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Growth and grazing rates of the prostomatid ciliate *Tiarina fusus* on red-tide and toxic algae

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ABSTRACT: We investigated growth and grazing rates of the prostomatid ciliate *Tiarina fusus* when feeding on several species of red-tide and/or toxic algae (RTA). *T. fusus* ingested the dinoflagellates *Lingulodinium polyedrum*, *Scrippsiella trochoidea*, *Heterocapsa triquetra*, *Prorocentrum minimum*, *Amphidinium carterae*, and the raphidophyte *Heterosigma akashiwo*, but rarely consumed the dinoflagellate *Ceratium fusus*, and did not feed on the dinoflagellate *Prorocentrum micans*. *T. fusus* exhibited positive growth on *L. polyedrum*, *S. trochoidea*, and *H. akashiwo*. Specific growth rates of *T. fusus* increased rapidly with increasing density of *L. polyedrum*, *S. trochoidea*, and *H. akashiwo* before saturating between 500 and 1000 ng C ml^{-1}. Maximum specific growth rate of *T. fusus* feeding on *L. polyedrum* (0.47 d^{-1}) was much higher than when feeding on *S. trochoidea* (0.13 d^{-1}) or *H. akashiwo* (0.10 d^{-1}). Threshold prey concentrations (where net growth = 0) for *L. polyedrum*, *S. trochoidea*, and *H. akashiwo* were 34 to 160 ng C ml^{-1}. Maximum ingestion rates of *T. fusus* on *L. polyedrum*, *S. trochoidea*, and *H. akashiwo* were 23.4, 10.2, and 6.5 ng C predator^{-1} d^{-1}, respectively, while maximum clearance rates were 4.5, 0.2, and 0.6 µl predator^{-1} h^{-1}, respectively. *T. fusus* exhibited comparable or higher maximum growth, ingestion, and clearance rates than previously reported for the mixotrophic dinoflagellate *Fragilidium* cf. *mexicanum* or the heterotrophic dinoflagellates *Protoperidinium* cf. *divergens* and *P. crassipes*, when grown on the same prey species. Grazing coefficients calculated by combining field data on abundances of *T. fusus* and co-occurring RTA with laboratory data on ingestion rates obtained in the present study suggest that *T. fusus* sometimes has a considerable grazing impact on the populations of *H. akashiwo*.

KEY WORDS: Dinoflagellate · Feeding · Harmful algal bloom · Ingestion · Protist · Raphidophyte

INTRODUCTION

Algal blooms, often referred to as 'red tides', can alter the balance of food webs and cause large-scale mortalities of fish and shellfish (ECOHAB 1995). Studies of red tide formation and persistence suggest that grazing pressure may play an important role in bloom dynamics (Watras et al. 1985). In particular, grazing by microzooplankton is believed to contribute to the decline of algal blooms (Holmes et al. 1967, Eppley & Harrison 1975). The prostomatid ciliate *Tiarina fusus* sometimes dominates the ciliate abundance and/or biomass in many coastal (Beers & Stewart 1969, Elbrächter 1973, Morey-Gaines 1980, Smetacek 1981, Reid et al. 1985, Tumantseva & Kopylov 1985, Dale & Dahl 1987, Dale 1988, Nomura et al. 1992) and oceanic waters (Mamaeva 1983, Moiseyev 1986, Sleigh et al. 1996). It is often abundant during blooms dominated by the dinoflagellate *Ceratium* spp. (Smetacek 1981, Nielsen 1991, Nielsen & Kiørboe 1994) and/or the raphidophyte *Heterosigma akashiwo* (authors' unpubl. data), and can itself cause red tides (Dale & Dahl 1987; maximum density = 34 000 cells ml^{-1}). However, no data are available for *T. fusus* growth and grazing rates as a function of prey concentration, prey selec-

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tion, threshold prey concentrations, and grazing impact on prey populations.

To better understand the ecological role of *Tiarina fusus* in the planktonic community, we established a monoclonal culture of *T. fusus* and conducted experiments to examine its numerical and functional responses when grown on a variety of toxic and/or red-tide algae (RTA). Our goal was to explore the predator-prey relationship between *T. fusus* and RTA by determining threshold prey concentrations, optimal prey species, and the ciliate's maximum growth, ingestion, and clearance rates. We also estimated grazing coefficients attributable to *Tiarina* on RTA using our data for ingestion rates and accounts of predator and prey abundances in the field samples.

Maximum growth and grazing rates of *Tiarina fusus* on unialgal diets are compared to literature data on mixotrophic or heterotrophic dinoflagellates and other ciliates feeding on the same prey species. Results of the present study provide a basis for understanding the potential of *T. fusus* to influence the population dynamics of RTA.

MATERIALS AND METHODS

Culture of phytoplankton prey. RTA (Table 1) were grown at 19°C in enriched f/2 seawater media (Guillard & Ryther 1962) without silicate, under continuous illumination of 100 µE m^{-2} s^{-1} provided by cool white fluorescent lights. Only cultures in exponential growth phase were used for feeding experiments. The toxic dinoflagellate *Amphidinium carterae* (ACKS 0010) has a toxicity of 1 MU/1.3 × 10^8 cells (Jeong et al. 2001b). Carbon contents for RTA were estimated from cell volume according to Strathmann (1967).

