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Interactions Between the Kleptoplastidic Dinoflagellate *Shimiella gracilenta* and Several Common Heterotrophic Protists

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The newly described dinoflagellate, *Shimiella gracilenta*, is known to survive for approximately 1 month on the plastids of ingested prey cells during starvation, indicating kleptoplastidy. To understand the population dynamics of this dinoflagellate in marine planktonic food webs, its growth and mortality rate due to predation should be assessed. Thus, we investigated the feeding occurrence of eight common heterotrophic protists on *S. gracilenta*. We also determined the growth and ingestion rates of *Oxyrrhis marina* and the naked ciliate, *Rimostrombidium* sp. on *S. gracilenta* as a function of the prey concentration. The common heterotrophic dinoflagellates (HTDs) *Gyrodinium dominans*, *O. marina*, and *Pfiesteria piscicida* and a naked ciliate *Rimostrombidium* sp. were able to feed on *S. gracilenta*; whereas the HTDs *Aduncodinium glandula*, *Gyrodinium jinhaense*, *Oblea rotunda*, and *Polykrikos kofoidii* were not. *Shimiella gracilenta* supported positive growth of *O. marina* and *Rimostrombidium* sp. but did not support that of *G. dominans* and *P. piscicida*. With increasing prey concentrations, the growth and ingestion rates of *O. marina* and *Rimostrombidium* sp. on *S. gracilenta* increased and became saturated. The maximum growth rates of *O. marina* and *Rimostrombidium* sp. on *S. gracilenta* were 0.645 and 0.903 day^{-1}, respectively. Furthermore, the maximum ingestion rates of *O. marina* and *Rimostrombidium* sp. on *S. gracilenta* were 0.11 ng C $predator\ day^{-1}$ (1.6 cells $predator^{-1}\ day^{-1}$) and 35 ng C $predator\ day^{-1}$ (500 cells $predator^{-1}\ day^{-1}$), respectively. The maximum ingestion rate of *O. marina* on *S. gracilenta* was lower than that on any other algal prey reported to date, although its maximum growth rate was moderate. In conclusion, *S. gracilenta* had only a few common heterotrophic protist predators but could support moderate growth rates of the predators. Thus, *S. gracilenta* may not be a common prey species for diverse heterotrophic protists but may be a suitable prey for a few heterotrophic protists.

Keywords: ciliate, grazer, microbial food web, mixotrophy, predation

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INTRODUCTION

Dinoflagellates are ubiquitous protists and one of the major components of marine ecosystems (Coats, 1999; Taylor et al., 2008; Jeong et al., 2010b). They play diverse ecological roles in marine food webs as primary producers, predators of diverse prey types (including bacteria, microalgae, and metazoans), prey for heterotrophic protists and metazoans (Shumway, 1990; Stoecker, 1999; Jeong et al., 2010b; Johnson, 2015; Mitra et al., 2016; Ward and Follows, 2016), symbiotic partners (Jeong et al., 2012; Lee et al., 2016; LaJeunesse et al., 2018), and parasites (Park et al., 2013b). Their diverse ecological roles in marine ecosystems may be related to their diverse trophic modes (i.e., autotrophy, heterotrophy, kleptoplastidy, and mixotrophy) (Jeong et al., 2010b; Lim et al., 2015). In particular, mixotrophic dinoflagellates perform photosynthesis using their own plastids, whereas kleptoplastidic dinoflagellates perform photosynthesis using plastids acquired from algal prey (Mitra et al., 2016; Ward and Follows, 2016; Jeong et al., 2021). Kleptoplastidic dinoflagellates can survive for certain long periods under starvation but eventually die if they do not subsequently feed on prey, unlike mixotrophic dinoflagellates (Gast et al., 2007; Mitra et al., 2016; Ok et al., 2021). Far less kleptoplastidic dinoflagellate species have been reported than mixotrophic dinoflagellate species; however, the number of studies describing new kleptoplastidic dinoflagellates is increasing (e.g., Jacobson and Anderson, 1986, 1996; Park et al., 2006, 2013a; Gast et al., 2007; Jeong et al., 2010a; Ok et al., 2021).

The dinoflagellate *Shimiella gracilenta* SGJH1904 that was isolated from the waters of Jinhae Bay, Korea, has been recently described (Ok et al., 2021). This dinoflagellate is known to survive without added prey for approximately 1 month on chloroplasts obtained from the prey, a cryptophyte called *Teleaulax amphioxeia*, indicating its "kleptoplastidy" (Ok et al., 2021). To understand the ecological roles of a newly described heterotrophic, kleptoplastic, or mixotrophic dinoflagellate, its prey and predators should be first identified (Potvin et al., 2013; Jeong et al., 2018a,b; Kang et al., 2019). Based on the results of the studies on the prey and predators, the transfer of elements from prey (i.e., the target dinoflagellate) to the predators in cycling of elements and food webs can be understood (Jeong et al., 2010b). To explore the ecological role of *S. gracilenta* as a predator, the kind of prey that *S. gracilenta* is able to feed on, growth and ingestion rates of *S. gracilenta* on prey, and grazing impact by *S. gracilenta* on prey populations should be assessed. On the other hand, to explore the ecological role of *S. gracilenta* as prey, the kind of predators that are able to feed on *S. gracilenta*, growth and ingestion rates of the predator on *S. gracilenta*, and predation impact by the predator on *S. gracilenta* populations should be assessed. Furthermore, to understand the population dynamics of the dinoflagellate, its growth rate (k) and mortality rate due to predation (g) under a given condition should be determined (Jeong et al., 2015). To determine the mortality rate due to predation, first, predators that are able to feed on the dinoflagellate prey should be identified (Berge et al., 2008; Lim et al., 2015). Second, the ingestion and growth rates of the predators on the dinoflagellate prey should be determined (Jeong et al., 2016; Anderson and Menden-Deuer, 2017). The ingestion rate of a predator on dinoflagellate prey is proportional to the clearance rate that, in turn, is proportional to g in bottle incubation experiments (Jeong et al., 2011; Kang et al., 2011). When data on the abundances of the target dinoflagellate and its co-occurring predator species in marine environments are available, the mortality rate due to predation by multiple predators can be estimated (Yoo et al., 2013a; Lim et al., 2017). Thus, revealing predators that are able to feed on *S. gracilenta* and determining the ingestion and growth rates of the predators on *S. gracilenta* are needed.

