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Feeding by phototrophic red-tide dinoflagellates: five species newly revealed and six species previously known to be mixotrophic

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ABSTRACT: We report here for the first time that 5 red-tide dinoflagellates (*Gymnodinium catenatum*, *G. impudicum*, *Lingulodinium polyedrum*, *Prorocentrum donghaiense*, and *P. triestinum*) which had been previously thought to be exclusively autotrophic dinoflagellates are mixotrophic species. We investigated the feeding behaviors, the kinds of prey species that 11 mixotrophic red-tide dinoflagellates (*Akashiwo sanguinea*, *Alexandrium tamarense*, *G. catenatum*, *G. impudicum*, *Heterocapsa triquetra*, *L. polyedrum*, *P. donghaiense*, *P. micans*, *P. minimum*, *P. triestinum*, and *Scrippsiella trochoidea*) fed on, and the effects of the prey concentration on the growth and ingestion rates of *P. donghaiense*, *H. triquetra*, *P. micans*, and *L. polyedrum* when feeding on algal prey. We have also calculated grazing coefficients by combining field data on abundances of *P. donghaiense*, *H. triquetra*, *P. micans*, and *L. polyedrum* and co-occurring prey species. All algal predators tested in the present study ingested small phytoplankton species that had equivalent spherical diameters (ESDs) < 12 µm. *A. sanguinea* and *L. polyedrum* were able to ingest large phytoplankton species such as *H. triquetra*, *S. trochoidea*, and *A. tamarense*. *Prorocentrum* spp. fed on prey by engulfing the prey cell through body sutures, while *S. trochoidea* engulfed prey through the apical horn as well as through the sulcus. Specific growth rates of *P. donghaiense*, *H. triquetra*, and *P. micans* on a cryptophyte and *L. polyedrum* on *P. minimum* and *S. trochoidea* increased with increasing mean prey concentration, with saturation occurring at mean prey concentrations of 110 to 480 ng C ml^{-1}. The maximum specific growth rates (mixotrophic growth) of *P. donghaiense*, *H. triquetra*, and *P. micans* on the cryptophyte were 0.510, 0.283, and 0.197 d^{-1}, respectively, under a 14:10 h light:dark cycle of 20 µE m^{-2} s^{-1}, while their growth rates (phototrophic growth) under the same light conditions without added prey were 0.375, 0.184, and 0.106 d^{-1}, respectively. The maximum specific growth rates of *L. polyedrum* on *P. minimum* and *S. trochoidea* were 0.254 and 0.303 d^{-1}, respectively, under a 14:10 h light:dark cycle of 50 µE m^{-2} s^{-1}, while their growth rates without added prey were 0.157 and 0.182 d^{-1}, respectively. Maximum ingestion rates of *P. donghaiense*, *H. triquetra*, and *P. micans* on the cryptophyte were much lower than those of *L. polyedrum* on *S. trochoidea* and *P. minimum*. The calculated grazing coefficients of *P. donghaiense*, *H. triquetra*, and *P. micans* on the cryptophyte were up to 2.67, 0.091, and 0.041 h^{-1}, respectively, while those of *L. polyedrum* on small *Prorocentrum* spp. and *S. trochoidea* were up to 0.026 and 0.011 h^{-1}, respectively. The results of the present study suggest that the algal predators sometimes have a potentially considerable grazing impact on populations of the algal prey.

KEY WORDS: Feeding process · Harmful algal bloom · Ingestion · Marine · Protist · Red tide

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INTRODUCTION

Recently, several red-tide dinoflagellates which had previously been thought to be exclusively autotrophic dinoflagellates have been found to be mixotrophic dinoflagellates (i.e. capable of both photosynthesis and ingesting prey) (Bockstahler & Coats 1993, Chang & Carpenter 1994, Jacobson & Anderson 1996, Granéli et al. 1997, Stoecker et al. 1997, Smalley et al. 1999, Stoecker 1999, Skovgaard 2000, Jeong et al. 2004, 2005). If a red-tide dinoflagellate thought to be an autotrophic dinoflagellate is revealed to be mixotrophic, studies on the ecology, physiology, and biochemistry of that red-tide dinoflagellate should be conducted, taking into consideration the mixotrophic property of the dinoflagellate and also the models for predicting the outbreak, persistence, and decline of red tides dominated by the red-tide dinoflagellate, and the related management strategies should be adjusted to reflect these facts. However, mixotrophy in many red-tide dinoflagellate species have been not explored yet, even though these dinoflagellates have formed huge red tides which have sometimes caused large-scale mortalities of fin-fish and shellfish and thus great losses to the aquaculture and tourist industries of many countries (ECOHAB 1995).

Recently, we found food vacuoles inside 5 red-tide dinoflagellates (*Prorocentrum donghaiense*, *P. triestinum*, *Gymnodinium catenatum*, *G. impudicum*, and *Lingulodinium polyedrum*) which had previously been known as autotrophic dinoflagellates. *P. donghaiense* (previously *P. dentatum* in Korean, Chinese and Japanese waters, and in some USA waters, Qi & Wang 2003; reported maximum concentrations = 360 000 cells ml^{-1}, Lu et al. 2002) has often formed huge red tide patches in Korean, Chinese, and Japanese waters (Yanagi et al. 1994, NFRDI 1998, Liu & Wang 2002). *P. triestinum* has often formed huge red tide patches in the waters off many countries (Hernandez-Becerril et al. 2000, Labib 2000, Lu & Hodgkiss 2004). *G. catenatum*, known as a toxic species, has caused fish kills and/or paralytic shellfish poisoning in many areas (Anderson et al. 1989, Hallegraeff & Fraga 1998, McMinn et al. 2001, Glibert et al. 2002). *G. impudicum* has also sometimes caused fish kills (Glibert et al. 2002). *L. polyedrum* (previously *Gonyaulax polyedra*; reported maximum concentrations = 25 000 cells ml^{-1}, Marasović 1989; 22 200 cells ml^{-1}, Sweeney 1975) has caused red tides in the coastal waters off many countries (Holmes et al. 1967, Sweeney 1975, Marasović 1989, Bruno et al. 1990, Legović et al. 1991, Altamirano et al. 1996, Zhu et al. 1997, Kudela & Cochlan 2000, Bennouna et al. 2002). In particular, *L. polyedrum* is one of the most common causative species of red tides off southern California, USA (Eppley & Harrison 1975, Morey-Gaines 1980, Jeong 1995, Kudela & Cochlan 2000), and is one of the most studied red-tide organisms to date (reviewed by Lewis & Hallett 1997). There have been some studies on the possible uptake of amino acids and B_{12} (Carlucci 1970, Gaines & Elbrächter 1987, Nakamura et al. 1993), but there has been no report on the phagotrophy of *L. polyedrum* yet. There have been a large number of studies on the cell chemistry, bioluminescence, life cycle, physiology, ecology, and/or the cysts of these dinoflagellates; however, most studies have been conducted under the assumption that these dinoflagellates are autotrophic dinoflagellates. Therefore, whether these dinoflagellates are exclusively autotrophic or mixotrophic should be tested.

The red-tide dinoflagellates *Akashiwo sanguinea*, *Alexandrium tamarense*, *Heterocapsa triquetra*, *Prorocentrum micans*, *P. minimum*, and *Scrippsiella trochoidea* were previously thought to be mixotrophic dinoflagellates (Bockstahler & Coats 1993, Nygaard & Tobiesen 1993, Jacobson & Anderson 1996, Legrand et al. 1998). *A. sanguinea* has been known to feed on small ciliates (Bockstahler & Coats 1993) and *A. tamarense* on bacteria (Nygaard & Tobiesen 1993), but whether these dinoflagellates are able to feed on co-occurring phytoplankton prey has not been tested yet. *P. minimum* has been known to feed on cryptophytes (Stoecker et al. 1997). Legrand et al. (1998) reported that when the cyanobacteria *Synechococcus* spp., the diatom *Thalassiosira pseudonana*, and a small unidentified autotrophic flagellate were provided as prey, the small flagellate and the diatom were sometimes observed inside *H. triquetra*, in contrast to the cyanobacterium which was never observed inside this dinoflagellate. Jacobson & Anderson (1996) reported that *P. micans* and *S. trochoidea* were mixotrophic because food vacuoles were observed inside the predators. However, there have been few reports on the feeding behaviors and the kinds of prey species that these red-tide dinoflagellates feed on when diverse phytoplankton species are provided as prey.

The mixotrophic red-tide dinoflagellate *Gonyaulax polygramma* has been known to feed on phytoplankton cells by engulfing the prey through both the apical horn and the sulcus (Jeong et al. 2005), while other engulfment-feeding mixotrophic and heterotrophic dinoflagellates have only been known to engulf a prey cell through the sulcus (Schnept & Elbrächter 1992, Skovgaard 1996, Jeong et al. 1997, 1999, Hansen & Calado 1999). Two interesting questions arise in the case of engulfment-feeding mixotrophic dinoflagellates. (1) Is there any other dinoflagellate that engulfs the prey through both the apical horn and the sulcus like *G. polygramma*? (2) Are there any further feeding behaviors other than that of

engulfing the prey through the apical horn and/or the sulcus? The feeding behaviors of *Prorocentrum* spp., which are not known as yet, are of interest because they have no apical horn or sulcus. The periflagellar area and the suture between 2 valves, which are the only openings for *Prorocentrum* spp., could be candidates for the feeding sites.

Exploring the kinds of prey species that red-tide dinoflagellates feed on is important from an ecological perspective for the following reasons: (1) based on the results of these experiments, we can judge whether each red-tide dinoflagellate is a potential predator, prey, or competitor of other phytoplankton prey for nutrients. The results of this study may reveal predator–prey relationships among phototrophic organisms so far unknown. (2) If the red-tide dinoflagellates and newly discovered prey species co-occur, we should consider the competition between red-tide dinoflagellates and co-occurring heterotrophic protists and/or metazooplankton on the common algal prey species. We must also consider the possibility that *in situ* grazing impacts by microzooplankton on the algal prey have been overestimated because red-tide dinoflagellates may significantly reduce the populations of co-occurring algal prey. (3) The predation of the algal predator on the algal prey can be a driving force for the succession of the dominant species during red tides in series if the algal predator has a great grazing impact on the populations of the algal prey and if the algal prey supports the growth of the algal predators. The results of these experiments may provide ideas for testing algal predation as a potential mechanism for succession of the dominant species during serial red tides.

We established monoclonal cultures of 11 red-tide dinoflagellates (*Akashiwo sanguinea*, *Alexandrium tamarense*, *Gymnodinium catenatum*, *G. impudicum*, *Heterocapsa triquetra*, *Lingulodinium polyedrum*, *Prorocentrum donghaiense*, *P. micans*, *P. minimum*, *P. triestinum*, and *Scrippsiella trochoidea*) and observed the feeding behavior and determined the prey species therein. We conducted experiments to determine the effects of prey concentration on the growth and ingestion rates of *P. donghaiense*, *H. triquetra*, and *P. micans* on an unidentified cryptophyte species (equivalent spherical diameter, ESD = 5.6 µm) and *L. polyedrum* when feeding on unialgal diets of *P. minimum* and *S. trochoidea*. We also estimated grazing coefficients attributable to *P. donghaiense*, *H. triquetra*, and *P. micans* on co-occurring cryptophytes and *L. polyedrum* on co-occurring small *Prorocentrum* spp. and *S. trochoidea* using our data for ingestion rates obtained from the laboratory experiments and the abundances of predator and prey in the field. The results of the present study provide a basis for understanding the feeding behaviors of mixotrophic red-tide dinoflagellates, the interactions among the red-tide dinoflagellates and between the red-tide dinoflagellates and co-occurring phytoplankton belonging to other classes, and the dynamics of red tides dominated by red-tide dinoflagellates.

