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Feeding by the heterotrophic dinoflagellates *Gyrodinium dominans* and *G. spirale* on the red-tide dinoflagellate *Prorocentrum minimum*

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ABSTRACT: To investigate the roles of *Gyrodinium dominans* and *G. spirale*, which have been reported to be abundant heterotrophic dinoflagellates in many coastal waters at different stages of red tides dominated by the dinoflagellate *Prorocentrum minimum*, we measured their growth and ingestion rates when feeding on *P. minimum* and calculated grazing coefficients by combining field data on abundances of *G. dominans*, *G. spirale*, and co-occurring *P. minimum* with laboratory data on ingestion rates obtained in the present study. In addition, the grazing coefficients of *G. dominans* and *G. spirale* on *P. minimum* were compared to those for co-occurring copepods, *Acartia* spp. Specific growth rates of *G. dominans* and *G. spirale* increased rapidly with increasing mean prey concentration before saturating at the *P. minimum* concentrations of ca. 150 and 80 ng C ml^{-1}, respectively. The maximum specific growth rate of *G. dominans* on *P. minimum* (1.13 d^{-1}) was higher than that of *G. spirale* (0.79 d^{-1}). Threshold prey concentrations (where net growth = 0) were 15 ng C ml^{-1} for *G. dominans* and 23 ng C ml^{-1} for *G. spirale*. Maximum ingestion and clearance rates of *G. dominans* on *P. minimum* (1.2 ng C $grazer^{-1}$ d^{-1} and 0.9 µl $grazer^{-1}$ h^{-1}, respectively) were much lower than those of *G. spirale* on the prey (13.6 ng C $grazer^{-1}$ d^{-1} and 5.3 µl $grazer^{-1}$ h^{-1}, respectively). Calculated grazing coefficients for *G. dominans* on *P. minimum* (up to 0.066 h^{-1}, i.e. 6.3% of *P. minimum* populations were removed by a *G. dominans* population in 1 h) or those by *G. spirale* (up to 0.231 h^{-1}, i.e. 39% of *P. minimum* populations were removed in 1 h) were much higher than those for co-occurring *Acartia* spp. (up to 0.001 h^{-1}, i.e. 0.1% of *P. minimum* populations were removed by *Acartia* spp. populations in 1 h). The results of the present study suggest that *G. dominans* and/or *G. spirale* sometimes have considerable grazing impacts on populations of *P. minimum* and are the most effective zooplanktonic grazers on the prey.

KEY WORDS: Copepod · Food web · Harmful algal bloom · Ingestion · Mixotroph · Protist

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INTRODUCTION

Dinoflagellate blooms, often referred to as red tides, can alter the balance of food webs and cause large-scale mortalities of fish and shellfish (ECOHAB 1995). Studies of red-tide formation and persistence suggest that grazing pressure may play an important role in bloom dynamics (Watras et al. 1985). In particular, grazing by microzooplankton is believed to contribute to the decline of red tides (Holmes et al. 1967, Eppley & Harrison 1975, Jeong 1995). *Prorocentrum minimum* is a common mixotrophic dinoflagellate which often forms red tides in the waters off many countries (Trigueros & Orive 2000, Yallop 2001, Gallegos & Jordan 2002). A few heterotrophic protistan grazers have been reported to grow on *P. minimum*; the large ciliates *Strombidinopsis* sp., *Favella taraikaensis*, and *F. ehrenbergii* are known to grow on *P. minimum* (Stoecker et al. 1981, Taniguchi & Kawakami 1985, Jeong et al. 1999), but common heterotrophic dino-

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flagellate *Polykrikos kofoidii* and the ciliate protostomid *Tiarina fusus* do not grow on this dinoflagellate prey (Jeong et al. 2001, 2002).

Heterotrophic dinoflagellates are ubiquitous protists in marine environments and play diverse ecological roles in the marine planktonic community (Lessard 1991, Jeong 1999, Sherr & Sherr 2000, Tillmann & Reckermann 2002). The heterotrophic dinoflagellates *Gyrodinium* spp. are ubiquitous and often abundant in many coastal waters (e.g. Haigh & Taylor 1991), in particular, during red tides dominated by *Prorocentrum minimum* (Sournia et al. 1991, Borkman et al. 1993, Fiala et al. 1998, Hori et al. 1998, Johnson et al. 2003). High abundance of *Gyrodinium* spp. during red tides dominated by *P. minimum* suggests that these grazers may grow well on *P. minimum* and have a considerable grazing impact on the populations of *P. minimum*. Hansen (1992) reported on the growth rate of *G. spirale* on *P. minimum*. However, no study has reported growth and grazing rates of *Gyrodinium* spp. on *P. minimum* as a function of prey concentration, and few studies have estimated their grazing impact on the prey (Johnson et al. 2003).

To understand the role of *Gyrodinium* spp. in the dynamics of *Prorocentrum minimum*, we established a monoclonal culture of *G. dominans* and *G. spirale* and conducted experiments to examine its numerical and functional responses when grazing on *P. minimum*. We also estimated the grazing coefficients attributable to *Gyrodinium* spp. feeding on *P. minimum* by combining field data on the abundances of *G. dominans*, *G. spirale*, and co-occurring *P. minimum* with laboratory data on the ingestion rates obtained in the present study.