Typically, to identify predators of specific dinoflagellates, mixotrophic and/or heterotrophic organisms, which are abundant during or after the bloom of the target dinoflagellate (Yoo et al., 2013a; Lim et al., 2017; Eom et al., 2021), are selected as the potential predators. Alternatively, predators of the target dinoflagellate can be identified by observing the feeding behavior under a microscope after mixing the target dinoflagellate cells with potential predators commonly found in many marine environments (Yoo et al., 2010, 2015; Potvin et al., 2013; Ok et al., 2017; Kim et al., 2019). The heterotrophic dinoflagellates (HTDs) *Gyrodinium dominans*, *Oblea rotunda*, *Oxyrrhis marina*, *Pfiesteria piscicida*, and *Polykrikos kofoidii* and the naked ciliate *Rimostrombidium* sp. are commonly present in the waters of many countries (e.g., Costello et al., 2001; Jakobsen et al., 2002; Rhodes et al., 2006; Rublee et al., 2006; Sherr and Sherr, 2007; Felder and Camp, 2009; Agatha, 2011; Watts et al., 2011; Kilias et al., 2013; McCarthy, 2013). They have also been regarded as potential heterotrophic protist predators on many mixotrophic or kleptoplastidic dinoflagellates (Jacobson and Anderson, 1986, 1996; Jeong et al., 2001a, 2007a, 2017, 2018a,b; Ok et al., 2017). The newly described HTD, *Gyrodinium jinhaense*, is commonly found in Korean coastal waters (Lee et al., 2021). The HTD *Aduncodinium glandula* has been used as a potential predator in several studies (Jang et al., 2016; Jeong et al., 2018a). These heterotrophic protists have been reported to be present in the eastern South Sea of Korea, where *S. gracilenta* SGJH1904 was isolated (Jeong et al., 2006, 2011; Kang et al., 2015, 2019; Lim et al., 2017; Jung et al., 2021). Thus, *S. gracilenta* is likely to encounter these heterotrophic protists in natural environments. Moreover, these protists exhibit diverse sizes and shapes and adopt various feeding mechanisms, such as engulfment, peduncle, and pallium feeding.

In the present study, using the clonal cultures of *S. gracilenta* SGJH1904, we investigated the feeding occurrence of these potential heterotrophic protist predators on *S. gracilenta* and also determined the growth and ingestion rates of *O. marina* and *Rimostrombidium* sp. on *S. gracilenta* as a function of prey concentration. This was done because *S. gracilenta* supported the growth of only these two predators. Additionally, we compared the growth rate of *O. marina* feeding on *S. gracilenta* to that on other algal prey species. The results of this study can contribute to the understanding of interactions between *S. gracilenta* and common heterotrophic protists, as well as the understanding of ecological roles of *S. gracilenta* in marine planktonic food webs.

MATERIALS AND METHODS

Preparation of Experimental Organisms

Shimiella gracilenta SGJH1904 cells were isolated from surface waters off the coast of Jinhae, Korea on April 6, 2019 (Ok et al., 2021). A clonal culture of *S. gracilenta* was established using two serial single cell isolations, and a culture of *S. gracilenta* was grown on *T. amphioxeia* (30,000–40,000 cells ml^{-1}). *Teleaulax amphioxeia* was originally isolated from the coastal waters of Gomso Bay, Korea.

The HTDs *A. glandula*, *G. dominans*, *G. jinhaense*, *O. rotunda*, *O. marina*, and *P. kofoidii*, isolated from plankton samples collected from the coastal waters of Masan, Jeongok, Jinhae, Kunsan, and Jangheung during 2001–2019, were used in this study (**Table 1**). The clonal culture of *P. piscicida* was obtained from the National Center for Marine Algae and Microbiota (NCMA) in the USA. To isolate and cultivate the naked ciliate *Rimostrombidium* sp., plankton samples were collected from the coastal waters of Saemankeum, Korea, in July 2020 (**Table 1**).

Determination of Carbon Content and Cell Volume

The carbon contents of the potential predators and *S. gracilenta* were estimated based on cell volume (Menden-Deuer and Lessard, 2000). The cell volumes of *A. glandula*, *G. jinhaense*, *G. dominans*, *O. rotunda*, *O. marina*, *P. kofoidii*, *P. piscicida*, and *Rimostrombidium* sp. were estimated following the method described by Jang et al. (2016), Kang et al. (2020), Jeong et al. (2001b, 2007a, 2008), Ok et al. (2017), and Eom et al. (2021). The cell volume of *S. gracilenta* was also measured in the present study.