Table 1. Species of autotrophic or mixotrophic prey and predator used in the present study, listed in order of cell volume. Volume (µm^3) of preserved prey cells (to the nearest hundred) was calculated according to the equation: volume = $4/3\pi(ESD/2)^3$. ESD (mean equivalent spherical diameter) was measured with a PAMAS-SVSS particle counter. Cell volume of the predator was estimated from geometrical forms after being satiated with *Lingulodinium polyedrum* and then starved for 1 d. Carbon contents (ng C) per prey and predator were estimated from cell volume according to Strathmann (1967) and Putt & Stoecker (1989), respectively. The number of cells measured (n) was >2000 for prey and 70 for the predator

Species	Approximate volume (±SE)	Carbon content $cell^{-1}$
Heterosigma akashiwo	700 (8)	0.11
Heterocapsa triquetra	1100 (3)	0.15
Prorocentrum minimum	1100 (4)	0.15
Amphidinium carterae	2200 (16)	0.27
Scrippsiella trochoidea	8300 (31)	0.85
Prorocentrum micans	9200 (50)	0.94
Ceratium fusus	11600 (9)	1.26
Lingulodinium polyedrum	28500 (216)	2.50
Tiarina fusus	25400 (76)	4.83

Isolation and culture of *Tiarina fusus*. A 30 cm diameter, 20 µm mesh plankton net was used to collect samples from coastal waters off Jinhae, Korea, during April 2001, when the water temperature was 17°C. The samples were screened gently through 154 µm Nitex mesh and placed in 1 l polycarbonate (PC) bottles. Bottles were spiked with 50 ml of f/2 media, and a mixture of *Lingulodinium polyedrum* and *Scrippsiella trochoidea* was added as food. Bottles were placed on a shelf and incubated at 19°C under continuous illumination of 10 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 *Tiarina fusus* were obtained, they were transferred to 500 or 1000 ml PC bottles of fresh prey every 2 or 3 d. Experiments were conducted when a large volume of *T. fusus* culture was available.

Growth and ingestion rates. Expts 1 to 8 were designed to measure growth, ingestion, and clearance rates of *Tiarina fusus*, as a function of the prey concentration, when feeding on RTA.

Two days before these experiments were conducted, dense cultures of *Tiarina fusus* growing on *Lingulodinium polyedrum* were transferred into 1 l PC bottles containing low concentrations of the target prey. This was done to acclimate the predator to the target prey and minimize possible residual growth resulting from ingestion of prey during batch culture. The bottles were filled to capacity with filtered seawater and placed on a shelf to incubate as above, except that illumination was provided on a 12:12 h light:dark cycle. The abundances of *T. fusus* and prey were determined by enumerating cells in three 1 ml Sedgwick-Rafter counting chambers (SRCs).

For Expts 1 to 8, initial concentrations of *Tiarina fusus* and target prey were established using an autopipette to deliver predetermined volumes of known cell concentrations to the bottles. Triplicate 80 ml PC experiment bottles (mixtures of predator and prey) and triplicate control bottles (prey only) were set up at each predator-prey combination. Triplicate control bottles containing only *T. fusus* were also established at 1 predator concentration. Ten ml of f/2 media were added to all bottles, which were then filled to capacity with freshly filtered seawater and capped. To determine actual predator and prey densities at the beginning of the experiment and after 24, 48, and 72 h incubation, 5 ml aliquots were removed from each

bottle and fixed with 5% Lugol's solution, and all *Tiarina* and all or >200 prey cells in three 1 ml SRCs were enumerated. The range of the actual predator densities at the beginning of Expts 1 to 8 was 4 to 90 *Tiarina* ml^{-1}. Prior to taking subsamples, the condition of *T. fusus* and its prey was assessed with a dissecting microscope. The bottles were filled again to capacity with freshly filtered seawater, capped, and placed on a shelf under the environmental conditions described above. Dilution of the cultures associated with refilling the bottles was considered in calculating growth and ingestion rates.

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

$$\mathrm{IGR} = \frac{\ln(S_{t^2} / S_{t^1})}{t_2 - t_1} \times 24 \quad (1)$$

where S_{t1} and S_{t2} = the concentration of *T. fusus* at consecutive samplings. The final t_2 for calculation was 48 h, which provided the highest specific growth rate.

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

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

where $\mu_{\max}$ = the maximum growth rate (d^{-1}); x = prey concentration (cells ml^{-1} or ng C ml^{-1}), x' = threshold prey concentration (the prey concentration where μ = 0), K_{GR} = the prey concentration sustaining $^1/_2$ $\mu_{\max}$. Data were iteratively fitted to the model using DeltaGraph® (Delta Point).

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

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

where $I_{\max}$ = the maximum ingestion rate (cells predator^{-1} d^{-1} or ng C predator^{-1} d^{-1}); x = prey concentration (cells ml^{-1} or ng C ml^{-1}), K_{IR} = the prey concentration sustaining $^1/_2$ $I_{\max}$.