MATERIALS AND METHODS

Preparation of experimental organisms. Phytoplankton species were grown at 20°C in enriched f/2 seawater media (Guillard & Ryther 1962) without silicate, under continuous illumination of 50 µE m^{-2} s^{-1} provided by cool white fluorescent lights (Table 1). The mean ESD (± SD) was measured using an electronic particle counter (Coulter Multisizer II, Coulter Corporation).

We conducted experiments to determine the effects of prey concentration on the growth and ingestion rates of *Heterocapsa triquetra*, *Prorocentrum donghaiense*, *P. micans*, and *Lingulodinium polyedrum* when feeding on unialgal diets of algal prey. For the isolation and culture of *H. triquetra* (HTMS0402), plankton samples collected with a 40 cm diameter, 25 µm mesh plankton net were taken from the waters

Table 1. Taxa, sizes, and concentration of phytoplankton species offered as food to algal predators in Expts 1 and 2. The taxa whose initial prey concentrations were not provided were used for predators only. Mean equivalent spherical diameter (ESD, µm) ± SD was measured before the start of the experiments. n > 2000 for each species. *PRY: Prymnesiophyceae; CRP: Cryptophyceae; RAP: Raphidophyceae; DIN: Dinophyceae. The densities of algal predators were 4000 to 5500 cells ml^{-1} (*P. donghaiense*, *P. minimum*, and *P. triestinum*) and 1000 to 1500 cells ml^{-1} (others)

Species	ESD (±SD)	Initial prey conc. (cells ml^{-1})
Isochrysis galbana (*PRY)	5.2 (1.0)	200000
Unidentified cryptophyte (CRP)	5.6 (1.5)	100000
Amphidinium carterae (DIN)	6.6 (1.8)	55000
Rhodomonas salina (CRP)	7.0 (2.0)	30000
Heterosigma akashiwo (RAP)	11.5 (1.9)	20000
Prorocentrum minimum (DIN)	12.1 (2.5)	13000
Prorocentrum triestinum (DIN)	12.6 (2.0)	13000
Prorocentrum donghaiense (DIN)	13.3 (2.0)	13000
Heterocapsa triquetra (DIN)	15.0 (4.3)	13000
Gymnodinium impudicum (DIN)	17.8 (2.6)	
Scrippsiella trochoidea (DIN)	22.8 (2.7)	5000–6000
Cochlodinium polykrikoides (DIN)	25.9 (2.9)	3000–5000
Prorocentrum micans (DIN)	26.6 (2.8)	3000–5000
Alexandrium tamarense (DIN)	28.1 (3.1)	3000–4000
Akashiwo sanguinea (DIN)	30.8 (3.5)	1000–3000
Gymnodinium catenatum (DIN)	33.9 (1.6)	1000–3000
Lingulodinium polyedrum (DIN)	38.2 (3.6)	

of Masan Bay, Korea, during February 2004, when the water temperature and salinity were 7.5°C and 30.5 psu, respectively. The samples were screened gently through a 154 µm Nitex mesh and placed in 1 l polycarbonate (PC) bottles. Fifty ml of f/2 media was added as food. The bottles were placed on shelves and incubated at 20°C under continuous illumination of 50 µE m^{-2} s^{-1} of cool white fluorescent light. After 3 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 *H. triquetra* were obtained, they were transferred to 2 l PC bottles containing ca. 500 ml of fresh f/2 seawater media (final culture volume = ca. 1 l) every 2 wk. Approximately 1 mo before the feeding experiments were conducted, the bottles containing *H. triquetra* were incubated under a 14:10 h light:dark cycle of 20 µE m^{-2} s^{-1} of cool white fluorescent light.

For the isolation and culture of *Prorocentrum donghaiense* (PDHMS0206), plankton samples collected with a clean bucket were taken from the coastal waters off Masan, during June 2002, when the water temperature and salinity were 22.6°C and 27.5 psu, respectively. The samples were screened and placed in 1 l PC bottles to which 50 ml of f/2 nutrient medium was added. 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}. Once dense cultures of *P. donghaiense* were obtained, they were transferred every 2 wk to 2 l PC bottles of fresh f/2 seawater medium.

For the isolation and culture of *Prorocentrum micans* (PMCJH99), plankton samples collected with a clean bucket were taken from the coastal waters off Jinhae, Korea, during June 1999, when the water temperature and salinity were 21.3°C and 27.7 psu, respectively. Fifty ml of f/2 media was added as food. The bottles were placed on shelves and incubated at 20°C under continuous illumination of 50 µE m^{-2} s^{-1} of cool white fluorescent light. Approximately 1 mo before the feeding experiments were conducted, the bottles containing *P. micans* were incubated under a 14:10 h light:dark cycle of 20 µE m^{-2} s^{-1} of cool white fluorescent light.

A culture of *Lingulodinium polyedrum* (LpSIO95), originating from Scripps Institution of Oceanography, University of California, San Diego, USA (Jeong & Latz 1994), has been maintained in our laboratory since 1995. Dense cultures of *L. polyedrum* incubated at 20°C under continuous illumination of 50 µE m^{-2} s^{-1} were transferred to 2 l PC bottles containing ca. 500 ml of fresh f/2 seawater media (final culture volume = ca. 1 l) every 2 wk. Approximately 1 mo before the feeding experiments were conducted, the bottles containing *L. polyedrum* were incubated under a 14:10 h light:dark cycle of 50 µE m^{-2} s^{-1} of cool white fluorescent light. *L. polyedrum* became unhealthy under a 14:10 h light:dark cycle of 20 µE m^{-2} s^{-1}.

Prey species. Expt 1 was designed to investigate whether or not an algal predator was able to feed on each target phytoplankton species when unialgal diets of diverse phytoplankton species were provided (Table 1). The initial concentrations of each phytoplankton species offered were similar in terms of their carbon biomass. To confirm no ingestion by the algal predator on some phytoplankton species, additional higher prey concentrations were provided.

A dense culture of an algal predator maintained in f/2 media and growing photosynthetically in an exponential growth phase was transferred to a 1 l 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 algal predator's concentration.

In this experiment, the initial concentrations of an algal predator and each target phytoplankton species 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 (mixtures of the algal predator and phytoplankton) and triplicate predator control bottles (containing the algal predator only) were set up for each target phytoplankton species. The bottles were filled to capacity with freshly filtered seawater, capped, and then placed on a vertically rotating plate rotating at 0.9 rpm and incubated at 20°C under continuous illumination of 20 µE m^{-2} s^{-1} (but 50 µE m^{-2} s^{-1} for *Lingulodinium polyedrum* because this species became unhealthy under a 14:10 h light:dark cycle of 20 µE m^{-2} s^{-1}) of cool white fluorescent light. After 6 h incubation, a 5 ml aliquot was removed from each bottle and transferred into a 10 ml bottle. Aliquots (0.2 ml) were placed on slides and then cover-glasses were added. Under these conditions, the algal predator cells were alive, but almost motionless. The protoplasms of more than 100 algal predator cells were carefully examined with a compound microscope and/or an epifluorescent microscope at a magnification of 100 to 400× to determine whether or not the algal predator was able to feed on the target prey species. Pictures of the algal predator at several different stages of the feeding process were taken using an Olympus camera on a compound microscope at a magnification of 100 to 400×.

Feeding behaviors. Expt 2 was designed to investigate the feeding mechanisms of 11 red-tide dinoflagellates on a cryptophyte (*Amphidinium carterae*, *Heterosigma akashiwo*, *P. minimum*, *H. triquetra*, *S. trochoidea*, and/or *A. tamarense*). The initial concentrations of predator and prey were the same as in Expt 1.

The initial concentrations of an algal predator and its target phytoplankton species were established using an autopipette to deliver a predetermined volume of culture with a known cell density to the experimental bottles. One 80 ml PC bottle (mixtures of the algal predator and phytoplankton) was set up for each target phytoplankton species. The bottle was filled to capacity with freshly filtered seawater, capped, and then well mixed. After 1 min incubation, a 1 ml aliquot was removed from the bottle and transferred into a 1 ml Sedgwick-Rafter chamber. By monitoring the behavior of more than 30 unfed algal predator cells for each target phytoplankton under a compound microscope at a magnification of 100×, the feeding behaviors were determined. In addition, a 0.1 ml aliquot was removed from the bottle and placed on slides and then coverglasses were added. A series of pictures showing the feeding process of the algal predator cell were taken using a digital camera on a compound microscope at a magnification of 100 to 400×.

The behavior of 112 unfed *Prorocentrum micans* cells when fed the cryptophyte was monitored using a compound microscope (400×). Frequencies of *P. micans* engulfing prey cells through sutures on the anterior and posterior ends, on the lower-right and the lower-left parts of the right valve were obtained.

Additional experiments to determine the time for an algal prey cell to be completely engulfed by an algal predator after the prey cell was contacted by the predator (i.e. handling time) were set up in the same way as Expt 2. After 1 min incubation, a 1 ml aliquot was removed from the bottle and transferred into a 1 ml Sedgwick-Rafter chamber. The time for a cryptophyte cell (ESD = 5.6 µm) to be completely engulfed by *Prorocentrum donghaiense*, *Heterocapsa triquetra*, and *P. micans* after the prey cell was contacted by the predator was measured by tracking 5 unfed *P. donghaiense*, 6 unfed *H. triquetra* cells, and 5 unfed *P. micans* cells under a compound microscope at a magnification of 100 to 400×. In addition, by monitoring the behavior of 5 to 7 unfed *Lingulodinium polyedrum* cells for each prey species, the time for a cryptophyte, *Heterosigma akashiwo*, *P. minimum*, and *Scrippsiella trochoidea* cell to be completely engulfed by *L. polyedrum* was measured.

Effects of the prey concentration. Expt 3 was designed to investigate the effects of prey concentration on the growth and ingestion rate of *Prorocentrum donghaiense*, *Heterocapsa triquetra*, *P. micans*, and *Lingulodinium polyedrum* (Table 2). We measured the growth, ingestion, and clearance rates of *P. donghaiense*, *H. triquetra*, and *P. micans* on a cryptophyte species (carbon content per cell = 0.017 ng C, Strathmann 1967) and those of *L. polyedrum* on unialgal diets of *P. minimum* PminUSA (carbon content per cell = 0.13 ng C) and *Scrippsiella trochoidea* STKP9909 (0.67 ng C) as a function of prey concentration.

A dense culture of an algal predator, maintained in f/2 medium and growing photosynthetically under a 14:10 h light:dark cycle of 20 µE m^{-2} s^{-1} (50 µE m^{-2} s^{-1} for *Lingulodinium polyedrum*) for approximately 1 mo, 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 algal predator, and the cultures were then used to conduct experiments.