Maximum growth and grazing rates of *Gyrodinium dominans* and *G. spirale* on *Prorocentrum minimum* are compared with those of heterotrophic dinoflagellates and ciliates feeding on the same prey species, and grazing coefficients attributable to *Gyrodinium* spp. on *P. minimum* were compared with those of the copepods. Results of the present study provide a basis for understanding the potential of *Gyrodinium* spp. to influence the population dynamics of *P. minimum*.

MATERIALS AND METHODS

Culture of phytoplankton prey. *Prorocentrum minimum* (PMJH00) was grown at 20°C in enriched f/2 seawater media (Guillard & Ryther 1962) without silicate, with continuous illumination at 100 µE m^{-2} s^{-1} provided by cool white fluorescent lights. Only cultures in an exponential growth phase were used for feeding experiments. The carbon content for this dinoflagellate (0.15 ng C $cell^{-1}$, $n > 2000$) was estimated from cell volume (1100 µm) according to Strathmann (1967).

Isolation and culture of *Gyrodinium* spp. Plankton samples collected with water samplers were taken from coastal waters off Masan, Korea, during April 2003, when the water temperature and salinity were 18.5°C and 25 psu, respectively. The samples were screened gently through a 154 µm Nitex mesh and placed in 6-well tissue culture plates, and a monoclonal culture of *Gyrodinium dominans* (or *G. spirale*) was established by 2 serial single-cell isolations. As the concentration of *G. dominans* (or *G. spirale*) feeding on *Prorocentrum minimum* increased, the grazers were subsequently transferred to 32, 270, and 500 ml polycarbonate (PC) bottles containing fresh *P. minimum*. The bottles were again filled to capacity with freshly filtered seawater, capped, and placed on a rotating wheel at 0.9 rpm at 20°C at 10 µE m^{-2} s^{-1} of cool white fluorescent light on a 12:12 h light:dark cycle. Once dense cultures of *Gyrodinium* spp. were obtained, they were transferred to 500 ml PC bottles of fresh prey every 2 d. Experiments were conducted when large volumes of *Gyrodinium* spp. culture were available. The carbon contents for *G. dominans* and *G. spirale* were estimated from cell volume (see next subsection) according to Menden-Deuer & Lessard (2000).

Cell volume. Cell length and maximum width of *Gyrodinium dominans* and *G. spirale* preserved in 5% acid Lugol's solution were measured using a compound or inverted microscope. The shapes of these *Gyrodinium* species were estimated as 2 cones joined at the cell equator (= maximum width of the cell). Cell volumes of both preserved *Gyrodinium* species were calculated according to the equation: volume = $1/3[\pi(\text{cell width}/2)^2](\text{cell length})$.

Swimming speed. Swimming speeds of *Gyrodinium dominans* and *G. spirale* starved for 12 h were measured at 20°C using a video-analysis system. For each species, aliquots from a dense culture were added to multiwell plates and allowed to acclimatize for 30 min. Swimming was then observed and recorded at 40×, with mean and maximum swimming velocity analyzed for fast-swimming cells that exhibited linear paths. Average swimming speed was calculated based on the linear displacement of cells in 1 s during single-frame playback. Swimming speeds of 30 cells for each *Gyrodinium* species were measured.

Growth and ingestion rates. Expts 1 and 2 were designed to measure growth, ingestion, and clearance rates of *Gyrodinium dominans* and *G. spirale*, respectively, as a function of the prey concentration, when feeding on *Prorocentrum minimum* (Table 1).

One or 2 d before these experiments were conducted, dense cultures of *Gyrodinium dominans* (or

G. spirale) grazing on *Prorocentrum minimum* were transferred into 1 l PC bottles containing low concentrations of the target prey. This was done to acclimatize the grazer to the target prey and minimize possible residual growth resulting from the ingestion of prey during batch culture. The bottles were filled to capacity with filtered seawater and placed on a rotating wheel to incubate as above. The abundances of *G. dominans* (or *G. spirale*) and prey were determined by enumerating cells in three 1 ml Sedgwick-Rafter counting chambers (SRCs).

The initial concentrations of *Gyrodinium dominans* (or *G. spirale*) and target prey were established using an autopipette to deliver predetermined volumes of known cell concentrations to the bottles. Triplicate 80 ml PC experiment bottles (mixtures of predator and prey) and triplicate control bottles (prey only) were set up for each predator–prey combination. Triplicate control bottles containing only *G. dominans* (or *G. spirale*) were also established at 1 predator concentration. Ten ml of f/2 medium were added to all bottles, which were then filled to capacity with freshly filtered seawater and capped. To determine actual predator and prey concentrations at the beginning of the experiment and after 24, 48, and 72 h incubation, a 5 ml aliquot for *G. dominans* (10 ml aliquot for *G. spirale*) was removed from each bottle and fixed with 5% acid Lugol's solution, and all predator cells and all or >200 prey cells in three 1 ml SRCs were enumerated. Prior to taking subsamples, the condition of *G. dominans* (or *G. spirale*) and its prey was assessed using a dissecting microscope. The bottles were filled again to capacity with freshly filtered seawater, capped, and placed on rotating wheels under the environmental conditions described above. Dilution of the cultures associated with refilling the bottles was considered in calculating growth and ingestion rates.

The specific growth rate of *Gyrodinium dominans* (or *G. spirale*) (μ, d^{-1}), was calculated by averaging the instantaneous growth rates (IGR) for each sampling interval, calculated as:

$$\mathrm{IGR} = \frac{\mathrm{Ln}(S_{t_2} / S_{t_1})}{t_2 - t_1} \times 24 \quad (1)$$

where S_{t_1} and S_{t_2} are the concentrations of *Gyrodinium* spp. at consecutive samplings. The final values of t_2 for calculation were 24 h for *G. spirale* and 48 h for *G. dominans*, which provided the highest specific growth rate. After 24 h, prey concentrations for *G. spirale* had already been largely reduced (ca. 35 to 75% of the initial concentrations).

