

## Feeding by Phototrophic Red-Tide Dinoflagellates on the Ubiquitous Marine Diatom *Skeletonema costatum*

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**ABSTRACT.** We investigated feeding by phototrophic red-tide dinoflagellates on the ubiquitous diatom *Skeletonema costatum* to explore whether dinoflagellates are able to feed on *S. costatum*, inside the protoplasm of target dinoflagellate cells observed under compound microscope, confocal microscope, epifluorescence microscope, and transmission electron microscope (TEM) after adding living and fluorescently labeled *S. costatum* (FLSc). To explore effects of dinoflagellate predator size on ingestion rates of *S. costatum*, we measured ingestion rates of seven dinoflagellates at a single prey concentration. In addition, we measured ingestion rates of the common phototrophic dinoflagellates *Prorocentrum micans* and *Gonyaulax polygramma* on *S. costatum* as a function of prey concentration. We calculated grazing coefficients by combining field data on abundances of *P. micans* and *G. polygramma* on co-occurring *S. costatum* with laboratory data on ingestion rates obtained in the present study. All phototrophic dinoflagellate predators tested (i.e. *Akashiwo sanguinea*, *Amphidinium carterae*, *Alexandrium catenella*, *Alexandrium tamarense*, *Cochlodinium polykrikoides*, *G. polygramma*, *Gymnodinium catenatum*, *Gymnodinium impudicum*, *Heterocapsa rotundata*, *Heterocapsa triquetra*, *Lingulodinium polyedrum*, *Prorocentrum donghaiense*, *P. micans*, *Prorocentrum minimum*, *Prorocentrum triestinum*, and *Scrippsiella trochoidea*) were able to ingest *S. costatum*. When mean prey concentrations were 170–260 ng C/ml (i.e. 6,500–10,000 cells/ml), the ingestion rates of *G. polygramma*, *H. rotundata*, *H. triquetra*, *L. polyedrum*, *P. donghaiense*, *P. micans*, and *P. triestinum* on *S. costatum* (0.007–0.081 ng C/dinoflagellate/d [0.2–3.0 cells/dinoflagellate/d]) were positively correlated with predator size. With increasing mean prey concentration of ca 1–3,440 ng C/ml (40–132,200 cells/ml), the ingestion rates of *P. micans* and *G. polygramma* on *S. costatum* continuously increased. At the given prey concentrations, the maximum ingestion rates of *P. micans* and *G. polygramma* on *S. costatum* (0.344–0.345 ng C/grazer/d; 13 cells/grazer/d) were almost the same. The maximum clearance rates of *P. micans* and *G. polygramma* on *S. costatum* were 0.165 and 0.020 µl/grazer/h, respectively. The calculated grazing coefficients of *P. micans* and *G. polygramma* on co-occurring *S. costatum* were up to 0.100 and 0.222 h, respectively (i.e. up to 10% and 20% of *S. costatum* populations were removed by *P. micans* and *G. polygramma* populations in 1 h, respectively). Our results suggest that *P. micans* and *G. polygramma* sometimes have a considerable grazing impact on populations of *S. costatum*.

**Key Words.** Grazing, harmful algal bloom, ingestion, mixotroph, protist.

**D**IATOMS and phototrophic dinoflagellates are two major components of marine net-phytoplankton in most marine environments and they often co-occur (Allen 1949). For a long time, the primary interaction between diatoms and phototrophic dinoflagellates has been thought to be a competition for nutrients. In general, the half-saturation constants ( $K_s$ ) for nitrogen and phosphate uptake by diatoms are lower than those of phototrophic dinoflagellates (Smayda 1997). The phototrophic growth rates of diatoms are usually higher than those of phototrophic dinoflagellates when their sizes are similar (Banse 1982). Usually a bloom dominated by diatoms occurs first, and then one dominated by phototrophic dinoflagellates follows (Bianchi et al. 2002; Gilbert 2001; Trigueros and Orive 2001). The lower  $K_s$  for nitrogen and phosphate uptake and higher growth rates may enable the diatoms to outcompete phototrophic dinoflagellates, explaining why they bloom first when nutrient concentrations increase. Slow-growing phototrophic dinoflagellates have been thought to form a subsequent bloom using nutrients released from dead diatoms. However, if co-occurring phototrophic dinoflagellates are able to feed on the dominant diatoms and also have a considerable grazing impact on diatom populations, in particular at the decline stage of the diatom bloom, then grazing by phototrophic dinoflagellates on diatoms may be one of the driving forces for, or at least accelerate, the succession of diatom blooms by phototrophic dinoflagellate

blooms, even when a large amount of nutrients are not released from diatoms.

Phototrophic dinoflagellates often form red tides (Eppley and Harrison 1975; Jeong 1995). Many phototrophic red-tide dinoflagellates are now considered to be mixotrophic (i.e. capable of both photosynthesis and ingesting prey) (Bockstahler and Coats 1993a, b; Burkholder, Glibert, and Skelton 2008; Chang and Carpenter 1994; Granéli et al. 1997; Jacobson and Anderson 1996; Jeong et al. 1997, 1999, 2004c, 2005a, b, c; Legrand, Granéli, and Carlsson 1998; Seong et al. 2006; Skovgaard 1996; Smalley, Coats, and Adam 1999; Stoecker 1999; Stoecker et al. 1997). Indeed, Jeong et al. (2005a) suggested that most phototrophic dinoflagellates may be mixotrophic. There is a high possibility that most phototrophic dinoflagellates feed on co-occurring diatoms because they usually co-exist. However, there have been a few studies reporting feeding by phototrophic dinoflagellates on diatoms. Legrand, Granéli, and Carlsson (1998) reported that the phototrophic red-tide dinoflagellate *Heterocapsa triquetra* was able to ingest the diatom *Thalassiosira pseudonana* in nutrient-depleted cultures, but it did not ingest the diatom in nutrient-replete cultures. Also, the ingestion rate of *H. triquetra* on *T. pseudonana* obtained in their study was very low (0.09 cells/dinoflagellate/d) and no dividing cells were observed. Bockstahler and Coats (1993a) observed small diatom frustules inside the protoplasm of the phototrophic dinoflagellate *Akashiwo sanguinea* in natural water samples. However, there have been no studies on the kinds of phototrophic red-tide dinoflagellate species that are able to ingest diatoms (except *H. triquetra* and *A. sanguinea*), their feeding behavior, the numerical and functional responses of phototrophic red-tide dinoflagellates to diatoms, and the grazing

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impact by dinoflagellates on the populations of diatoms. Thus the interactions between phototrophic red-tide dinoflagellates and diatoms, with respect to predator–prey relationships remain poorly understood.

