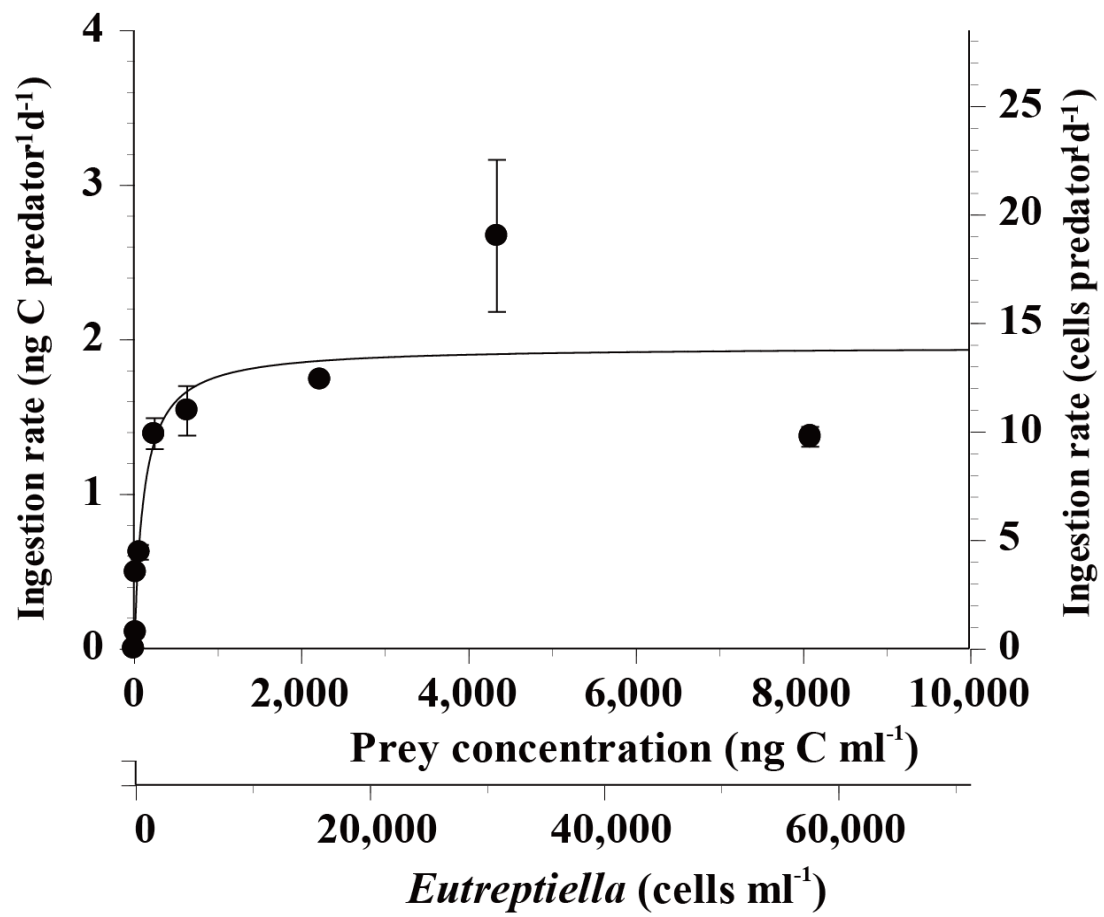


Fig. 11

