

Feeding by protists and copepods on the heterotrophic dinoflagellates *Pfiesteria piscicida*, *Stoeckeria algicida*, and *Luciella masanensis*

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ABSTRACT: To investigate interactions between the heterotrophic dinoflagellates *Pfiesteria piscicida*, *Stoeckeria algicida*, and *Luciella masanensis* and their protozoan and metazoan predators, we measured the growth and/or ingestion rates of the heterotrophic dinoflagellate *Oxyrrhis marina*, the ciliate *Strombidinopsis jeokjo*, and the calanoid copepods *Acartia* spp. (*A. hongii* and *A. omorii*) when fed on *P. piscicida*, *S. algicida*, and *L. masanensis*. The maximum growth and ingestion rates of *O. marina* fed on *P. piscicida* (0.66 d⁻¹ and 0.33 ng C predator⁻¹ d⁻¹, respectively) were markedly higher than those of the same predator fed on *S. algicida* (0.22 d⁻¹ and 0.14 ng C predator⁻¹ d⁻¹, respectively) or *L. masanensis* (0.04 d⁻¹ and 0.07 ng C predator⁻¹ d⁻¹, respectively). The maximum growth and ingestion rates of *S. jeokjo* fed on *P. piscicida* and *S. algicida* (1.61 to 1.77 d⁻¹ and 44 to 49 ng C predator⁻¹ d⁻¹, respectively) were much higher than when fed on *L. masanensis* (–0.1 d⁻¹ and 10 ng C predator⁻¹ d⁻¹, respectively). *S. jeokjo* had significantly higher attack ratios (number of attempted captures relative to number of physical contacts between predator and prey) when fed on *P. piscicida* and *S. algicida* (18 to 25 %) than on *L. masanensis* (5 %). Similarly, successful capture (number of prey ingested relative to number of attempted captures) of *P. piscicida* and *S. algicida* (82 to 87 %) was significantly higher than that of *L. masanensis* (2 %). *L. masanensis* may have defensive behavior or chemical protection against predation. However, maximum ingestion rates of *Acartia* spp. fed on these dinoflagellate species were similar. In understanding the population dynamics and predator–prey interactions of these 3 closely related dinoflagellate species, it is important to distinguish between predation by protists and by copepods.

KEY WORDS: Graze · Growth · Harmful algal bloom · Ingestion · Marine · Protist · Red tide

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INTRODUCTION

Since the small heterotrophic dinoflagellate *Pfiesteria piscicida* (order Peridiniales and family Pfiesteriaceae) was first discovered in the early 1990s (Steidinger et al. 1996), several more dinoflagellate species in the family Pfiesteriaceae, such as *Cryptoperidiniopsis brodyi*, *Luciella atlantis*, *L. masanensis*, *Pseudopfiesteria shumwayae*, and *Stoeckeria algicida*, have been discovered (Jeong et al. 2005b, Litaker et al. 2005, Steidinger et al. 2006, Mason et al. 2007). Both scientists and the public have paid attention to these

dinoflagellates because some of the species are harmful to fish (Noga et al. 1996, Glasgow et al. 2001), shellfish (Springer et al. 2002, Shumway et al. 2006), and humans (Schmechel & Koltai 2001). These dinoflagellates often co-occur in estuaries as well as in coastal waters (e.g. Lewitus et al. 2002). Their cell length and width are approximately 5 to 25 µm and 3 to 20 µm, respectively, and the ranges of the cell lengths and widths overlap between species (Jeong et al. 2006). Further, their shapes are very similar, whereas their plate patterns and DNA sequences clearly differ (Steidinger et al. 1996, Jeong et al. 2005b, 2006, Litaker et

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al. 2005, Rublee et al. 2005, Marshall et al. 2006). Therefore, it is very difficult to distinguish one species from the others in fixed samples. They feed on prey with the same feeding mechanism, i.e. by using a peduncle (a feeding tube) (Burkholder & Glasgow 1995, Jeong et al. 2005a). An important question arises: do they have similar ecological roles in marine plankton communities? With respect to their ecological roles, their feeding and mortality due to predation are important factors. Recent studies (Jeong et al. 2006, 2007a) have revealed that the kinds of prey species which *L. masanensis* (previously *Lucy*) feeds on were very similar to those consumed by *P. piscicida*. However, the kinds of prey species which *P. piscicida* and *L. masanensis* feed on are very different from those consumed by *S. algicida*, which is known to feed only on the raphidophyte *Heterosigma akashiwo* and blood cells (Jeong et al. 2005b, 2007a). Also, the growth and ingestion rates of *P. piscicida* feeding on optimal and suboptimal algal prey and fish blood cells were usually higher than those of *L. masanensis* feeding on the same prey species (Jeong et al. 2006, 2007a). Therefore, with regard to feeding, *P. piscicida*, *L. masanensis*, and *S. algicida* have different roles.

With regard to mortality due to predation, limited studies have thus far reported on the growth and/or ingestion rates of the predators on *Pfiesteria piscicida* (Mallin et al. 1995, Stoecker et al. 2000, Stoecker & Gustafson 2002, Gransden & Lewitus 2003, Set  l   et al. 2005, Lewitus et al. 2006); these predators include the naked ciliates *Euplotes* spp., *Strombidium* spp., and *Strobilidium* sp., the tintinnid ciliates *Tintinnopsis* spp., *Tintinnidium* spp., *Nolaculus* spp., *Favella* spp., rotifers, and the copepod *Acartia tonsa* (Stoecker et al. 2000, Stoecker & Gustafson 2002, Gransden & Lewitus 2003, Lewitus et al. 2006). Moreover, no studies have thus far been conducted on predators that feed on *Luciella masanensis* and *Stoeckeria algicida*. Therefore, to investigate the mortality rates due to predation for these 2 dinoflagellates and to investigate whether they play ecological roles similar to *P. piscicida*, we need to measure the numerical (i.e. growth rate) and functional responses (i.e. ingestion rate) of common predators to prey concentration when fed on *P. piscicida*, *S. algicida*, and *L. masanensis*.

Heterotrophic dinoflagellates, ciliates, and copepods are some of the major components in marine planktonic food webs. Heterotrophic dinoflagellates and ciliates are ubiquitous and occasionally dominate within the microzooplankton in terms of abundance and/or biomass, while copepods dominate similarly within the mesozooplankton (Lessard 1991, Jeong 1999, Kimmel & Roman 2004, Turner et al. 2005). These 3 groups sometimes have considerable grazing or predation

impact on populations of diverse prey (Verity et al. 1999, Kim & Jeong 2004). Heterotrophic dinoflagellates feed on a variety of prey (for review, see Jeong 1999). Ciliates also feed on diverse prey, including bacteria (e.g. Sherr & Sherr 2002), algae (Montagnes et al. 1996, Kamiyama & Arima 2001), and heterotrophic dinoflagellates (Jeong et al. 2004). However, no studies have been conducted on predator–prey relationships among heterotrophic dinoflagellates, and only a few studies have been conducted on predation by ciliates on heterotrophic dinoflagellates (Stoecker et al. 2000, Gransden & Lewitus 2003, Jeong et al. 2004, Lewitus et al. 2006). The lack of information regarding the interactions among heterotrophic dinoflagellates and between ciliates and heterotrophic dinoflagellates restricts our understanding of the cycling of materials, energy flow, and population dynamics of dominant heterotrophic dinoflagellates in marine food webs. Copepods feed on diverse prey, including algae (e.g. Turner et al. 2005), heterotrophic dinoflagellates, and ciliates (Gifford & Dagg 1991, Jeong et al. 2001, Roman et al. 2006). However, information available on predation by copepods on heterotrophic dinoflagellates is also much less than that for phototrophic dinoflagellate prey. When *Pfiesteria piscicida*, *Stoeckeria algicida*, and *Luciella masanensis* are offered singularly as prey to heterotrophic dinoflagellates, ciliates, and copepods, these predators may display different patterns in their functional responses to the concentration of each prey species.