*Skeletonema costatum* is a ubiquitous diatom and often dominates the abundance and/or biomass of diatoms and total phytoplankton in the coastal waters due to its very high maximum growth rates of three to four divisions per day (Balkis 2003; Durbin and Durbin 1981; Marshall and Ranasinghe 1989; Pratt 1965; Ramaiah and Furuya 2002; Reid, Lange, and White 1985). So far, heterotrophic protists (Hansen 1992; Jeong et al. 2004b) and copepods (Conover 1956; Deason 1980; Martin 1965; Paffenhöfer 1976) have been known to be two major grazers on *S. costatum* in marine plankton communities. Recently we have found that many phototrophic dinoflagellate species were able to actively ingest *S. costatum*. However, the feeding by phototrophic dinoflagellates on *S. costatum* has not been investigated at all yet even though they usually co-exist (>95% among our unpublished data,  $n > 1,000$ ). Therefore, to understand the population dynamics of *S. costatum* and phototrophic red-tide dinoflagellates and the total grazing pressure exerted by grazers on *S. costatum*, we investigated feeding by phototrophic dinoflagellates on *S. costatum* and the grazing impact by co-occurring phototrophic dinoflagellates on *S. costatum*.

## MATERIALS AND METHODS

**Preparation of experimental organisms.** *Skeletonema costatum* were grown at 20 °C in enriched f/2 seawater media (Guillard and Ryther 1962) under a 14:10 h light–dark cycle of 20  $\mu\text{E}/\text{m}^2/\text{s}$  of cool white fluorescent light, while phototrophic-dinoflagellate predators were grown in enriched f/2 seawater media without silicate. Phototrophic dinoflagellate cultures in their exponential growth phase and diatom cultures in their lag phase, were used for feeding experiments. The carbon content for *S. costatum* (0.026 ng C/cell) was calculated according to Menden-Deuer and Lessard (2000). Mean equivalent spherical diameters (ESD) were measured by an electronic particle counter (Coulter Multisizer II, Coulter Corporation, Miami, FL).

**Feeding occurrence.** Experiment 1 was designed to investigate whether or not each dinoflagellate species was able to feed on *S. costatum* (Table 1). We observed *S. costatum* inside the dinoflagellate predator using a compound microscope, confocal microscope, epifluorescence microscope, and transmission electron microscope (TEM) after adding living *S. costatum* for compound microscopy and TEM and fluorescently labeled *S. costatum* (FLSc) for epifluorescence microscopy and confocal microscope. *Skeletonema costatum* was fluorescently labeled according to Sherr, Sherr, and Fallon (1987).

For the compound, confocal, and epifluorescence microscopy, a dense culture of each dinoflagellate predator, maintained in f/2 media and growing photosynthetically in its exponential growth phase on shelves and incubated under a 14:10 h light–dark cycle of 50  $\mu\text{E}/\text{m}^2/\text{s}$  for *Cochlodinium polykrikoides* and *Lingulodinium polyedrum* and 20  $\mu\text{E}/\text{m}^2/\text{s}$  for the other dinoflagellate species, was transferred to a 1-L polycarbonate (PC) bottle containing freshly filtered seawater. Three 1-ml aliquots were then removed from the bottle and examined using a compound microscope to determine the dinoflagellate concentration.

The initial concentrations of each dinoflagellate predator (1,000–20,000 cells/ml) and *S. costatum* or FLSc (ca 100,000 cells/ml) were established using an autopipette to deliver a predetermined volume of culture with a known cell density to the experimental bottles. Triplicate 80-ml PC bottles with mixtures of dinoflagellate predator and *S. costatum* or FLSc and triplicate predator control bottles containing dinoflagellate predator only were set up at a

Table 1. The cultured dinoflagellate species used as predators on the diatom *Skeletonema costatum*<sup>a</sup> in Experiment 1.

Predator species	ESD ( $\pm$ SD)	Initial predator concentration (cells/ml)	Feeding
<i>Heterocapsa rotundata</i>	5.8 (0.4)	20,000	Y
<i>Amphidinium carterae</i>	9.7 (1.6)	10,000	Y
<i>Prorocentrum minimum</i>	12.1 (2.5)	10,000	Y
<i>Prorocentrum triestinum</i>	12.6 (2.0)	10,000	Y
<i>Prorocentrum donghaiense</i>	13.3 (2.0)	10,000	Y
<i>Heterocapsa triquetra</i>	15.0 (4.3)	8,000	Y
<i>Gymnodinium impudicum</i>	17.8 (2.6)	2,000	Y
<i>Scrippsiella trochoidea</i>	22.8 (2.7)	2,000	Y
<i>Cochlodinium polykrikoides</i>	25.9 (2.9)	2,000	Y
<i>Prorocentrum micans</i>	26.6 (2.8)	2,000	Y
<i>Alexandrium tamarense</i>	28.1 (3.1)	2,000	Y
<i>Akashiwo sanguinea</i>	30.8 (3.5)	2,000	Y
<i>Gonyaulax polygramma</i>	32.5 (3.0)	2,000	Y
<i>Alexandrium catenella</i>	32.6 (2.7)	2,000	Y
<i>Gymnodinium catenatum</i>	33.9 (1.6)	1,000	Y
<i>Lingulodinium polyedrum</i>	38.2 (3.6)	1,000	Y

Y, a dinoflagellate predator was observed to contain food cells in the protoplasm; N, a dinoflagellate predator was observed not to contain food cells. Mean equivalent spherical diameter (ESD,  $\mu\text{m}$ )  $\pm$  standard deviation of the mean was measured by an electronic particle counter (Coulter Multisizer II, Coulter Corporation, Miami, Florida, USA).  $n > 2,000$  for each species.