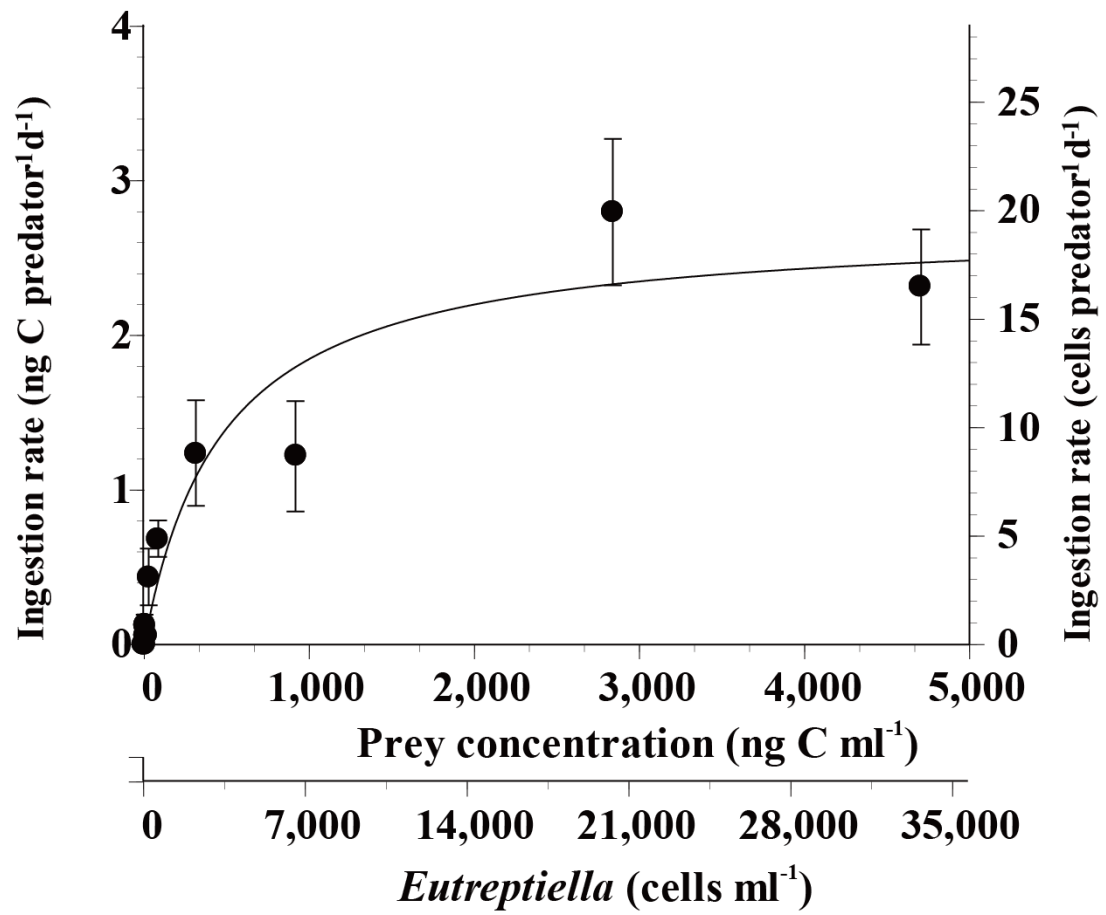


Fig. 12

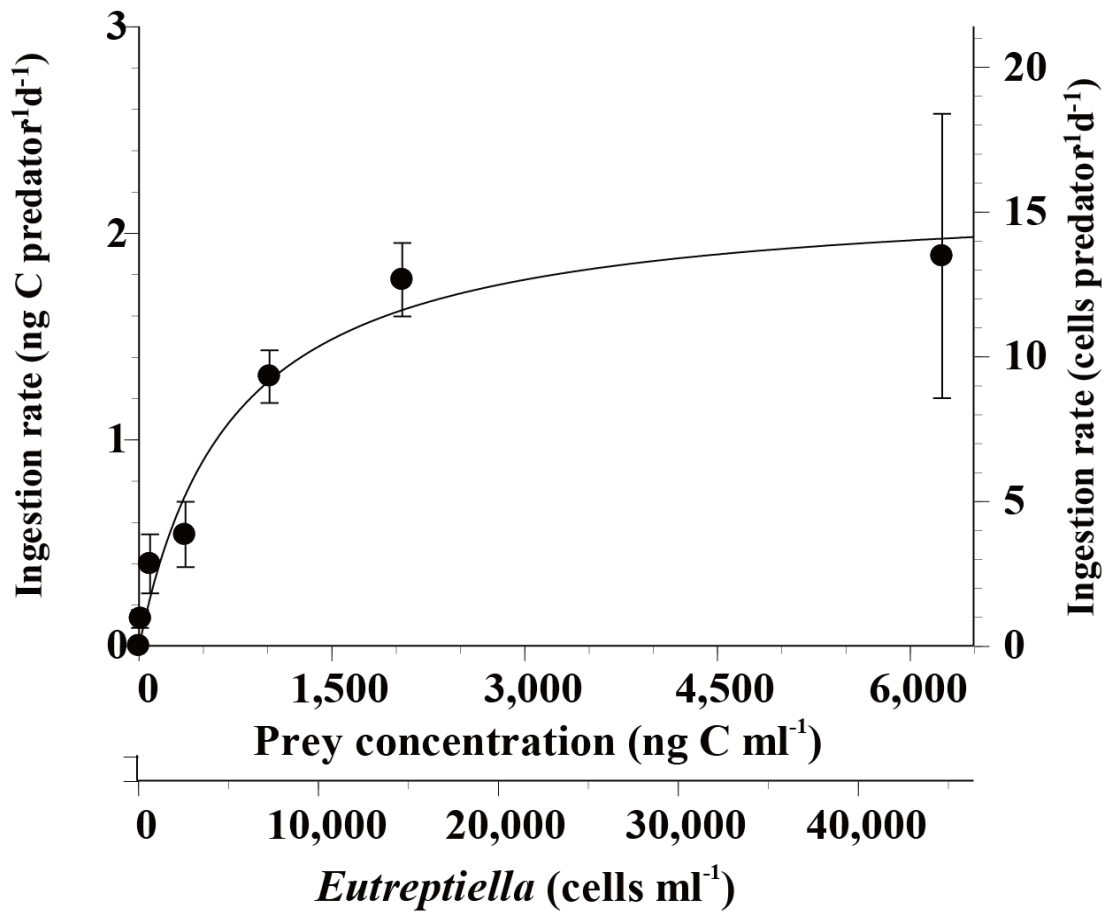