Determination of Feeding Capability

Experiment 1 was designed to examine whether the selected potential heterotrophic protists could feed on *S. gracilenta* after mixing the two species. *Shimiella gracilenta* cells were added to 42-ml polycarbonate (PC) bottles at a concentration of 15,000 cells ml^{-1}. Next, each of the potential predators was added. A predator control bottle (no prey) and a prey control bottle (no predator) were also set up for each experiment. The initial concentration of each target heterotrophic protist was set up, considering its carbon contents or the maximum cell abundances as described in **Supplementary Table 1**. The bottles were placed on a plankton wheel rotating at 0.9 rpm (0.00017 × *g*) and incubated at 20°C under 20-μE m^{-2} s^{-1} illumination with cool white fluorescent light and a 14:10-h light-and-dark cycle.

After 1, 2, 6, 24, and 48 h of incubation, 5-ml aliquots were collected from each bottle using an autopipette and transferred into six-well plate chambers. When prey cells were not eaten by a target predator, >40 of the cells of the predator were observed under a dissecting microscope at a magnification of × 10–63 to determine the feeding occurrence of the potential predators on *S. gracilenta*. However, when a prey cell was eaten by a target predator, >15 cells of the predator were observed. The attack ratio (i.e., number of attempted captures relative to the number of physical contacts between a predator and prey) and capture success (i.e., number of prey ingested relative to the number of attempted captures) were determined by monitoring the behavior of the potential dinoflagellate predators in the presence of *S. gracilenta*. The ratios for *Rimostrombidium* sp. were not measured because this predator quickly jumped.

To explore the process of feeding, wells containing both a predator and *S. gracilenta* were placed under a light microscope (Zeiss-Axiovert 200M; Carl Zeiss Ltd., Göttingen, Germany), equipped with a video-analyzing system (Sony DXC-C33; Sony Co., Tokyo, Japan). The feeding process of the target species was recorded at a magnification of × 200–630. Cells of each target predator species and *S. gracilenta* were photographed on a confocal dish with cover glasses using a digital camera (Zeiss AxioCam 506; Carl Zeiss Ltd.), attached to a light and an epifluorescence microscope at a magnification of × 400–1,000.

Measurement of Growth and Ingestion Rates as a Function of Prey Concentration

In the preliminary test, *S. gracilenta* supported the positive growth rate of only two of the investigated potential predators, namely *O. marina* and *Rimostrombidium* sp. Thus, Experiments 2 and 3 were designed to determine the growth and ingestion rates of *O. marina* and *Rimostrombidium* sp. on *S. gracilenta*.

In Experiment 2, when prey cells were undetected under 1-ml Sedgewick–Rafter chamber (SRC), a dense culture of *O. marina* was transferred into a round 1-L PC bottle (Triforest® PC Centrifuge/Wide-mouth bottles) containing *S. gracilenta* (approximately 2,000 *S. gracilenta* cells ml^{-1} and 2,000 *O. marina* cells ml^{-1}). The bottle was filled to the capacity with freshly filtered seawater to decrease the damage to the organisms, capped and placed on a plankton wheel rotating at 0.9 rpm (0.00017 × *g*). It was then incubated at 20°C under an illumination of 20 μE m^{-2} s^{-1} and placed in a 14:10-h light-and-dark cycle. Triplicate 1-ml aliquots were removed from the bottle every day, and cells of *S. gracilenta* and *O. marina* were counted under a light microscope to determine complete consumption of *S. gracilenta* and cell concentration and residual growth of *O. marina* (i.e., no difference in the growth rates of *O. marina* with and without added prey). After subsampling, the bottle was refilled with freshly filtered seawater and placed on the plankton wheel once again. The predetermined volumes of *O. marina* and *S. gracilenta* were transferred to PC bottles using an autopipette (**Supplementary Table 1**). Triplicate 42-ml PC experimental bottles (containing mixtures of predators and prey) and triplicate control bottles (containing only prey) were set up for each predator–prey combination. Triplicate control bottles containing only predators were also set up at a single predator concentration. Cultures of predator cells were passed through a 0.2-μm disposable syringe filter (DISMIC-25CS type, 25 mm; Advantec, Toyo Roshi Kaisha Ltd., Chiba, Japan), and then the filtrates were added to the prey control bottles as the same volume as that of the predator culture added to the experimental bottles for each predator—prey combination to ensure similar water conditions. All the bottles were then filled to capacity with freshly filtered seawater and capped. At the start of the experiment, a 5-ml aliquot was collected from each bottle, fixed in 5% Lugol's solution, and

TABLE 1 | Conditions for the isolation and maintenance of the experimental organisms.

Organisms	Strain name	Type	FM	ESD	Location	Time	T	S	Prey
Predators									
Aduncodinium glandula	AGMS1303	HTD	PD	21.0	Masan, Korea	Mar 2013	8.1	30.3	As
Gyrodinium dominans	GDJK1907	HTD	EG	11.6	Jeongok, Korea	Jul 2019	25.2	31.9	Ac
Gyrodinium jinhaense	GSJH1710	HTD	EG	10.2	Jinhae, Korea	Oct 2017	21.6	32.5	HKDs
Oblea rotunda	ORJH1504	HTD	PA	21.6	Jinhae, Korea	Apr 2015	12.6	31.2	Ac
Oxyrrhis marina	OMKS0105	HTD	EG	15.6	Kunsan, Korea	May 2001	16.0	27.7	Ac
Pfiesteria piscicida	CCMP2091	KPD	PD	13.5	Neuse River, USA	Jan 1998	–	–	Ac
Polykrikos kofoidii	PKJH1607	HTD	EG	43.5	Jangheung, Korea	Jul 2016	23.6	26.4	Am
Rimostrombidium sp.	RSSMK2007	NC	EG	29.8	Saemankeum, Korea	Jul 2020	27.1	18.8	Hr
Prey									
Shimiella gracilenta	SGJH1904	KPD	PD	9.3	Jinhae, Korea	Apr 2019	14.6	33.6	Ta