Data for *Gyrodinium* growth rate were fitted to a Michaelis-Menten equation:

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

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

Ingestion and clearance rates were calculated using the equations of Frost (1972) and Heinbokel (1978). Incubation time for calculating ingestion and clearance rates was the same as for estimating growth rate. Ingestion rate data for *Gyrodinium dominans* were fitted to a linear regression equation, and those for *G. spirale* to a Michaelis-Menten equation:

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

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

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

Grazing impact. With some assumptions (see Table 2), we estimated grazing coefficients attributable to *Gyrodinium* spp. on *Prorocentrum minimum* by combining field data on abundances of *Gyrodinium* spp. and prey with ingestion rates of the predators on the prey obtained in the present study. For comparison (of the grazing coefficients between *Gyrodinium* spp. and the copepods *Acartia*

Table 1. Design of experiments. Values in prey and predator columns represent actual initial concentrations (cells ml^{-1}) followed by calculated carbon biomass (ng C ml^{-1}) in parentheses. Concentrations of *Gyrodinium dominans* and *G. spirale* in control bottles were 92 (Expt 1) and 45 cells ml^{-1} (Expt 2), respectively

Expt	Predator		Prey
	Species	Concentration	Concentration
1	*Gyrodinium dominans*	7.6–136.2	108 (16), 200 (30), 507 (76), 983 (148), 2955 (443), 7220 (1083), 18608 (2791)
2	*Gyrodinium spirale*	7.3–46.4	99 (15), 167 (25), 413 (62), 1139 (171), 3831 (571), 6227 (934), 12416 (1861)

spp. on *P. minimum*), we also estimated grazing coefficients attributable to co-occurring dominant copepods *Acartia* spp. on *P. minimum* by combining field data on abundances of *Acartia* spp. and *P. minimum* with ingestion rates of the grazer on the prey obtained from the equation of Besiktepe & Dam (2002). The data on the abundances of *P. minimum*, *Gyrodinium* spp., and co-occurring *Acartia* spp. used in this estimation were obtained from water samples and net-towed samples collected from the coastal waters at the same stations off Kwangyang (in 2000) and Masan (in 2003), Korea.

Grazing coefficients (g, h^{-1}) were calculated as:

$$g = (1/\Delta t)\ln[C_i/(C_i - C_e)] \quad (4)$$

where Δt (h) is a time interval, C_e (cells ml^{-1}) is the number of prey cells eaten by the *Gyrodinium* spp. (or *Acartia* spp.) population in 1 ml of seawater in 1 h, and C_i (cells ml^{-1}) is the initial cell concentration of prey for a given hour. The values of C_e were calculated as:

$$C_e = PIR \times 1\ h = IR \times G \times 1\ h \quad (5)$$

where PIR is the population ingestion rate of *Gyrodinium* spp. (or *Acartia* spp.) on *Prorocentrum minimum* in 1 ml of seawater (prey eaten $ml^{-1}\ h^{-1}$), IR is the ingestion rate (prey eaten $grazer^{-1}\ h^{-1}$) of *Gyrodinium* spp. (or *Acartia* spp.) on *P. minimum*, and G is the abundance (grazers ml^{-1}) of *Gyrodinium* spp. (or *Acartia* spp.) at the same time as C_i.

RESULTS

Swimming speed

Gyrodinium dominans swam faster than *G. spirale*. The average (±SE, n = 30) and maximum swimming speeds of *G. dominans* were 1463 (±78) and 2533 µm s^{-1}, respectively, while those of *G. spirale* were 815 (±54) and 1175 µm s^{-1}, respectively.

Growth rates

Both *Gyrodinium dominans* and *G. spirale* grew well on *Prorocentrum minimum*. The specific growth rates of *G. dominans* feeding on a unialgal diet of *P. minimum* increased with increasing mean prey concentration up to ca. 150 ng C ml^{-1}, but were saturated at higher prey concentrations (Fig. 1). When the data were fitted to Eq. (2), the maximum specific growth rate (μ_{max}) of *G. dominans* was 1.13 d^{-1}. A threshold prey concentration (where net growth = 0) for *G. dominans* was 14.7 ng C ml^{-1} (98 cells ml^{-1}).

The specific growth rates of *Gyrodinium spirale* feeding on a unialgal diet of *Prorocentrum minimum* increased with increasing mean prey concentration up to ca. 80 ng C ml^{-1}, but were saturated at higher prey concentrations (Fig. 2). When the data were fitted to Eq. (2), μ_{max} of *G. spirale* was 0.786 d^{-1}. A threshold