Fig. 13

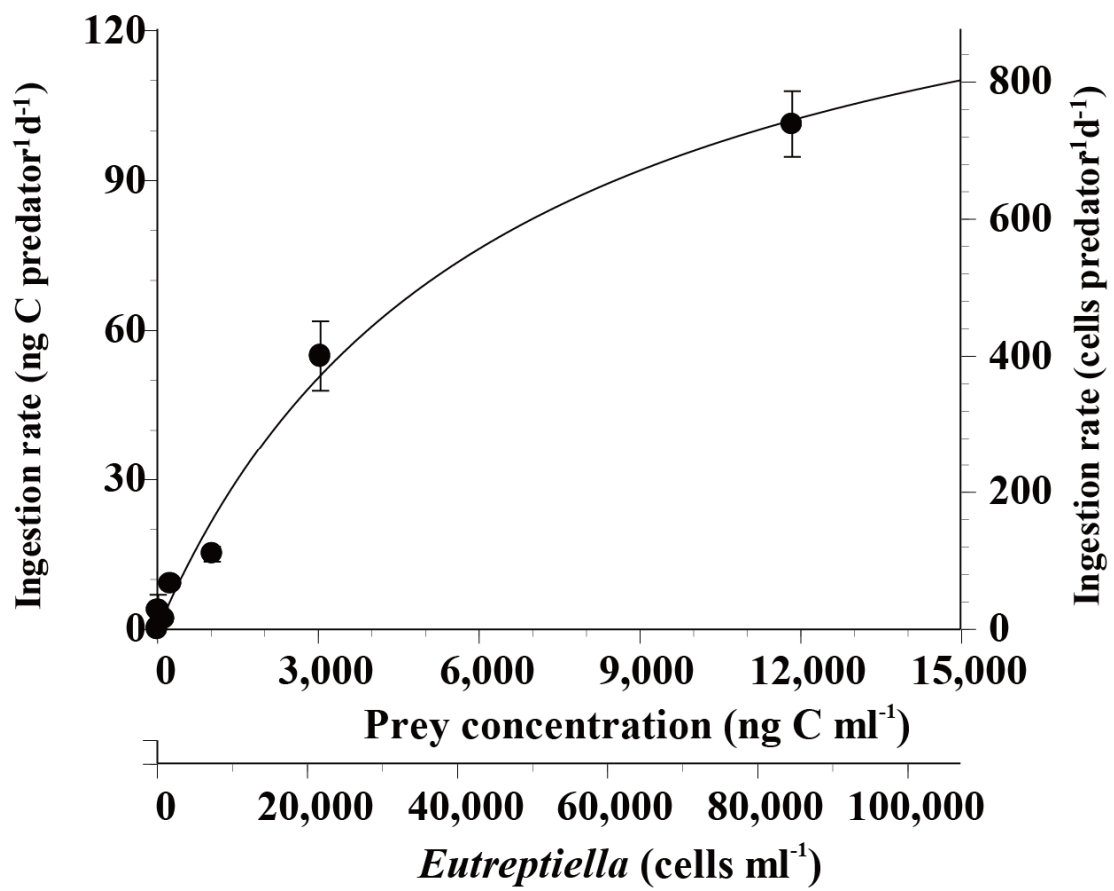