FM, feeding mechanism; ESD, equivalent spherical diameter (μm); T, temperature (°C); S, salinity; HTD, heterotrophic dinoflagellate; NC, naked ciliate; KPD, kleptoplastidic dinoflagellate; PD, peduncle feeder; EG, engulfment feeder; PA, pallium feeder; As, Akashiwo sanguinea; HKDs, heat-killed Dunaliella salina; Ac, Amphidinium carterae; Am, Alexandrium minutum CCMP1888; Hr, Heterocapsa rotundata; Ta, Teleaulax amphioxeia.

enumerated under a light microscope to determine the actual predator and prey abundances. The bottles were refilled to the capacity with freshly filtered seawater and placed on rotating wheels under the conditions described above. Dilution of the cultures by refilling the bottles was considered when calculating the growth and ingestion rates. After 48 h of incubation, a 10-ml aliquot was collected from each bottle and fixed in 5% Lugol's solution. The predator and prey abundance sampled at 0 and 48 h after setting up the experiment was determined by counting all (or over 200) cells using 1-ml SRC in triplicate.

In Experiment 3, when the prey cells were completely consumed, a dense culture of *Rimostrombidium* sp. was transferred to a 500-ml PC bottle containing *S. gracilenta* (approximately 600 *S. gracilenta* cells ml^{-1} and 20 *Rimostrombidium* sp. cells ml^{-1}), and the bottle was filled with filtered seawater. The bottles were incubated under the same conditions as described above. Every 12 h of incubation, triplicate 1-ml aliquots were collected from the bottle, and the cell concentration and residual growth of *Rimostrombidium* sp. were determined under a light microscope. The initial concentration of *Rimostrombidium* sp. and *S. gracilenta* was established using an autopipette to deliver predetermined volumes of known cell concentrations to the bottles (**Supplementary Table 1**). The experiment was conducted using the methodology described above. After 24 h of incubation, a 10-ml aliquot was collected from each bottle, fixed in 5% Lugol's solution, and enumerated under an inverted microscope (BX51, Olympus, Japan). Triplicate 10-ml aliquots were collected from the bottles with the three lowest concentrations and all predator control bottles and enumerated in six-well plate chambers under a dissecting microscope (SZX2-ILLB, Olympus, Japan) without fixation.

The specific growth rate of each heterotrophic protist predator, μ (day^{-1}), was calculated as follows:

$$\mu\ (day^{-1}) = [\mathrm{Ln}(P_t/P_0)]/t \quad (1)$$

where P_0 and P_t are the concentrations of predators at 0 and 24 h for *Rimostrombidium* sp. or at 0 and 48 h for *O. marina*, respectively. *Rimostrombidium* sp. depleted *S. gracilenta* cells in <48 h, and, thus, was incubated for 24 h.

The calculated growth rate was fitted to the Michaelis–Menten equation as follows:

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

where μ_{max} is the maximum growth rate (day^{-1}); x is the prey concentration (cells ml^{-1} or ng C ml^{-1}); x' is the threshold prey concentration (prey concentration where $\mu = 0$); and K_{GR} is the prey concentration sustaining 1/2 μ_{max}.

Data were iteratively fitted to the model using Delta Graph (IBM-SPSS Inc., Armonk, NY, USA).

The ingestion and clearance rates were calculated using the modified equations described by Frost (1972) and Heinbokel (1978). The incubation time for calculating the ingestion and clearance rates was the same as that for estimating the growth rate. The calculated ingestion rate (IR; cells $predator^{-1}$ day^{-1}) of each heterotrophic protist was fitted to the Michaelis–Menten equation as follows:

$$IR = [I_{max}(x)]/[K_{IR} + (x)] \quad (3)$$

where I_{max} is the maximum ingestion rate (cells $predator^{-1}$ day^{-1} or ng C $predator^{-1}$ day^{-1}); x is the prey concentration (cells ml^{-1} or ng C ml^{-1}); and K_{IR} is the prey concentration sustaining 1/2 I_{max}.

Measurement of Swimming Speed

A culture of *S. gracilenta* with approximately 40,000 cells ml^{-1} growing on *T. amphioxeia* was transferred into a 1-L PC bottle. To determine the presence of any prey cells in the *S. gracilenta* culture, a 5 ml aliquot was removed from the bottle, fixed with 5% Lugol's solution, and examined under a light microscope. When no prey cells were detected, an

TABLE 2 | Feeding capability and comparison of the swimming speeds of predator species and *Shimiella gracilenta*.