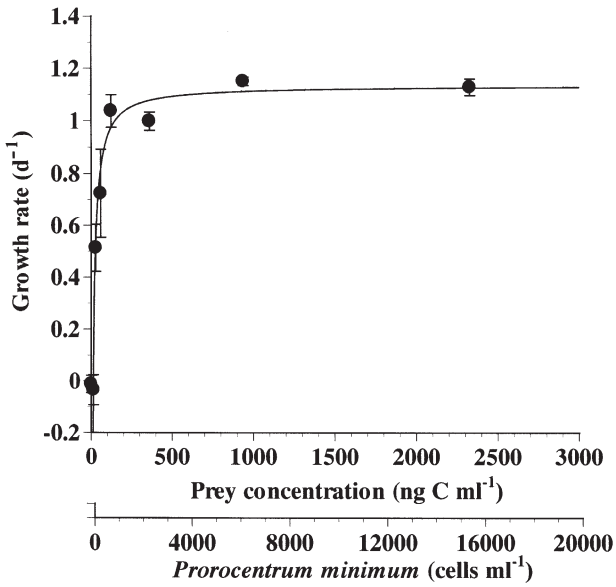

Fig. 1. *Gyrodinium dominans*. Specific growth rates on *Prorocentrum minimum* as a function of mean prey concentration (x). Symbols represent treatment means ±1 SE. The curve is fitted by a Michaelis-Menten equation (Eq. 2) using all treatments in the experiment. Growth rate (GR, d^{-1}) = $1.13\{(x - 14.7)/[18.1 + (x - 14.7)]\}$, $r^2 = 0.915$

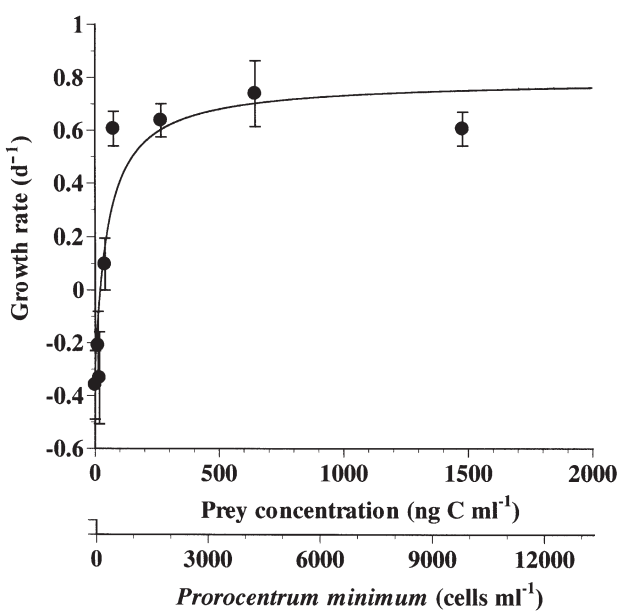

Fig. 2. *Gyrodinium spirale*. Specific growth rates on *Prorocentrum minimum* as a function of mean prey concentration (x). Symbols and curve as in Fig. 1. Growth rate (GR, d^{-1}) = $0.786\{(x - 22.8)/[73.8 + (x - 22.8)]\}$, $r^2 = 0.784$

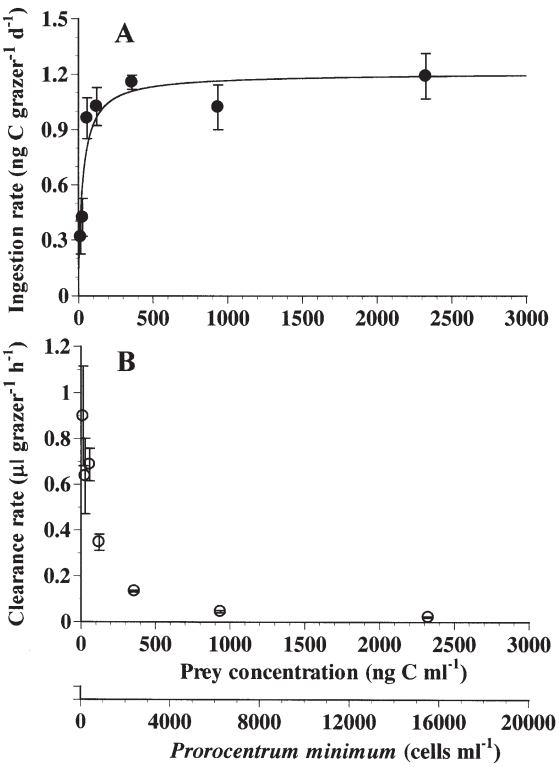

Fig. 3. *Gyrodinium dominans.* (A) Ingestion and (B) clearance rates on *Prorocentrum minimum* as a function of mean prey concentration (x). Symbols and curve as in Fig. 1. Ingestion rate (IR, ng C grazer^{-1} d^{-1}) = 1.2[x/(30.6 + x)], r^2 = 0.751

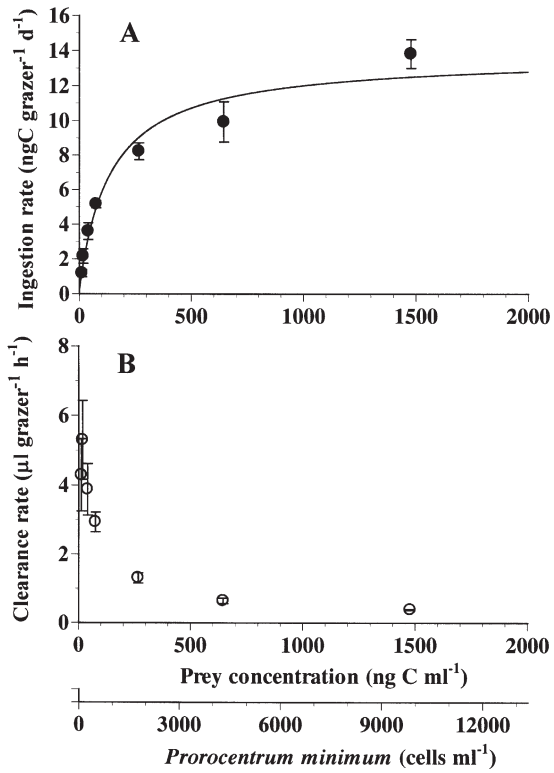

Fig. 4. *Gyrodinium spirale.* (A) Ingestion and (B) clearance rates on *Prorocentrum minimum* as a function of mean prey concentration (x). Symbols and curve as in Fig. 1. Ingestion rate (IR, ng C grazer^{-1}d^{-1}) = 13.6[x/(137 + x)], r^2 = 0.917

prey concentration (where net growth = 0) for *G. spirale* was 22.8 ng C ml^{-1} (152 cells ml^{-1}).