Fig. 14

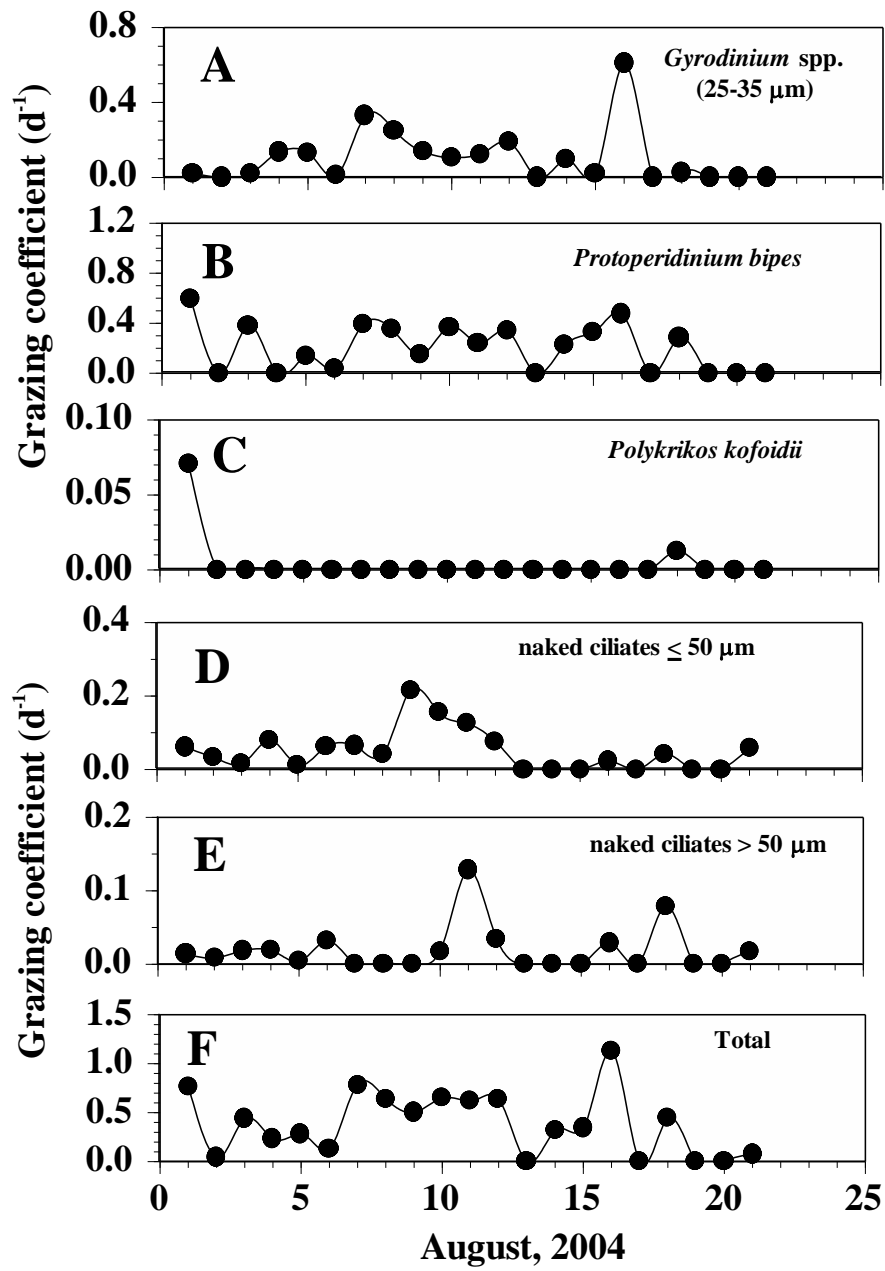


Fig. 15