To explore differential feeding by heterotrophic dinoflagellates, ciliates, and copepods on heterotrophic dinoflagellates, we established cultures of *Pfiesteria piscicida*, *Stoeckeria algicida*, and *Luciella masanensis* as prey, and the heterotrophic dinoflagellate *Oxyrrhis marina*, the ciliate *Strombidinopsis jeokjo*, and the calanoid copepods *Acartia* spp. (*A. hongii* and *A. omorii*) as predators, and conducted experiments to measure the growth and/or ingestion rates of each predator feeding on each prey species. These prey and predators often coexist in Masan Bay and/or the coastal waters off Kunsan, Korea. The results of the present study provide a basis for understanding the interactions between *P. piscicida*, *S. algicida*, and *L. masanensis* and their predators and the ecological roles of these 3 heterotrophic dinoflagellates in marine planktonic communities.

MATERIALS AND METHODS

Preparation of experimental organisms. For the isolation and culture of *Pfiesteria piscicida* (GenBank Accession number AM231031), *Stoeckeria algicida* (AJ841809), and *Luciella masanensis* (AM050344),

plankton samples were collected using water samplers from the surface waters off Incheon and Masan Bay, Korea (Table 1). The mixotrophic dinoflagellate *Amphidinium carterae* or the raphidophyte *Heterosigma akashiwo* was provided as prey, and a clonal culture of each prey species was established by 2 serial single-cell isolations as described in Jeong et al. (2005a, 2006, 2007a). These prey cultures were maintained at 20°C for >3 mo before experiments were conducted. The volume of *P. piscicida*, *S. algicida*, and *L. masanensis* cells (n = 20 for each species), collected just before experiments began, was calculated by geometric formula, and the carbon content of *P. piscicida* (0.06 ng C cell⁻¹), *S. algicida* (0.08), and *L. masanensis* (0.06) was estimated from the cell volume according to the method of Menden-Deuer & Lessard (2000).

For the isolation and culture of the predator *Oxyrrhis marina* (or *Strombidinopsis jeokjo*), plankton samples were collected with a 25 cm diameter, 25 µm mesh plankton net (or a 40 cm diameter, 25 µm mesh net) (Table 1). A clonal culture of each protistan predator was established by 2 serial single-cell isolations as described in Jeong et al. (2003, 2004). These predator cultures were maintained at 20°C for >1 mo before experiments were conducted.

Using a 303 µm mesh net, copepods were collected from the mouth of the Keum Estuary, Kunsan, Korea, in November 2005 and were then acclimatized in a 20°C room in the presence of *Prorocentrum minimum* for 1 wk (Table 1). Adult female *Acartia* spp. (*A. hongii* and *A. omorii*) were used for these experiments. *A. hongii* (Soh & Suh 2000) and *A. omorii*, which coexist in the coastal waters off western Korea, are similar and it is impossible to distinguish between the 2 species when they are in a viable state.

Growth and ingestion rates. These experiments were designed to measure the growth and/or ingestion rates of *Oxyrrhis marina*, *Strombidinopsis jeokjo*, and *Acartia* spp. as a function of the prey concentration when fed on each of *Pfiesteria piscicida*, *Stoeckeria algicida*, and *Luciella masanensis* (Table 2).

One day before these experiments were conducted, dense cultures of *Oxyrrhis marina* growing on *Amphidinium carterae* were transferred into 500 ml polycarbonate (PC) bottles containing 2 different concentrations of the target prey (ca. 50 cells ml⁻¹ for 5 lower prey concentrations and ca. 1000 cells ml⁻¹ for 4 upper prey concentrations; see Table 2). This was done to minimize possible residual growth resulting from the ingestion of prey during batch culture. The bottles were filled to capacity with freshly filtered seawater,

Table 1. Isolation and maintenance conditions of the experimental organisms

Organism	Location	Time	Temp. (°C)	Salinity (psu)	Prey species	Concentration (cells ml ⁻¹)	Source
<i>Pfiesteria piscicida</i>	Off Incheon	Jul 2005	24.0	25.4	<i>Amphidinium carterea</i>	20 000–30 000	Jeong et al. (2006)
<i>Stoeckeria algicida</i>	Masan Bay	Jul 2004	24.8	20.6	<i>Heterosigma akashiwo</i>	30 000	Jeong et al. (2005a)
<i>Luciella masanensis</i>	Masan Bay	Apr 2005	16.0	28.0	<i>Amphidinium carterea</i>	30 000–40 000	Jeong et al. (2007a)
<i>Oxyrrhis marina</i>	Keum Estuary	May 2001	16.0	27.7	<i>Amphidinium carterea</i>	8000	Jeong et al. (2003)
<i>Strombidinopsis jeokjo</i>	Off Kunsan	Aug 2005	25.1	27.0	<i>Prorocentrum micans</i>	5000	As in Jeong et al. (2004)
<i>Acartia</i> spp. ^a	Keum Estuary	Nov 2005	12.5	24.6	<i>Prorocentrum minimum</i>	10 000	

^a*A. hongii* and *A. omorii*

Table 2. Design of experiments

Expt	Prey		Predator	
	Species	Density (cells ml ⁻¹)	Species	Density (cells ml ⁻¹) ^{a,b}
1	<i>Pfiesteria piscicida</i>	0, 36, 153, 298, 530, 1170, 3500, 8260, 15 370	<i>Oxyrrhis marina</i>	9–361 (363)
2	<i>Stoeckeria algicida</i>	0, 48, 190, 428, 976, 2970, 4589, 10 510, 15 940	<i>Oxyrrhis marina</i>	9–490 (493)
3	<i>Luciella masanensis</i>	0, 57, 104, 210, 477, 1170, 3080, 9820, 15 260	<i>Oxyrrhis marina</i>	14–452 (452)
4	<i>Pfiesteria piscicida</i>	0, 42, 65, 162, 388, 924, 1570, 4130, 8200, 15 090	<i>Strombidinopsis jeokjo</i>	3.5–8.3 (6.9)
5	<i>Stoeckeria algicida</i>	0, 40, 85, 170, 488, 846, 1760, 3650, 6020, 11 640	<i>Strombidinopsis jeokjo</i>	2.8–7.5 (6.6)
6	<i>Luciella masanensis</i>	0, 61, 100, 242, 478, 1050, 2160, 5410, 10 680, 17 420	<i>Strombidinopsis jeokjo</i>	4.4–12.7 (9.2)
7	<i>Pfiesteria piscicida</i>	39, 67, 239, 775, 2570, 8560, 21 790	<i>Acartia</i> spp. ^c	20
8	<i>Stoeckeria algicida</i>	95, 416, 965, 2940, 5350, 8140, 14 460	<i>Acartia</i> spp.	20
9	<i>Luciella masanensis</i>	49, 95, 266, 1020, 2980, 10 870, 27 810	<i>Acartia</i> spp.	20

^aInd. l⁻¹ for *Acartia* spp.; ^bValues in parentheses are from control bottles; ^c*A. hongii* and *A. omorii*

capped, and placed on plankton wheels rotating at 0.9 rpm and incubated at 20°C under the illumination of $20 \mu E m^{-2} s^{-1}$ on a 14 h light:10 h dark cycle. To monitor the conditions and interaction between predator and prey species, the cultures were periodically removed from the rotating wheels, observed through the surface of the capped bottles with a dissecting microscope, and then returned to the rotating wheels. Once the target prey cells were no longer detectable, three 1 ml aliquots from each bottle were counted using a compound microscope to determine the cell concentrations of *O. marina*, and the cultures were then used to conduct experiments.

