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NOTE

Feeding by the marine planktonic ciliate *Strombidinopsis jeokjo* on common heterotrophic dinoflagellates

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ABSTRACT: To investigate the interactions between the ciliate *Strombidinopsis jeokjo* and the heterotrophic dinoflagellates *Gyrodinium dominans* and *Oxyrrhis marina*, we measured the growth and ingestion rates of *S. jeokjo* (mean length and width of fixed specimens = 149 × 70 µm, n = 30) when feeding on each of the heterotrophic dinoflagellates, and calculated grazing coefficients by combining field data on abundances of large *Strombidinopsis* spp. (>100 µm in length) and co-occurring heterotrophic dinoflagellates with laboratory data on ingestion rates obtained in the present study. The specific growth rates of *S. jeokjo* when feeding on *G. dominans* and *O. marina* increased rapidly with increasing prey concentration (ca. <300 ng C ml^{-1}), but were saturated or slightly increasing at higher concentrations. The maximum specific growth rate of *S. jeokjo* feeding on *G. dominans* (0.54 d^{-1}) was similar to that when fed on *O. marina* (0.59 d^{-1}). Threshold prey concentrations (where net growth = 0) were 79 ng C ml^{-1} for *G. dominans* and 36 ng C ml^{-1} for *O. marina*. The maximum ingestion and clearance rates of *S. jeokjo* feeding on *G. dominans* (108 ng C grazer^{-1} d^{-1} and 14.5 µl grazer^{-1} h^{-1}, respectively) were comparable to those when fed on *O. marina* (87 ng C grazer^{-1} d^{-1} and 13.4 µl grazer^{-1} h^{-1}, respectively). Calculated grazing coefficients for large *Strombidinopsis* spp. feeding on *G. dominans* and *O. marina* were 0.01 to 0.39 h^{-1} (i.e. 1 to 33% of *G. dominans* populations were removed by *Strombidinopsis* spp. populations in 1 h) and 0.002 to 0.004 h^{-1} (i.e. 0.2 to 0.4% of *O. marina* populations were removed), respectively. The results of the present study suggest that *Strombidinopsis* spp. can sometimes have a considerable grazing impact on populations of *G. dominans* and *O. marina*.

KEY WORDS: Feeding · Food web · *Gyrodinium* · Ingestion · *Oxyrrhis* · Plankton · Protist

INTRODUCTION

Ciliates and heterotrophic dinoflagellates are often abundant and ubiquitous protists in marine environments and play diverse ecological roles in the marine planktonic community (Stoecker et al. 1984, Hansen 1991b, Lessard 1991, Strom & Buskey 1993, Jeong 1994, 1999, Jeong & Latz 1994, Jeong et al. 1999, 2001, 2002, Tillmann 2004); they prey on a wide variety of organisms, including phytoplankton and copepod eggs and early naupliar stages. They are, in turn, important prey for some metazoans and larval fish (e.g. Stoecker & Govoni 1984). Ciliates and heterotrophic dinoflagellates may have several ecologically important interactions because they are often abundant simultaneously (e.g. Jeong 1995, Johnson et al. 2003) and are believed to compete with each other for common prey. If one component is able to feed on the other, the former can

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severely affect the population dynamics of the latter, and vice versa. However, there have been few studies on the predator–prey relationship between ciliates and heterotrophic dinoflagellates (Hansen 1991a), and no studies have been conducted on the growth and grazing rates and grazing impact of the predator on prey as a function of prey concentration.

The naked ciliates *Strombidinopsis* spp. and the heterotrophic dinoflagellates *Gyrodinium dominans* and *Oxyrrhis marina* are often abundant and ubiquitous protists and are known to grow well on diverse red-tide dinoflagellates (Nakamura et al. 1995, Jeong et al. 1999, Kim & Jeong 2004). They often dominate the abundance of heterotrophic protists during red tides and are thus believed to have a considerable grazing impact on the populations of red-tide organisms (Nakamura et al. 1992, 1995, Johnson et al. 2003). However, the total grazing impact caused by ciliates and heterotrophic dinoflagellates may be reduced if ciliates feed on heterotrophic dinoflagellates or vice versa.