<sup>a</sup>The densities of *Skeletonema costatum* were ca 100,000 cells/ml for these experiments.

single prey concentration. The bottles were filled to capacity with freshly filtered seawater, capped, and then placed on a vertically rotating plate at 0.9 rpm at 20 °C under a 14:10 h light–dark cycle of 20 or 50  $\mu\text{E}/\text{m}^2/\text{s}$  for *C. polykrikoides* and *L. polyedrum* to provide it with better conditions. After 10 and 60 min, and 6, 12, and 24-h incubation, a 5-ml aliquot was removed from each bottle and transferred into a 10-ml bottle. Two 0.1-ml aliquots were placed on slides and then cover glasses were added. Under these conditions, the dinoflagellate predator cells were alive, but almost motionless. The protoplasm of 50–100 dinoflagellate predator cells was carefully examined with a compound microscope, confocal microscope, and/or epifluorescence microscope at a magnification of 100–630X. Pictures of the dinoflagellate predator at several different stages of the feeding process were taken using a Nikon Coolpix 4500 camera (Nikon, Chiyoda-ku, Tokyo, Japan) on an Olympus compound microscope (BX-51) or an AxioCam HRC camera on a Zeiss Axiovert 200 M (Carl Zeiss Ltd., Göttingen, Germany) inverted microscope at a magnification of 100–630X.

Additionally one 80-ml PC bottle with mixtures of the dinoflagellate predator and *S. costatum* was set up. The bottle was filled to capacity with freshly filtered seawater, capped, and then well mixed. After 12 h incubation, a 1-ml aliquot was removed from the bottle and transferred into a clean 1-ml Sedgwick-Rafter chamber (SRC). By monitoring the behavior of ca 30 unfed cells of each dinoflagellate predator under the inverted microscope at a magnification of 100–630X, the feeding behaviors were determined.

**Transmission electron microscopy.** For transmission electron microscopy, predator and/or prey cells were fixed for 1.5–2 h in 2.5% (v/v) glutaraldehyde in culture medium. Cells were centrifuged, and the pellet was embedded in 1% agar (w/v). After several medium rinses, the cells were postfixed in 1% (w/v) osmium tetroxide with deionized water. Dehydration was accomplished using a graded ethanol series (i.e. 50%, 60%, 70%, 80%, 90%, and 100% ethanol, followed by two 100% ethanol steps). The material was embedded in Spurr's low-viscosity resin

(Spurr 1969). Sections were obtained with a RMC MT-XL ultramicrotome (Boeckeler Instruments Inc., Tucson, AZ) and post-stained with 3% (w/v) aqueous uranyl acetate followed by lead citrate. Stained sections were viewed with a JEOL-1010 electron microscope (Jeol Ltd., Tokyo, Japan).

**Ingestion rates at single prey concentrations.** Experiment 2 was designed to compare the ingestion rates of seven phototrophic red-tide dinoflagellates (*Gonyaulax polygramma*, *Heterocapsa rotundata*, *H. triquetra*, *L. polyedrum*, *Prorocentrum donghaiense*, *Prorocentrum micans*, and *Prorocentrum triestinum*) on *S. costatum* at single prey concentration.

A dense culture of each dinoflagellate predator, maintained in f/2 medium and growing photosynthetically under a 14:10 h light–dark cycle of 20 or 50  $\mu\text{E}/\text{m}^2/\text{s}$  for *L. polyedrum*, was transferred into a 1-L PC bottle. Three 1-ml aliquots from the bottle were counted using a compound microscope to determine the cell concentrations of the dinoflagellate predator, and the cultures were then used to conduct experiments.

The initial concentrations of each dinoflagellate predator and *S. costatum* were established using an autopipette to deliver predetermined volumes of known cell concentrations to the bottles. Triplicate 42-ml PC experiment bottles containing mixtures of predator and prey and triplicate prey control bottles containing prey only were set up at a single prey concentrations. Actual initial prey concentration were ca 1,700–2,000 cells/ml for all predators and actual initial predator concentrations were ca 90–120 cells/ml for *G. polygramma* and *L. polyedrum* and ca 340–1,150 cell/ml for the other predators. Triplicate predator control bottles containing only the dinoflagellate predator were also established. To make the water conditions similar, the water of a predator culture was filtered through 0.7  $\mu\text{m}$  GF/F filter and then added to the prey control bottles in the same amount as the volume of the predator culture added to the predator control bottles and the experimental bottles for each predator–prey combination. Also, the water of a prey culture was filtered through 0.7  $\mu\text{m}$  GF/F filter and then added to the predator control bottles in the same amount as the volume of the prey culture added to the prey control bottles and the experimental bottles. Five milliliters 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 2 d incubation, a 5-ml aliquot was removed from each bottle and fixed with 5% (v/v) acid Lugol's solution, and all or > 200 predator and prey cells in three 1-ml SRCs were enumerated. Before taking subsamples, the condition of the predator and its prey was assessed using a dissecting microscope. The bottles were filled again to capacity with freshly filtered seawater, capped, and placed on a vertically rotating wheel at 0.9 rpm at 20 °C under an illumination of 20 or 50  $\mu\text{E}/\text{m}^2/\text{s}$  for *L. polyedrum* of cool white fluorescent light on a 14:10 h light–dark cycle. Dilution of the cultures associated with refilling the bottles was considered in calculating ingestion rates.

The ingestion and clearance rates were calculated using the equations of Frost (1972) and Heinbokel (1978).

**Effects of prey concentration.** Experiment 3 was designed to measure the ingestion and clearance rates of *P. micans* and *G. polygramma* as a function of the prey concentration, when feeding on *S. costatum*.