For each experiment, the initial concentrations of *Oxyrrhis marina* and a target prey species (each of *Pfiesteria piscicida*, *Stoeckeria algicida*, and *Luciella masanensis*) were established using an autopipette to deliver predetermined volumes of known cell concentrations to the bottles. Triplicate 42 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 *O. marina* were also established at 1 predator concentration. To obtain similar water conditions, the water of a predator culture was filtered through a 0.7 μm GF/F filter (Whatman) and then added to the prey control bottles in the same amount as the volume of the predator culture added into the experiment bottles for each predator–prey combination. All the bottles were then filled to capacity with freshly filtered seawater and capped. To determine the actual predator and prey densities at the beginning of the experiment, a 5 ml aliquot was removed from each bottle, fixed with 5% Lugol's solution, and examined with a compound microscope to determine predator and prey abundance by enumerating the cells in three 1 ml Sedgwick-Rafter chambers (SRCs). The bottles were refilled to capacity with freshly filtered seawater, capped, and placed on rotating wheels under the conditions described above. Dilution of the cultures associated with refilling the bottles was considered in calculating growth and ingestion rates. A 10 ml aliquot was taken from each bottle at 48 h and fixed with 5% Lugol's solution, and the abundances of *O. marina* and the target prey were determined by counting all or >300 cells in three 1 ml SRCs. Prior to taking subsamples, the condition of *O. marina* and its prey was assessed using a dissecting microscope as described above.

One day before these experiments were conducted, dense cultures of *Strombidinopsis jeokjo* growing on *Prorocentrum micans* were transferred into a 500 ml PC bottle containing 2 concentrations of the target prey (50 cells ml⁻¹ for 6 lower prey concentration and 1000 cells ml⁻¹ for 4 upper prey concentration; see

Table 2). The bottle was filled to capacity with filtered seawater and placed on a rotating wheel for incubation as described above. When the prey cells were undetectable, the abundance of *S. jeokjo* was determined by enumerating cells in three 1 ml SRCs.

The initial concentrations of *Strombidinopsis jeokjo* and the target prey were established using an autopipette. Triplicate 42 ml PC experiment bottles and triplicate control bottles (prey only) for each predator–prey combination and triplicate control bottles containing only *S. jeokjo* at 1 predator concentration were also established as described above. To determine actual predator and prey concentrations at the beginning of the experiment, a 5 ml aliquot was removed from each bottle and, after 24 h of incubation, a 10 ml aliquot was removed and fixed with 5% Lugol's solution; all predator cells and all or >200 prey cells in three to five 1 ml SRCs were enumerated. The bottles were refilled to capacity with freshly filtered seawater, capped, and placed on rotating wheels under the environmental conditions described above.

The specific growth rate of *Oxyrrhis marina* (or *Strombidinopsis jeokjo*), μ (d⁻¹), was calculated as:

$$\mu (d) = [\ln (P_t/P_0)] / t \quad (1)$$

where P_0 and P_t are the concentration of *O. marina* (or *S. jeokjo*) at 0 h and 48 h (or 24 h for *S. jeokjo*), respectively.

Data for *Oxyrrhis marina* (or *Strombidinopsis jeokjo*) growth rates were fitted to a Michaelis-Menten equation:

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

where μ_{\max} is the maximum growth rate d⁻¹, x is prey concentration (cells ml⁻¹ or ng C ml⁻¹), x' is threshold prey concentration (the prey concentration where $\mu = 0$), and K_{GR} is the prey concentration sustaining 0.5 μ_{\max} . Data were iteratively fitted to the model using DeltaGraph® (Delta Point).

Ingestion and clearance rates were calculated using the equations of Frost (1972) and Heinbokel (1978). The incubation time was the same as that for estimating the growth rate. Ingestion rate data for *Oxyrrhis marina* (or *Strombidinopsis jeokjo*) were fitted to a Michaelis-Menten equation:

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

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 0.5 I_{\max} .

For the experiment on the feeding by copepods, initial concentrations of the target prey were established

using an autopipette, and those of *Acartia* spp. were obtained by individually transferring the copepods using a Pasteur pipette (Table 2). Triplicate 500 ml PC experiment bottles and triplicate control bottles (prey only) were set up at each predator–prey combination. To determine actual prey densities at the beginning of the experiment, a 20 ml aliquot was removed from each bottle, fixed with 5% Lugol's solution, and examined with a compound microscope to determine prey abundance by enumerating cells in three 1 ml SRCs. The bottles were filled again to capacity with freshly filtered seawater, capped, and placed on rotating plankton wheels and incubated at 20°C as described above.

After 48 h of incubation, 20 ml aliquots were taken from each bottle and fixed with 5% Lugol's solution, and the abundance of the target prey was determined by counting all or >300 cells in three 1 ml SRCs. After incubation for 48 h, *Acartia* spp. were counted. Mortality of *Acartia* spp. was zero at the end of the incubation. Ingestion and clearance rates were calculated using the equations of Frost (1972) as described above.

Attack ratio and successful capture. This experiment was designed to investigate why the growth and ingestion rates of *Strombidinopsis jeokjo* feeding on *Luciella masanensis* were much lower than those achieved on a diet of *Pfiesteria piscicida* or *Stoeckeria algicida*.

In this experiment the attack ratio (i.e. the number of attempted captures relative to the number of physical contacts between predator and prey) and successful capture ratio (i.e. the number of prey ingested relative to the number of attempted captures) were determined by monitoring the behavior of *Strombidinopsis jeokjo* in the presence of *Pfiesteria piscicida*, *Stoeckeria algicida*, or *Luciella masanensis*. Attempted captures represented generation of feeding current by undulating cilia. Successful captures were attacks that resulted in the prey being ingested. Additionally, to explore possible adverse effects (i.e. chemical effects) of the extract of *L. masanensis*, the water of an *L. masanensis* culture (density = ca. 20 000 cells⁻¹) was filtered through a 0.7 µm GF/F filter and then added into bottles containing the optimal prey species, *P. piscicida*.

Individual *Strombidinopsis jeokjo* cells starved for 1 d were transferred to a Petri dish (50 mm in diameter) containing each prey species (*Pfiesteria piscicida*, *Stoeckeria algicida*, and *Luciella masanensis*) and then each predator was tracked under a dissecting microscope until it successfully engulfed a prey cell or until ca. 10 min had elapsed. For each prey species, the number of predator–prey encounters, attempted prey captures, and ingestion of prey were recorded for 10 to 20 *S. jeokjo* cells (i.e. 10 to 20 replicates).