To understand the interactions between ciliates and heterotrophic dinoflagellates, we established a monoclonal culture of *Strombidinopsis jeokjo* (Jeong et al. 2004), *Gyrodinium dominans*, and *Oxyrrhis marina*, and conducted experiments to examine the numerical and functional responses of the ciliate when fed on the heterotrophic dinoflagellates. We also estimated grazing coefficients attributable to large *Strombidinopsis* spp. (>100 µm in length) feeding on the heterotrophic dinoflagellates by combining field data on abundances of the predator and co-occurring prey with laboratory data on ingestion rates obtained in the present study.

The maximum growth and grazing rates of *Strombidinopsis jeokjo* feeding on *Gyrodinium dominans* and *Oxyrrhis marina* are compared to those when fed on red-tide dinoflagellates. The results of the present study provide a basis for understanding the potential of large ciliates to influence the population dynamics of heterotrophic dinoflagellates.

MATERIALS AND METHODS

Preparation of experimental organisms. For the isolation and culture of *Strombidinopsis jeokjo*, plankton samples (collected with a 40 cm diameter, 25 µm mesh plankton net) were taken from the mouth of the Mankyeong Estuary, Kunsan, Korea, during October 2003, when the water temperature and salinity were 18.4°C and 30.3 psu, respectively. The samples were gently screened through a 202 µm Nitex mesh and placed in 1 l polycarbonate (PC) bottles. *Prorocentrum micans* (ca. 5000 cells ml^{-1}) and 50 ml of f/2 media were added as food. The bottles were placed on plankton wheels rotating at 0.9 rpm and incubated at 20°C under continuous illumination of 20 µE m^{-2} s^{-1} of cool white fluorescent light. After 2 d, aliquots of the enriched water were transferred to 6-well tissue culture plates and a monoclonal culture was established by 2 serial single-cell isolations. Once dense cultures of *S. jeokjo* (mean length and width of fixed specimens = 149 × 70 µm, n = 30) were obtained, they were transferred to 500 ml PC bottles containing fresh *P. micans* (ca. 4500 to 5500 cells ml^{-1}) every 2 or 3 d.

For the isolation and culture of *Gyrodinium dominans*, 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 on 6-well tissue culture plates and a monoclonal culture of *G. dominans* was established by 2 serial single-cell isolations. As the concentration of *G. dominans* feeding on *Prorocentrum minimum* increased, the grazers were subsequently transferred to 32, 270, and 500 ml PC bottles of 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 under continuous illumination of 10 µE m^{-2} s^{-1} of cool white fluorescent light on a 12:12 h light:dark cycle. Once dense cultures of *G. dominans* were obtained, they were transferred to 500 ml PC bottles containing fresh prey every 2 d.

For the isolation and culture of *Oxyrrhis marina*, plankton samples (collected with a 25 cm diameter, 25 µm mesh plankton net) were taken from the mouth of the Keum Estuary, Kunsan, Korea, during May 2001, when the water temperature and salinity were 16°C and 27.7 psu, respectively. The samples were screened gently through a 154 µm Nitex mesh and placed in 1 l PC bottles. *Amphidinium carterae* (ca. 8000 cells ml^{-1}) and 50 ml of f/2 media were added as food. The bottles were placed on plankton wheels rotating at 0.9 rpm and incubated at 20°C under continuous illumination of 20 µE m^{-2} s^{-1} of cool white fluorescent light. After 2 d, aliquots of the enriched water were transferred to 6-well tissue culture plates and a monoclonal culture was established by 2 serial single-cell isolations. Once dense cultures of *O. marina* were obtained, they were transferred to 500 or 1000 ml PC bottles containing fresh *Heterosigma akashiwo* prey (ca. 15000 cells ml^{-1}) every 2 or 3 d.