Attack ratio and successful capture. Expt 9 was designed to determine attack ratio (i.e. number of attempted captures relative to number of physical contacts between predator and prey) and successful capture (i.e. number of prey ingested relative to number of attempted captures) by monitoring the behavior of *Tiarina fusus* in the presence of different RTA. Attempted captures represented physical contacts where the predator remained associated with the prey for longer than 2 s. Successful captures were attacks that resulted in the prey being ingested. Individual *T. fusus* cells starved for 1 d were transferred to a Petri-dish (49 mm in diameter) containing unialgal prey (*Lingulodinium polyedrum*, *Scrippsiella trochoidea*, or *Prorocentrum micans*) with concentrations of 1250 to 1269 ng C ml^{-1}, and each predator was tracked under a dissecting microscope until it successfully engulfed a prey cell or until 1 h had elapsed. For each prey species, the number of predator-prey encounters, attempted prey captures, and ingested prey were recorded for 8 *T. fusus* (i.e. 8 replicates). *Heterosigma akashiwo* cells were too small to clearly detect predator encounters and/or attacks.

Swimming speed. Swimming speeds of 2 prey species (*Heterosigma akashiwo* and *Heterocapsa triquetra*) previously unreported and *Tiarina fusus* were measured at 19°C using a video analyzing system. For each species, aliquots from a dense culture were added to multiwell plates and allowed to acclimate for 30 min. Swimming was then observed and recorded at 40×, with mean and maximum swimming velocity analyzed for fast-swimming cells that exhibited straight linear paths. Average swimming speed was calculated based on the linear displacement of cells in 1 s during single-frame playback. Swimming speeds of more than 10 cells were measured for each species.

Grazing impact. We estimated grazing coefficients attributable to *Tiarina* on RTA by combining field data on abundances of *Tiarina* and prey with ingestion rates of the predator on the prey obtained in the present study.

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

$$g = (1/\Delta t)\{\ln[C_{\mathrm{i}}/(C_{\mathrm{i}} - C_{\mathrm{e}})]\} \quad (4)$$

where Δt (d) is a time interval, C_{e} (cells ml^{-1}) is the number of prey cells eaten by the *Tiarina* population in 1 ml of seawater in 1 d, and C_{i} (cells ml^{-1}) is the initial prey cell concentration on a given day. The values of C_{e} were calculated as:

$$C_{\mathrm{e}} = \mathrm{PIR} \times 1\ \mathrm{d} = \mathrm{IR} \times G \times 1\ \mathrm{d} \quad (5)$$

where PIR is the population ingestion rate of *Tiarina* on a RTA in 1 ml of seawater (prey eaten ml^{-1} d^{-1}), IR is the ingestion rate (prey eaten *Tiarina*$^{-1}$ d^{-1}) of *Tiarina* on a RTA, and G is the abundance (cells ml^{-1}) of *Tiarina* on the same day as C_{i}.

RESULTS

Feeding process and prey species

Tiarina fusus feeds on RTA by engulfment and can contain several prey cells simultaneously. Among RTA offered as prey, *T. fusus* ingested *Lingulodinium poly-*

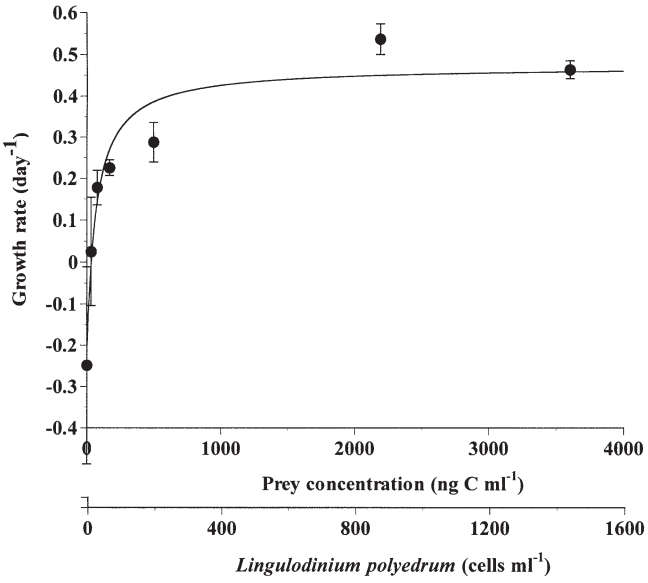

Fig. 1. *Tiarina fusus.* Specific growth rates on *Lingulodinium polyedrum* as a function of mean prey concentration. Symbols represent treatment means ± 1 SE. The curves are fitted by a Michaelis-Menten equation (Eq. 2) using all treatments (see Table 2)