A dense culture of *P. micans* or *G. polygramma* maintained in f/2 medium and growing photosynthetically for approximately 1 mo, was transferred into a 1 L PC bottle and three 1-ml aliquots from the bottle were counted as described above. Triplicate 42 ml PC experimental bottles, triplicate prey control bottles, and triplicate predator control bottles were set up for each predator–prey combination. Also, to make the water conditions similar between the experimental and prey control bottles, the waters of the cul-

tures were filtered and then added into the bottles as described above. Five milliliters of f/2 medium were added to all bottles, which were then filled to capacity with freshly filtered seawater and capped. To determine the actual initial predator and prey densities (cells/ml) at the beginning of the experiment (*P. micans*/*S. costatum* = 10/19, 19/45, 46/57, 485/837, 1,800/1,900, 3,120/5,280, 3,800/9,500, 3,580/26,250, 5,510/76,250, 5,200/141,690; *G. polygramma*/*S. costatum* = 65/105, 1,220/2,420, 3,830/7,750, 4,060/18,350, 3,800/28,960, 5,370/93,090, 5,090/138,950) and after 2 d incubation, 5-ml aliquots were removed from each bottle and enumerated as described above. The bottles were filled again to capacity with f/2 medium, capped, placed on a vertically rotating plate at 0.9 rpm, and incubated as described above. Ingestion and clearance rates for 2 d were also calculated as described above. Ingestion rate data were fitted by linear regression.

**Potential grazing impact.** We estimated the grazing coefficients attributable to *P. micans* and *G. polygramma* on co-occurring *S. costatum* by combining field data on abundances of the predators and the prey with ingestion rates of the grazers on the prey obtained in the present study. Data on the abundances of *P. micans* and the prey used in this estimate were obtained from the water samples taken in Masan Bay, Korea in 2003–2004 and in the coastal waters off Tongyoung, Korea in 2003. Data on the abundances of *G. polygramma* and the prey used in this estimate were obtained from the water samples taken in the coastal waters off Saemankeum, Korea in 1999–2002, Kwangyang, Korea in 1999, and Tongyoung, Korea in 2004.

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

$$g = \text{CR} \times \text{GC} \quad (1)$$

where CR is a clearance rate (ml/predator/h) of a dinoflagellate predator on *S. costatum* at a given prey concentration and GC is a predator concentration (cells/ml). Clearance rates were calculated as

$$\text{CR} = \text{IR}/X \quad (2)$$

where IR is the ingestion rate (cells eaten/predator/h) of the dinoflagellate predator on the prey and X is a prey concentration (cells/ml). CRs were corrected using  $Q_{10} = 2.8$  (Hansen, Bjornsen, and Hansen 1997) because in situ water temperatures and the temperature used in the laboratory for this experiment (20 °C) were sometimes different.

## RESULTS

**Predator species.** All red-tide dinoflagellates tested ingested *S. costatum* (Table 1; Fig. 1–11). The smallest red-tide dinoflagellate *H. rotundata* attacked and fed on only a single cell of *S. costatum*, but did not attack chain-formed cells. However, the other dinoflagellate predators attacked cells in a chain. Two to four cells forming a chain were sometimes observed inside the protoplasm of all dinoflagellates except the two smallest species *Amphidinium carterae* and *H. rotundata* (Fig. 5–11).

**Ingestion rates at a single prey concentration.** When mean prey concentrations were 170–260 ng C/ml (i.e. 6,500–10,000 cells/ml), the ingestion rates of selected dinoflagellate predators on *S. costatum* were 0.007–0.081 ng C/dinoflagellate/d (0.2–3.0 cells/dinoflagellate/d; Table 2). The ingestion rates of these seven red-tide dinoflagellate predators on *S. costatum* correlated positively with the predator size ( $P < 0.05$ , linear regression ANOVA; Fig. 12).

**Effects of prey concentration.** With increasing mean prey concentration, ingestion rates of *P. micans* and *G. polygramma* on *S. costatum* continuously increased at mean prey concentrations ca 140–3,440 ng C/ml (i.e. 5,000–132,000 cells/ml) (Fig. 13, 14).