Organisms	Type	ESD	Attack (%)	Capture success (%)	Feeding	Growth	SS	MSS	Ref*
Predators									
Gyrodinium jinhaense	HTD	10.2	0	0	N		243	331	(1, 2)
Gyrodinium dominans	HTD	11.6	6	100	Y[a]	–	299	440	(1, 3)
Pfiesteria piscicida	KPD	13.5	33	100	Y	–	300	670	(4, 5)
Oxyrrhis marina	HTD	15.6	14	100	Y	+	474	590	(3)
Aduncodinium glandula	HTD	21.0	0	0	N		439	546	(4)
Oblea rotunda	HTD	21.6	0	0	N		420		(6, 7)
Polykrikos kofoidii	HTD	43.5	0	0	N		657	911	(8, 9)
Rimostrombidium sp.	NC	29.8			Y	++	220 ±10	420	This study
Prey									
Shimiella gracilenta	KPD	9.3					160 ± 14 (357 ± 44)	500 (700)	This study

ESD, equivalent spherical diameter (μm); SS, swimming speed (μm s^{-1}, ± standard error); MSS, maximum swimming speed (μm s^{-1}); N, no feeding; Y, feeding; Y[a], rarely feeding; HTD, heterotrophic dinoflagellate; NC, naked ciliate; KPD, kleptoplastidic dinoflagellate; Ref: reference for ESD, SS, and MSS; (1) Kang et al. (2020); (2) Our unpublished data; (3) Jeong et al. (2018a); (4) Jang et al. (2016); (5) Burkholder and Glasgow (1997); (6) Ok et al. (2017); (7) Buskey et al. (1993); (8) Jeong et al. (2001b); (9) Jeong et al. (2002). The number in parenthesis in SS and MSS columns is the jumping speed of S. gracilenta. ++: >0.8 day^{-1}; +: 0.8 to >0.5 day^{-1}; –: no growth.*

aliquot of *S. gracilenta* culture was transferred to a 38-ml cell culture flask (BD Biosciences, USA) and allowed to acclimate for 30 min to avoid the interference of water flow. A video camera was focused on a single frame on the cell culture flask under a stereomicroscope (SZX2-ILLK, Olympus, Japan) at 20°C. Swimming of *S. gracilenta* cells was recorded at a magnification of × 25 using a video-analyzing system (SRD-1673 DN, Samsung, Korea) and a CCD camera (DXC-C33, SONY, Japan). The speed of all swimming cells viewed within 10–70 min was measured, and the average swimming speed (n = 30) was calculated based on the straight line of the cells during single-frame playback.

Statistical Analysis

Pearson's correlation analysis was used to examine the association among the variables [i.e., equivalent spherical diameter (ESD) of prey species, μ_{max} and I_{max} of *O. marina* feeding on dinoflagellate prey species, maximum swimming speed (MSS) of prey species, and μ_{max} and I_{max} of *O. marina* feeding on dinoflagellate prey species]. Statistical analyses were performed using SPSS ver. 25.0 (IBM-SPSS Inc., Armonk, NY, USA).

RESULTS

Feeding Occurrence by Heterotrophic Protists on *Shimiella gracilenta*

The HTDs *O. marina*, *P. piscicida*, and *G. dominans*, as well as the naked ciliate *Rimostrombidium* sp., were able to feed on *S. gracilenta* SGJH1904 (**Table 2**; **Supplementary Figures 1, 2**; **Supplementary Video 1**). Cells of *O. marina*, *G. dominans*, and *Rimostrombidium* sp. engulfed prey cells, while *P. piscicida* cells fed on prey cells using a peduncle (**Supplementary Figures 1**, **2**). The attack ratios of *G. dominans*, *P. piscicida*, and *O. marina* to *S. gracilenta* were 6, 33, and 14%, respectively (**Table 2**). Once these predators attacked *S. gracilenta*, they successfully fed on *S. gracilenta* (i.e., 100%).

The HTDs *A. glandula*, *G. jinhaense*, *O. rotunda*, and *P. kofoidii* did not feed on *S. gracilenta* (**Table 2**; **Supplementary Figure 3**). Cells of *A. glandula*, *G. jinhaense*, *O. rotunda*, and *P. kofoidii* did not attack *S. gracilenta* cells. Furthermore, *S. gracilenta* cells were observed quickly jumping backward when *A. glandula*, *G. jinhaense*, *O. rotunda*, and *P. kofoidii* touched them. However, it was observed that *O. marina* spun very quickly around an *S. gracilenta* cell and engulfed the prey cell (**Supplementary Video 1**). Cells of *Rimostrombidium* sp. made feeding currents to draw prey cells and intercepted prey cells inside the feeding currents. Often, several cells of *P. piscicida* attacked an *S. gracilenta* cell together.

Growth Rates of *Rimostrombidium* sp. and *Oxyrrhis marina* Feeding on *Shimiella gracilenta* as a Function of Prey Concentration

With increasing mean prey concentrations, the specific growth rate of *Rimostrombidium* sp. feeding on *S. gracilenta* increased at mean prey concentrations ≤204 ng C ml^{-1} (2,919 cells ml^{-1}), but this became saturated at higher mean prey concentrations (**Figure 1A**). When the data were fitted to Equation (2), the calculated maximum growth rate (μ_{max}) of *Rimostrombidium* sp. feeding on *S. gracilenta* was 0.903 day^{-1}.

The specific growth rate of *O. marina* feeding on *S. gracilenta* rapidly increased with the increase of mean prey concentrations, with the highest growth rate at a mean prey concentration of 9.4 ng C ml^{-1} (134 cells ml^{-1}; **Figure 1B**). However, this slightly decreased at higher mean prey concentrations. When the data were fitted to Equation (2), the calculated μ_{max} of *O. marina* on *S. gracilenta* was 0.645 day^{-1}.