RESULTS

Growth rates

Oxyrrhis marina grew well feeding on *Pfiesteria piscicida* and *Stoeckeria algicida*, but failed to grow when fed *Luciella masanensis* (Fig. 1). The specific growth rates of *O. marina* consuming *P. piscicida* and *S. algicida* increased rapidly with increasing mean prey concentration (ca. 30 to 60 ng C ml⁻¹) but increased only slightly at higher concentrations (Fig. 1A,B). When the

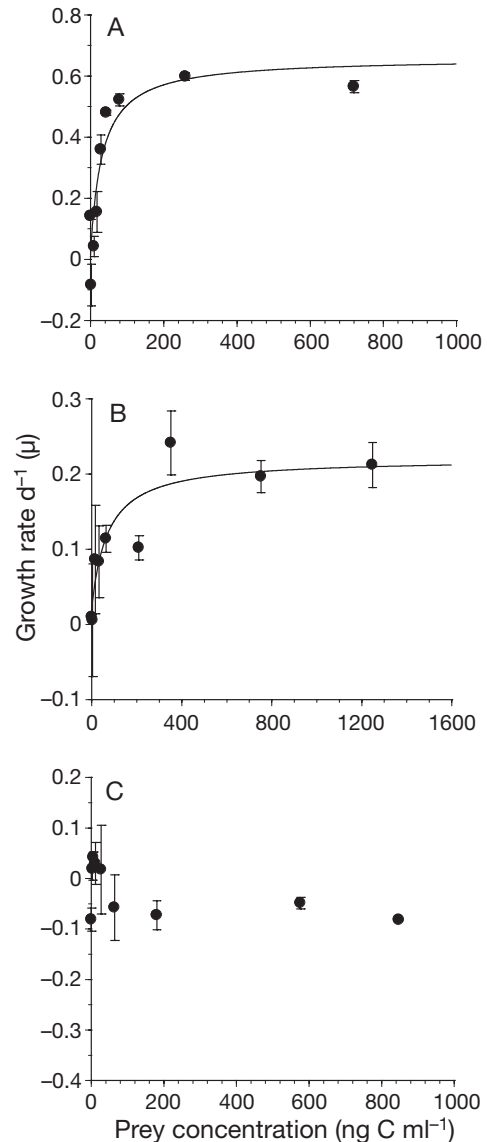


Fig. 1. Mean (± 1 SE) specific growth rates of *Oxyrrhis marina* feeding on (A) *Pfiesteria piscicida*, (B) *Stoeckeria algicida*, and (C) *Luciella masanensis* as a function of mean prey concentration (x). The curves are fitted by a Michaelis-Menten equation (Eq. 2) using all treatments in the experiment; (A) $\mu = 0.66 ([x - 0.4]/[21 + (x - 0.4)])$, $r^2 = 0.797$. (B) $\mu = 0.22 ([x + 5]/[64 + (x + 5)])$, $r^2 = 0.528$

data were fitted to Eq. (2), the maximum specific growth rate (μ_{\max}) of *O. marina* consuming *P. piscicida* (0.66 d^{-1}) was 3 times higher than when fed *S. algicida* (0.22 d^{-1}) (Table 3). The specific growth rates of *O. marina* consuming *L. masanensis* were between -0.08 and 0.04 d^{-1} (Fig. 1C).

Like the *Oxyrrhis marina* predator, *Strombidinopsis jeokjo* also grew well with *Pfiesteria piscicida* and *Stoeckeria algicida* as prey, but failed to grow when consuming *Luciella masanensis* (Fig. 2A–C). The specific growth rates of *S. jeokjo* when fed *P. piscicida* and *S. algicida* increased rapidly with increasing mean prey concentration (up to ca. 50 ng C ml^{-1}) but increased only slightly at higher concentrations (Fig. 2A,B). Unlike the *O. marina* predator, when the data were fitted to Eq. (2), μ_{\max} of *S. jeokjo* consuming *P. piscicida* (1.77 d^{-1}) was slightly higher than when fed *S. algicida* (1.61 d^{-1}). The specific growth rates of *S. jeokjo* feeding on *L. masanensis* were between -0.83 and -0.11 d^{-1} (Fig. 2C).

Ingestion and clearance rates

The ingestion rates of *Oxyrrhis marina* feeding on *Pfiesteria piscicida* and *Stoeckeria algicida* increased rapidly with increasing mean prey concentration < ca. 210 to 260 ng C ml^{-1} , but were saturated at higher concentrations (Fig. 3A,B), while rates when feeding on *Luciella masanensis* increased rapidly with increasing mean prey concentration (up to ca. 65 ng C ml^{-1}) but increased slowly at higher concentrations (Fig. 3C). When the data were fitted to Eq. (3), the maximum ingestion rate (I_{\max}) of *O. marina* consuming *P. piscicida* ($0.33 \text{ ng C predator}^{-1} \text{ d}^{-1}$) was considerably higher

than when consuming *S. algicida* ($0.14 \text{ ng C predator}^{-1} \text{ d}^{-1}$) and much higher than with *L. masanensis* as prey ($0.07 \text{ ng C predator}^{-1} \text{ d}^{-1}$) (Table 3). The maximum clearance rates of *O. marina* feeding on *P. piscicida* and *S. algicida* (0.34 to $0.61 \text{ } \mu\text{l predator}^{-1} \text{ h}^{-1}$) were also much higher than that with *L. masanensis* as prey ($0.02 \text{ } \mu\text{l predator}^{-1} \text{ h}^{-1}$).

The ingestion rates of *Strombidinopsis jeokjo* feeding on *Pfiesteria piscicida* and *Stoeckeria algicida* increased rapidly with increasing mean prey concentration (ca. 40 to 50 ng C ml^{-1}) but increased slowly at higher concentrations (Fig. 4A,B). The ingestion rates of *S. jeokjo* consuming *Luciella masanensis* increased with increasing mean prey concentration (up to ca. 270 ng C ml^{-1}) but decreased at higher concentrations (Fig. 4C). When the data were fitted to Eq. (3), I_{\max} values of *S. jeokjo* consuming *P. piscicida* and *S. algicida* (44 to $49 \text{ ng C predator}^{-1} \text{ d}^{-1}$) were markedly higher than when feeding on *L. masanensis* ($10 \text{ ng C predator}^{-1} \text{ d}^{-1}$). The maximum clearance rate of *S. jeokjo* consuming *P. piscicida* ($15.4 \text{ } \mu\text{l predator}^{-1} \text{ h}^{-1}$) was higher than those with *S. algicida* and *L. masanensis* as prey (5.4 to $6.6 \text{ } \mu\text{l predator}^{-1} \text{ h}^{-1}$).

The ingestion rate of *Acartia* spp. feeding on *Pfiesteria piscicida* and *Luciella masanensis* increased continuously with increasing mean prey concentration (up to $1300 \text{ ng C ml}^{-1}$) while that resulting from ingestion of *Stoeckeria algicida* increased with increasing mean prey concentration (up to ca. 650 ng C ml^{-1}) but was saturated at the highest concentration (Fig. 5). The highest values among the ingestion rates of *Acartia* spp. feeding on *P. piscicida*, *S. algicida*, and *L. masanensis* were 3850 , 3640 , and $3490 \text{ ng C predator}^{-1} \text{ d}^{-1}$, respectively, at mean prey concentrations of 1050 , 650 , and $1330 \text{ ng C ml}^{-1}$, respectively. The maximum clear-

Table 3. Growth and grazing data for *Oxyrrhis marina*, *Strombidinopsis jeokjo*, and *Acartia* spp. (*A. hongii* and *A. omorii*). Parameters are for numerical and/or functional response from Eqs. (2) & (3) as presented in Figs. 1–4. μ_{\max} (maximum growth rate, d^{-1}), K_{GR} (prey concentration sustaining $0.5 \mu_{\max}$, ng C ml^{-1}), x' (threshold prey concentration, ng C ml^{-1}), I_{\max} (maximum ingestion rate, $\text{ng C predator}^{-1} \text{ d}^{-1}$), K_{IR} (prey concentration sustaining $0.5 I_{\max}$, ng C ml^{-1}), C_{\max} (maximum clearance rate, $\mu\text{l predator}^{-1} \text{ d}^{-1}$)