Ingestion and clearance rates

The ingestion rates of *Gyrodinium dominans* on a unialgal diet of *Prorocentrum minimum* increased with increasing mean prey concentration up to ca. 400 ng C ml^{-1}, but were saturated at higher prey concentrations (Fig. 3A). When the data were fitted to Eq. (3), the maximum ingestion rate was 1.2 ng C grazer^{-1} d^{-1} (8 prey cells grazer^{-1} d^{-1}). The maximum clearance rate on *Prorocentrum minimum* was 0.9 µl grazer^{-1} h^{-1} (Fig. 3B), and the maximum volume-specific clearance rate was 1.5×10^6 h^{-1}.

The ingestion rates of *Gyrodinium spirale* on a unialgal diet of *Prorocentrum minimum* continuously increased with increasing mean prey concentration (Fig. 4A). When the data were fitted to Eq. (3), the maximum ingestion rate was 13.6 ng C grazer^{-1} d^{-1} (91 prey cells grazer^{-1} d^{-1}). The maximum clearance rates on *Prorocentrum minimum* were 5.3 µl grazer^{-1} h^{-1} (Fig. 4B), and the maximum volume-specific clearance rate was 6.5×10^5 h^{-1}.

Cell volume

After 48 h incubation, the cell volume of *Gyrodinium dominans* fed *Prorocentrum minimum* at the lowest mean prey concentration of 16 ng C ml^{-1} (590 µm^3) was similar to that of *G. dominans* without added prey (570 µm^3), but at the higher prey concentration cell volume increased continuously from 860 to 1720 µm^3 with increasing mean prey concentration (Fig. 5A). The cell length distribution after 48 h incubation varied from a range of 13–20 µm (mean ± SE = 17.9 ± 0.5 µm) without added prey to 20–30 µm (mean ± SE = 25.9 ± 0.6 µm) at the highest mean prey concentration.

After 24 h incubation, the cell volume of *Gyrodinium spirale* fed *Prorocentrum minimum* at the lowest mean prey concentration of 11 ng C ml^{-1} (8000 µm^3) was larger than that of *G. dominans* without added prey (5890 µm^3), and at the higher prey concentration cell volume increased continuously from 8110–16 860 µm^3 with increasing mean prey concentration (Fig. 5B). The cell length distribution after 24 h incubation varied from a range of 58–71 µm (mean ± SE = 63.6 ± 1.5) without added prey to 65–90 µm (mean ± SE = 72.3 ± 1.3) at the highest mean prey concentration.

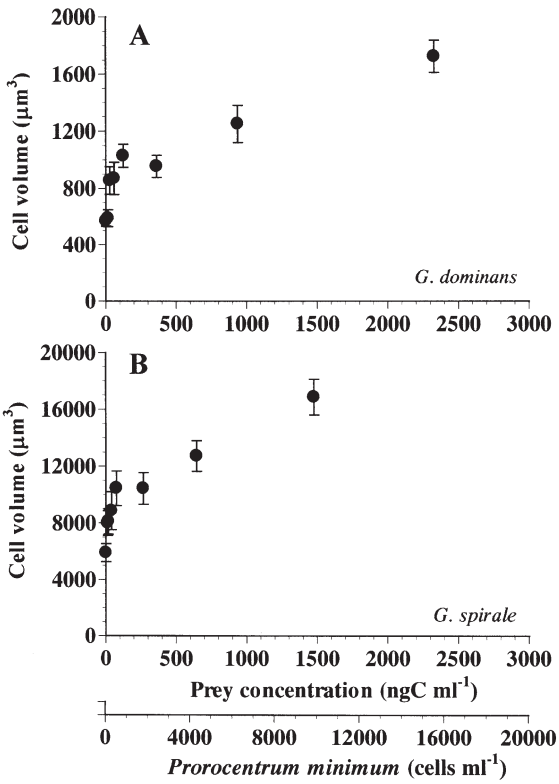

Fig. 5. (A) *Gyrodinium dominans* and (B) *G. spirale*. Cell volume of dinoflagellates fed *Prorocentrum minimum* as a function of mean prey concentration. Symbols represent treatment means ± 1 SE