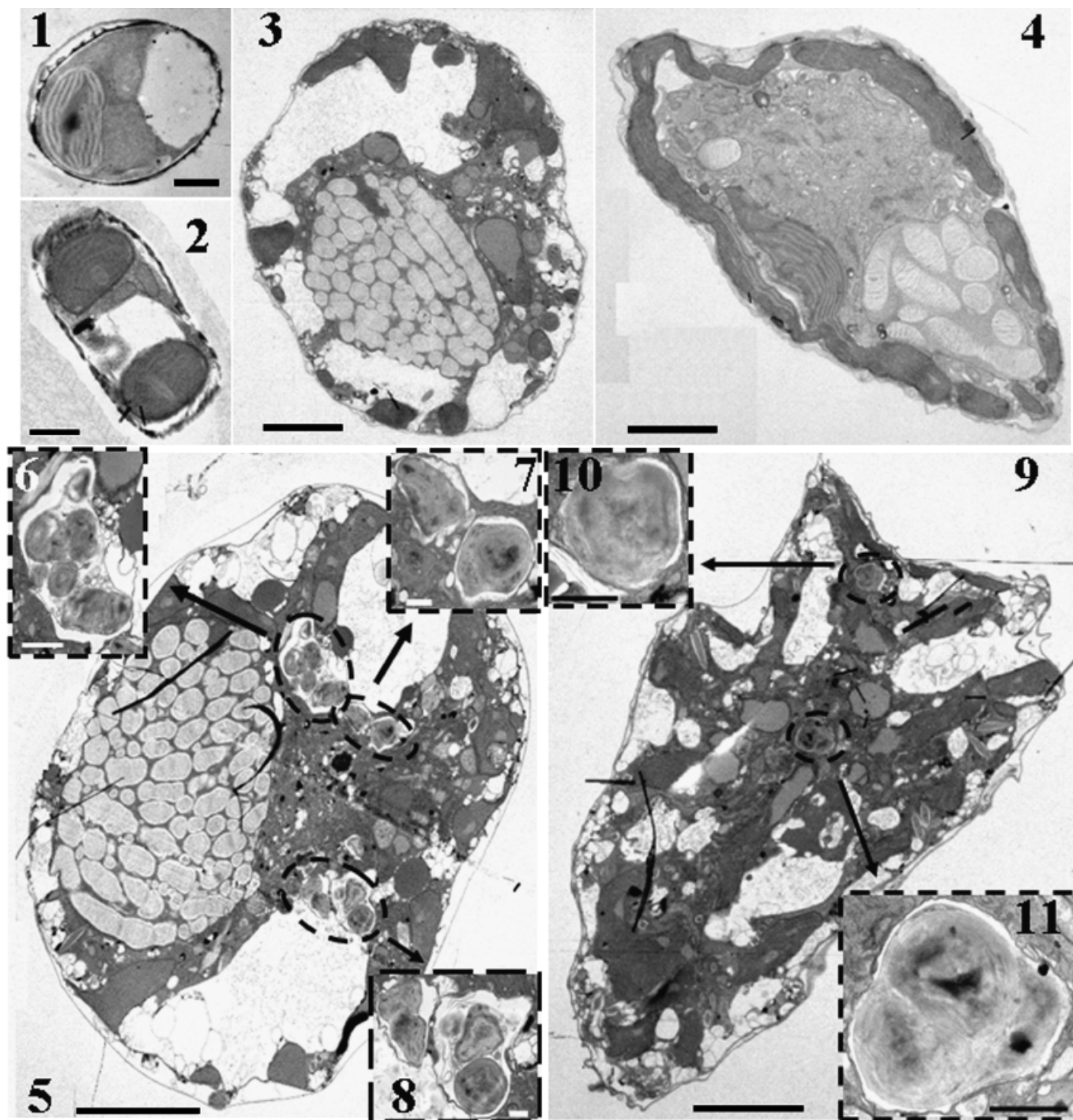


Fig. 1–11. Transmission electron micrographs (TEM) of phototrophic dinoflagellates feeding on *Skeletonema costatum*. 1. A transversally sectioned *S. costatum* cell. 2. A longitudinally sectioned *S. costatum* cell. 3. A longitudinally sectioned *Gonyaulax polygramma* cell. 4. A longitudinally sectioned *Prorocentrum micans* cell. 5. A *G. polygramma* cell with three food vacuole packages containing two to four ingested *S. costatum* cells. 6. Enlarged from Fig. 5. The food vacuole package contained four ingested *S. costatum* cells. 7, 8. Enlarged from Fig. 5. Each food vacuole package contained two ingested *S. costatum* cells. 9. A *P. micans* cell with two food vacuole packages containing one to two ingested *S. costatum* cells. 10. Enlarged from Fig. 9. The food vacuole contained one ingested *S. costatum* cell. 11. Enlarged from Fig. 9. The food vacuole packages contained three ingested *S. costatum* cells. Scale bars = 1  $\mu\text{m}$  for Fig. 1, 2, 6, 7, 8, 10 and 11 and 5  $\mu\text{m}$  for Fig. 3, 4, 5 and 9.

At the given prey concentrations, the maximum ingestion rate of *P. micans* on *S. costatum* (0.345 ng C/grazer/d [13.3 cells/dinoflagellate/d]) was similar to that of *G. polygramma* (0.344 ng C/grazer/d [13.2 cells/dinoflagellate/d]). The maximum clearance

rates of *P. micans* and *G. polygramma* on *S. costatum* were 0.165 and 0.020  $\mu\text{l}/\text{predator}/\text{h}$ .

**Potential grazing impact.** When the abundances of *P. micans* and *S. costatum* ( $n = 42$ ) in Masan Bay in 2003–2004 and in the

Table 2. Mean ingestion rates ( $n = 3$ ) of the dinoflagellate predators on *Skeletonema costatum* at a single mean prey concentration.

Predator species	Mean prey concentrations (ng C/ml)	Ingestion rate (ng C/dinoflagellate/d)
<i>Heterocapsa rotundata</i>	259 (13)	0.007 (0.004)
<i>Prorocentrum triestinum</i>	234 (28)	0.007 (0.005)
<i>Prorocentrum donghaiense</i>	195 (7)	0.012 (0.004)
<i>Heterocapsa triquetra</i>	174 (6)	0.029 (0.005)
<i>Prorocentrum micans</i>	241 (8)	0.081 (0.007)
<i>Gonyaulax polygramma</i>	191 (4)	0.052 (0.013)
<i>Lingulodinium polyedrum</i>	180 (8)	0.069 (0.031)

Standard errors of the means in parentheses.

coastal waters off Tongyoung in 2003 were 58–6,944 cells/ml (mean  $\pm$  SE = 919  $\pm$  192 cells/ml) and 20–13,200 cells/ml (1,567  $\pm$  419 cells/ml), respectively, grazing coefficients attributable to *P. micans* on co-occurring *S. costatum* were 0.001–0.100 h (mean  $\pm$  SE = 0.024  $\pm$  0.004 h; Fig. 15). In general grazing coefficients increased with increasing *P. micans* concentration.

When the abundances of *G. polygramma* and *S. costatum* ( $n = 21$ ) in the coastal waters off Saemankeum in 1999–2002, Kwangyang in 1999, and Tongyoung, Korea in 2004 were 1–1,810 cells/ml (mean  $\pm$  SE = 300  $\pm$  120 cells/ml) and 16–4,533 cells/ml (843  $\pm$  289 cells/ml), respectively, grazing coefficients attributable to *G. polygramma* on co-occurring *S. costatum* were 0.001–0.222 h (mean  $\pm$  SE = 0.036  $\pm$  0.014 h; Fig. 16). In general grazing coefficients also increased with increasing *G. polygramma* concentration.