Figs.	Species	μ_{\max}	K_{GR}	x'	r^2	I_{\max}	K_{IR}	r^2	C_{\max}
<i>Oxyrrhis marina</i>									
1A & 3A	<i>Pfiesteria piscicida</i>	0.657	21	0.4	0.797	0.334	83	0.876	0.34
1B & 3B	<i>Stoeckeria algicida</i>	0.220	64	-4.7	0.528	0.138	89	0.359	0.61
1C & 3C	<i>Luciella masanensis</i>	0.042 ^a				0.065	132	0.335	0.01
<i>Strombidinopsis jeokjo</i>									
2A & 4A	<i>Pfiesteria piscicida</i>	1.77	90	23	0.783	43.5	92	0.973	15.4
2B & 4B	<i>Stoeckeria algicida</i>	1.61	36	16	0.847	49.3	187	0.955	6.6
2C & 4C	<i>Luciella masanensis</i>	-0.11 ^a				9.8 ^a			5.4
<i>Acartia</i> spp.									
5A	<i>Pfiesteria piscicida</i>					3850 ^a			153
5B	<i>Stoeckeria algicida</i>					3640 ^a			782
5C	<i>Luciella masanensis</i>					3490 ^a			432

^aMaximum value of mean growth and/or ingestion rates measured at the given prey concentrations

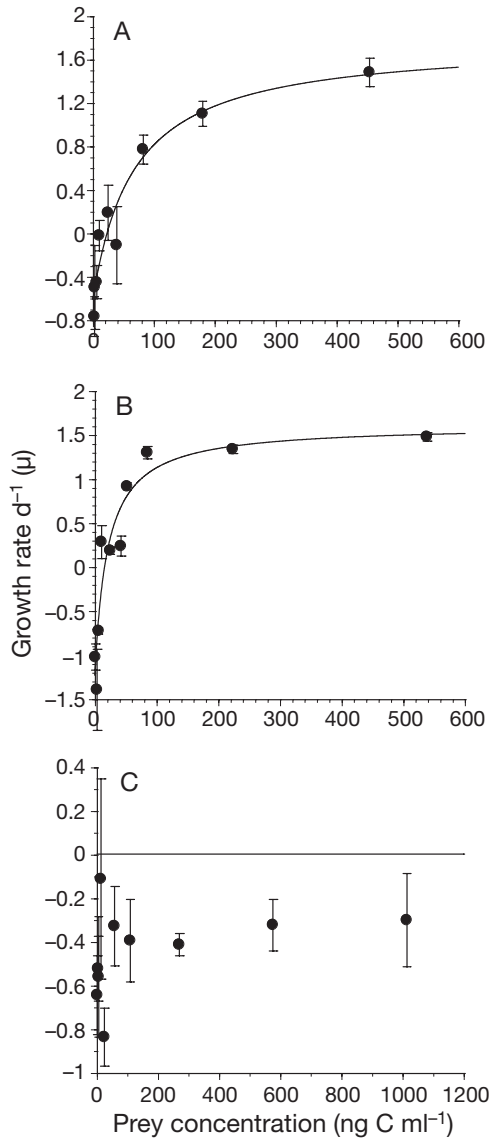


Fig. 2. Mean (± 1 SE) specific growth rates of *Strombidinopsis jeokjo* feeding on (A) *Pfiesteria piscicida*, (B) *Stoeckeria algicida*, and (C) *Luciella masanensis* as a function of mean prey concentration (x). The curves are fitted by a Michaelis-Menten equation (Eq. 2) using all treatments in the experiment; (A) $\mu = 1.77$ ($[(x - 23)/(90 + (x - 23))]$), $r^2 = 0.783$. (B) $\mu = 1.61$ ($[(x - 16)/(36 + (x - 16))]$), $r^2 = 0.847$

ance rates of *Acartia* spp. feeding on *P. piscicida*, *S. algicida*, and *L. masanensis* were 153, 782, and 432 $\mu\text{l predator}^{-1} \text{h}^{-1}$, respectively.

Attack ratio and successful capture

Strombidinopsis jeokjo had a significantly higher attack ratio, (number of attempted captures)/(number of physical contacts), when feeding on *Pfiesteria pisci-*

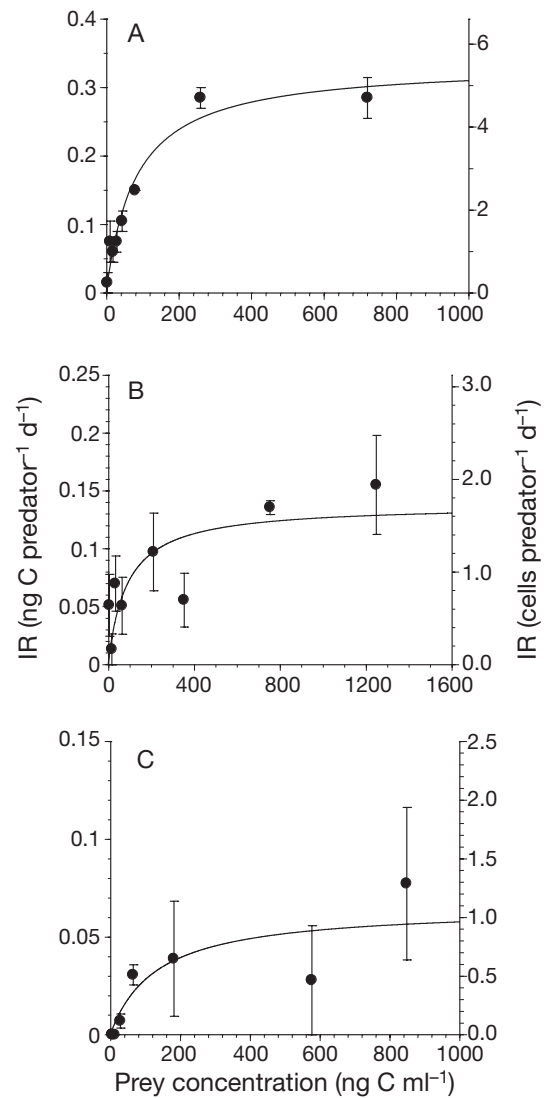


Fig. 3. Mean (± 1 SE) ingestion rates (IR) of *Oxyrrhis marina* feeding on (A) *Pfiesteria piscicida*, (B) *Stoeckeria algicida*, and (C) *Luciella masanensis* as a function of mean prey concentration (x). The curves are fitted by a Michaelis-Menten equation (Eq. 3) using all treatments in the experiment; (A) IR, $\text{ng C predator}^{-1} \text{d}^{-1} = 0.33$ ($x/[83 + x]$), $r^2 = 0.876$. (B) IR, $\text{ng C predator}^{-1} \text{d}^{-1} = 0.14$ ($x/[89 + x]$), $r^2 = 0.359$. (C) IR, $\text{ng C predator}^{-1} \text{d}^{-1} = 0.07$ ($x/[132 + x]$), $r^2 = 0.335$

cida (mean \pm SE = $25 \pm 5\%$) than when consuming *Luciella masanensis* ($5 \pm 1\%$) (1-tailed t-test, $p < 0.005$), but not significantly higher than with *Stoeckeria algicida* as prey ($18 \pm 3\%$) ($p > 0.1$) (Fig. 6A). *S. jeokjo* also had a significantly higher attack ratio when feeding on *P. piscicida* without added filtered water of a *L. masanensis* culture than with added filtered water ($9 \pm 3\%$) (1-tailed t-test, $p < 0.05$).