The initial concentrations of an algal predator and each target phytoplankton species were established using an autopipette to deliver predetermined volumes of known cell concentrations to the bottles. Triplicate 80 ml PC experimental bottles (containing mixtures of predator and prey) and triplicate prey control bottles (containing prey only) were set up for each predator–prey combination. Triplicate predator control bottles (containing the predator only) were also established at 1 predator concentration. A f/2 medium (36 ml) was added to all bottles, which were then filled to capacity with freshly filtered seawater and capped. Here, we added only 36 ml so as to add the same amount of f/2 medium to all bottles, because in the bottles containing the highest prey concentrations, a volume of only approximately 40 ml remained after adding the prey and predator. To determine the actual initial predator and prey densities (cells ml^{-1}) at the beginning of the experiment and after 24, 48, and 72 h incubation, 6 ml aliquots were removed from each bottle and fixed with 5% Lugol's solution, and all algal predator cells and all

Table 2. Design of Expt 3. Values in prey and predator columns represent the actual initial concentrations (density columns, cells ml^{-1})

Predator		Prey	
Species	Density	Species	Density
Prorocentrum donghaiense	5–2763	Cryptophyte	0, 46, 167, 691, 1686, 6130, 12254, 27448
Heterocapsa triquetra	21–2268	Cryptophyte	0, 53, 160, 656, 1689, 4709, 11291
P. micans	8–3790	Cryptophyte	0, 65, 214, 939, 2638, 7353, 16917, 32513,
Lingulodinium polyedrum	5–1243	*Prorocentrum minimum*	0, 18, 47, 95, 268, 804, 1796, 5059, 8475
L. polyedrum	6–605	*Scrippsiella trochoidea*	0, 9, 20, 36, 151, 624, 1783

or >300 prey cells in three 1 ml Sedgwick-Rafter counting chambers were enumerated. Prior to taking subsamples, the condition of the algal predator and its prey was assessed under a dissecting microscope. The bottles were filled again to capacity with f/2 medium, capped, placed on a vertically rotating plate at 0.9 rpm, and incubated at 20°C under a 14:10 h light:dark cycle of 20 µE m^{-2} s^{-1} (50 µE m^{-2} s^{-1} for *Lingulodinium polyedrum*) of cool white fluorescent light. The dilution of the cultures associated with refilling the bottles was taken into consideration in calculating growth and ingestion rates.

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

$$\mathrm{IGR} = \frac{\mathrm{In}\left(S_{t_2}/S_{t_1}\right)}{t_2 - t_1} \quad (1)$$

where S_{t_1} and S_{t_2} are the concentration of the algal predator at consecutive samplings. The final sampling time (t_2) for the calculation was 48 h. In some experimental bottles (i.e. containing high prey concentrations), increases in the growth rates of the algal predator at 48 to 72 h incubation were depressed. Mean prey concentrations for 48 h were also calculated by averaging the instantaneous mean prey concentrations at 0 to 24 and 24 to 48 h. The instantaneous mean prey concentration for each sampling interval was calculated using the equations of Frost (1972). The prey concentrations after subsampling were lower than those before subsampling due to the dilution of the cultures associated with refilling the bottles and thus the prey concentrations before and after subsampling were dependent. Therefore, we calculated the specific growth rate of the algal predator by averaging the IGR for each sampling interval rather than by plotting prey concentrations over sampling times.

Data for the algal predator's growth rate were fitted to a Michaelis-Menten equation:

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

where $\mu_{\max}$ is the maximum growth rate (d^{-1}); x is prey concentration (cells ml^{-1} or ng C ml^{-1}); x' = threshold prey concentration (where µ = 0); and K_{GR} is the prey concentration sustaining ½ $\mu_{\max}$. Data were iteratively fitted to the model using Delta Graph® (SPSS).

Ingestion and clearance rates for 48 h were also 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 were fitted to a Michaelis-Menten equation:

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

where $I_{\max}$ is the maximum ingestion rate (cells $predator^{-1}$ d^{-1} or ng C $predator^{-1}$ d^{-1}); x is prey concentration (cells ml^{-1} or ng C ml^{-1}); and K_{IR} is the prey concentration sustaining ½ $I_{\max}$.

Potential grazing impact. We estimated the grazing coefficients attributable to *Prorocentrum donghaiense*, *Heterocapsa triquetra*, and *P. micans* on cryptophytes and attributable to *Lingulodinium polyedrum* on small *Prorocentrum* spp. and *Scrippsiella trochoidea* by combining field data on abundances of the grazers and the target prey with ingestion rates of the grazers on the prey obtained in the present study. Data on the abundances of *H. triquetra* and co-occurring cryptophytes used in this estimate were obtained from the water samples taken in Masan Bay, Korea (in 2003 to 2004). Data on the abundances of *P. donghaiense* and co-occurring cryptophytes used in this estimation were obtained from the water samples off Kohung (in 1998 to 1999), Kwangyang (in 1999 to 2003), Tongyoung (in 1998 to 2003), and Masan (in 2003), Korea. Data on the abundances of *P. micans* and co-occurring cryptophytes used in this estimate were obtained from water samples off Kohung (in 1998), Tongyoung (in 2003), and Masan (in 2003), Korea. Data on the abundances of *L. polyedrum* and co-occurring small *Prorocentrum* spp. (*P. minimum* + *P. triestinum*) used in this estimate were obtained from water samples taken off Kohung (in 1999) and Saemankeum (in 1999), Korea, and in the Krka Estuary, Croatia (east Adriatic coast) (Legović et al. 1991). Data on the abundances of *L. polyedrum* and co-occurring *S. trochoidea* used in this estimate were obtained from waters in the Los Angeles–Long Beach harbor, California, USA (Morey-Gaines 1980), and Kohung (in 2001) and Saemankeum (in 1999), Korea.

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

$$g = \mathrm{CR} \times \mathrm{GC} \quad (4)$$

where CR (ml $grazer^{-1}$ h^{-1}) is clearance rate of an algal predator on a target prey at a certain prey concentration and GC is grazer concentration (cells ml^{-1}). CRs were calculated as:

$$\mathrm{CR} = \mathrm{IR}/x \quad (5)$$

where IR (cells eaten $grazer^{-1}$ h^{-1}) is the ingestion rate of the algal predator on the target prey and x (cells ml^{-1}) is prey concentration. CRs were corrected using Q_{10} = 2.8 (Hansen et al. 1997) because *in situ* water temperatures and the temperature used in the laboratory for this experiment (20°C) were sometimes different.

RESULTS

Prey species

Among the phytoplankton prey offered, all algal predators tested in the present study (*Akashiwo sanguinea*, *Alexandrium tamarense*, *Gymnodinium catenatum*, *G. impudicum*, *Heterocapsa triquetra*, *Lingulodinium polyedrum*, *Prorocentrum donghaiense*, *P. micans*, *P. triestinum*, and *Scrippsiella trochoidea*) ingested the small phytoplankton species (the prymnesiophyte *Isochrysis galbana*, an unidentified cryptophyte, the dinoflagellate *Amphidinium carterae*, the cryptophyte *Rhodomonas salina*, and the raphidophyte *Heterosigma akashiwo*) which had ESDs < 12 µm (Table 3, Fig. 1).

Alexandrium tamarense, *Gymnodinium catenatum*, *Heterocapsa triquetra*, *Prorocentrum donghaiense*, *P. triestinum*, and *Scrippsiella trochoidea* were able to feed on *P. minimum* which had an ESD of 12.1 µm, but they were not able to ingest the larger prey species (Table 3). *P. micans* was able to ingest *H. triquetra* which had an ESD of 15 µm, but it did not feed on the larger prey species. *Akashiwo sanguinea* and *Lingulodinium polyedrum* were able to ingest *H. triquetra*, *S. trochoidea*, and *A. tamarense*, but they did not feed on *Cochlodinium polykrikoides*, *Gymnodinium catenatum* or *P. micans*.

Feeding behaviors

The predators *Prorocentrum* spp. fed on prey by engulfing the prey cell through the sutures on the side of several parts of their bodies (Figs. 2 & 3). The frequencies of engulfing cryptophyte cells (n = 112) of *P. micans* through the suture at the anterior end, the posterior end, the side of the upper-right part, the upper-left part, the lower-right part, and the lower-left part when viewed from the right valve were 25, 20, 20, 19, 11, and 6%, respectively. Up to 4 cryptophyte cells were observed to be simultaneously or consequently engulfed by a *P. micans* cell (Fig. 3M,N).

Scrippsiella trochoidea fed on phytoplankton cells by engulfing the prey through both the apical horn and the sulcus. *S. trochoidea* fed on small phytoplankton cells (*Isochrysis galbana* and an unidentified cryptophyte) by engulfing the prey through the apical horn, while it fed on large phytoplankton cells (*Rhodomonas salina*, *Amphidinium carterae*, *Heterosigma akashiwo*, and *Prorocentrum minimum*) through the sulcus. However, *Akashiwo sanguinea*, *Alexandrium tamarense*, *Gymnodinium catenatum*, *G. impudicum*, *Heterocapsa triquetra*, and *Lingulodinium polyedrum* fed on phytoplankton cells by engulfing the prey only through the sulcus. A tow filament to anchor the prey cell was not observed for these algal predators.

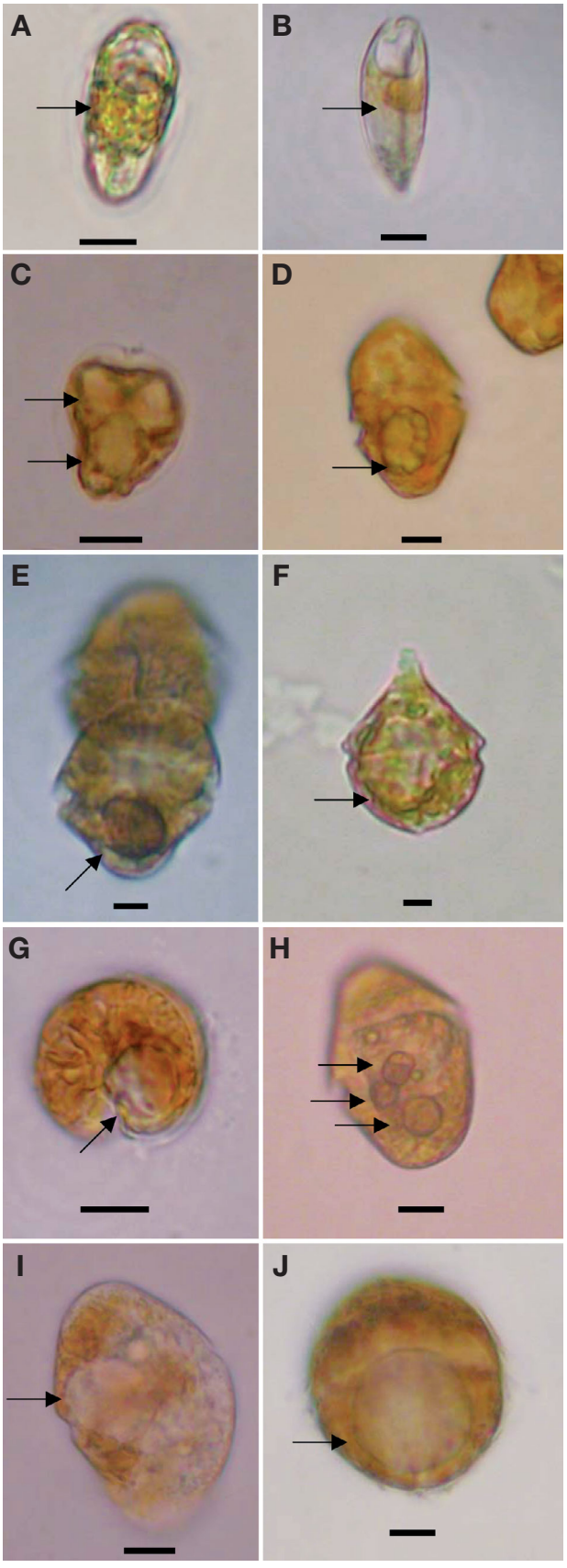
The time (mean ± SE) for an unidentified cryptophyte cell (ESD = 5.6 µm) to be completely engulfed by *Lingulodinium polyedrum* after the prey cell was contacted by the predator (73 ± 8 s, n = 5) was much shorter than that by *Prorocentrum donghaiense* (357 ± 43 s, n = 5), *Heterocapsa triquetra* (549 ± 30 s, n = 6), or *P. micans* (629 ± 84 s, n = 5). The mean times (±SE) for a cryptophyte, *Heterosigma akashiwo*, *P. minimum*, and *Scrippsiella trochoidea* cell to be completely engulfed by *L. polyedrum* after the prey cell was contacted by the predator, 73 (8) s, 178 (18) s, 293 (41) s, and 756 (81) s, respectively, increased with increasing prey size (Fig. 4).