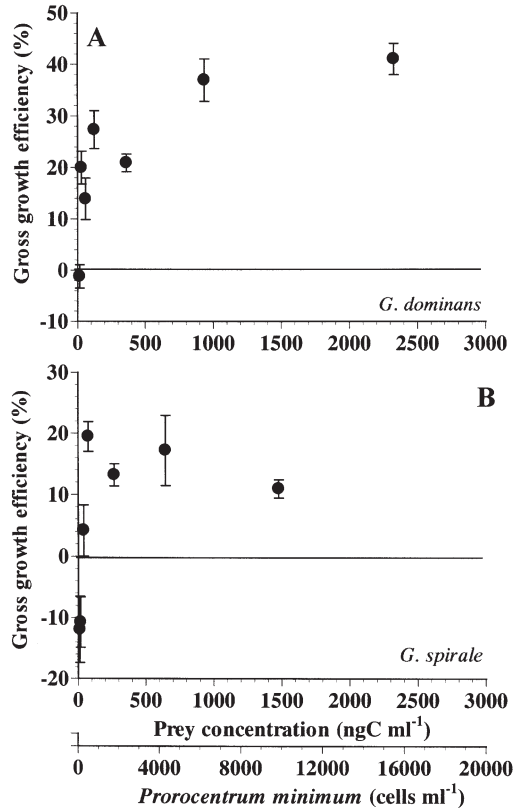

Fig. 6. (A) *Gyrodinium dominans*; (B) *G. spirale*. Gross growth efficiency (GGE), defined as *Gyrodinium* biomass produced (+) or lost (–) per *Prorocentrum minimum* biomass ingested, as a function of mean prey concentration. Symbols represent treatment means ± 1 SE

The cell volumes of *Gyrodinium dominans* and *G. spirale* where maximum volume-specific clearance rate were obtained were 590 and 8110 µm^3, respectively.

Gross growth efficiency

GGEs of *Gyrodinium dominans* on *Prorocentrum minimum* were negative at the mean prey concentration of 16 ng C ml^{-1}, but increased up to 41% with increasing mean prey concentration (Fig. 6A).

GGEs of *Gyrodinium spirale* on *Prorocentrum minimum* were negative at the mean prey concentration of 17 ng C ml^{-1}, increased up to 17% at 75 ng C ml^{-1}, but were saturated at the higher prey concentrations (Fig. 6B).

Grazing impact

Grazing coefficients attributable to *Gyrodinium dominans* on co-occurring *Prorocentrum minimum* in the coastal waters off Kwangyang and Masan were 0 to 0.066 h^{-1}, while those for *G. spirale* were 0 to 0.231 h^{-1} (i.e. up to 39% of *P. minimum* populations were removed by a *G. spirale* population in 1 h) (Fig. 7A,B, Table 2). Grazing coefficients attributable to *G. dominans* plus *G. spirale* at the *P. minimum* concentrations of 60 to 300 cells ml^{-1} (0.027 to 0.296 h^{-1}) were much higher than those at the lower or higher *P. minimum* concentrations (0 to 0.01 h^{-1}). Grazing coefficients attributable to co-occurring *Acartia* spp. on *P. minimum* were 0 to 0.001 h^{-1} (Fig. 7C, Table 2).

DISCUSSION

Protistan predators on *Prorocentrum minimum*

Both *Gyrodinium dominans* and *G. spirale* grew well on *Prorocentrum minimum* in the present study. The heterotrophic dinoflagellates *Oblea rotunda* and *Polykrikos kofoidii* have been known not to grow on *P. minimum* (Strom & Buskey 1993, Jeong et al. 2001). The heterotrophic dinoflagellates *Protoperidinium*

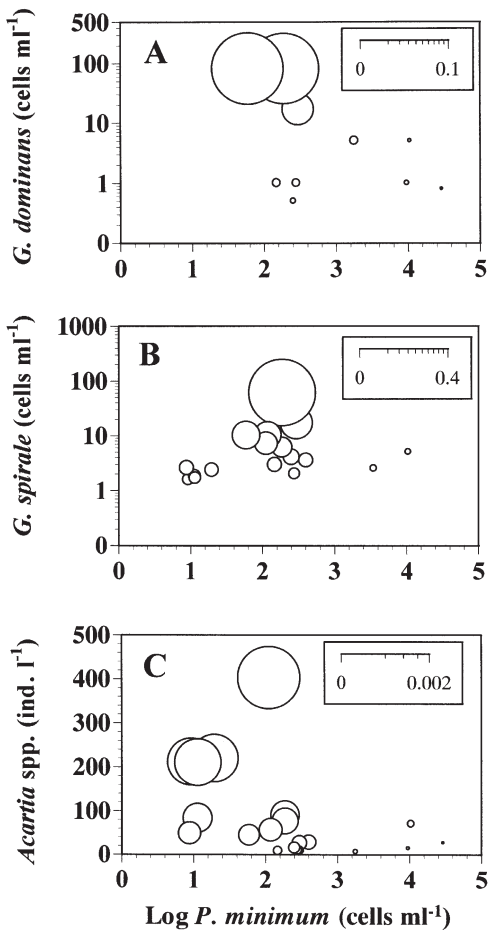

Fig. 7. (A) *Gyrodinium dominans*, (B) *G. spirale*, and (C) *Acartia* spp. Calculated grazing coefficients (g, h^{-1}) on *Prorocentrum minimum* (see text for calculation). N = 29

divergens and *P. crassipes* may also not grow on the prey, because these *Protoperidinium* species did not grow on *Prorocentrum balticum*, which is similar to *P. minimum* in its size and shape (Jeong & Latz 1994). Large ciliates *Strombidinopsis* sp. and *Favella taraikaensis* grew on the prey (Taniguchi & Kawakami 1985, Jeong et al. 1999), while a small prostomatid ciliate *Tiarina fusus* did not grow (Jeong et al. 2002). Therefore, *G. dominans* and *G. spirale* are the only heterotrophic dinoflagellate grazers so far reported to grow on *P. minimum*.