Similarly, *Strombidinopsis jeokjo* had a significantly higher successful capture ratio, (number of prey

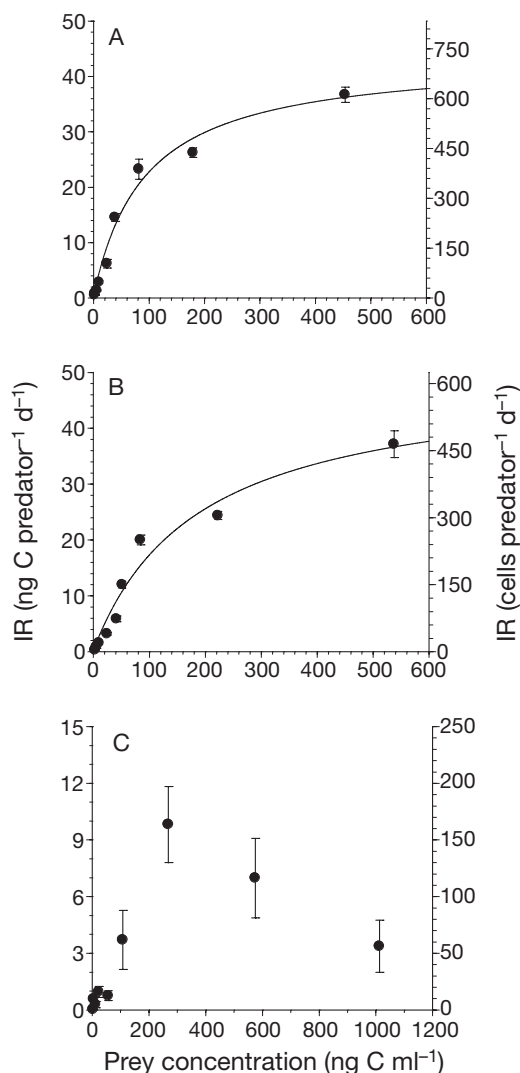


Fig. 4. Mean (± 1 SE) ingestion rates (IR) of *Strombidinopsis jeokjo* feeding on (A) *Pfiesteria piscicida*, (B) *Stoeckeria algicida*, and (C) *Luciella masanensis* as a function of mean prey concentration (x). The curves are fitted by a Michaelis-Menten equation (Eq. 3) using all treatments in the experiment; (A) IR, $\text{ng C predator}^{-1} \text{d}^{-1} = 44 (x/[92 + x])$, $r^2 = 0.973$. (B) IR, $\text{ng C predator}^{-1} \text{d}^{-1} = 49 (x/[187 + x])$, $r^2 = 0.955$

ingested)/(number of attempted captures), when feeding on *Pfiesteria piscicida* (mean \pm SE = $82 \pm 6\%$) than when consuming *Luciella masanensis* ($2 \pm 2\%$) (1-tailed t-test, $p < 0.005$); however, the former ratio was not significantly lower than that for *S. jeokjo* feeding on *Stoeckeria algicida* ($87 \pm 5\%$) ($p > 0.1$) (Fig. 6B). *S. jeokjo* also had a significantly higher successful capture ratio when feeding on *P. piscicida* without added filtered water of a *L. masanensis* culture than with added filtered water ($49 \pm 5\%$) (1-tailed t-test, $p < 0.01$). In the case of unsuccessful captures, *S. jeokjo* rejected the prey cells delivered to the mouth area.

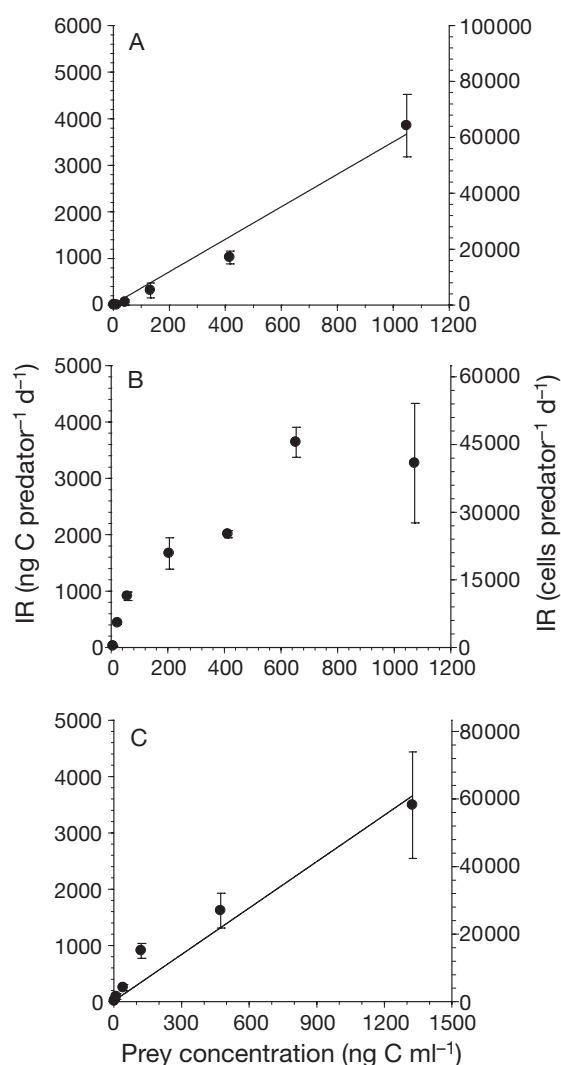


Fig. 5. Mean (± 1 SE) ingestion rates (IR) of *Acartia* spp. (*A. hongii* and *A. omorii*) feeding on (A) *Pfiesteria piscicida*, (B) *Stoeckeria algicida*, and (C) *Luciella masanensis* as a function of mean prey concentration (x). The curves are fitted by the equation of the linear regression (A,C) and a Michaelis-Menten equation (B) using all treatments in the experiment; (A) IR, $\text{ng C predator}^{-1} \text{d}^{-1} = 3.49 (x)$, $r^2 = 0.905$. (B) IR, $\text{ng C predator}^{-1} \text{d}^{-1} = 3070 (x/[140 + x])$, $r^2 = 0.754$. (C) IR, $\text{ng C predator}^{-1} \text{d}^{-1} = 2.75 (x)$, $r^2 = 0.787$

DISCUSSION

Differential feeding

The present study reveals that despite the fact that *Pfiesteria piscicida*, *Stoeckeria algicida*, and *Luciella masanensis* belonging to the family Pfiesteriaceae have similar sizes and shapes, they caused different functional responses by *Oxyrrhis marina* and *Strombidinopsis jeokjo*. In particular, while *P. piscicida* and