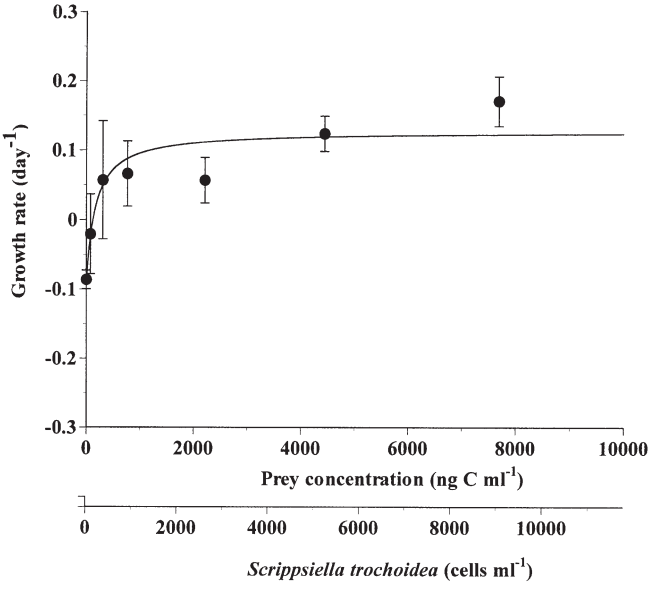

Fig. 2. *Tiarina fusus.* Specific growth rates on *Scrippsiella trochoidea* as a function of mean prey concentration. Symbols represent treatment means ± 1 SE. The curves are fitted as in Fig. 1

edrum, *Scrippsiella trochoidea*, *Heterosigma akashiwo*, *Prorocentrum minimum*, *Amphidinium carterae*, and *Heterocapsa triquetra*, but did not ingest *Prorocentrum micans*. *T. fusus* was able to engulf part of a living *Ceratium fusus* cell or a fragment of a dead cell,

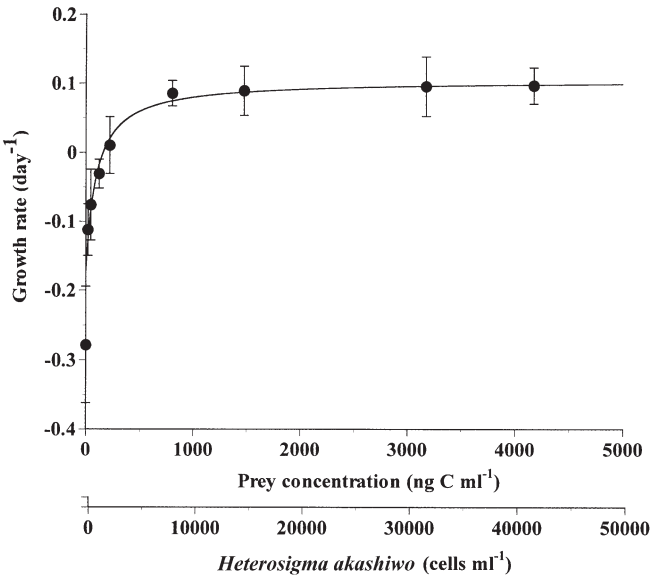

Fig. 3. *Tiarina fusus.* Specific growth rates on *Heterosigma akashiwo* as a function of mean prey concentration. Symbols represent treatment means ± 1 SE. The curves are fitted as in Fig. 1

but could not ingest a whole *C. fusus* because this prey was too long to be included inside the protoplasm of the predator. Between 4 and 5 min after engulfing a single *L. polyedrum*, *T. fusus* was able to ingest a second prey item of the same species. A maximum of 7 semi- or almost completely digested *L. polyedrum* cells were observed inside the protoplasm of individual predators.

Growth rates

Tiarina fusus grew on *Lingulodinium polyedrum*, *Scrippsiella trochoidea*, and *Heterosigma akashiwo*, but failed to grow on *Prorocentrum minimum*, *Ceratium fusus*, *Amphidinium carterae*, *Heterocapsa triquetra*, and *P. micans* (Figs. 1–3, Table 2).

The specific growth rates of *Tiarina fusus* feeding on unialgal diets of *Lingulodinium polyedrum*, *Scrippsiella trochoidea*, and *Heterosigma akashiwo* increased with increasing mean prey concentration below ca. 500 to 1000 ng C ml^{-1}, but were saturated or showed only a slight increase at higher prey concentrations (Figs. 1–3). When the data were fitted to Eq. (2), the maximum specific growth rates (μ_{max}) of *T. fusus* on the different diets were 0.471 d^{-1} for *L. polyedrum*, 0.127 for *S. trochoidea*, and 0.104 for *H. akashiwo* (Table 2). Threshold prey concentrations (where net growth = 0) were 34 (14), 121 (142), and 160 ng C ml^{-1} (1600 cells ml^{-1}) for *L. polyedrum*, *S. trochoidea*, and *H. akashiwo*, respectively (Table 2).

Table 2. *Tiarina fusus* growth and grazing data. Parameters are for numerical and functional response from Eqs. (2) & (3) as presented in Figs. 1–6. μ_{max} (maximum growth rate, d^{-1}), K_{GR} (prey concentration sustaining 0.5 μ_{max}, ng C ml^{-1}), x' (threshold prey concentration, ng C ml^{-1}), I_{max} (maximum ingestion rate, ng C *Tiarina*$^{-1}$ d^{-1}), K_{IR} (prey concentration sustaining 0.5 I_{max}, ng C ml^{-1})