Effects of prey concentration

With increasing mean prey concentration the specific growth rates of *Prorocentrum donghaiense*, *Heterocapsa triquetra*, and *P. micans* on a cryptophyte (ESD = 5.6 µm) increased, with saturation at mean prey concentrations

Table 3. Feeding occurrences by algal predators on the phytoplankton species in Expts 1 and 2. Y: an algal predator was observed to contain food cells in the protoplasm; N: the algal predator was observed not to contain food cells. Pd: *Prorocentrum donghaiense*; Pt: *P. triestinum*; Pmin: *P. minimum*; Ht: *Heterocapsa triquetra*; Gi: *Gymnodinium impudicum*; St: *Scrippsiella trochoidea*; Pmic: *P. micans*; At: *Alexandrium tamarense*; As: *Akashiwo sanguinea*; Gc: *Gymnodinium catenatum*; Lp: *Lingulodinium polyedrum*

Species	Pmin	Pt	Pd	Ht	Gi	St	Pmic	At	As	Gc	Lp
Isochrysis galbana	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
Unidentified cryptophyte	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
Amphidinium carterae	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
Rhodomonas salina	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
Heterosigma akashiwo	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
Prorocentrum minimum		Y	Y	Y	N	Y	Y	Y	Y	Y	Y
Prorocentrum triestinum	N		N	N	N	N	Y	N	Y	N	Y
Prorocentrum donghaiense	N	N		N	N	N	Y	N	Y	N	Y
Heterocapsa triquetra	N	N	N		N	N	Y	N	Y	N	Y
Scrippsiella trochoidea	N	N	N	N	N		N	N	Y	N	Y
Cochlodinium polykrikoides	N	N	N	N	N	N	N	N	N	N	N
Prorocentrum micans	N	N	N	N	N	N		N	N	N	N
Alexandrium tamarense	N	N	N	N	N	N	N		Y	N	Y
Akashiwo sanguinea	N	N	N	N	N	N	N	N		N	N
Gymnodinium catenatum	N	N	N	N	N	N	N	N	N		N
Lingulodinium polyedrum	N	N	N	N	N	N	N	N	N	N	



of approximately 110 to 480 ng C ml^{-1} (i.e. 6410 to 28 240 cells ml^{-1}) (Figs. 5 to 7). When the data were fitted to Eq. (2), the maximum specific growth rate of *P. donghaiense*, *H. triquetra*, and *P. micans* on a cryptophyte (mixotrophic growth) was 0.510, 0.283, and 0.197 d^{-1}, respectively, under a 14:10 h light:dark cycle of 20 µE m^{-2} s^{-1}, while its growth rate under the same light conditions without any added prey (phototrophic growth) was only 0.375, 0.184, and 0.106 d^{-1}, respectively.

With increasing mean prey concentration the specific growth rates of *Lingulodinium polyedrum* on *Prorocentrum minimum* increased, with saturation at a mean prey concentration of approximately 210 ng C ml^{-1} (i.e. 1620 cells ml^{-1}) (Fig. 8). When the data were fitted to Eq. (2), the maximum specific growth rate of *L. polyedrum* on *P. minimum* (mixotrophic growth) was 0.254 d^{-1}, under a 14:10 h light:dark cycle of 50 µE m^{-2} s^{-1}, while its growth rate under the same light conditions without added prey (phototrophic growth) was only 0.157 d^{-1}.

With increasing mean prey concentration the specific growth rates of *Lingulodinium polyedrum* on *Scrippsiella trochoidea* increased, with saturation at a mean prey concentration of approximately 170 ng C ml^{-1} (i.e. 250 cells ml^{-1}) (Fig. 9). When the data were fitted to Eq. (2), the maximum specific growth rate of *L. polyedrum* on *S. trochoidea* (mixotrophic growth) was 0.303 d^{-1}, under a 14:10 h light:dark cycle of 50 µE m^{-2} s^{-1}, while its growth rate under the same light conditions without added prey (phototrophic growth) was only 0.182 d^{-1}.

The ingestion rates of *Prorocentrum donghaiense*, *Heterocapsa triquetra*, and *P. micans* on a cryptophyte increased continuously with increasing mean prey concentration offered in the present study (Figs. 10 to 12). When the data were fitted to Eq. (3), the maximum ingestion rate of *P. donghaiense*, *H. triquetra*, and *P. micans* on a cryptophyte were 0.026, 0.038, and 0.041 ng C $grazer^{-1}$ d^{-1} (1.5, 2.2, and 2.4 cells $grazer^{-1}$ d^{-1}, respectively). The maximum clearance rates of *P. donghaiense*, *H. triquetra*, and *P. micans* on a cryptophyte were 0.041, 0.051, and 0.054 µl $grazer^{-1}$ h^{-1}, respectively.

Fig. 1. Feeding by algal predators on algal prey. (A) *Prorocentrum donghaiense* with an ingested *Amphidinium carterae* cell. (B) *P. triestinum* with an ingested cryptophyte cell. (C) *P. minimum* with ingested *Heterosigma akashiwo* cells. (D) *Heterocapsa triquetra* with an ingested *H. akashiwo* cell. (E) *Gymnodinium impudicum* with an ingested *H. akashiwo* cell. (F) *Scrippsiella trochoidea* with an ingested *P. minimum* cell. (G) *Alexandrium tamarense* with an ingested *H. akashiwo* cell. (H) *G. catenatum* with ingested *H. akashiwo* cells. (I) *Akashiwo sanguinea* with an ingested *A. tamarense* cell. (J) *Lingulodinium polyedrum* with an ingested *A. tamarense* cell. Arrows indicate prey cells. Scale bars = 5 µm (A to F) and 10 µm (G to J)

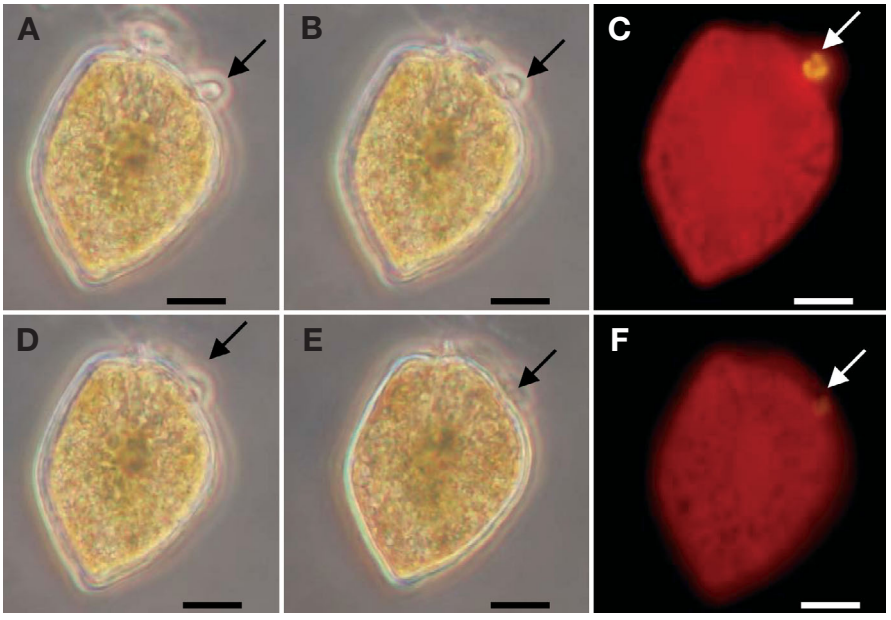


Fig. 2. Feeding process by *Prorocentrum micans* on a cryptophyte cell. These pictures in sequence were taken using a digital camera on a compound microscope. (A) *P. micans* has captured a cryptophyte cell. (B–C) *P. micans* has engulfed approximately ½ of the body of a cryptophyte cell. (D) *P. micans* has engulfed approximately ¾ of the body of a cryptophyte cell. (E–F) *P. micans* has almost engulfed a cryptophyte cell. Arrows indicate the prey cell. The predator and prey cells in (A) to (F) were the same. (A), (B), (D) and (E) are phase photomicrographs and (C) and (F) are photomicrographs taken using epifluorescence. Scale bars = 10 µm

With increasing mean prey concentration the ingestion rates of *Lingulodinium polyedrum* on *Prorocentrum minimum* increased, with saturation at a mean prey concentration of approximately 1180 ng C ml^{-1} (i.e. 9080 cells ml^{-1}) (Fig. 13). When the data were fitted to Eq. (3), the maximum ingestion rate of *L. polyedrum* on *P. minimum* was 0.20 ng C $grazer^{-1}$ d^{-1} (1.5 cells $grazer^{-1}$ d^{-1}). The maximum clearance rate of *L. polyedrum* on *P. minimum* was 0.13 µl $grazer^{-1}$ h^{-1}.

The ingestion rates of *Lingulodinium polyedrum* feeding on a unialgal diet of *Scrippsiella trochoidea* increased continuously with increasing mean prey concentration offered in the present study (Fig. 14). When the data were fitted to Eq. (3), the maximum ingestion rate of *L. polyedrum* on *S. trochoidea* was 0.36 ng C $grazer^{-1}$ d^{-1} (0.5 cells $grazer^{-1}$ d^{-1}). The maximum clearance rate of *L. polyedrum* on *S. trochoidea* was 0.14 µl $grazer^{-1}$ h^{-1}.

Potential grazing impact

Grazing coefficients attributable to *Prorocentrum donghaiense* on co-occurring cryptophytes in the coastal waters off Kohung, Kwangyang, Tongyoung, and Masan, Korea, were up to 2.67 h^{-1}, while those attributable to *Heterocapsa triquetra* on co-occurring cryptophytes in the waters of Masan Bay, Korea, were up to 0.091 h^{-1} (Fig. 15A,B). In addition, grazing coefficients attributable to *P. micans* on co-occurring cryptophytes in the coastal waters off Kohung, Tongyoung, and Masan, Korea, were up to 0.043 h^{-1} (Fig. 15C).

Grazing coefficients attributable to *Lingulodinium polyedrum* on co-occurring small *Prorocentrum* spp. (*P. minimum* + *P. triestinum*) in the coastal waters off Kohung and Saemankeum, Korea, and in the Krka Estuary, Croatia, were up to 0.026 h^{-1} (Fig. 15D), while those on co-occurring *Scrippsiella trochoidea* in the waters in the Los Angeles–Long Beach harbor, USA, and Kohung and Saemankeum, Korea, were up to 0.011 h^{-1} (Fig. 15E).