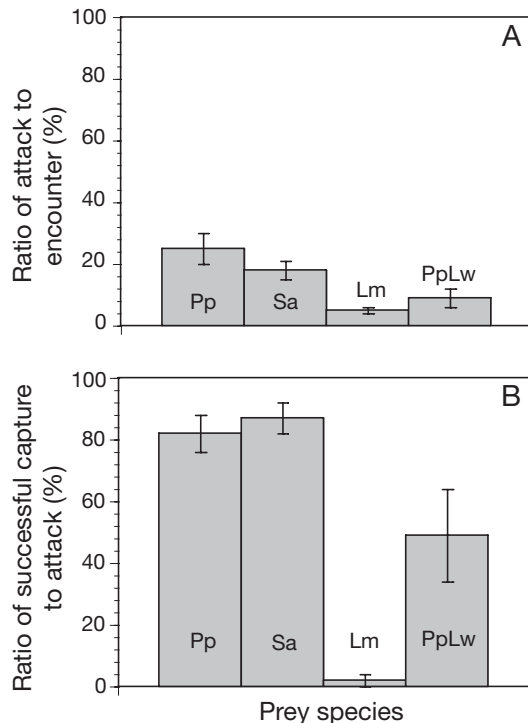


Fig. 6. Mean (± 1 SE) ratios of (A) attack by *Strombidinopsis jeokjo* feeding on *Pfiesteria piscicida* (Pp), *Stoeckeria algicida* (Sa), *Luciella masanensis* (Lm), and *Pfiesteria piscicida* with added filtered water of a *L. masanensis* culture (PpLw) relative to encounter and of (B) successful capture relative to attack. Values are treatment means ± 1 SE

S. algicida did support positive growth of the protist predators *O. marina* and *S. jeokjo*, *L. masanensis* did not. I_{\max} of *S. jeokjo* feeding on *P. piscicida* or *S. algicida* was substantially higher than when fed *L. masanensis*.

Several possible explanations exist for these prey dependent differences in ingestion rate and growth rate of *Strombidinopsis jeokjo*. (1) *L. masanensis* may be less attractive to *S. jeokjo* as prey compared to *P. piscicida* and *S. algicida*. *S. jeokjo* has much lower attack ratios when fed on *L. masanensis* than when fed on *P. piscicida* and *S. algicida*. Also, *S. jeokjo* had significantly higher attack and successful capture ratios when fed on *P. piscicida* without added filtered water of an *L. masanensis* culture than with added filtered water. This suggests that chemicals excreted from *L. masanensis* may inhibit feeding by *S. jeokjo*. Recently, Moeller et al. (2007) reported the nature of toxins produced by *P. piscicida* (i.e. metal complexes and free radical toxins) by using 5 different analytical methods. *L. masanensis* may have toxins that are more potent than those of *P. piscicida*; however, the presence and toxicity of the toxins of *L. masanensis* should be investigated in future studies. (2) *S. jeokjo* may have more difficulty in handling *L. masanensis* than *P. piscicida*

and *S. algicida*. *S. jeokjo* has much lower successful capture ratios when fed on the former dinoflagellate prey than when fed on the latter dinoflagellate prey. (3) Some *L. masanensis* cells were observed to attack *S. jeokjo*, while no *P. piscicida* or *S. algicida* cells attacked their predators. This attack may be partially responsible for the decrease in the ingestion rate of *L. masanensis* by *S. jeokjo* at mean prey concentrations >270 ng C ml⁻¹ and indicates direct reversal of predator-prey relationships among heterotrophic protists. Only a few other reports have indicated the same; the heterotrophic dinoflagellate *Proto-peridinium divergens* and the mixotrophic dinoflagellate *Fragilidium* cf. *mexicanum* were able to feed on each other (Jeong et al. 1997).

To understand the population dynamics of *Pfiesteria piscicida*, *Stoeckeria algicida*, and *Luciella masanensis*, data on the prey species, their growth rates (k) and mortality rates due to predation (g) should be obtained. *P. piscicida* and *L. masanensis* feed on diverse prey species and have several optimal and suboptimal prey species that support their high growth rates, such as fish blood cells, *Amphidinium carterae*, cryptophytes, and *Heterosigma akashiwo* (0.8 to 1.8 d⁻¹) (Burkholder & Glasgow 1995, 1997, Parrow et al. 2002, Seaborn et al. 2002, Lin et al. 2004, Jeong et al. 2005b, 2006, 2007a). However, *S. algicida* feeds only on *H. akashiwo* and blood cells (Jeong et al. 2005a, 2007a). When combining the kind of prey species, growth rates, and mortality rates due to predation, *L. masanensis* (with many prey species, high k and low g) is the most competitive, followed by *P. piscicida* (with many prey species, high k and high g), and finally *S. algicida* (with a few prey species, high k on a few prey species but zero or low k on many other co-occurring plankton, and high g) and the least competitive. *L. masanensis* is likely to dominate the assemblage of *P. piscicida*, *S. algicida*, and *L. masanensis* when protistan predators are abundant. Gransden & Lewitus (2003) reported that the growth rate of *P. piscicida* feeding on the cryptophyte *Storeatula major* was significantly higher than that of *Cryptoperidiniopsis* sp. and suggested that the euplotid ciliate *Euplotes woodruffi* had a greater ability to control the population growth of *P. piscicida* than *Cryptoperidiniopsis* sp. Therefore, *P. piscicida*, *S. algicida*, *L. masanensis*, and *Cryptoperidiniopsis* sp. have different ecological niches in marine planktonic food webs.

The results of the present study suggest that the predator with the lowest I_{\max} (*Oxyrrhis marina*) has a clearly different I_{\max} on these 3 different prey species (specialist), while the predators with the highest I_{\max} (*Acartia* spp.) have relatively similar I_{\max} values on these 3 different prey species (generalists). And the predator with a moderate I_{\max} (*Strombidinopsis jeokjo*)

shows a combination of specialist and generalist. The smallest predator *O. marina* may detect differences in taste, nutrition, and/or behavior of these 3 different prey species, but the largest predator *Acartia* spp. may not detect such differences. Feeding by some copepods is affected by some toxic mixotrophic dinoflagellates (e.g. Huntley et al. 1986). However, feeding of *Acartia* spp. was not affected by any chemicals excreted from *Luciella masanensis*, which might have inhibited the feeding of *S. jeokjo*. Also, *Acartia tonsa* was reported to graze both non-toxic and potentially toxic strains of *Pfiesteria piscicida* at approximately equal rates (Roman et al. 2006). Therefore, with regard to *Acartia* spp., the effect of the toxicity of the chemicals excreted from *L. masanensis* or *P. piscicida* is likely to be less than that of toxic mixotrophic dinoflagellates.

Growth and ingestion rates

Heterotrophic dinoflagellates feed on bacteria (Lessard & Swift 1985, Strom 1991, H. J. Jeong, K. A. Seong, T. H. Kim unpubl. data), algae (Jacobson 1987, Johnson et al. 2003, Menden-Deuer et al. 2005), heterotrophic nanoflagellates (Jeong et al. 2007b), ciliates (Burkholder & Glasgow 1995), eggs and naupliar stages of copepods (Jeong 1994), larvae of bivalves (Burkholder & Glasgow 1997, Springer et al. 2002), the blood of finfish (Burkholder & Glasgow 1997, Parrow et al. 2005, Jeong et al. 2006), and the epidermis, muscle, and gills of finfish (Burkholder & Glasgow 1997). However, prior to the present study, there had been no studies on the feeding by a heterotrophic dinoflagellate species on other heterotrophic dinoflagellate species. To enhance understanding of material cycling and energy flow in marine planktonic food webs, we should consider predator-prey relationships among heterotrophic dinoflagellates because usually several heterotrophic dinoflagellate species coexist (e.g. Jacobson 1987). The μ_{\max} of *Oxyrrhis marina* feeding on *Pfiesteria piscicida* (0.66 d⁻¹; present study) is lower than that resulting from consumption of *Heterosigma akashiwo* (1.43 d⁻¹; Jeong et al. 2003), *Amphidinium carterae* (1.17 d⁻¹; Jeong et al. 2001), and the diatom *Phaeodactylum tricornutum* (1.30 d⁻¹; Goldman et al. 1989); however, it is comparable to that arising from predation on the phototrophic flagellates *Dunaliella tertiolecta* and *Isochrysis galbana* (0.79 d⁻¹) or the raphidophyte *Fibrocapsa japonica* (0.72 d⁻¹; Tillmann & Reckermann 2002), when corrected to 20°C using $Q_{10} = 2.8$ (Hansen et al. 1997). The I_{\max} of *O. marina* feeding on *P. piscicida* (0.33 ng C predator⁻¹ d⁻¹) is much lower than I_{\max} values arising from consumption of all these algal prey species (1.3 to 7 ng C predator⁻¹