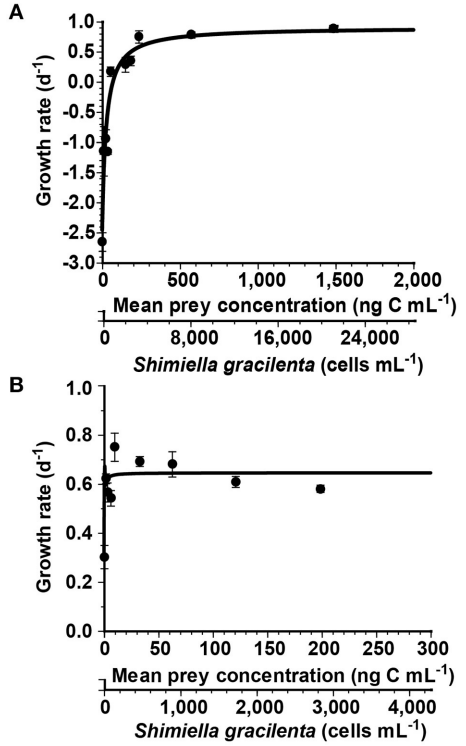

FIGURE 1 | Growth rates of *Rimostrombidium* sp. **(A)** and *Oxyrrhis marina* **(B)** feeding on *Shimiella gracilenta* as a function of mean prey concentration (x). Symbols represent treatment means ± standard error (SE). The curves are fitted by the Michaelis–Menten equation (Equation 2), using all treatments in the experiment. **(A)** The growth rate (day^{-1}) = 0.90 {(x – 69.1)/[94.5 + (x – 69.1)]}, r^2 = 0.89. **(B)** The growth rate (day^{-1}) = 0.65 {(x + 0.12)/[0.14 + (x + 0.12)]}, r^2 = 0.63.

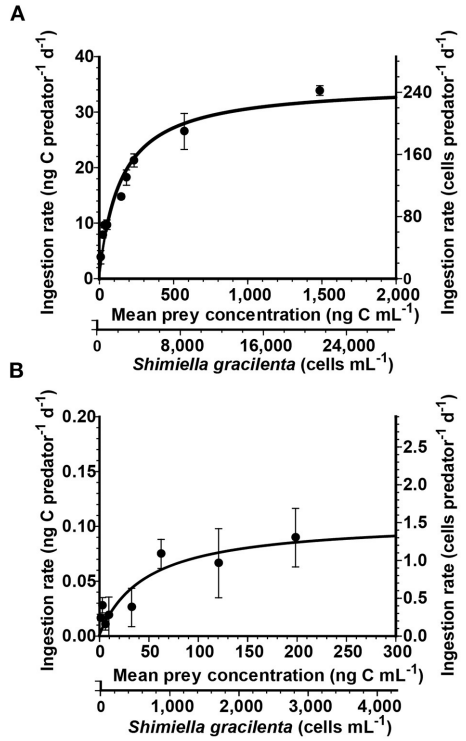

FIGURE 2 | Ingestion rates of *Rimostrombidium* sp. **(A)** and *Oxyrrhis marina* **(B)** feeding on *Shimiella gracilenta* as a function of mean prey concentration (x). Symbols represent treatment means ± standard error (SE). The curves are fitted by the Michaelis–Menten equation (Equation 3), using all treatments in the experiment. **(A)** The ingestion rate (ng C predator^{-1} day^{-1}) = 35 [x/(146 + x)], r^2 = 0.92. **(B)** The ingestion rate (ng C predator^{-1} day^{-1}) = 0.11 [x/(47.1 + x)], r^2 = 0.46.

Ingestion Rates of *Rimostrombidium* sp. and *Oxyrrhis marina* Feeding on *Shimiella gracilenta* as a Function of Prey Concentration

With increasing mean prey concentrations, the ingestion rate of *Rimostrombidium* sp. feeding on *S. gracilenta* rapidly increased at mean prey concentrations ≤204 ng C ml^{-1} (2,919 cells ml^{-1}) but slowly increased at higher mean prey concentrations (**Figure 2A**). When the data were fitted to Equation (3), the calculated maximum ingestion rate (I_{max}) of *Rimostrombidium* sp. feeding on *S. gracilenta* was 35 ng C predator^{-1}day^{-1} (500 cells predator^{-1} day^{-1}).

With increasing mean prey concentrations, the ingestion rate of *O. marina* feeding on *S. gracilenta* increased at mean prey concentrations ≤62.3 ng C ml^{-1} (890 cells ml^{-1}) but became almost saturated at higher mean prey concentrations (**Figure 2B**). When the data were fitted to Equation (3), the calculated I_{max} of *O. marina* on *S. gracilenta* was 0.11 ng C predator^{-1} day^{-1} (1.6 cells predator^{-1} day^{-1}).

Swimming Speed

The average (± SE, n = 30) and maximum swimming speeds of *S. gracilenta* under experiment conditions were 160 (± 14) and 500 μm s^{-1}, respectively, with the maximum jumping speed of 700 μm s^{-1} (**Table 2**).