Fig.	Species	μ_{max}	K_{GR}	x'	r^2	I_{max}	K_{IR}	r^2
1 & 4	*Lingulodinium polyedrum*	0.471	101	34	0.68	23.4	669	0.81
2 & 5	*Scrippsiella trochoidea*	0.127	285	121	0.56	10.2	6310	0.79
3 & 5	*Heterosigma akashiwo*	0.104	255	160	0.65	6.5	1850	0.68
6	*Prorocentrum minimum*	−0.006[a]				1.8	5170	0.40
	Ceratium fusus	−0.031[a]						
6	*Amphidinium carterae*	−0.039[a]				2.7	1430	0.46
6	*Heterocapsa triquetra*	−0.081[a]				2.6	1180	0.58
	Prorocentrum micans	−0.338[a]						

[a]Maximum value among the mean growth rates measured at the given prey concentrations

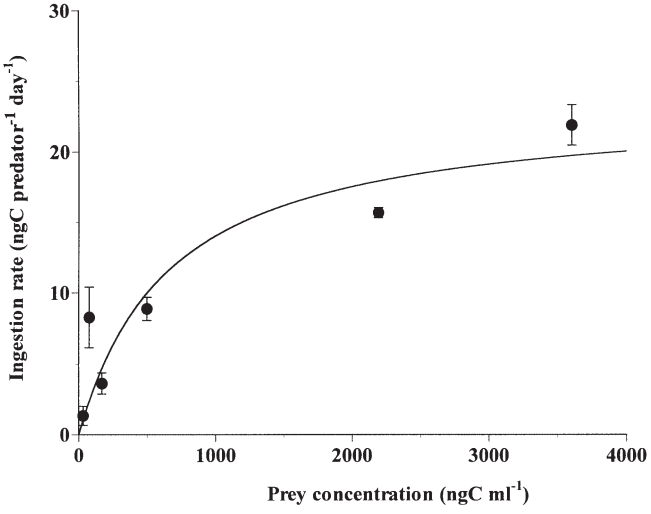

Fig. 4. *Tiarina fusus.* Ingestion rates on *Lingulodinium polyedrum* as a function of mean prey concentration. Symbols represent treatment means ± 1 SE. The curves are fitted by a Michaelis-Menten equation (Eq. 3) using all treatments (see Table 2)

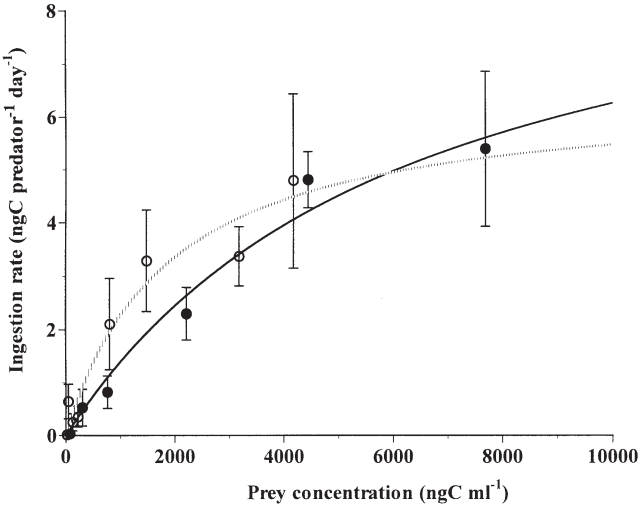

Fig. 5. *Tiarina fusus.* Ingestion rates on *Scrippsiella trochoidea* (●) and *Heterosigma akashiwo* (○) as a function of mean prey concentration. Symbols represent treatment means ± 1 SE. The curves for *S. trochoidea* (solid line) and *H. akashiwo* (dashed line) are fitted as in Fig. 4

Ingestion and clearance rates

The ingestion rates of *Tiarina fusus* on unialgal diets of *Lingulodinium polyedrum*, *Scrippsiella trochoidea*, *Heterosigma akashiwo*, *Prorocentrum minimum*, and *Heterocapsa triquetra* increased rapidly with increasing mean prey concentration below ca. 500 to 4000 ng C ml^{-1} and slowly, but continuously, increased at higher prey concentrations (Figs. 4–6). The ingestion rate of *T. fusus* on *Amphidinium carterae* increased rapidly with increasing mean prey concentrations up to ca. 3000 ng C ml^{-1}, but showed a slight decrease at a higher prey concentration (Fig. 6). When the data were fitted to Eq. (3), the maximum ingestion rates of *T. fusus* in ng C predator^{-1} d^{-1} (and prey cells predator^{-1} d^{-1}) were 23.4 (9.4), 10.2 (12), 6.5 (65), 1.8 (12), 2.7 (10.8), and 2.6 (17) for *L. polyedrum*, *S. trochoidea*, *H. akashiwo*, *P. minimum*, *A. carterae*, and *H. triquetra*, respectively (Table 2).

Maximum clearance rates of *Tiarina fusus* were 4.5 µl predator^{-1} h^{-1} for *Lingulodinium polyedrum*, 0.6 for *Heterosigma akashiwo*, 0.2 for *Scrippsiella trochoidea* and *Prorocentrum minimum*, 0.1 for *Amphidinium carterae*, and 0.01 for *Heterocapsa triquetra*.