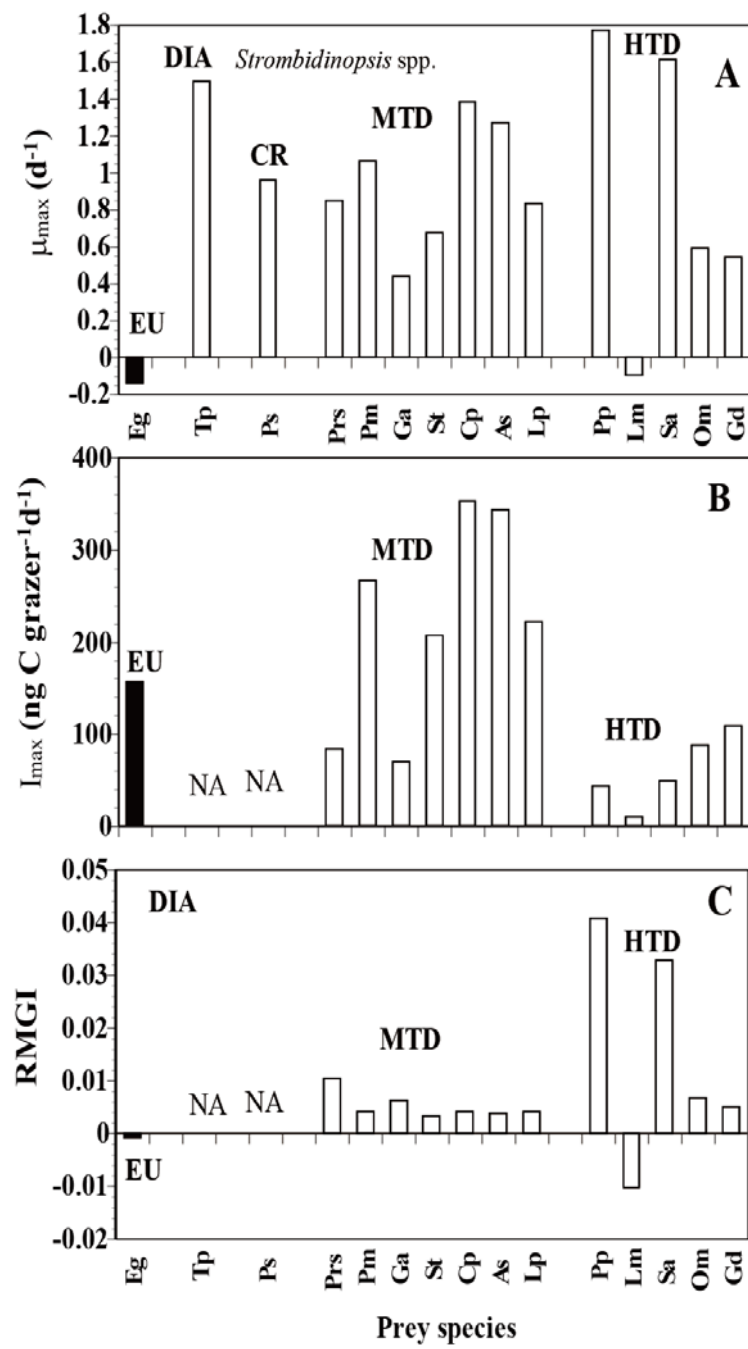


Fig. 16A-C