Growth and ingestion rates. These experiments were designed to measure the growth, ingestion, and clearance rates of *Strombidinopsis jeokjo*, as a function of prey concentration, when feeding on each of *Gyrodinium dominans* and *Oxyrrhis marina*.

One day before the experiments were conducted, dense cultures of *Strombidinopsis jeokjo* grazing on *Prorocentrum micans* were transferred into a 1 l PC

bottle containing a low concentration of *P. micans* (ca. 200 cells ml^{-1}). This was done to make the growth rate of *S. jeokjo* almost zero at the end of this pre-incubation. The bottle was filled to capacity with filtered seawater and placed on a rotating wheel to incubate as above. When prey cells were undetectable, the abundance of *S. jeokjo* was determined by enumerating cells in three 1 ml Sedgwick-Rafter counting chambers (SRCs).

One day before the experiments were conducted, a dense culture of *Gyrodinium dominans* grazing on *Prorocentrum minimum* (or that of *Oxyrrhis marina* grazing on *Heterosigma akashiwo*) was transferred into a 1 l PC bottle containing a low concentration of the prey (ca. 500 cells ml^{-1} for each prey species). The bottle was filled to capacity with filtered seawater and placed on a rotating wheel to incubate as above. When prey cells were undetectable, the abundance of *G. dominans* (or *O. marina*) was determined by enumerating cells in three 1 ml SRCs.

The initial concentrations of *Strombidinopsis jeokjo* and target heterotrophic dinoflagellate prey were established using an autopipette to deliver predetermined volumes of known cell concentrations to the bottles. Triplicate 270 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 *S. jeokjo* were also established at 1 predator concentration. Thirty ml of f/2 medium was 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 6, 12, 18, 24 h incubation, a 10 ml aliquot for *S. jeokjo* was removed from each bottle and fixed with 5% Lugol's solution, and all predator cells and all or >200 prey cells in five 1 ml SRCs were enumerated. The ranges of the actual prey (and predator) concentrations for the *Gyrodinium dominans* and *Oxyrrhis marina* experiments were 47 to 7134 (2.3 to 6.0) and 44 to 8987 cells ml^{-1} (1.7 to 5.1 cells ml^{-1}), respectively. Prior to taking subsamples, the condition of *S. jeokjo* 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.

Cell length and maximum width of *Gyrodinium dominans* and *Oxyrrhis marina* preserved in 5% acid Lugol's solution after 18 h incubation were measured using a compound or inverted microscope. The shape of the heterotrophic dinoflagellates was estimated as 2 cones joined at the cell equator (=maximum width of the cell). Cell volumes of both preserved heterotrophic dinoflagellates were calculated according to the equation: volume = $1/3 \times [\pi(\text{cell width}/2)^2] \times (\text{cell length})$. The carbon content for *G. dominans* and *O. marina* (0.15 ng C per cell for both species) was estimated from cell volume according to Menden-Deuer & Lessard (2000).

The specific growth rate (μ, d^{-1}) of *Strombidinopsis jeokjo* was calculated by averaging the instantaneous growth rates (IGR) for each sampling interval, calculated as:

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

where S_{t_1} and S_{t_2} = the concentration of *S. jeokjo* at consecutive samplings. The final t_2 for calculation was 18 h, which provided high specific growth rates. After 18 h prey concentrations had already been largely reduced.