Attack ratio and successful capture

Tiarina fusus had a significantly higher attack ratio on *Lingulodinium polyedrum* (mean ± SE: 53 ± 13%) than on *Prorocentrum micans* (0%) (1-tailed *t*-test, $p < 0.01$), but not significantly higher than on *Scrippsiella*

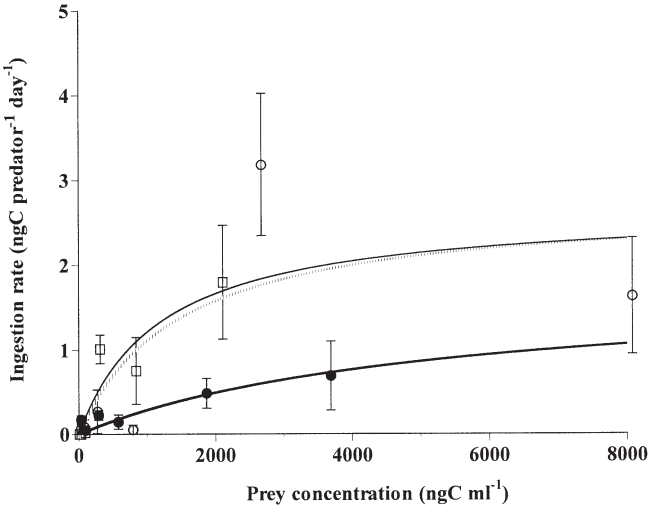

Fig. 6. *Tiarina fusus.* Ingestion rates on *Prorocentrum minimum* (●) and *Amphidinium carterae* (○), and *Heterocapsa triquetra* (□) as a function of mean prey concentration. Symbols represent treatment means ± 1 SE. The curves for *P. minimum* (thick solid line), *A. carterae* (dashed), and *H. triquetra* (thin solid line) are fitted as in Fig. 4

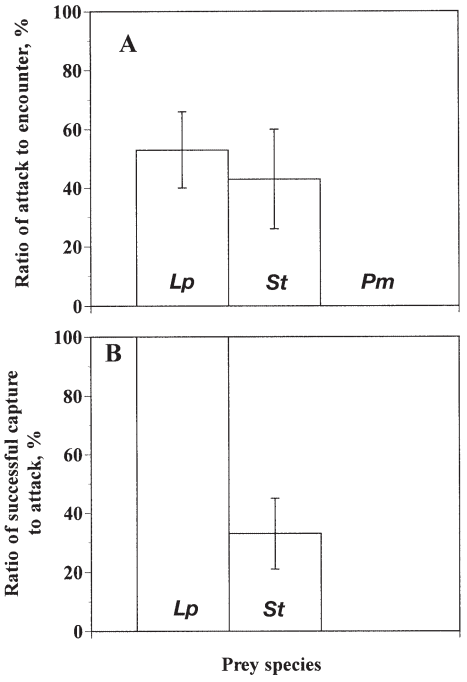

Fig. 7. *Tiarina fusus.* Ratios (%) of attack on *Lingulodinium polyedrum* (*Lp*), *Scrippsiella trochoidea* (*St*), and *Prorocentrum micans* (*Pm*) relative to encounter (A) and of successful capture relative to attack (B). Values are treatment means ± 1 SE

trochoidea (47 ± 17%) ($p > 0.1$) (Fig. 7A). The attack ratio on *S. trochoidea* was significantly higher than on *P. micans* ($p < 0.01$). Similarly, capture success on *L. polyedrum* (100%) was significantly higher than on *S. trochoidea* (33 ± 8%) ($p < 0.01$) (Fig. 7B).

Swimming speed

The average (±SE) and maximum swimming speeds of *Tiarina fusus*, 1353 (±140) and 3125 µm s^{-1}, respectively, were much greater than those of *Heterocapsa triquetra*, 370 (±14) and 496, *Heterosigma akashiwo*, 211 (±9) and 299, or the other prey species offered in the present study (Jeong et al. 1999b).

DISCUSSION

Prey species

Few previous studies have considered prey species of *Tiarina fusus* (Hansen 1991, Nielsen 1991), with *Dinophysis* sp., *Heterocapsa triquetra*, and *Ceratium furca* reported to be eaten by this ciliate. Among the algal prey offered in the present study, *T. fusus* ingested *Lingulodinium polyedrum*, *Scrippsiella trochoidea*, *Heterocapsa triquetra*, *Prorocentrum minimum*, *Amphidinium carterae*, *Heterosigma akashiwo*, and pieces of *Ceratium fusus*. Therefore, *T. fusus* has diverse prey species.

Only a few heterotrophic protists are known to feed on *Heterosigma akashiwo*, a raphidophyte that can cause large-scale mortalities of fish when forming red tides (Honjo 1993). For example, the heterotrophic dinoflagellate *Gyrodinium dominans* can grow on *H. akashiwo* (Nakamura et al. 1995). However, the large tintinnid ciliate *Favella* spp. did not ingest this prey (Taniguchi & Takeda 1988), or ingestion rate was undetectable even though this prey was ingested during the initial incubation (Kamiyama & Arima 2001). Therefore, *Tiarina fusus* is one of a few protistan grazers so far reported to grow and/or prey on *H. akashiwo*.