DISCUSSION

Mixotrophy in red-tide dinoflagellates

We report here for the first time that 5 red-tide dinoflagellates (*Gymnodinium catenatum*, *G. impudicum*, *Lingulodinium polyedrum*, *Prorocentrum donghaiense*, and *P. triestinum*) which had been previously thought to be exclusively autotrophic dinoflagellates, are mixotrophic species. Before the present study, approximately 40 marine dinoflagellates have been reported to be mixotrophic (reviewed by Stoecker 1999, Jeong et al. 2004, 2005). Most dinoflagellates may be mixotrophic species, but the trophic modes of many dinoflagellates have not been tested yet to ascertain whether they are exclusively autotrophic or mixotrophic. To understand the ecology and physiology of these dinoflagellates better, their trophic modes should be revealed.

Algal predators and prey species

All algal predators tested in the present study were able to feed on phytoplankton belonging to diverse classes such as Prymnesiophyceae, Cryptophyceae, Raphidophyceae, and Dinophyceae. However, in gen-

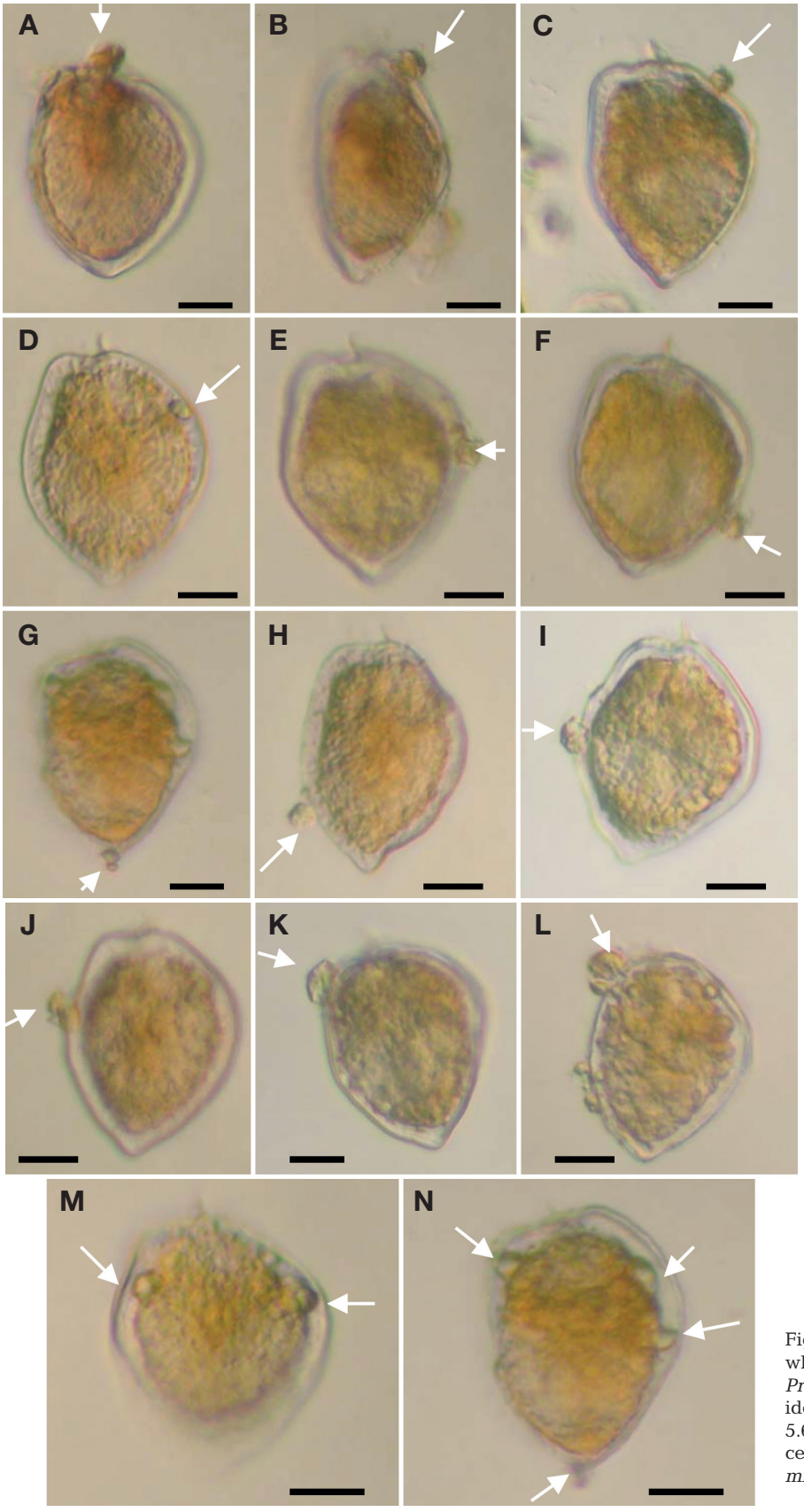


Fig. 3. (A–L) Diverse sites through which prey cells were engulfed when *Prorocentrum micans* fed on an unidentified cryptophyte species (ESD = 5.6 µm). Two (M) and 4 (N) cryptophyte cells simultaneously engulfed by a *P. micans* cell. Arrows indicate prey cells. Scale bars = 10 µm

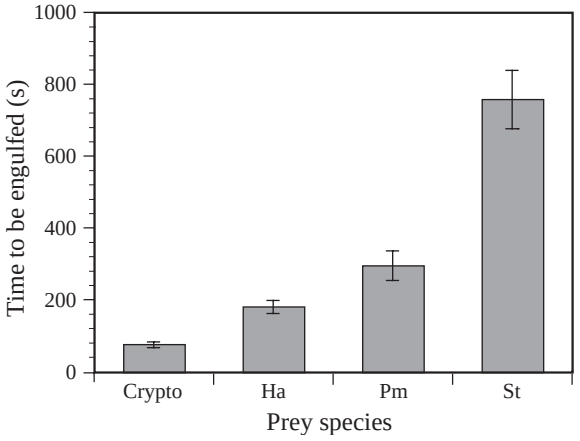


Fig. 4. Mean time (± SE) for a cryptophyte (Crypto; ESD = 5.6 µm), *Heterosigma akashiwo* (Ha), *Prorocentrum minimum* (Pm), and *Scrippsiella trochoidea* cell (St) to be completely engulfed through the sulcus of *Lingulodinium polyedrum* after the prey cell was contacted by the predator. N = 5 to 7 for each prey species

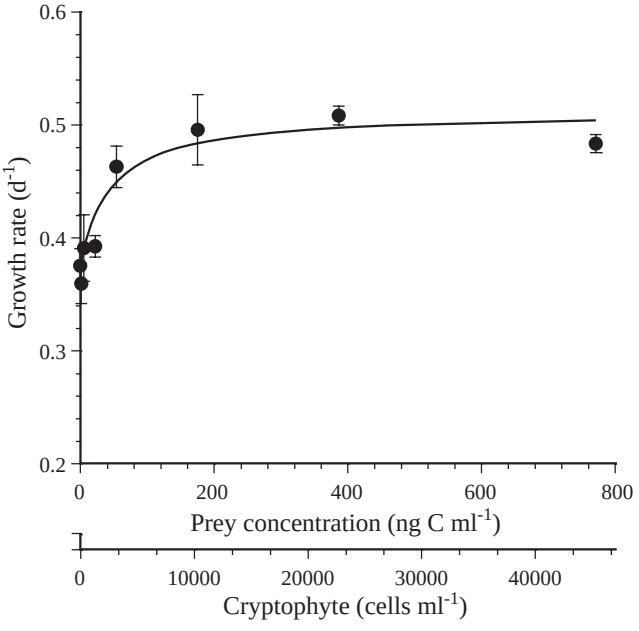


Fig. 5. Specific growth rates (d^{-1}) of *Prorocentrum donghaiense* on an unidentified cryptophyte (ESD = 5.6 µm) as a function of mean prey concentration (ng C ml^{-1} and cells ml^{-1}). Symbols represent treatment means ± 1 SE. The curves were fitted by a Michaelis-Menten equation (Eq. 2) using all treatments in the experiment. Growth rate (GR, d^{-1}) = 0.510 {(x + 32)/[12 + (x + 32)]}, r^2 = 0.47

eral, whether these algal predators are able to ingest a phytoplankton species or not appears to be mainly affected by the sizes of the prey and predator species; all algal predators tested in the present study ingested the small phytoplankton species which had ESD < 12 µm. All the algal predators which had ESDs ≥ 12.6 µm were able to feed on *Prorocentrum minimum*.

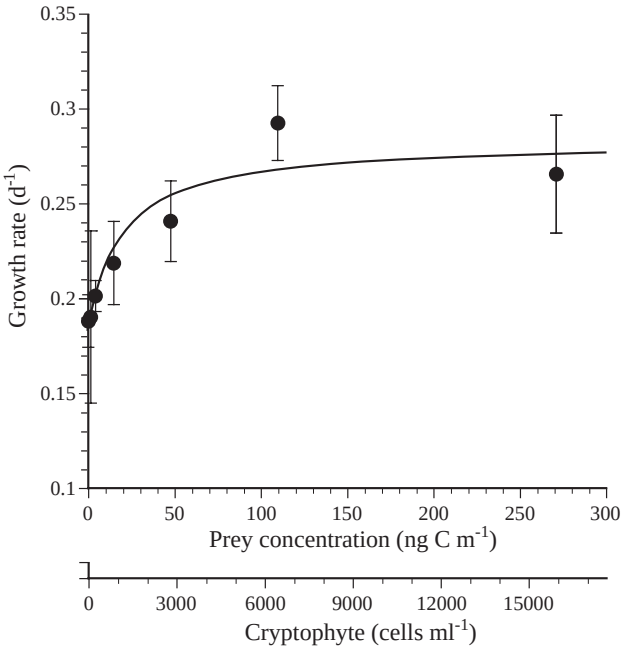


Fig. 6. Specific growth rates (d^{-1}) of *Heterocapsa triquetra* on an unidentified cryptophyte (ESD = 5.6 µm) as a function of mean prey concentration (ng C ml^{-1} and cells ml^{-1}). Symbols represent treatment means ± 1 SE. The curve was fitted by a Michaelis-Menten equation (Eq. 2) using all treatments in the experiment. Growth rate (GR, d^{-1}) = 0.283 {(x +12.6)/[6.8+(x+12.6)]}, r^2 = 0.42