DISCUSSION

**Predators on *Skeletonema costatum*.** Before the present study, there had been no report on the feeding by phototrophic dinoflagellates on the ubiquitous diatom *S. costatum*. Our study showed that all phototrophic red-tide dinoflagellates tested were able to ingest *S. costatum*. Thus several phototrophic dinoflagellates may compete with one another for *S. costatum* prey because *S. costatum* is present almost all year round in many areas and

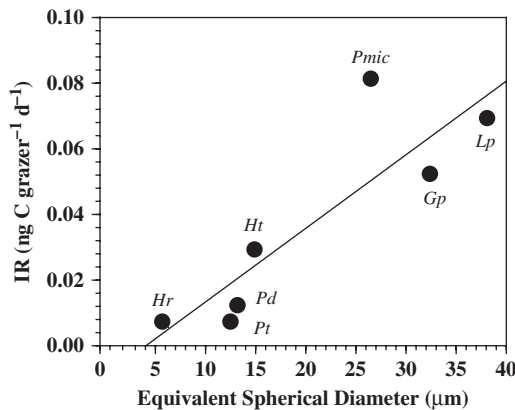


Fig. 12. Ingestion rates (IR) of seven phototrophic red-tide dinoflagellates on *Skeletonema costatum* as a function of dinoflagellate size (equivalent spherical diameters [ESD],  $\mu\text{m}$ ). The equation of the regression was  $\text{IR (ng C/grazer/d)} = 0.0023 (\text{ESD}) - 0.001$ ,  $r^2 = 0.761$  when the ESD was 5.8–38.2  $\mu\text{m}$ . Gp, *Gonyaulax polygramma*; Hr, *Heterocapsa rotundata*; Ht, *Heterocapsa triquetra*; Lp, *Lingulodinium polyedrum*; Pd, *Prorocentrum donghaiense*; Pmic, *Prorocentrum micans*; Pt, *Prorocentrum triestinum*.

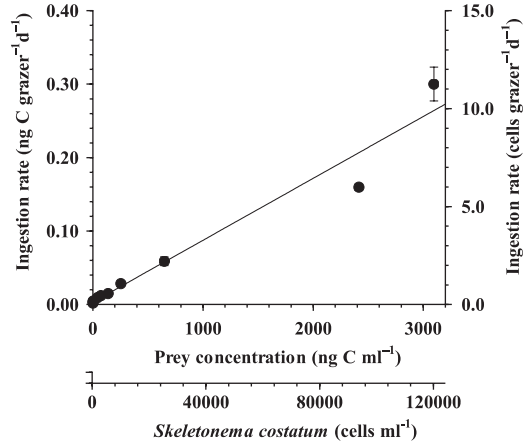


Fig. 13. Ingestion rates (IR) of *Prorocentrum micans* on *Skeletonema costatum* as a function of mean prey concentration ( $x$ , ng C/ml). Symbols represent treatment means  $\pm$  1 SE. The curves are fitted by linear equation using all treatments in the experiment.  $\text{IR (ng C/grazer/d)} = 0.00008 (x) + 0.00292$ ,  $r^2 = 0.955$ .

diverse phototrophic dinoflagellate species often co-existed with this diatom. Several metazoan grazers (Conover 1956; Deason 1980; Jordana et al. 2001; Martin 1965; Paffenhöfer 1976) and some heterotrophic protists, such as the pallium-feeding heterotrophic dinoflagellates *Proto-peridinium bipes* (Jeong et al. 2004b), *Proto-peridinium pellucidum* (Hansen 1992), *Proto-peridinium spinulosum* (Jacobson and Anderson 1986), and *Diplopsalis lenticula* (Naustvoll 1998), have been known to feed on *S. costatum*. Therefore, phototrophic red-tide dinoflagellates may compete with these heterotrophic protists and metazooplankton grazers for *S. costatum* prey. The relative contribution by red-tide dinoflagellates, heterotrophic protists, and metazooplankton to the total grazing impact on *S. costatum* will be affected by the combination of the relative abundances of these predator groups and the relative ingestion rates of the predators on the diatom.

Phototrophic red-tide dinoflagellates are able to feed on diverse prey such as diatoms, heterotrophic bacteria (Nygard and Tobiesen 1993; Seong et al. 2006), the cyanobacterium *Synechococcus*

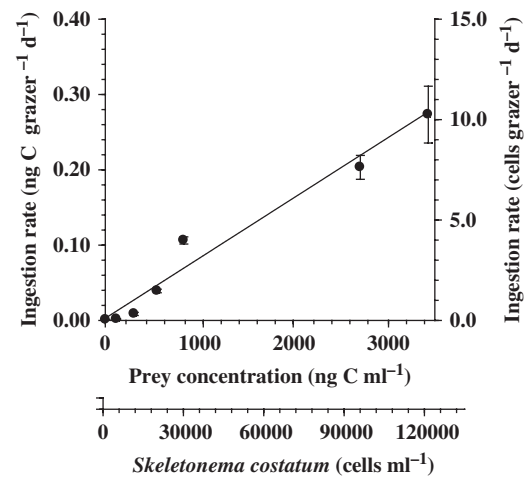


Fig. 14. Ingestion rates (IR) of *Gonyaulax polygramma* on *Skeletonema costatum* as a function of mean prey concentration ( $x$ , ng C/ml). Symbols represent treatment means  $\pm$  1 SE. The curves are fitted by linear equation using all treatments in the experiment.  $\text{IR (ng C/grazer/d)} = 0.00008 (x) + 0.00394$ ,  $r^2 = 0.908$ .

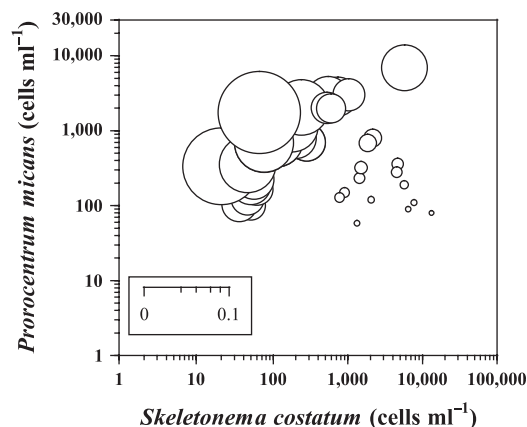


Fig. 15. Calculated grazing coefficients attributable to *Prorocentrum micans* (A,  $n = 42$ ) on *Skeletonema costatum* (see text for calculation). The scale of the circles in the inset box is  $g$  (h).

(Jeong et al. 2005c), phytoflagellates (Jeong et al. 2005a,b; Stoecker et al. 1997), other phototrophic dinoflagellates (Legrand, Granéli, and Carlsson 1998; Jeong et al. 1999, 2005a), heterotrophic dinoflagellates (Jeong et al. 1997), and ciliates (Bockstahler and Coats 1993b). However, the predator–prey relationships between phototrophic red-tide dinoflagellates and other microbes and ingestion rates of the dinoflagellates on the prey seem to depend on the relative abundances of the dinoflagellate predators and their prey (Jeong et al. 2005a,c). Each red-tide dinoflagellate also has different preferences for prey among diverse prey items, and thus it is worthwhile investigating selective feeding by phototrophic red-tide dinoflagellates among the diverse prey items mentioned above.