d⁻¹). *O. marina* may have more difficulty and thus use more energy in capturing the heterotrophic dinoflagellate prey compared to the algal prey. However, *P. piscicida* as prey for *O. marina* may be more nutritional than the algal prey.

This is the first study on predation by *Strombidinopsis* spp. on *Pfiesteria piscicida*, *Stoeckeria algicida*, and *Luciella masanensis*. The μ_{\max} of *Strombidinopsis jeokjo* feeding on *P. piscicida* and *S. algicida* (1.61 to 1.77 d⁻¹) was much higher than that resulting from the consumption of the heterotrophic dinoflagellates *Gyrodinium dominans* and *Oxyrrhis marina* prey (0.54 to 0.59 d⁻¹; Jeong et al. 2004) and also clearly higher than that from feeding on the optimal algal prey *Cochlodinium polykrikoides* and *Akashiwo sanguinea* (1.41 to 1.53 d⁻¹; Jeong et al. 1999), when corrected to 20°C using $Q_{10} = 2.8$ (Hansen et al. 1997). The μ_{\max} in the present study is the highest observed value for *S. jeokjo* to date and thus *P. piscicida* and *S. algicida* are the optimal prey for culturing *S. jeokjo*. However, the I_{\max} of *S. jeokjo* feeding on *P. piscicida* and *S. algicida* (44 to 49 ng C predator⁻¹ d⁻¹) in the present study was lower than that observed for *G. dominans* and *O. marina* as prey (87 to 106 ng C predator⁻¹ d⁻¹; Jeong et al. 2004) and much lower than that from feeding on the optimal algal prey (229 to 391 ng C predator⁻¹ d⁻¹; Jeong et al. 1999), when corrected to 20°C. These results suggest that (1) *P. piscicida* and *S. algicida* may sometimes comprise important prey for the growth of large *Strombidinopsis* species; and (2) *P. piscicida* and *S. algicida* are more nutritional as prey for *S. jeokjo* than *G. dominans*, *O. marina*, and algal prey. In natural environments, a higher abundance of *S. jeokjo* is expected when it co-occurs with *P. piscicida* and *S. algicida* compared to co-occurrence with *G. dominans*, *O. marina*, and algal prey.

The naked ciliates *Euplotes* spp., *Strombidium* spp., and *Strobilidium* sp. and the tintinnid ciliates *Tintinnopsis* spp., *Tintinnidium* spp., *Nolacclusilis* spp., and *Favella* sp. also feed on *Pfiesteria piscicida* (Stoecker et al. 2000, Lewitus et al. 2006). The maximum clearance rate of *Strombidinopsis jeokjo* feeding on *P. piscicida* (15 μ l predator⁻¹ h⁻¹) is comparable to that of *Tintinnopsis* spp. (4 to 19 μ l predator⁻¹ h⁻¹ with an exception of 109 μ l predator⁻¹ h⁻¹) or *Strombidium* spp. (3 to 46 μ l predator⁻¹ h⁻¹; Stoecker et al. 2000, Setälä et al. 2005), when corrected to 20°C using $Q_{10} = 2.8$ (Hansen et al. 1997). Therefore, *S. jeokjo* may compete with these ciliates for *P. piscicida* prey in cases where they coexist. To enhance understanding of the interactions between dominant ciliates and *P. piscicida*, *Stoeckeria algicida*, and *Luciella masanensis* in marine environments, it is necessary to explore the numerical and functional responses of the ciliates to the prey concentration when fed on these 3 dinoflagellate prey.

The calanoid copepod *Acartia tonsa* feeds on *Pfiesteria piscicida* (Mallin et al. 1995, Roman et al. 2006). The highest value (64 180 cells predator⁻¹ d⁻¹) among the ingestion rates of *Acartia* spp. (*A. hongii* and *A. omorii*) on *P. piscicida* at mean prey concentrations <17 500 cells ml⁻¹ is greater than rates for consumption of both non-toxic and toxic strains of *P. piscicida* (31 920 and 29 760 cells predator⁻¹ d⁻¹, respectively) (Roman et al. 2006). *A. hongii* or *A. omorii* are considerably longer than *A. tonsa*. This difference in size among *Acartia* species and variation in the *P. piscicida* strains ingested may be responsible for the difference in ingestion rates.

Only a few studies have reported on predation by copepods on *Pfiesteria piscicida* and other species belonging to the family Pfiesteriaceae. Thus, to enhance understanding of the interactions between these dinoflagellates and copepods in the natural environment, it would be worthwhile to investigate feeding by dominant copepods on *P. piscicida* and other dinoflagellate species.

Microzooplankton occasionally have considerable predation impact on the populations of *Pfiesteria piscicida*, and hence control the prey population; however, metazooplankton, including copepods, usually do not affect the prey populations (Stoecker & Gustafson 2002, Roman et al. 2006). Nevertheless, it is very difficult to measure *in situ* ingestion rates of *Oxyrrhis marina* or *Strombidinopsis jeokjo* feeding on *Stoeckeria algicida* and/or *Luciella masanensis* or to calculate the predators' impact by combining the data on their ingestion rates and abundance because (1) differentiating among *P. piscicida*, *S. algicida*, and *L. masanensis* and then measuring their abundances in fixed natural samples remains difficult because advanced methods (such as DNA probes) of identifying *S. algicida* and *L. masanensis* have not been developed yet; (2) ingestion rates of *O. marina* or *S. jeokjo* feeding on each of *P. piscicida*, *S. algicida*, and *L. masanensis* differ greatly from those observed for consumption of the other prey species. Therefore, to enhance understanding of the interactions between *P. piscicida*, *S. algicida*, and *L. masanensis* and their predators at the population level, advanced methods for identifying these 3 dinoflagellates must be developed.

For a long time, species belonging to the family Pfiesteriaceae were probably not easily recognized due to their small size and the difficulty of establishing monoclonal cultures. However, recently, several new species in this family have been discovered (Jeong et al. 2005b, Litaker et al. 2005, Mason et al. 2007). The present study suggests that species in this family may have a distinct ecological niches and may be differentiated from each other based on their prey species, differential growth and ingestion rates (Lin et al. 2004,

Jeong et al. 2005a, 2006, 2007a) as well as the differential mortality rate due to predation as shown in the present study. Thus, to understand the roles of a newly discovered species in marine planktonic food webs, predator-prey relationships between the species and coexisting prey species, its growth and ingestion rates resulting from feeding on diverse prey, and the numerical and functional responses of the potential predators, in particular, heterotrophic protists should be investigated simultaneously.

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