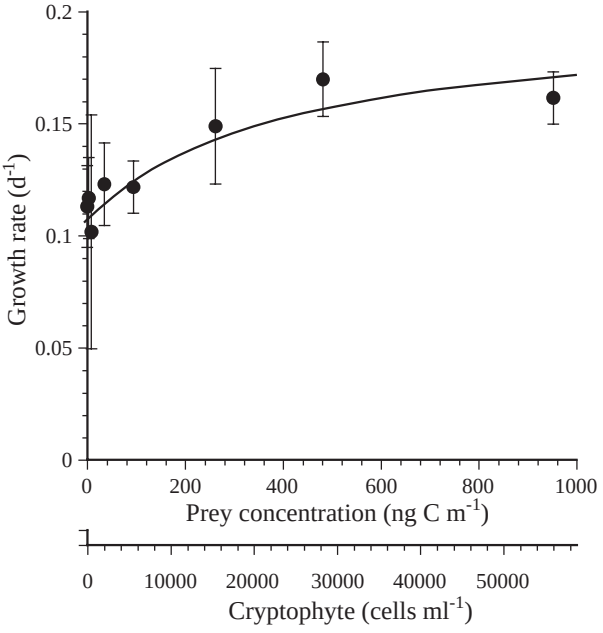


Fig. 7. Specific growth rates (d^{-1}) of *Prorocentrum micans* on an unidentified cryptophyte (ESD = 5.6 µm) as a function of mean prey concentration (ng C ml^{-1} and cells ml^{-1}). Symbols represent treatment means ± 1 SE. The curve was fitted by a Michaelis-Menten equation (Eq. 2) using all treatments in the experiment. Growth rate (GR, d^{-1}) = 0.197 {(x + 211)/[181+ (x+211)]}, r^2 = 0.26

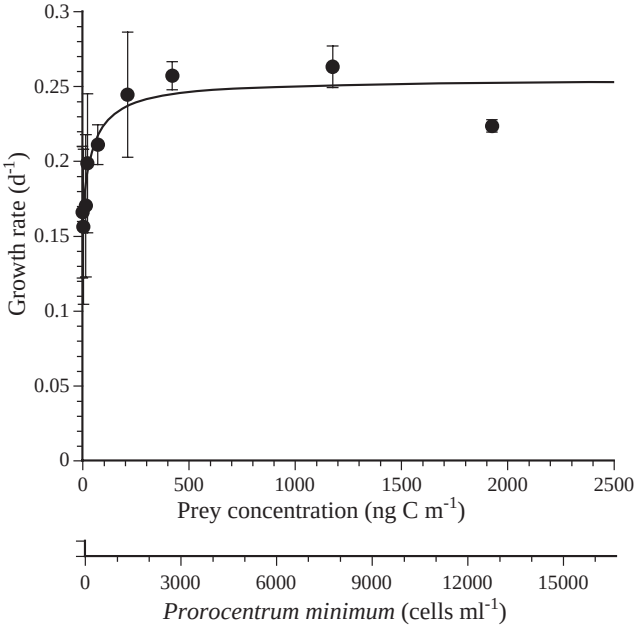


Fig. 8. Specific growth rates (d^{-1}) of *Lingulodinium polyedrum* on *Prorocentrum minimum* as a function of mean prey concentration (ng C ml^{-1} and cells ml^{-1}). Symbols represent treatment means ± 1 SE. The curve was fitted by a Michaelis-Menten equation (Eq. 2 using all treatments in the experiment. Growth rate (GR, d^{-1}) = 0.254 {(x + 30)/[18 + (x + 30)]}, r^2 = 0.32

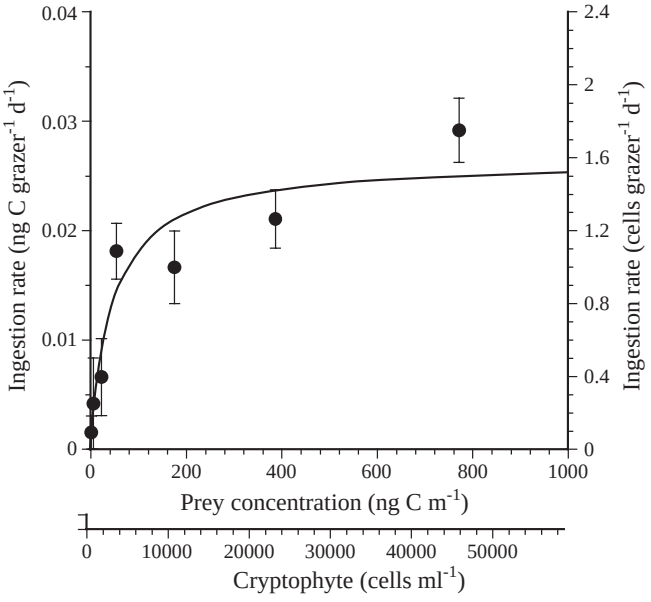


Fig. 10. Ingestion rate (ng C $grazer^{-1}$ d^{-1} and cells $grazer^{-1}$ d^{-1}) of *Prorocentrum donghaiense* on an unidentified cryptophyte (ESD = 5–6 µm) as a function of mean prey concentration (ng C ml^{-1} and cells ml^{-1}). Symbols represent treatment means ± 1 SE. The curve was fitted by a Michaelis-Menten equation (Eq. 3) using all treatments in the experiment. Ingestion rate (IR, ng C $grazer^{-1}$ d^{-1}) = 0.026 [x/(44.7 + x)], r^2 = 0.731

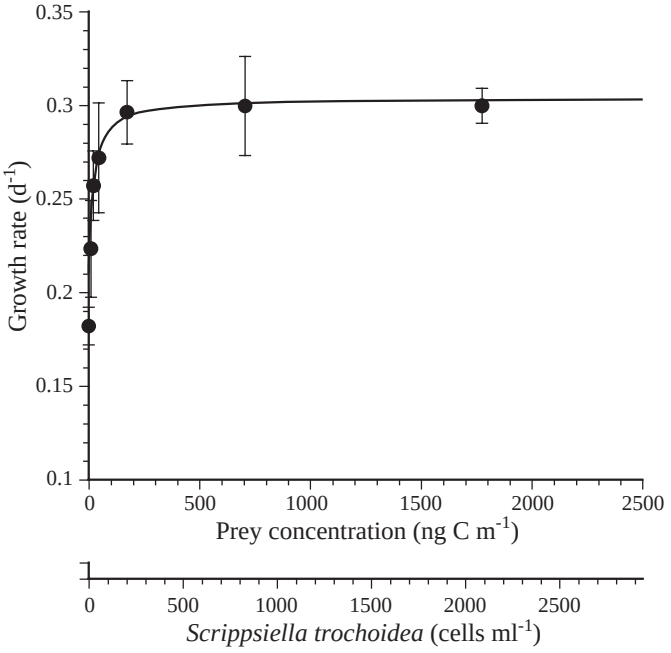


Fig. 9. Specific growth rates (d^{-1}) of *Lingulodinium polyedrum* on *Scrippsiella trochoidea* as a function of mean prey concentration (ng C ml^{-1} and cells ml^{-1}). Symbols represent treatment means ± 1 SE. The curve was fitted by a Michaelis-Menten equation (Eq. 2) using all treatments in the experiment. Growth rate (GR, d^{-1}) = 0.303 {(x+10)/[6 + (x+10)]}, r^2 = 0.67

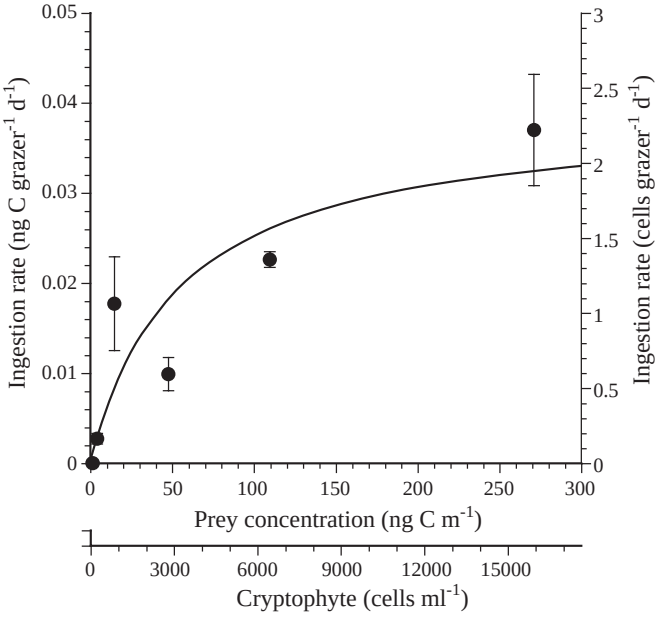


Fig. 11. Ingestion rate (ng C $grazer^{-1}$ d^{-1} and cells $grazer^{-1}$ d^{-1}) of *Heterocapsa triquetra* on an unidentified cryptophyte (ESD = 5.6 µm) as a function of mean prey concentration (ng C ml^{-1} and cells ml^{-1}). Symbols represent treatment means ± 1 SE. The curve was fitted by a Michaelis-Menten equation (Eq. 3) using all treatments in the experiment. Ingestion rate (IR, ng C $grazer^{-1}$ d^{-1}) = 0.038 [x/(48.8 + x)], r^2 = 0.689

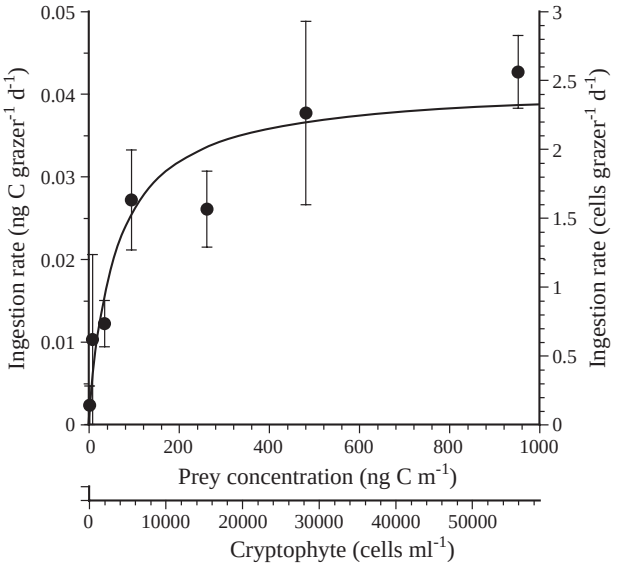


Fig. 12. Ingestion rate (ng C grazer^{-1} d^{-1} and cells grazer^{-1} d^{-1}) of *Prorocentrum micans* on an unidentified cryptophyte as a function of mean prey concentration (ng C ml^{-1} and cells ml^{-1}). Symbols represent treatment means ± 1 SE. The curve was fitted by a Michaelis-Menten equation (Eq. 3) using all treatments in the experiment. Ingestion rate (IR, ng C grazer^{-1} d^{-1}) = 0.041 [x/(59 + x)], r^2 = 0.62

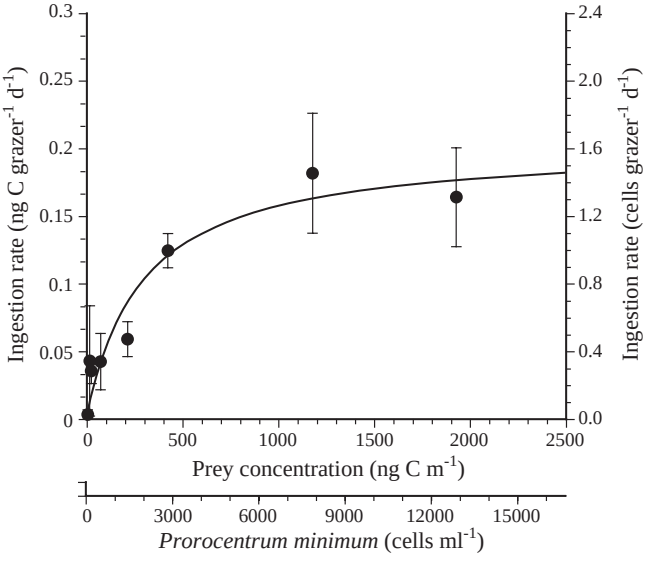


Fig. 13. Ingestion rate (ng C grazer^{-1}d^{-1} and cells grazer^{-1} d^{-1}) of *Lingulodinium polyedrum* on *Prorocentrum minimum* as a function of mean prey concentration (ng C ml^{-1} and cells ml^{-1}). Symbols represent treatment means 1 SE. The curve was fitted by a Michaelis-Menten equation (Eq. 3) using all treatments in the experiment. Ingestion rate (IR, ng C grazer^{-1} d^{-1}) = 0.20 [x/(292 + x)], r^2 = 0.66