Data for the *Strombidinopsis jeokjo* growth rate were fitted to a Michaelis-Menten equation:

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

where μ_{max} = the maximum growth rate (d^{-1}); x = prey concentration (cells ml^{-1} or ng C ml^{-1}), x' = threshold prey concentration (the prey concentration where $\mu = 0$), and K_{GR} = 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). The incubation time for calculating ingestion and clearance rates was the same as for estimating the growth rate. Ingestion rate (IR) data for *Strombidinopsis jeokjo* were fitted to a Michaelis-Menten equation:

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

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

Grazing impact. We estimated grazing coefficients attributable to large *Strombidinopsis* spp. (>100 µm in length) feeding on each of *Gyrodinium dominans* and *Oxyrrhis marina*, by combining field data on abundances of *Strombidinopsis* spp. and the prey with ingestion rates of the predator on the prey obtained in the present study (see Table 1). The data on the abundances of large *Strombidinopsis* spp. (>100 µm in length) and co-occurring *G. dominans* and *O. marina* used in this estimation were obtained from water samples collected from the coastal waters off Koheung (in 1997), Saemankeum (in 1999–2000), 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 *Strombidinopsis* spp. populations 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 *Strombidinopsis* spp. feeding on a heterotrophic dinoflagellate in 1 ml of seawater (prey eaten ml^{-1} h^{-1}), IR is the ingestion rate (prey eaten $grazer^{-1}$ h^{-1}) of *Strombidinopsis* spp. feeding on heterotrophic dinoflagellate prey, and G is the abundance (grazers ml^{-1}) of *Strombidinopsis* spp. at the same time as C_i.

RESULTS

Growth rates

Strombidinopsis jeokjo grazed on *Gyrodinium dominans* and *Oxyrrhis marina*. The specific growth rates of *S. jeokjo* feeding on *G. dominans* and *O. marina* increased rapidly with increasing prey concentration ca. <300 ng C ml^{-1}, respectively, but were saturated or slightly increasing at higher concentrations (Figs. 1 & 2). When the data were fitted to Eq. (2), the maximum specific growth rates (μ_{max}) of *G. dominans* and *O. marina* were 0.54 and 0.59 d^{-1}, respectively. Threshold prey concentrations (where net growth = 0) were 79 ng C ml^{-1} for *G. dominans* and 36 ng C ml^{-1} for *O. marina*.

Ingestion and clearance rates

The ingestion rates of *Strombidinopsis jeokjo* feeding on *Gyrodinium dominans* and *Oxyrrhis marina* increased continuously with increasing mean prey concentration (Figs. 3 & 4). When the data were fitted to Eq. (3), the maximum ingestion rates of *S. jeokjo* feeding on *G. dominans* and *O. marina* were 108 ng C $grazer^{-1}$ d^{-1} (720 prey cells $grazer^{-1}$ d^{-1}) and 87 ng C $grazer^{-1}$ d^{-1} (580 prey cells $grazer^{-1}$ d^{-1}), respectively.

The maximum clearance rates of *Strombidinopsis jeokjo* feeding on *Gyrodinium dominans* and *Oxyrrhis marina* were 14.5 and 13.4 µl $grazer^{-1}$ h^{-1}, respectively.

Grazing impact

Grazing coefficients attributable to large *Strombidinopsis* spp. (>100 µm in length) feeding on co-occurring *G. dominans* and *O. marina* in the coastal waters