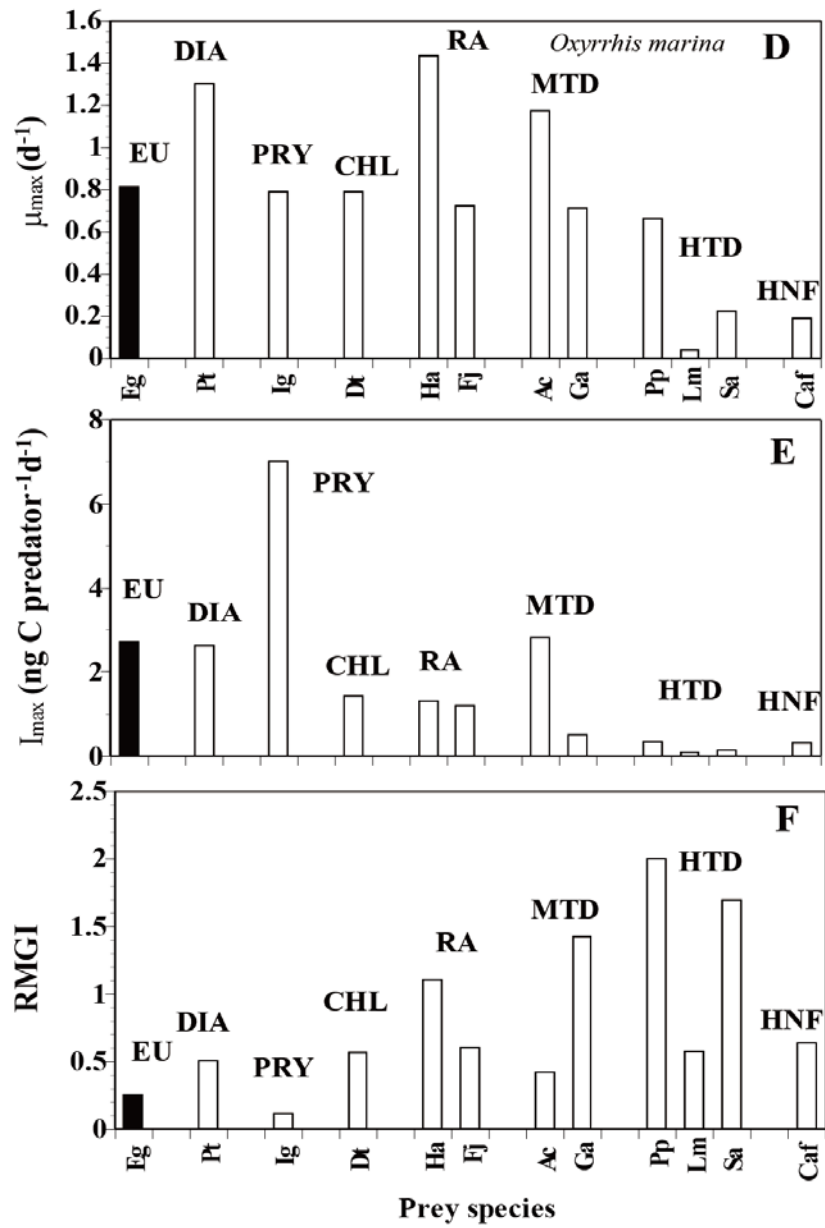


Fig. 16D-F

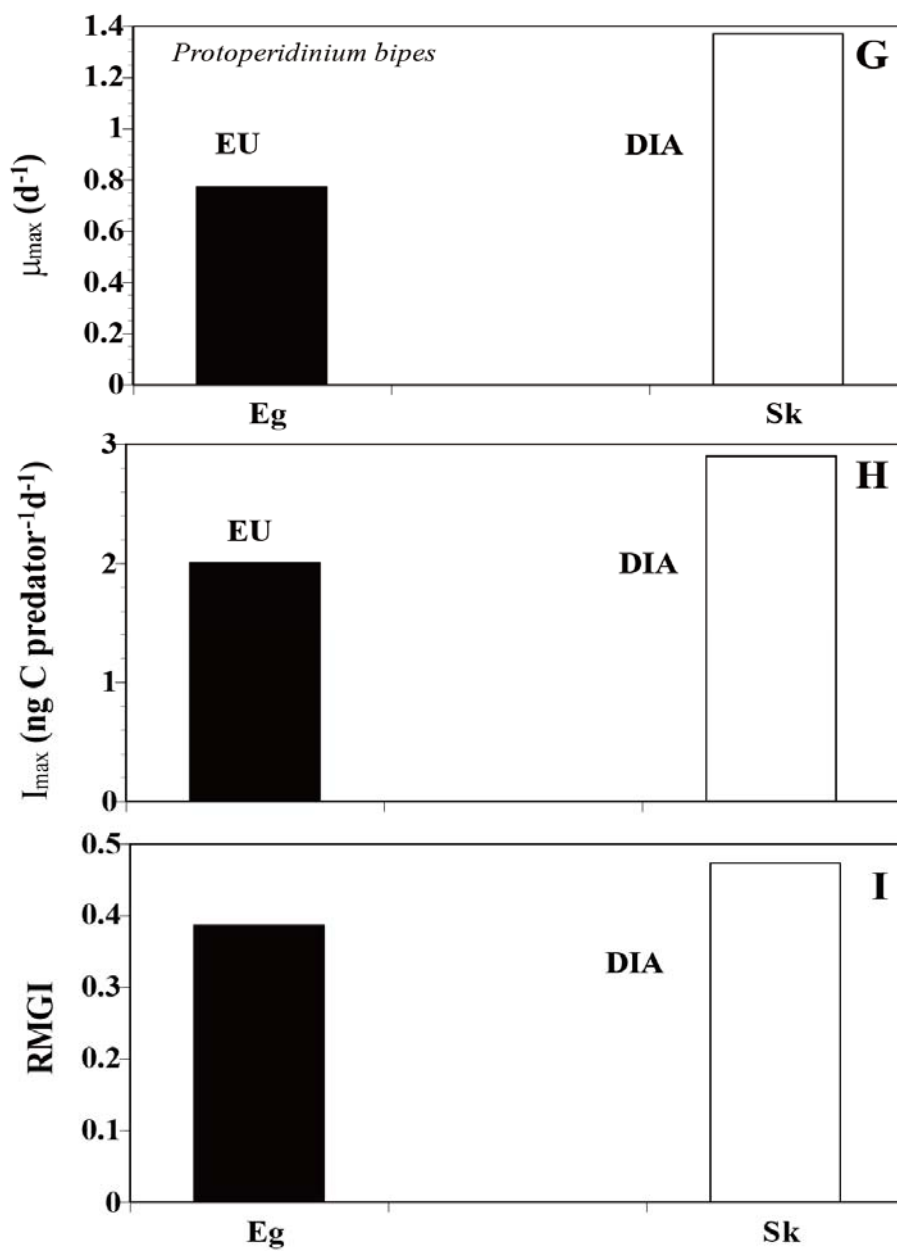