The large predators *P. micans*, *Akashiwo sanguinea*, and *Lingulodinium polyedrum* were able to ingest *Heterocapsa triquetra* which had an ESD of 15 µm. In addition, *A. sanguinea* and *L. polyedrum* were able to

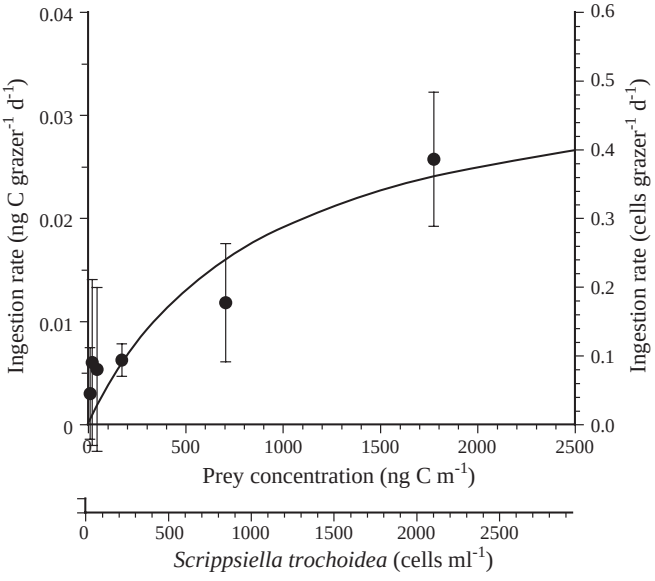


Fig. 14. Ingestion rate (ng C grazer^{-1} d^{-1} and cells grazer^{-1} d^{-1}) of *Lingulodinium polyedrum* on *Scrippsiella trochoidea* as a function of mean prey concentration (ng C ml^{-1} and cells ml^{-1}). Symbols represent treatment means ± 1 SE. The curve was fitted by a Michaelis-Menten equation (Eq. 3) using all treatments in the experiment. Ingestion rate (IR, ng C grazer^{-1} d^{-1}) = 0.36 [x/(895 + x)], r^2 = 0.66

ingest *Scrippsiella trochoidea* and *Alexandrium tamarense* which had ESDs of 23 to 28 µm. The length of the sulcus of *L. polyedrum* (ESD = 38 µm) is almost ¾ of the whole body length due to a big displacement in the girdle. This long sulcus may be responsible for engulfing large prey species such as *A. tamarense* (ESD = 28 µm). However, *A. sanguinea* and *L. polyedrum* did not feed on *Cochlodinium polykrikoides* (26 µm) and *P. micans* (22 µm) (Table 3). The maximum swimming speed of *C. polykrikoides* (1450 µm s^{-1}) is much higher than that of *A. sanguinea* (280 µm s^{-1}) or *L. polyedrum* (380 µm s^{-1}) (Jeong et al. 1999). The high swimming speed of *C. polykrikoides* may be partially responsible for its not being eaten by *L. polyedrum*.

Feeding behaviors

Before the present study, the feeding mechanisms of *Prorocentrum* spp. had not been known. Surprisingly, *Prorocentrum* spp. fed on prey by engulfing the prey cell through the sutures on the sides of several parts of their bodies. This predator is also able to engulf several prey cells at several different sites simultaneously or consequently. *Scrippsiella trochoidea* fed on phytoplankton cells by engulfing the prey through the apical horn as well as the sulcus, as observed for *Gonyaulax polygramma* (Jeong et al. 2005). However, *Heterocapsa triquetra* and *Lingulodinium polyedrum* fed on phyto-

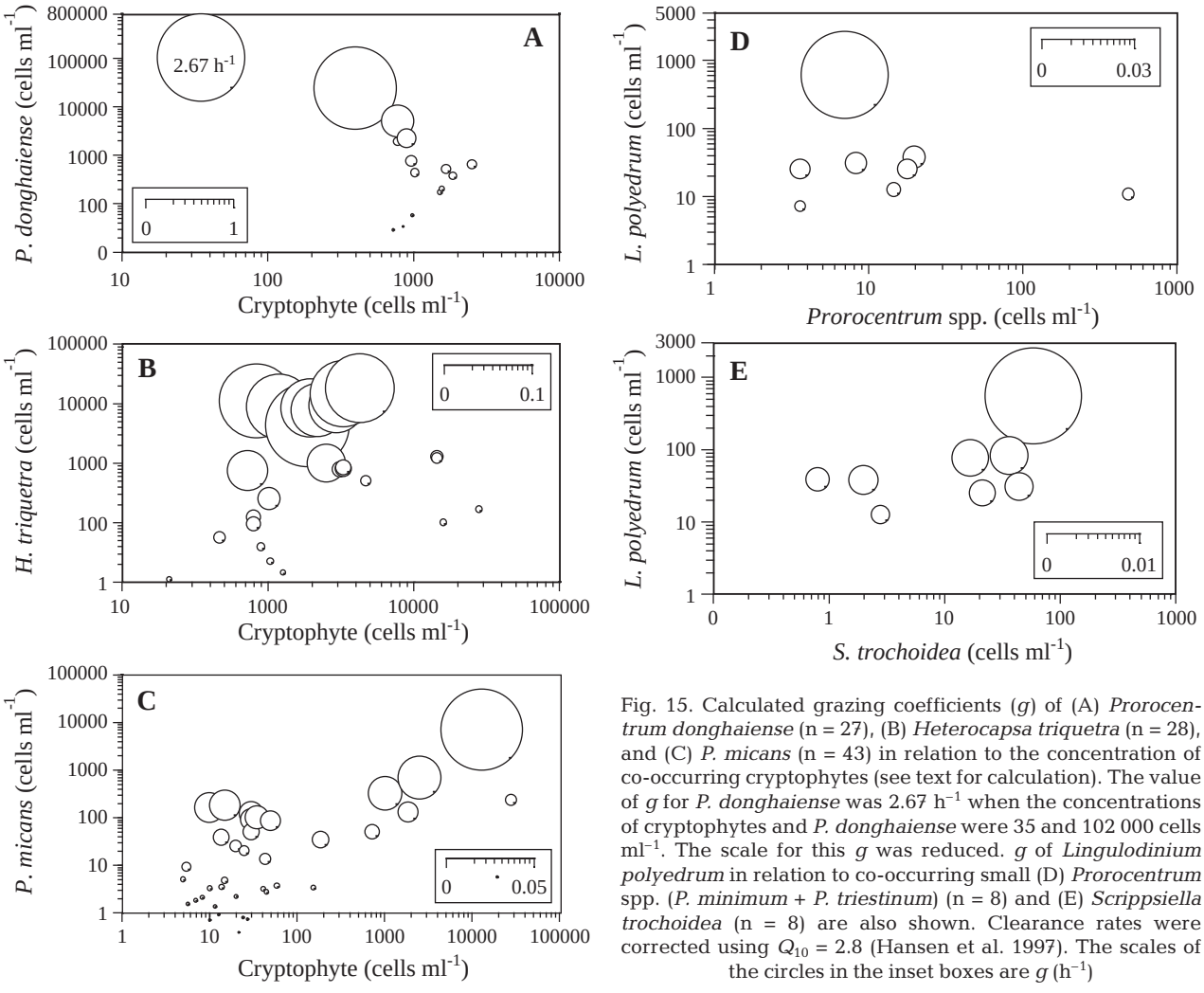


Fig. 15. Calculated grazing coefficients (*g*) of (A) *Prorocentrum donghaiense* (n = 27), (B) *Heterocapsa triquetra* (n = 28), and (C) *P. micans* (n = 43) in relation to the concentration of co-occurring cryptophytes (see text for calculation). The value of *g* for *P. donghaiense* was 2.67 h^{-1} when the concentrations of cryptophytes and *P. donghaiense* were 35 and 102 000 cells ml^{-1}. The scale for this *g* was reduced. *g* of *Lingulodinium polyedrum* in relation to co-occurring small (D) *Prorocentrum* spp. (*P. minimum* + *P. triestinum*) (n = 8) and (E) *Scrippsiella trochoidea* (n = 8) are also shown. Clearance rates were corrected using Q_{10} = 2.8 (Hansen et al. 1997). The scales of the circles in the inset boxes are *g* (h^{-1})

plankton cells by engulfing the prey through only the sulcus. The length of the apical horn of *H. triquetra* and *L. polyedrum* is much shorter than those of *G. polygramma* and *S. trochoidea*. Therefore, the mixotrophic dinoflagellates may need an elongated apical horn to capture prey cells through that part of their structure. In conclusion, *Prorocentrum* spp. are able to engulf prey cells from diverse directions, *S. trochoidea* and *G. polygramma* from 2 directions, and most other mixotrophic or heterotrophic dinoflagellates from 1 direction. However, ingesting prey cells from more directions may not cause higher ingestion rates because the maximum ingestion rate of *P. donghaiense* or *P. micans* on a cryptophyte was lower than that of *G. polygramma*.

Growth and ingestion

A unialgal diet of a cryptophyte can support a population growth of *Prorocentrum donghaiense*, *Heterocapsa triquetra*, and *P. micans* 36 to 86% higher than that without added prey under the conditions provided in the present study, while unialgal diets of *P. minimum* and *Scrippsiella trochoidea* can also support a population growth of *Lingulodinium polyedrum* 62 to 67% higher than that without added prey under the conditions provided in the present study. This evidence suggests that these algal predators may be able to increase or maintain their populations by feeding on the algal prey under conditions which are less favorable for phototrophic growth if prey is abundant. To predict the outbreak of red tides dominated by these algal predators, the co-occurring phytoplankton species should be taken into consideration.

The maximum ingestion rates of *Lingulodinium polyedrum* feeding on unialgal diets of *Prorocentrum minimum* and *Scrippsiella trochoidea* under the conditions provided in the present study (0.20 to 0.36 ng C $grazer^{-1}$ d^{-1}) were comparable to or higher than those of *Cochlodinium polykrikoides* (0.16 ng C $grazer^{-1}$ d^{-1})

and *Gonyaulax polygramma* (0.18) on a cryptophyte (ESD = 5.6 µm) obtained under a 14:10 h light:dark cycle of 50 µE m^{-2} s^{-1} (Jeong et al. 2004, 2005). However, the maximum clearance rates of *L. polyedrum* feeding on unialgal diets of *P. minimum* and *S. trochoidea* under the conditions provided in the present study (0.13 to 0.14 µl $grazer^{-1}$ h^{-1}) were comparable to or lower than those of *C. polykrikoides* (0.33 µl $grazer^{-1}$ h^{-1}) and *G. polygramma* (0.18) on a cryptophyte. The lower swimming speed of *L. polyedrum* and consequent lower encounter rate between the predator and prey cells compared with that of *C. polykrikoides* may cause the maximum clearance rate of *L. polyedrum* to be lower than that of *C. polykrikoides*.