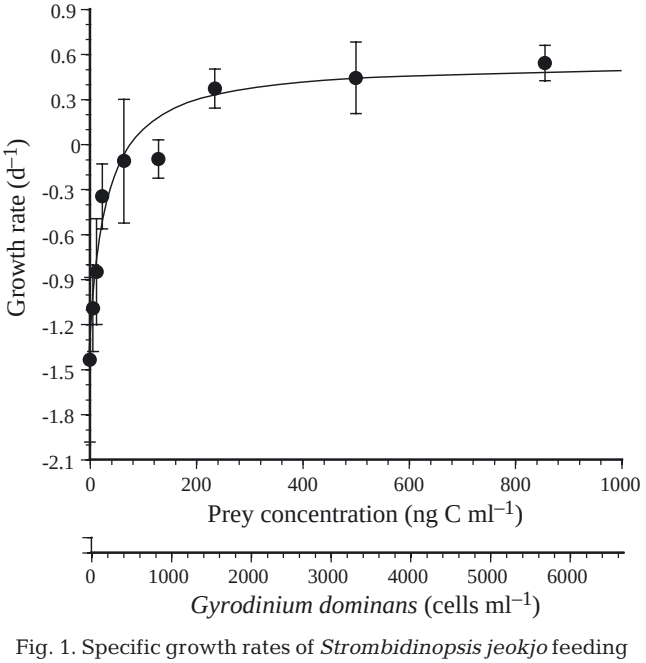

Fig. 1. Specific growth rates of *Strombidinopsis jeokjo* feeding on *Gyrodinium dominans* as a function of mean prey concentration (x). Symbols represent treatment means ± 1 SE. Curves are fitted by a Michaelis-Menten equation (Eq. 2) using all treatments in the experiment. Growth rate (d^{-1}) = $0.544\ \{(x - 79)/[109 + (x - 79)]\}$, $r^2 = 0.659$

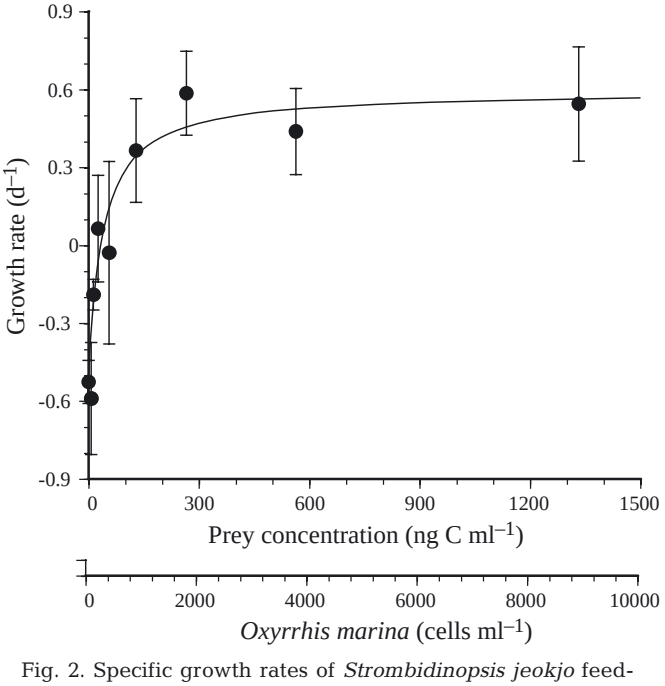

Fig. 2. Specific growth rates of *Strombidinopsis jeokjo* feeding on *Oxyrrhis marina* as a function of mean prey concentration (x). Symbols represent treatment means ± 1 SE. Curves are fitted by a Michaelis-Menten equation (Eq. 2) using all treatments in the experiment. Growth rate (d^{-1}) = $0.592\ \{(x - 36)/[72 + (x - 36)]\}$, $r^2 = 0.628$