Smetacek (1981) reported that *Tiarina fusus* was abundant when *Ceratium fusus* dominated the phytoplankton assemblage. We found that *T. fusus* could engulf part of a living *C. fusus* cell or pieces of broken cell, but could not ingest whole cells. Therefore, during the bloom dominated by *C. fusus*, *T. fusus* might grow by feeding on portions of living *Ceratium* cells and pieces of dead *Ceratium* cells, or by ingesting other co-occurring prey species.

Data from this study show that maximum growth and ingestion rates of *Tiarina fusus* are positively correlated with prey cell volume (Fig. 8A,B). This relationship suggests that prey cell volume generally has an effect on growth and ingestion of *T. fusus* on RTA. However, growth and ingestion rates of *T. fusus* on *Scrippsiella*

trochoidea were much higher than those for *Prorocentrum micans* or *Ceratium fusus*, even though those prey are similar in cell volume. In addition, growth and ingestion rates of *T. fusus* on smaller *Heterosigma akashiwo* were also much higher than on larger *Prorocentrum minimum*, *Heterocapsa triquetra*, and *Amphidinium carterae*. Thus, factors other than prey volume may in some cases be important to the feeding activity of *T. fusus*. Interestingly, like the heterotrophic dinoflagellate *Polykrikos kofoidii* (Jeong et al. 2001a), *T. fusus* had a significantly higher attack ratio (number of attempted captures/number of physical contacts) when feeding on *S. trochoidea* than when feeding on *P. micans*. These observations suggest that *S. trochoidea* may be more attractive to *T. fusus* as prey than *P. micans*.

Growth and ingestion

Maximum ingestion rates (I_{max}) of *Tiarina fusus* on red-tide dinoflagellates obtained in this study are comparable to or higher than those previously reported for a mixotrophic dinoflagellate and heterotrophic dinoflagellates, but lower than those for larger ciliates on the same prey (see Table 3). For example, the I_{max} of *T. fusus* on *Lingulodinium polyedrum* is similar to that of *Polykrikos kofoidii*, higher than that of *Fragilidium* cf. *mexicanum*, *Protoperidinium* cf. *divergens*, and *P. crassipes*, but much lower than that of *Strombidinopsis* sp. when corrected to 19°C using Q_{10} = 2.8 (Hansen et al. 1997). The I_{max} of *T. fusus* on *Scrippsiella trochoidea* is slightly lower than that for *P. kofoidii*, but much lower than those for *Strombidinopsis* sp. or *Favella* sp. This evidence suggests that raptorial feeding on prey directly captured by the narrow, but flexible ciliated mouth (*T. fusus*) is a similarly effective feeding mechanism to engulfing prey captured by a tow filament (*P. kofoidii*), more effective than pallium feeding on prey captured by a tow filament (*Protoperidinium* spp.), but less effective than engulfing prey using rows of cilia near the mouth (*Strombidinopsis* spp. and *Favella* spp.).

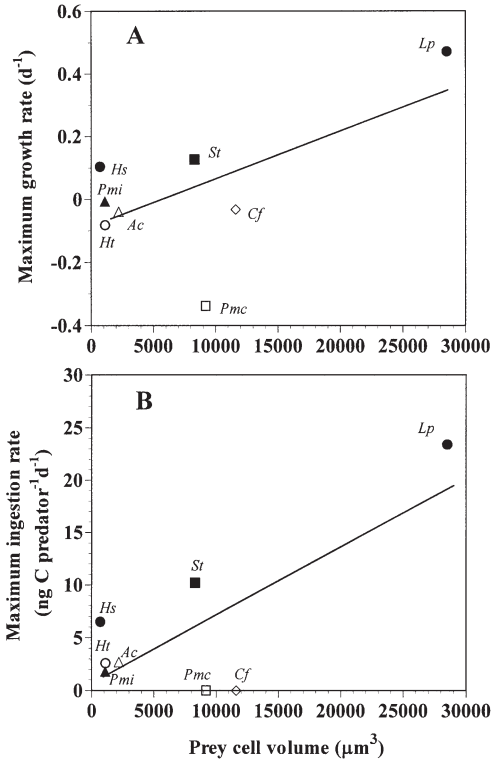

Fig. 8. *Tiarina fusus.* (A) Maximum growth (μ_{max}) and (B) ingestion (I_{max}) rates on 8 red-tide algal prey as a function of prey cell volume (pcv). The equations of the linear regression were (A) μ_{max} (d^{-1}) = 1.5×10^{-5} (pcv) – 9.2×10^{-2}, R^2 = 0.38, and (B) I_{max} (ng C predator d^{-1}) = 6.4×10^{-4} (pcv) + 0.86, R^2 = 0.59. *Ac*: *Amphidinium carterae*, *Cf*: *Ceratium fusus*, *Ha*: *Heterosigma akashiwo*, *Ht*: *Heterocapsa triquetra*, *Lp*: *Lingulodinium polyedrum*, *Pmc*: *Prorocentrum micans*, *Pmi*: *P. minimum*, *St*: *Scrippsiella trochoidea*

The maximum growth rate of *Tiarina fusus* on *Lingulodinium polyedrum* is much lower than that of *Polykrikos kofoidii* when corrected to 19°C using Q_{10} = 2.8 (Hansen et al. 1997) (Table 3), while the I_{max} of the former predator was similar to that of the latter predator. The average and maximum swimming speeds of *T. fusus*, 1353 and 3125 µm s^{-1}, respectively, are much higher than those of *P. kofoidii* (657 and 911 µm s^{-1}, respectively) (Jeong et al. 2001a). Thus, greater energy loss due to higher swimming speed of *T. fusus* relative to *P. kofoidii* might account for differences in growth rates.