Growth and ingestion

Gyrodinium dominans used in the present study has a higher maximum growth rate when feeding on *Prorocentrum minimum* (1.13 d^{-1}) than for any other prey so far reported (Table 3), when corrected to 20°C using Q_{10} = 2.8 (Hansen et al. 1997). However, the maximum growth rate of *G. spirale* on *P. minimum* (0.79 d^{-1}) obtained in the present study was lower than that on the dinoflagellate *Heterocapsa triquetra* (1.08 d^{-1}) (Hansen 1992). The cell volumes of *G. dominans* and *G. spirale* differ by strain, varying from ca. 1700 to 30 000 µm^3 and from ca. 11 500 to 16 900 µm^3, respectively (Table 3). In general, the smaller strain of *G. dominans* or *G. spirale* has a higher maximum growth rate than the larger strain.

The maximum ingestion rate of *Gyrodinium dominans* on *Prorocentrum minimum* (1.2 ng C grazer^{-1} d^{-1}) was lower than that on other phytoplankton prey so far reported (Table 3). However, the maximum ingestion

Table 2. Estimation of grazing impact by a *Gyrodinium* population or *Acartia* spp. populations on a *Prorocentrum minimum* population using the equations in Figs. 3 & 4 in this study, the equation in Fig. 1 of Besiktepe & Dam (2002) and the abundances of co-occurring *P. minimum*, *Gyrodinium* spp., and *Acartia* spp. obtained from water samples collected off Kwangyang in 2000 and Masan in 2003. PmC = *P. minimum* concentration; GdC = *G. dominans* concentration; GdPIR = *G. dominans* population ingestion rate; Gdg = *G. dominans* grazing coefficient; GsC = *G. spirale* concentration; GsPIR = *G. spirale* population ingestion rate; Gsg = *G. spirale* grazing coefficient; TGg = total *Gyrodinium* grazing coefficient; AD = *Acartia* spp. density; APIR = *Acartia* spp. population ingestion rate; Ag = *Acartia* spp. grazing coefficient

PmC (cells ml^{-1})	GdC (cells ml^{-1})	GdPIR (prey ml^{-1} h^{-1})	Gdg (h^{-1})	GsC (cells ml^{-1})	GsPIR (prey ml^{-1} h^{-1})	Gsg (h^{-1})	TGg (h^{-1})	AD (ind. l^{-1})	APIR[a] (prey ml^{-1} h^{-1})	Ag (h^{-1})
9	0	0	0	1.6	0.1	0.006	0.006	0.2104	0.01	0.0006
12	0	0	0	1.7	0.1	0.007	0.007	0.2090	0.01	0.0006
20	0	0	0	2.3	0.2	0.010	0.010	0.2181	0.01	0.0006
60	80.0	3.8	0.066	10.0	2.3	0.040	0.106	0.0435	0.01	0.0001
114	0	0	0	7.1	3.0	0.027	0.027	0.4013	0.11	0.0010
190	80.0	11.9	0.065	60.0	39.2	0.231	0.296	0.0889	0.04	0.0002
300	16.7	3.8	0.013	16.7	15.7	0.054	0.066	0.0252	0.02	0.0001
1800	5.0	1.5	0.001	0	0	0	0.001	0.0054	0.01	0.0000
3500	0	0	0	2.5	7.5	0.002	0.002	0.3994	0.72	0.0002
10600	5.0	1.6	0	5.0	17.5	0.002	0.002	0.0696	0.13	0.0000

[a]Assuming that the ingestion rate of *Acartia omorii*, the dominant copepod in the water samples collected off Kwangyang and Masan, on *Prorocentrum minimum* is the same as that of *A. tonsa* obtained in Besiktepe & Dam (2002)

Table 3. Comparison of growth, ingestion and clearance rates in the genus *Gyrodinium*. Rates are corrected to 20°C using Q_{10} = 2.8 (Hansen et al. 1997). PDV = predator volume ($\times 10^3$ µm^3); PYV = prey volume ($\times 10^3$ µm^3); μ_{max} = maximum growth rate (d^{-1}); I_{max} = maximum ingestion rate (ng C predator^{-1} d^{-1}); C_{max} = maximum clearance rate (µl predator^{-1} h^{-1}); SC_{max} = maximum specific clearance rate ($\times 10^5$ h^{-1}); GGE_{max} = maximum gross growth efficiency (%); SS_{max} = maximum swimming speed (mm s^{-1}); DN = dinoflagellate); DIA = diatom; RA = raphidophyte

Predator	PDV[a]	Prey	PYV	μ_{max}	I_{max}	C_{max}	SC_{max}	GGE_{max}	SS_{max}	Source
G. dominans	2	*Prorocentrum minimum* (DN)	1.1	1.13	1.2	0.9	15.3	41	2.5	This study
G. dominans	4	*Thalassiosira* sp. (DIA)	0.1	0.73						Nakamura et al. (1995)
G. dominans	4	*Heterocapsa triquetra* (DN)	1.9	0.54	2.3		5.3			Nakamura et al. (1995)
G. dominans	30	*Chattonella antiqua* (RA)	20.0	0.50	2.3					Nakamura et al. (1992)
G. spirale	12	*Heterocapsa triquetra* (DN)	2.1	1.08	7.5[b]	0.5	0.3	36		Hansen (1992)
G. spirale	17	*Prorocentrum minimum* (DN)	1.1	0.79	13.6	5.3	6.5	17	1.2	This study

[a]Maximum volume
[b]Maximum value among the ingestion rates measured at the given prey concentration