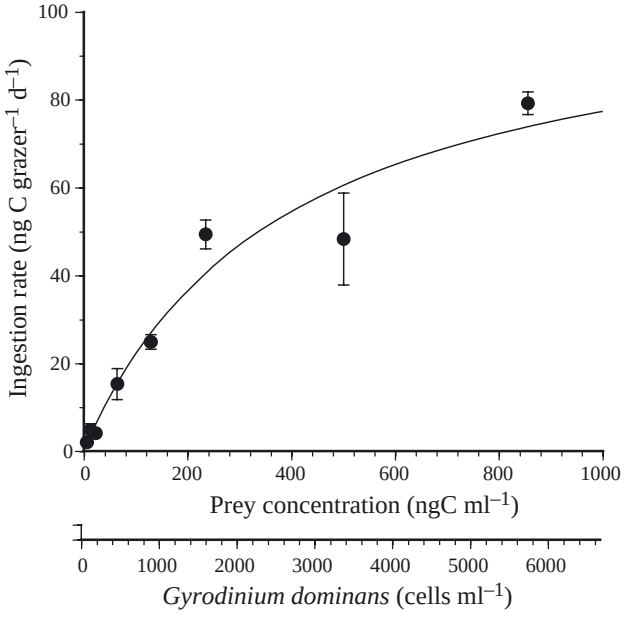

Fig. 3. Ingestion rates of *Strombidinopsis jeokjo* feeding on *Gyrodinium dominans* as a function of mean prey concentration (x). Symbols represent treatment means ± 1 SE. Curves are fitted by a Michaelis-Menten equation (Eq. 3) using all treatments in the experiment. Ingestion rate (ng C grazer^{-1} d^{-1}) = 108 [x/(393 + x)], r^2 = 0.903

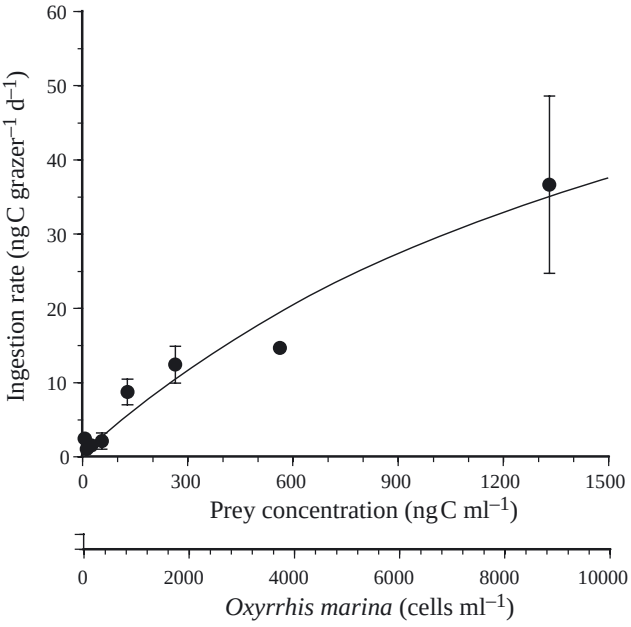

Fig. 4. Ingestion rates of *Strombidinopsis jeokjo* feeding on *Oxyrrhis marina* as a function of mean prey concentration (x). Symbols represent treatment means ± 1 SE. Curves are fitted by a Michaelis-Menten equation (Eq. 3) using all treatments in the experiment. Ingestion rate (ng C grazer^{-1} d^{-1}) = 87 [x/(1970 + x)], r^2 = 0.720

off Koheung, Saemankeum, and Masan, Korea, were 0.01 to 0.39 h^{-1} (i.e. 1 to 33% of *G. dominans* populations were removed by *Strombidinopsis* spp. populations in 1 h) and 0.002 to 0.004 h^{-1} (i.e. 0.2 to 0.4% of *O. marina* populations were removed), respectively (Table 1).

DISCUSSION

Interactions between ciliates and heterotrophic dinoflagellates

The results of the present study show that the ciliate *Strombidinopsis jeokjo* is able to graze on the common heterotrophic dinoflagellates *Gyrodinium dominans* and *Oxyrrhis marina*. Before the present study, there had been no studies on the feeding by ciliates on heterotrophic dinoflagellates, while there exist several studies on the feeding by mixotrophic or heterotrophic dinoflagellates on ciliates; the mixotrophic dinoflagellate *Gyrodinium instriatum* fed on the tintinnid ciliates *Favella azorica* and *Eutintinnus tubulosus* (Uchida et al. 1997); the mixotrophic dinoflagellate *Akashiwo sanguinea* (previously *Gymnodinium sanguineum*) fed on the naked ciliate *Strobilidium* (Bockstahler & Coats 1993); the heterotrophic dinoflagellate *Dinophysis* sp. fed on the ciliate *Tiarina fusus* (Hansen 1991a).