Legrand, Granéli, and Carlsson (1998) reported that the red-tide dinoflagellate *H. triquetra* was able to ingest the diatom *T. pseudonana* in nutrient-depleted cultures, but it did not ingest the diatom in nutrient-replete cultures. However, the *H. triquetra* used in the present study was able to feed on *S. costatum* in nutrient-replete cultures. Different strains of *H. triquetra* may cause these different results. Our strain of *H. triquetra*, originally isolated from the water in Masan Bay, where the concentrations of nitrate plus nitrite and phosphate are usually  $> 10$  and  $1 \mu\text{M}$ , respectively (e.g. Seong et al. 2006), seemed to have adapted to the eutrophicated water.

**Ingestion rates and grazing impact.** The maximum ingestion rate of *P. micans* on *S. costatum* ( $0.35 \text{ ng C/predator/d}$ ) is higher than that on an unidentified cryptophyte ( $\text{ESD} = 5.6 \mu\text{m}$ ;  $0.04 \text{ ng C/}$

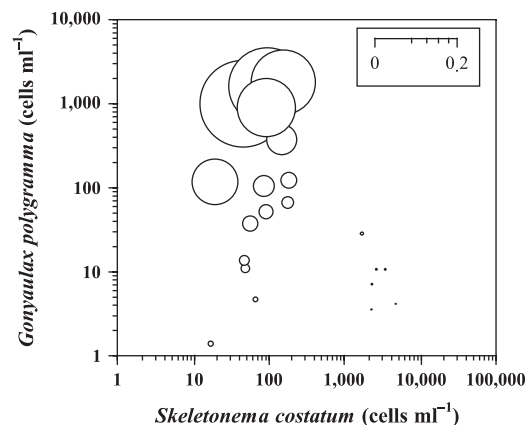


Fig. 16. Calculated grazing coefficients attributable to *Gonyaulax polygramma* (A,  $n = 21$ ) on *Skeletonema costatum* (see text for calculation). The scale of the circles in the inset box is  $g$  (h).

dinoflagellate/d; Jeong et al. 2005a). The maximum ingestion rate of *G. polygramma* on *S. costatum* ( $0.34 \text{ ng C/predator/d}$ ) is also higher than that on an unidentified cryptophyte ( $0.18 \text{ ng C/dinoflagellate/d}$ ; Jeong et al. 2005b; Table 3). Therefore, *S. costatum* is ingested more readily by *P. micans* or *G. polygramma*. Motionless *S. costatum* may be more easily captured and ingested by *P. micans* and *G. polygramma*, rather than the actively swimming cryptophyte.

Before the present study, there had been few studies measuring the ingestion and clearance rates of protists on *S. costatum* as a function of prey concentration, and providing maximum ingestion rates (i.e. the heterotrophic dinoflagellate *P. bipes*, Jeong et al. 2004b). The maximum ingestion and clearance rates of *P. micans* and *G. polygramma* on *S. costatum* ( $0.34\text{--}0.35 \text{ ng C/predator/d}$  and  $0.020\text{--}0.165 \mu\text{l/predator/h}$ , respectively) are much lower than that of *P. bipes* on the same prey ( $2.9 \text{ ng C/predator/d}$  and  $1.0 \mu\text{l/predator/h}$ , respectively; Jeong et al. 2004b), even though the volumes of *P. micans* (ca  $9,900 \mu\text{m}^3$ ) and *G. polygramma* (ca  $17,900 \mu\text{m}^3$ ) are much greater than that of *P. bipes* (ca  $1,000 \mu\text{m}^3$ ; Table 3). Engulfing a *S. costatum* cell through sutures (*P. micans*) or through the sulcus (*G. polygramma*) may be less efficient feeding mechanisms than ingesting the prey cell using the pallium (*P. bipes*). Also, the much lower swimming speeds of *P. micans* (average and maximum swimming speeds = ca  $270$  and  $380 \mu\text{m/s}$ , respectively; Jeong et al. 1999) and *G. polygramma* (average and maximum swimming speeds = ca  $380$  and  $550 \mu\text{m/s}$ , respectively,  $n = 30$ ; our unpubl. data) than that of *P. bipes* ( $4,000$  and  $8,300 \mu\text{m/s}$ , respectively; Jeong et al. 2004b) might cause a lower encounter rate between the phototrophic dinoflagellate predators and *S. costatum* compared with that between *P. bipes* and *S. costatum* and thus lead to the lower clearance rate of *P. micans* and *G. polygramma* on *S. costatum* compared with that of *P. bipes*. However, grazing coefficients attributable to *P. micans* ( $0.001\text{--}0.100 \text{ h}$ ) and *G. polygramma* ( $0.001\text{--}0.222 \text{ h}$ ) on co-occurring *S. costatum* obtained in the present study were higher than those of *P. bipes* and the calanoid copepod *Acartia* spp. on co-occurring *S. costatum* in Korean waters ( $0.001\text{--}0.034$  and  $< 0.002 \text{ h}$ , respectively; Jeong et al. 2004b). Much higher abundances of *P. micans* (maximum concentration = ca  $6,940 \text{ cells/ml}$ ) and *G. polygramma*

Table 3. Comparison of the ingestion rates of *Prorocentrum micans* (A) and *Gonyaulax polygramma* (B) on different prey items and those of protistan grazers on *Skeletonema costatum* (C).