Table 4. Comparison of growth, ingestion and clearance rates of *Gyrodinium* spp. and other protists on *Prorocentrum minimum*. Rates are corrected to 20°C using Q_{10} = 2.8 (Hansen et al. 1997). NC = naked ciliate; TC = tintinnid ciliate; HTD = heterotrophic dinoflagellate; other definitions as in Table 3

Predator	PDV	μ_{max}	I_{max}	C_{max}	Source
Gyrodinium dominans (HTD)	2	1.13	1.2	0.9	This study
Gyrodinium spirale (HTD)	17	0.79	13.6	5.3	This study
Tiarina fusus (NC)	25	−0.006[a]	2.0	0.2	Jeong et al. (2002)
Polykrikos kofoidii (HTD)	43	−0.03			Jeong et al. (2001)
Favella taraikaensis (TC)	401		233	19.7	Taniguchi & Kawakami (1985)
Strombidinopsis sp. (NC)	560	1.17	296	122	Jeong et al. (1999)

[a]This rate is obtained at 19°C without being corrected to 20°C because it is negative

rate of *G. spirale* on *P. minimum* (13.6 ng C grazer^{-1} d^{-1}) was higher than that on *Heterocapsa triquetra* (Hansen 1992). Unlike the maximum growth rate, the smaller strain of *G. dominans* or *G. spirale* has a lower maximum ingestion rate than the larger strain.

The maximum clearance rate of *Gyrodinium spirale* on *Prorocentrum minimum* (5.3 µl grazer^{-1} h^{-1}) was much higher than that on *Heterocapsa triquetra* (Table 3). *G. spirale* might capture and ingest *P. minimum* more efficiently at low prey concentration than *H. triquetra*. The maximum clearance rate of *G. dominans* on *P. minimum* (0.9 µl grazer^{-1} h^{-1}) was 5.9 times lower than that of *G. spirale*, while the cell volume of *G. dominans* used in the present study (ca. 600 µm^3), where the maximum volume-specific clearance rate was obtained, was 13.5 times smaller than that of *G. spirale* (8100 µm^3). The maximum swimming speed of *G. dominans* used in the present study (2.5 mm s^{-1}) was 2.1 times higher than that of *G. spirale* (1.2 mm s^{-1}). Therefore, the high swimming speed of *G. dominans* may increase the encounter rate between this grazer and *P. minimum* cells and thus enable the grazer to ingest a prey cell at a low prey concentration.

The maximum growth rate of *Gyrodinium dominans* on *Prorocentrum minimum* was comparable to that of *Strombidinopsis* sp. (1.17 d^{-1}), but higher than that of *Tiarina fusus* or *Polykrikos kofoidii* on the same prey at the same temperature (Table 4). The maximum ingestion rate of *G. spirale* was much lower than that of *Strombidinopsis* sp. or *Favella taraikaensis* on the same prey, but much higher than *T. fusus*. Whereas *P. kofoidii*, *Protoperidinium divergens*, *Protoperidinium crassipes*, and *Oblea rotunda*, which have no positive growth on *P. minimum*, use tow filaments to anchor and subsequently engulfment or a pallium to envelop the prey cells, *G. dominans*, *G. spirale*, *Strombidinopsis* sp., and *F. taraikensis*, which have positive growth on *P. minimum*, directly engulf the prey cells. Direct engulfment may be a more efficient or low-energy-cost feeding mechanism for capturing small and flattened in shape *P. minimum* cells than deploying tow filaments.

Grazing impact

Grazing coefficients attributable to *Gyrodinium dominans* on co-occurring *Prorocentrum minimum* in

the coastal waters off Kwangyang and Masan obtained in the present study were 0 to 0.066 h^{-1} (i.e. up to 6.4 % of *P. minimum* populations were removed by a *G. dominans* population in 1 h), while those for *G. spirale* were 0 to 0.231 h^{-1} (i.e. 39 % of *P. minimum* populations were removed by a *G. spirale* population in 1 h) (Table 2). The maximum grazing coefficient attributable to *G. dominans* plus *G. spirale* on *P. minimum* in the present study (0.296 h^{-1}) was higher than that for the microzooplanktonic grazers on the same prey, measured in Chesapeake Bay, USA (ca. 0.17 h^{-1}) (Johnson et al. 2003). Grazing coefficients attributable to *G. dominans* plus *G. spirale* at the *P. minimum* concentrations of 60 to 300 cells ml^{-1} (0.027 to 0.296 h^{-1}) were much higher than those at the lower or higher *P. minimum* concentration (0 to 0.01 h^{-1}). In particular, grazing coefficients attributable to *G. dominans* plus *G. spirale* on *P. minimum* during the red tides dominated by the prey were 0.002 h^{-1} or 0.04 d^{-1} (i.e. 4 % of *P. minimum* populations were removed by populations of *G. dominans* plus *G. spirale* in 1 d). Therefore, the populations of *G. dominans* and *G. spirale* may have considerable grazing impact on *P. minimum* at the developing or declining stages of red tides dominated by *P. minimum*, but small grazing impact at the fully developed stage of the red tides. Grazing coefficients attributable to *Acartia* spp. on *P. minimum* were 0 to 0.001 h^{-1} or 0 to 0.02 d^{-1} (i.e. up to only 2.4 % of *P. minimum* populations were removed by *Acartia* spp. populations in 1 d). The results of the present study suggest that *Gyrodinium* spp. may sometimes be much more effective grazers on *P. minimum* than *Acartia* spp.

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