Table 1. Estimation of grazing impact by large *Strombidinopsis* spp. (>100 µm in length) populations feeding on (A) *Gyrodinium dominans* and (B) *Oxyrrhis marina* populations using the equations in Figs. 3 & 4. Abundances of co-occurring large *Strombidinopsis* spp., *G. dominans*, and *O. marina* obtained from water samples collected off Koheung (in 1997), Saemankeum (in 1999–2000), and Masan (in 2003). SIR: population ingestion rate of *Strombidinopsis* spp.; S_g: grazing coefficient of *Strombidinopsis* spp.

Prey conc. (cells ml^{-1})	Predator conc. (cells ml^{-1})	SIR (prey ml^{-1} h^{-1})	S_g (h^{-1})
(A) *G. dominans* prey			
3.0	2.0	0.1	0.023
3.1	1.6	0.1	0.018
4.2	2.1	0.1	0.024
6.3	2.1	0.1	0.024
8.3	2.8	0.3	0.032
10.0	2.0	0.2	0.023
14.3	28.6	4.7	0.394
16.7	5.0	1.0	0.059
19.4	5.6	1.2	0.065
22.2	13.9	3.5	0.172
35.4	2.1	0.8	0.024
(B) *O. marina* prey			
0.5	1.4	0.001	0.003
138.0	1.0	0.25	0.002
209.0	2.0	0.76	0.004

Growth and ingestion

The maximum specific growth rates of *Strombidinopsis jeokjo* feeding on *Gyrodinium dominans* (0.54 d^{-1}) or *Oxyrrhis marina* (0.59) were lower than that when fed on the red-tide dinoflagellates *Cochlodinium polykrikoides* (1.38 d^{-1}), *Akashiwo sanguinea* (1.27), *Prorocentrum minimum* (1.06), *Lingulodinium polyedrum* (0.83), or *Scrippsiella trochoidea* (0.67) (Jeong et al. 1999). Heterotrophic dinoflagellates may sometimes comprise important prey for the growth of large *Strombidinopsis* species, particularly when heterotrophic dinoflagellates become abundant after greatly reducing the populations of the red-tide dinoflagellates.

Ingestion and clearance rates

The maximum ingestion rates of *Strombidinopsis jeokjo* feeding on *Gyrodinium dominans* (106 ng C $grazer^{-1}$ d^{-1}) and *Oxyrrhis marina* (87 ng C $grazer^{-1}$ d^{-1}) were considerably lower than those when fed on the red-tide dinoflagellates *Cochlodinium polykrikoides*, *Akashiwo sanguinea*, *Prorocentrum minimum*, *Lingulodinium polyedrum*, and *Scrippsiella trochoidea* (207 to 353 ng C $grazer^{-1}$ d^{-1}) (Jeong et al. 1999). Therefore, *S. jeokjo* may gain more energy from the red-tide dinoflagellates than from the heterotrophic dinoflagellates if both dinoflagellate prey varieties are abundant and there is no prey selection by *S. jeokjo* between the red-tide dinoflagellates and the heterotrophic dinoflagellates.

The ratios of the maximum growth rates relative to the maximum ingestion rates (RGIs) of *Strombidinopsis jeokjo* feeding on *Gyrodinium dominans* and *Oxyrrhis marina* were clearly higher than those when fed on the red-tide dinoflagellates (Fig. 5); the ratios of the RGIs of *S. jeokjo* feeding on *G. dominans* and *O. marina* to the RGI values interpolated using the equation of linear regression for the maximum growth rates of *S. jeokjo* feeding on the red-tide dinoflagellates as a function of the maximum ingestion rates were 1.8 and 2.8, respectively. Therefore, the food quality of the heterotrophic dinoflagellates as prey for the predator might be considerably higher than that of the red-tide dinoflagellates.