Prey	PYV	$I_{\text{max}}$	$C_{\text{max}}$	Source	
(A) <i>Prorocentrum micans</i> on different prey items					
Unidentified cryptophyte (CR)	90	0.04	0.05	Jeong et al. (2005a)	
<i>Skeletonema costatum</i> (DIA)	250	0.345	0.17	This study	
(B) <i>Gonyaulax polygramma</i> on different prey items					
Unidentified cryptophyte (CR)	90	0.18	0.18	Jeong et al. (2005b)	
<i>Skeletonema costatum</i> (DIA)	250	0.344	0.02	This study	
Predator	PDV	$I_{\text{max}}$	$C_{\text{max}}$	$SS_{\text{max}}$	Source
(C) Protistan grazers on <i>Skeletonema costatum</i>					
<i>Protoperidinium bipes</i> (HTD)	1,000	2.9	1.0	8,300	Jeong et al. (2004b)
<i>Prorocentrum micans</i> (MTD)	9,900	0.35	0.17	380	This study
<i>Gonyaulax polygramma</i> (MTD)	17,900	0.34	0.02	550	This study

Rates are corrected to  $20^\circ\text{C}$  using  $Q_{10} = 2.8$  (Hansen, Bjornsen, and Hansen 1997).  $C_{\text{max}}$ , maximum clearance rate as  $\mu\text{l/predator/h}$ ; CR, cryptophyte; DIA, diatom; HTD, heterotrophic dinoflagellate;  $I_{\text{max}}$ , maximum ingestion rate in  $\text{ng C/predator/d}$ ; MTD, mixotrophic dinoflagellate; PDV, predators' volume as  $\mu\text{m}^3$ ; PYV, preys' volume as  $\mu\text{m}^3$ ;  $SS_{\text{max}}$ , maximum swimming speed as  $\mu\text{m/s}$ .

(maximum concentration = ca 1,810 cells/ml), compared with those of *P. bipes* (137 cells/ml; Jeong et al. 2004b) and *Acartia* spp. (2 individual/Liter; Jeong et al. 2004b), may be responsible for their grazing impacts on *S. costatum* being greater than those of *P. bipes* and *Acartia* spp., even though ingestion rates of the former grazers are lower than those of the latter grazers. To understand further the contribution of grazing impacts by major grazers on co-occurring *S. costatum* in natural environments, it is worthwhile comparing the grazing rates of co-occurring phototrophic red-tide dinoflagellates, heterotrophic protists, and metazooplankton on natural populations of *S. costatum*.

Grazing coefficients attributable to *P. micans* and *G. polygramma* on co-occurring *S. costatum* obtained in the present study correspond to the removal of up to 10% (mean = 2.3%) and 20% (mean = 3.3%), respectively, of *S. costatum* populations by *P. micans* and *G. polygramma* populations in 1 h. The results of the present study suggest that *P. micans* and *G. polygramma* may sometimes have a considerable grazing impact on populations of co-occurring *S. costatum*. In particular, feeding by these dinoflagellate predators may accelerate the decline of blooms dominated by *S. costatum* or delay this diatom increase to form a bloom after a red tide dominated by *P. micans* and *G. polygramma*.

**Ecological importance.** The feeding by phototrophic red-tide dinoflagellates on the ubiquitous diatom *S. costatum* may be important in marine planktonic communities in the following ways: (1) a new pathway of materials and energy from *S. costatum* to phototrophic red-tide dinoflagellates is discovered. There may be diverse predator-prey relationships between phototrophic red-tide dinoflagellate species and *S. costatum*. Before the present study, *S. costatum* and phototrophic red-tide dinoflagellates had been thought to be purely competitors for nutrients. However, we suggest now that *S. costatum* and phototrophic red-tide dinoflagellates have quite different ecological niches in marine ecosystems and that they should be treated differently. (2) Many studies reported that a bloom dominated by *S. costatum* was followed by that dominated by phototrophic red-tide dinoflagellates (Bianchi et al. 2002; Gilabert 2001; Trigueros and Orive 2001). It has been suggested that when favorable conditions for photosynthesis are provided, differential growth rates between fast-growing *S. costatum* and slow-growing red-tide dinoflagellates may be responsible for this pattern in succession. Now, we suggest that feeding by phototrophic red-tide dinoflagellates on *S. costatum* could be one of the driving forces for the succession from *S. costatum* to phototrophic red-tide dinoflagellates during serial blooms. The bloom of phototrophic red-tide dinoflagellate species following a *S. costatum* bloom may be partially affected by its ability to feed on the diatom. To understand the mechanisms of succession further, it will be worthwhile exploring the mixotrophic growth rate and grazing impact of the dominant red-tide dinoflagellates on *S. costatum*, in addition to phototrophic growth rates of the dinoflagellates and the diatom. (3) There may also be competition between phototrophic red-tide dinoflagellates and co-occurring heterotrophic protists and metazooplankton for *S. costatum* prey. The ingestion rates of red-tide dinoflagellates on *S. costatum* are lower than those of heterotrophic protists or metazooplankton. However, the grazing impact by red-tide dinoflagellates on *S. costatum* may sometimes be higher than that of heterotrophic protists or metazooplankton because the abundances of the former grazers are usually much higher than that of the latter grazers. (4) *Skeletonema costatum* is a less favored prey for several predators than are some phototrophic red-tide dinoflagellates (e.g. Nakamura, Suzuki, and Hiromi 1995; Stoecker, Guillard, and Kavee 1981). Therefore, a change from *S. costatum* to phototrophic red-tide dinoflagellates as the dominant alga may increase the growth of these predators. Many phototrophic red-tide dinoflagellates are effective prey for diverse protistan and metazoan grazers (Buskey,

Coulter, and Brown 1994; Jeong and Latz 1994; Jeong et al. 2001, 2002, 2004a; Kim and Jeong 2004; Stoecker et al. 1981; Turner et al. 2001), but some phototrophic red-tide dinoflagellates are not good prey (Hansen 1989, 1995; Ianora et al. 2004). To better understand the interactions and transfer of materials and energy among *S. costatum*, phototrophic red-tide dinoflagellates, and protistan and/or metazoan grazers in marine planktonic food webs, it will be worthwhile exploring selective or differential feeding by protistan and metazoan grazers between *S. costatum* and the phototrophic red-tide dinoflagellates.

#### ACKNOWLEDGMENTS

We thank Tae Hoon Kim, Jeong Hyeok Kim, Kyeong Ah Seong, Jeong Eun Song for technical support. This paper was funded by a grant from the Korean Research Foundation (2005-070-C00143).

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