Fig. 16G-I

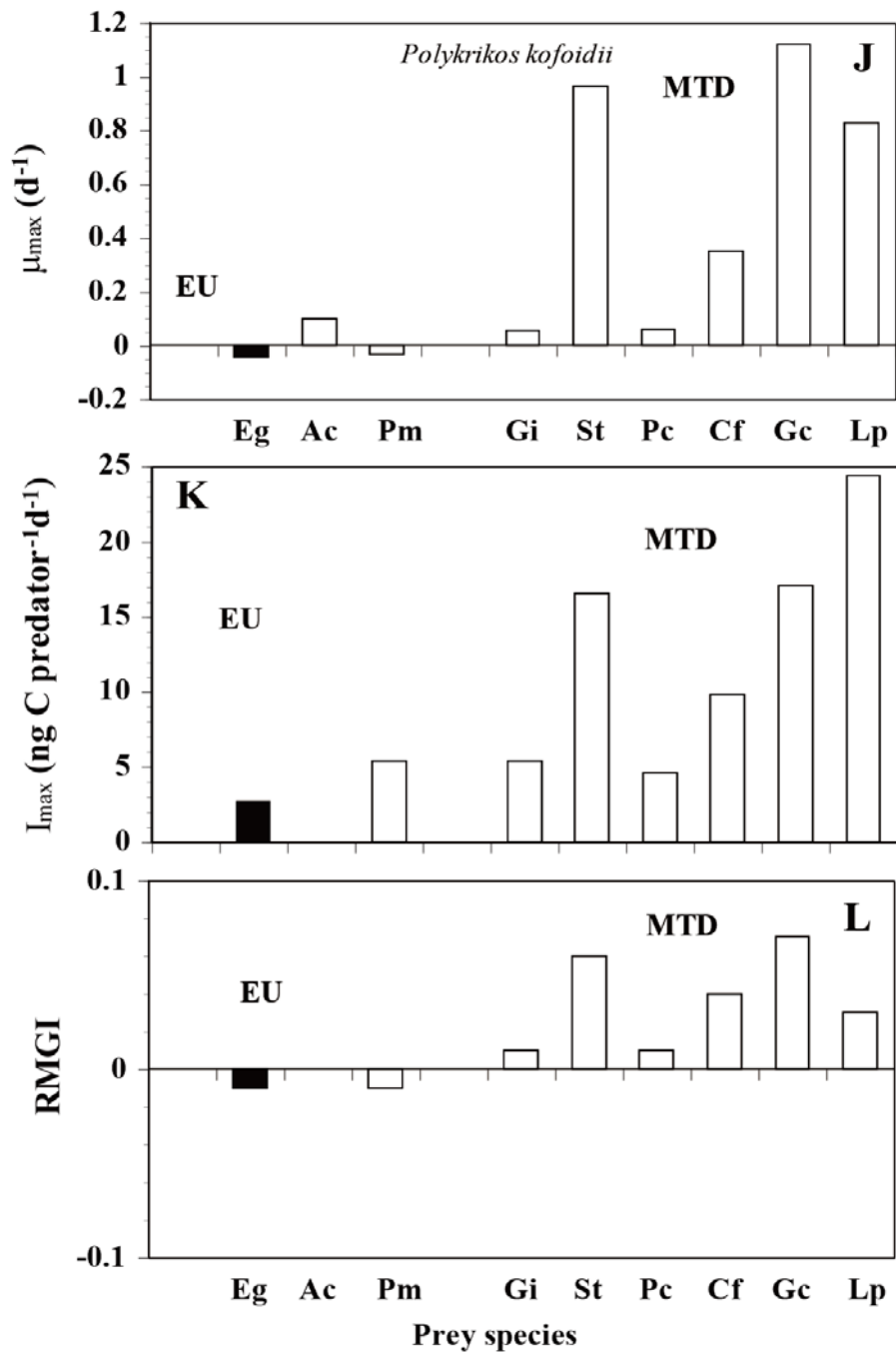