DISCUSSION

Feeding Ability of the Predators

Among the eight common heterotrophic protists tested in the present study, four species were able to feed on *S. gracilenta* SGJH1904, whereas the other four species did not feed at all. The feeding mechanism, behavior, size, and/or shape of protist predators, as well as the biochemistry, behavior, size, and/or shape of the prey, have been known to affect the feeding abilities of predators (Scharf et al., 2000; Strom et al., 2003; Evans and Wilson, 2008; Jeong et al., 2010b; Roberts et al., 2011). The engulfment feeders *G. dominans*, *O. marina*, and *Rimostrombidium* sp. ingested *S. gracilenta*, whereas other engulfment feeders, *G. jinhaense* and *P. kofoidii*, did not feed on the prey species. Furthermore, the peduncle feeder *P. piscicida* fed on *S. gracilenta*, whereas another peduncle feeder,

A. glandula, did not feed on the prey species. Therefore, feeding mechanisms are likely not to affect the feeding occurrence of these heterotrophic protists on *S. gracilenta*. Meanwhile, among the protists *G. dominans*, *P. piscicida*, *O. marina*, and *Rimostrombidium* sp., which were able to feed on *S. gracilenta*, the sizes were larger than those of *G. jinhaense*, which was not able to feed on *S. gracilenta* but smaller than that of *A. glandula*, *O. rotunda*, and *P. kofoidii*, which were not able to feed on the prey (**Table 2**). Therefore, the predator size may not affect the feeding occurrence of these heterotrophic protists on *S. gracilenta*.

Although *G. jinhaense* and *G. dominans* are included in the same genus and have similar ESD values, *G. dominans* is known to feed on *Mesodinium rubrum*, which has jumping behavior, whereas *G. jinhaense* does not (Lee et al., 2014b; Kang et al., 2020). Thus, the rapid jumping behavior of *S. gracilenta* may be an effective anti-predation tool against *G. jinhaense*, but not against *G. dominans*. Moreover, the maximum swimming speed of *G. dominans* (440 μm s^{-1}) is considerably greater than that of *G. jinhaense* (331 μm s^{-1}, **Table 2**). Therefore, the swimming speed of these two *Gyrodinium* species may affect this differential feeding occurrence on *S. gracilenta*.

Cells of *P. kofoidii* are known to deploy a nematocyst-taeniocyst complex to capture a prey cell (Matsuoka et al., 2000; Tillmann and Hoppenrath, 2013). However, cells of *P. kofoidii* were not observed deploying a nematocyst-taeniocyst complex on the surface of an *S. gracilenta* cell. The minimum prey size that *P. kofoidii* was able to feed on is known to be approximately 10 μm (Jeong et al., 2001b). Therefore, *P. kofoidii* may have difficulty deploying a nematocyst-taeniocyst complex on the surface of a small-sized *S. gracilenta* cell.

The pallium feeder, *O. rotunda*, was able to feed on smaller prey than *S. gracilenta* (Strom and Buskey, 1993). Ok et al. (2021) reported that many trichocysts were observed inside the cytoplasm of *S. gracilenta*. It is known that trichocysts of *Fibrocapsa japonica* may substantially complicate the capturing process involving the tow filament of *O. rotunda* (Tillmann and Reckermann, 2002). Thus, trichocysts in *S. gracilenta* may act mechanically as a grazer deterrent to *O. rotunda*.

Growth and Ingestion Rates of the Predators

Both the growth and ingestion rates of *O. marina* and *Rimostrombidium* sp. on *S. gracilenta* are affected by prey concentrations (**Figures 1**, **2**). The half-saturation constant for the growth (K_{GR}) of *O. marina* feeding on *S. gracilenta* (0.14 ng C ml^{-1}; 2 cells ml^{-1}) was lower than that of *Rimostrombidium* sp. (94.5 ng C ml^{-1}; 1,350 cells ml^{-1}). Additionally, the half-saturation constant for the ingestion (K_{IR}) of *O. marina* (47.1 ng C ml^{-1}; 673 cells ml^{-1}) was also lower than that of *Rimostrombidium* sp. (146 ng C ml^{-1}; 2,086 cells ml^{-1}). Thus, at low prey concentrations, the growth and ingestion rates of *O. marina* would respond more readily to changes in prey concentrations than those of *Rimostrombidium* sp. Until now, the maximum cell abundance of *S. gracilenta* in natural environments has been reported as 29.9 cells ml^{-1} (Back et al., 2021). Without considering spatial dependence and other physical effects, *O. marina* may grow under this *S. gracilenta* concentration, while *Rimostrombidium* sp. may not.

The threshold concentration of *S. gracilenta* for the growth of *Rimostrombidium* sp. was 69.1 ng C ml^{-1} (987 cells ml^{-1}). At this prey concentration, the ingestion rate of *Rimostrombidium* sp. on *S. gracilenta* was 11.2 ng C $predator^{-1}$ day^{-1} (160 cells ml^{-1}). Thus, this ingestion rate corresponds to the threshold prey concentration for basic maintenance in the abundance of *Rimostrombidium* sp. Meanwhile, the growth rate of *O. marina* without added *S. gracilenta* cells (i.e., predator control) was positive. *Oxyrrhis marina* is known to feed on bacteria and grow on dissolved nutrients (Jeong et al., 2008; Lowe et al., 2011). Thus, this physiological characteristic of *O. marina* may be the reason why it had a positive growth without added *S. gracilenta* cells in this study.