Data from these studies show that maximum ingestion rates of 5 red-tide dinoflagellates (*Cochlodinium polykrikoides*, *Gonyaulax polygramma*, *Heterocapsa triquetra*, *Prorocentrum donghaiense*, and *P. micans*) on a cryptophyte and *L. polyedrum* on unialgal diets of *P. minimum* and *S. trochoidea* are positively correlated with the ESDs of the dinoflagellates (Fig. 16). This relationship suggests that the sizes of the algal predators may be an important factor affecting their maximum ingestion rates on the algal prey. However, the maximum ingestion rate of *P. micans* (0.04 ng C $grazer^{-1}$ d^{-1}) feeding on a cryptophyte under the conditions provided in the present study was much lower than that of *C. polykrikoides* on the same prey (0.16 ng C $grazer^{-1}$ d^{-1}) despite having a similar ESD. When feeding on cryptophyte cells, the engulfment by *P. micans* through the suture on the sides of the body may be a less efficient mechanism than that of other mixotrophic dinoflagellates through the sulcus. The time for the cryptophyte cell to be completely engulfed by *P. micans* (629 s) was much longer than that by *C. polykrikoides* (245 s) (Jeong et al. 2004).

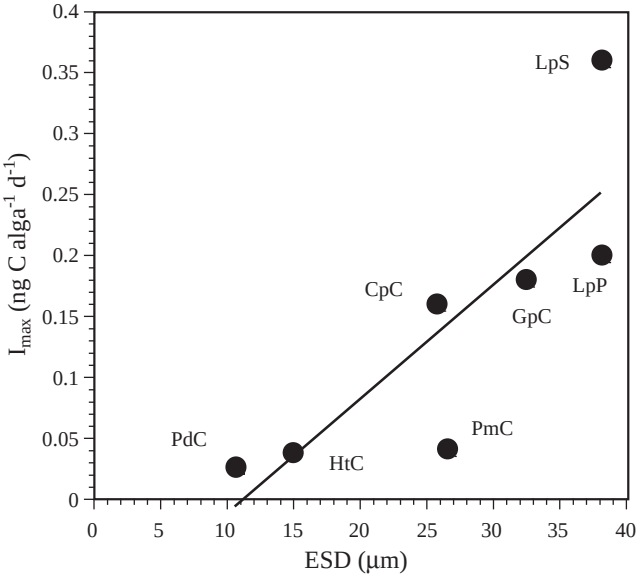


Fig. 16. Maximum ingestion rates (I_{max}) of 5 red-tide dinoflagellates on an unidentified cryptophyte species (ESD = 5.6 µm) and *Lingulodinium polyedrum* on *Scrippsiella trochoidea* and *Prorocentrum minimum* as a function of algal size (ESD, µm). The equation of the linear regression was I_{max} (ng C $alga^{-1}$ d^{-1}) = 0.00934 × (ESD) – 0.106, r^2 = 0.693. CpC: *Cochlodinium polykrikoides* fed on a cryptophyte × GpC: *Gonyaulax polygramma* on a cryptophyte; HtC: *Heterocapsa triquetra* on a cryptophyte; PdC: *P. donghaiense* on a cryptophyte; PmC: *P. micans* on a cryptophyte; LpP: *L. polyedrum* on *P. minimum*; LpS: *L. polyedrum* on *S. trochoidea*

Potential grazing impact

Grazing coefficients attributable to *Prorocentrum donghaiense* (2.67 h^{-1}), *Heterocapsa triquetra* (0.091 h^{-1}) and *P. micans* (0.043 h^{-1}) on co-occurring cryptophytes obtained in the present study correspond to the removals of 93.0, 9.1, and 4.2%, respectively, of cryptophyte populations by each of *P. donghaiense*, *H. triquetra*, and *P. micans* populations in 1 h. In addition, the grazing coefficients attributable to *Lingulodinium polyedrum* on co-occurring small *Prorocentrum* spp. (*P. minimum* + *P. triestinum*) obtained in the present study were up to 0.026 h^{-1} (i.e. up to 2.6% of small *Prorocentrum* spp. populations were removed by a *L. polyedrum* population in 1 h), while those on co-occurring *Scrippsiella trochoidea* were up to 0.011 h^{-1} (i.e. up to 1.1% of *S. trochoidea* populations were removed by a *L. polyedrum* population in 1 h). The results of the present study suggest that these algal predators may sometimes have a considerable grazing impact on populations of co-occurring prey species. However, the grazing rates of some mixotrophic dinoflagellates are known to be affected by light and/or nutrient conditions (Hansen & Nielsen 1997, Steocker et al. 1997, Jeong et al. 1999, Hansen et al. 2000, Jakobsen et al. 2000, Li et al. 2000, Skovgaard et al. 2000). Therefore, the grazing impact of algal predators on co-occurring phytoplankton may also be affected by light and/or nutrient conditions. Further, competition among algal predators for common prey species and predator–prey relationships among the algal predators may affect the grazing impact of the algal predators on co-occurring phytoplankton.

Ecological importance

The feeding by these red-tide dinoflagellates on diverse phytoplankton species may be important in marine planktonic communities in the following ways: (1) there may be broad predator and prey relationships between red-tide dinoflagellates and co-occurring

diverse phytoplankton species. In particular, the feeding by larger mixotrophic red-tide dinoflagellates on smaller red-tide dinoflagellates may be a driving force for succession of dominant species during serial red tides. For example, in Masan Bay, Korea, from June 21 to July, 6 2004, a bloom dominated by a mixture of *Amphidinium* sp. and *Heterosigma akashiwo* were followed by one dominated by a mixture of *Prorocentrum minimum* and *P. triestinum*, by *Cochlodinium polykrikoidea*, and then by *P. micans* in series (Fig. 17). In the present study and Jeong et al. (2004) *P. minimum* and *P. triestinum* which were able to feed on *Amphidinium carterae* and *H. akashiwo* were ingested in turn by *C. polykrikoidea* and *P. micans*. (2) There may be severe competition among red-tide dinoflagellates for common prey species if they co-occur. All algal predators tested in the present study may compete for the phytoplankton species which have ESDs < 12 µm, and *Akashiwo sanguinea* and *Lingulodinium polyedrum*, which are 2 of the most dominant species during the red tides off southern California, USA (Eppley & Harrison 1975, Morey-Gaines 1980, Fiedler 1982, Jeong 1995, Kudela & Cochlan 2000), may also compete for diverse phytoplankton species including *A. tamarense*, *H. triquetra*, and *S. trochoidea*. (3) There may also be competition between red-tide dinoflagellates and co-occurring heterotrophic protists and metazooplankton for common phytoplankton prey species. For example, the red-tide dinoflagellates which have ESDs ≥ 12.6 µm may compete with the heterotrophic dinoflagellates *Gyrodinium dominans* and *G. spirale* (Kim & Jeong 2004), the tintinnid ciliate *Favella taraikaensis* (Taniguchi & Kawakami 1985), and the naked ciliate *Strombidinopsis* sp. (Jeong et al. 1999) for *P. minimum*. *A. sanguinea* and *L. polyedrum* may also compete with *F. ehrenbergii* (Stoecker et al. 1981) and *Strombidinopsis* sp. (Jeong et al. 1999) for *S. trochoidea*. (4) Red-tide dinoflagellates may provide a link between a phytoplankton prey and co-occurring heterotrophic protists and metazooplankton for which phytoplankton is a poor prey item. The heterotrophic dinoflagellates *Protoperidinium* cf. *divergens* and *Polykrikos kofoidii* did not feed or rarely fed on small *Prorocentrum* spp. (*P. minimum* and *P. balticum*), while they fed actively on *L. polyedrum* and *S. trochoidea* which actively ingest small *Prorocentrum* spp. (Jeong & Latz 1994, Jeong et al. 2001). Therefore, the nutrients of the small *Prorocentrum* spp. may be transferred to *P.* cf. *divergens* and *P. kofoidii* via *L. polyedrum* and *S. trochoidea*. *L. polyedrum*, which has the widest phytoplankton prey species offered in the present study, is known to be the preferred prey for and/or to support the positive growth of many protozoan and metazoan grazers such as *Protoperidinium crassipes* (Jeong & Latz 1994), the mixotrophic dinoflagellate *Fragilidium* cf. *mexicanum* (Jeong et al. 1999), *F. ehrenbergii* (Stoecker et al. 1981), the prostomatid ciliate *Tiarina fusus* (Jeong et al. 2002), and the calanoid copepods *Acartia tonsa* and *Paracalanus parvus* (Morey-Gaines 1980) as well. Therefore, the change in dominant species from less preferred prey species to *L. polyedrum* during red tides in series may provide more favorable conditions for satiation and population growth of the heterotrophic predators.

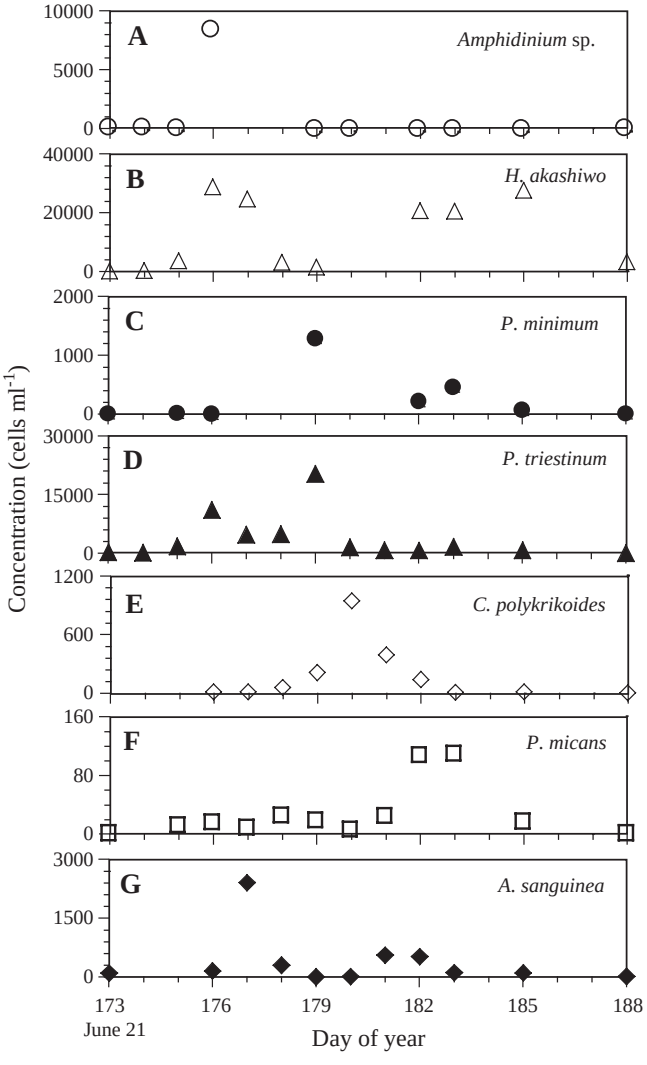


Fig. 17. Abundances of the red-tide organisms (A) *Amphidinium* sp., (B) *Heterosigma akashiwo*, (C) *Prorocentrum minimum*, (D) *P. triestinum*, (E) *Cochlodinium polykrikoides*, (F) *P. micans*, and (G) *Akashiwo sanguinea* at a pier in Masan Bay, Korea, from June 21 to July 6, 2004

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