Grazing impact

Grazing coefficients attributable to large *Strombidinopsis* spp. (>100 µm in length) feeding on co-occurring *Gyrodinium dominans* and *Oxyrrhis marina* in the coastal waters off Koheung, Saemankeum, and Masan, Korea, were 0.01 to 0.39 h^{-1} (i.e. 1 to 33% of *G. dominans* populations were removed by *Strombidinopsis* spp. populations in 1 h) and 0.002 to 0.004 h^{-1} (i.e. 0.2 to 0.4% of *O. marina* populations were removed in 1 h), respectively (Table 1). Therefore, the populations of *Strombidinopsis* spp. may have a considerable grazing impact on *G. dominans*.

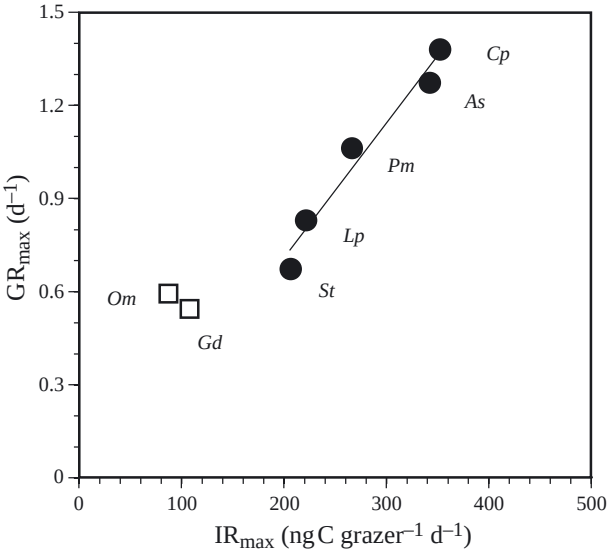

Fig. 5. Maximum growth rates (GR_{max}, d^{-1}) of *Strombidinopsis jeokjo* feeding on the heterotrophic dinoflagellates *Gyrodinium dominans* and *Oxyrrhis marina* (open squares) and 5 red-tide dinoflagellate species (solid circles) as a function of maximum ingestion rates (IR_{max}, ng C $grazer^{-1}$ d^{-1}). The equation of linear regression for 5 red-tide dinoflagellate prey was $GR_{max} = 0.0043(IR_{max}) - 0.16$, $r^2 = 0.97$. *Cp*: *Cochlodinium polykrikoides*, *As*: *Akashiwo sanguinea*, *Pm*: *Prorocentrum minimum*, *Lp*: *Lingulodinium polyedrum*, *St*: *Scrippsiella trochoidea*, *Gd*: *Gyrodinium dominans*, *Om*: *Oxyrrhis marina*

Ecological importance

The present study reports a new predator–prey relationship between ciliates and heterotrophic dinoflagellates. This predation may be important in planktonic communities in the following ways: (1) ciliates can survive at low phytoplankton prey concentration by feeding on heterotrophic dinoflagellates; however, in contrast, populations of the heterotrophic dinoflagellates may decrease rapidly due to predation by the ciliates. (2) An additional pathway between ciliates and heterotrophic dinoflagellates is found. (3) The grazing impact caused by heterotrophic dinoflagellate populations feeding on red-tide dinoflagellate prey can be reduced if ciliates co-occur.

In a preliminary test, we found that *Strombidinopsis jeokjo* also engulfed another heterotrophic dinoflagel-

late, *Polykrikos kofoidii*, even though the dinoflagellate did not support the growth of the ciliate. Feeding by large ciliates on heterotrophic dinoflagellates may commonly occur in marine ecosystems because there are numerous ciliates and heterotrophic dinoflagellates species and they are often abundant simultaneously. To better understand food webs in the marine planktonic community, new predator–prey relationships between other ciliates and heterotrophic dinoflagellates should be explored.

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