Grazing impact

Natural abundances of *Tiarina fusus* range from 0 to 34 500 cells ml^{-1} in coastal marine waters (Smetacek 1981, Dale & Dahl 1987, Dale 1988, Nielsen 1991, Nomura et al. 1992, Nielsen & Kiørboe 1994, F. Reid unpubl. data, authors' unpubl. data). However, the grazing impact by *T. fusus* on RTA is difficult to assess due to the lack of data on the abundances of this predator and its co-occurring prey. Grazing coefficients attributable to *T. fusus* on predominant co-occurring RTA, calculated by combining field data on abundances of *T. fusus* and co-occurring RTA with laboratory data on ingestion rates obtained in the present study, are 0.0004 to 0.23 d^{-1} (i.e. 0.04 to 26% of RTA populations were removed by a *Tiarina* population d^{-1}) (Table 4). In particular, the grazing coefficient of *T. fusus* on *Heterosigma akashiwo* in Korean coastal waters (maximum density = 8 *Tiarina* ml^{-1}) is 0.23 d^{-1}, and thus *T. fusus* may sometimes have a considerable

Table 3. Comparison of growth, ingestion and clearance rates of *Tiarina fusus* and other protists on the same red-tide algal prey. Rates are corrected to 19°C using Q_{10} = 2.8 (Hansen et al. 1997). PV: predators' volume as $\times 10^3$ µm^3; μ_{max}: maximum growth rate, d^{-1}; I_{max}: maximum ingestion rate, ng C predator^{-1} d^{-1}; C_{max}: maximum clearance rate, µl predator^{-1} h^{-1}; NC: naked ciliate; TC: tintinnid ciliate; HD: heterotrophic dinoflagellate; MD: mixotrophic dinoflagellate

Prey species	Predator	PV	μ_{max}	I_{max}	C_{max}	Source
Lingulodinium polyedrum	*Tiarina fusus* (NC)	23	0.47	23	4.5	This study
	Polykrikos kofoidii (HD)	43	0.83	24	5.9	Jeong et al. (2001a)
	Protoperidinium cf. *divergens* (HD)	119	0.48	12	0.7	Jeong & Latz (1994)
	Protoperidinium crassipes (HD)	204	0.31	5	0.5	Jeong & Latz (1994)
	Fragilidium cf. *mexicanum* (MD)	85	0.26	7	4.0	Jeong et al. (1999a)
	Strombidinopsis sp. (NC)	560	0.83	222	110	Jeong et al. (1999b)
Scrippsiella trochoidea	*Tiarina fusus* (NC)	23	0.13	10	0.1	This study
	Polykrikos kofoidii (HD)	43	0.97	17	1.1	Jeong et al. (2001a)
	Strombidinopsis sp. (NC)	560	0.67	207	41	Jeong et al. (1999b)
	Favella sp. (TC)			237	43	Stoecker et al. (1981)

Table 4. Estimation of grazing impact by a *Tiarina* population on a red-tide and/or toxic algae population using the equations in Figs. 4–6 and the abundances of *T. fusus* and RTA. PIR: population ingestion rate (prey eaten ml^{-1} d^{-1}); *g*: grazing coefficient (d^{-1})

Predator (*Tiarina*)	Prey species	Predator density (cells ml^{-1})	Prey density (cells ml^{-1})	PIR	*g*	Source
T. fusus	*Heterosigma akashiwo*	8.0	670	138	0.230	Authors' (unpubl. data)[a]
	Prorocentrum minimum	8.0	123	2.2	0.018	Authors' (unpubl. data)[a]
	Scrippsiella trochoidea	0.24	260	0.104	0.0004	F. Reid (unpubl. data)[b]
	Lingulodinium polyedrum	0.24	3.6	0.012	0.003	F. Reid (unpubl. data)[b]
	L. polyedrum	0.29	0.2	0.001	0.004	F. Reid (unpubl. data)[b]

[a]Samples were taken from the coastal waters off Masan, Korea
[b]Samples were taken from John Ruel's pier, CA, USA

grazing impact on *H. akashiwo* populations. Similarly, *T. fusus* abundance was highest (12.8 *Tiarina* ml^{-1}) in Tokyo Bay during May, when *H. akashiwo* forms red tides (Nomura et al. 1992, Han & Furuya 2000). Therefore, *T. fusus* may also play an important role in *H. akashiwo* bloom dynamics in Tokyo Bay. By contrast, the grazing coefficient of *T. fusus* on *Lingulodinium polyedrum* (0.004 d^{-1}) in a coastal water off southern California, USA, was low due to low abundance of the predator. However, *T. fusus* had a greater impact on *L. polyedrum* than co-occurring *Protoperidinium* spp. (0.002 d^{-1}). Clearly, additional studies that provide information on predator and prey abundances in the field are needed to better understand the role of *T. fusus* in the population dynamics of RTA.

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