Fig. 16J-L

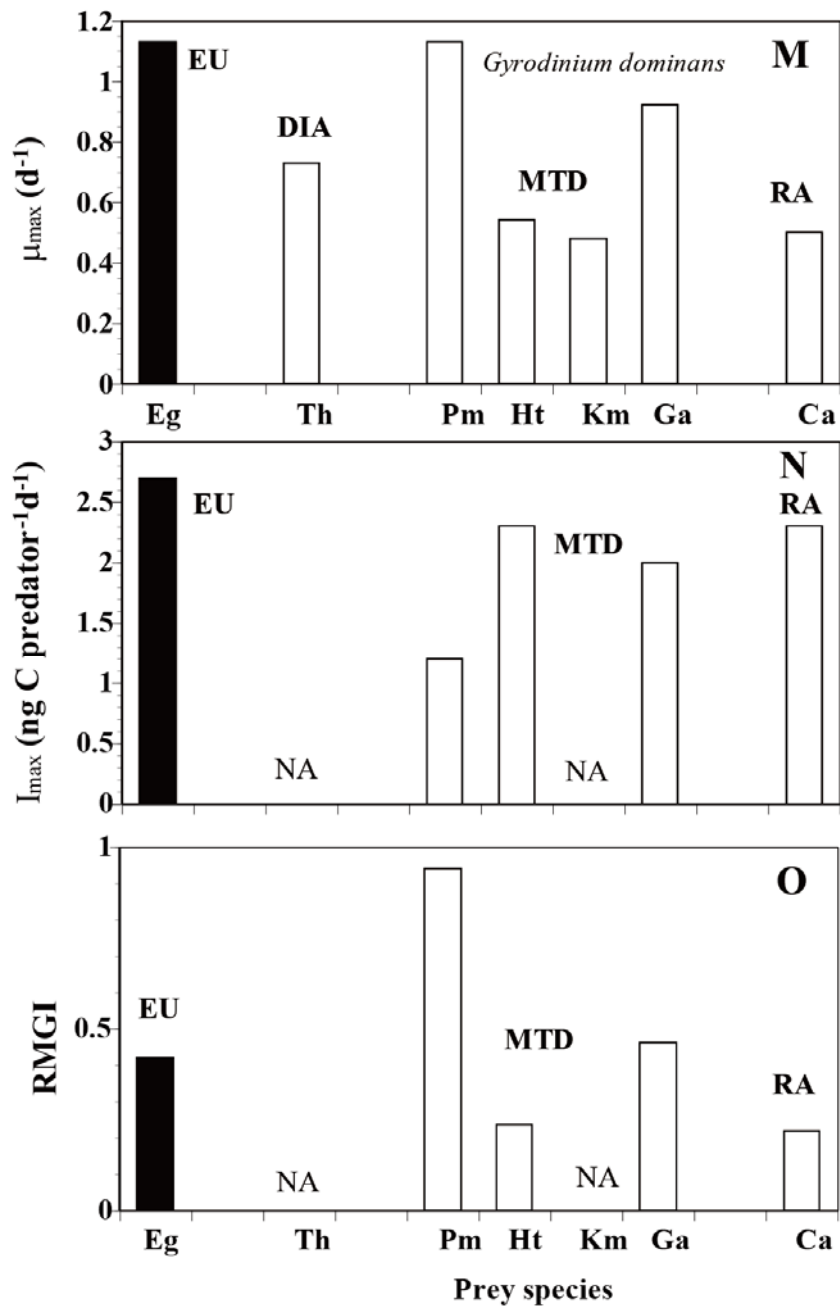


Fig. 16M-O