There have been three kleptoplastidic dinoflagellates whose predators were identified and on which the growth and ingestion rates of the predators were determined; *Gymnodinium smaydae*, *P. piscicida*, and *S. gracilenta* (**Supplementary Table 2**; Jeong et al., 2007a, 2018b). These three kleptoplastidic dinoflagellates were ingested by *O. marina*. The ranges of μ_{max} and I_{max} of *O. marina* on the three dinoflagellates were 0.41–0.66 day^{-1} and 0.11–0.33 ng C $predator^{-1}$ day^{-1}, respectively (**Supplementary Table 2**). These ranges of μ_{max} and I_{max} of *O. marina* on kleptoplastic dinoflagellates showed no distinct values compared with those of *O. marina* on phototrophic and heterotrophic dinoflagellates (0.16–1.20 day^{-1} and 0.07–6.36 ng C $predator^{-1}$ day^{-1}, respectively). Moreover, the K_{GR} of *O. marina* feeding on *G. smaydae* and *S. gracilenta* (1.4 and 0.14 ng C ml^{-1}, respectively) showed relatively low values, while that on *P. piscicida* (21 ng C ml^{-1}) was much higher (Jeong et al., 2007a, 2018b). Thus, the nutritional properties of each kleptoplastidic dinoflagellate as prey for a predator species may vary from species to species. More studies are needed to understand the nutritional values of kleptoplastidic dinoflagellates as prey in marine ecosystems.

Neither the I_{max} nor the μ_{max} of *O. marina* on target prey species was significantly correlated with prey size (>0.05, Pearson's correlation analysis; **Figures 3A,B**), and the μ_{max} was also not significantly correlated with the I_{max} (>0.05; **Figure 3C**). However, the maximum swimming speed (MSS) of the prey species was significantly and negatively correlated with the μ_{max} of *O. marina* on prey species (<0.05), but it was not correlated with the I_{max} (>0.05; **Figure 4**). The higher the MSS of prey species, the more the predator *O. marina* may spend energy in catching the prey cells. Thus, the growth rates of *O. marina* are likely to be affected by the MSS of prey species. Among the reported dinoflagellate prey species of *O. marina* having the size of 9–10 μm, the μ_{max} of *O. marina* on *S. gracilenta* was higher than those on *A.* cf. *poporum*, *B. adriatica*, *G. smaydae*, and a toxic strain of *K. veneficum* CCMP2064. Therefore, *O. marina* may spend less energy in capturing, ingesting, and digesting *S. gracilenta* than *A.* cf. *poporum*, *B. adriatica*, and *G. smaydae*. Among the 16 dinoflagellate prey species of *O. marina*, the I_{max} of *O. marina* on *S. gracilenta* was lower than that on the other prey

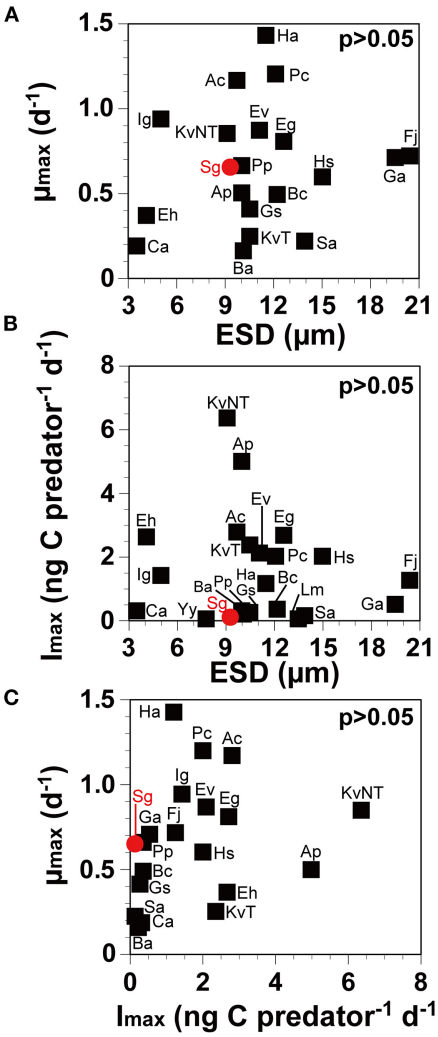

FIGURE 3 | The maximum growth rate (μ_{max}) and the ingestion rate (I_{max}) of *Oxyrrhis marina* on prey as a function of prey size (ESD, equivalent spherical diameter; μm) and μ_{max} as a function of I_{max}, as in **Supplementary Table 2**, respectively. The μ_{max} (**A**; $r = 0.15$, $p = 0.53$) and I_{max} (**B**; $r = 0.13$, $p = 0.57$) of *Oxyrrhis marina* on prey (black square) and *Shimiella gracilenta* (red circle), as a function of prey size (ESD). (**C**; $r = 0.26$, $p = 0.27$). The μ_{max} as a function of I_{max}. Ac, *Amphidinium carterae*; Ap, *Azadinium* cf. *poporum*; Ba, *Biecheleriopsis adriatica*; Bc, *Biecheleria cincta*; Ca, *Cafeteria* sp.; Eh, *Emiliania huxleyi*; Eg, *Eutreptiella gymnastica*; Ev, *Effrenium voratum*; Fj, *Fibrocapsa japonica*; Ga, *Gymnodinium aureolum*; Gs, *Gymnodinium smaydae*; Ha, *Heterosigma akashiwo*; Hs, *Heterocapsa steinii*; Ig, *Isochrysis galbana*; KvNT, *Karlodinium veneficum* (non-toxic; MD5); KvT, *K. veneficum* (toxic; CCMP2064); Lm, *Luciella masanensis*; Pc, *Prorocentrum cordatum*; Pp, *Pfiesteria piscicida*; Sa, *Stoeckeria algicida*; Sg, *Shimiella gracilenta*; Yy, *Yihiella yeosuensis*. Data were obtained from Lee (1998), Jeong et al. (2001a, 2003, 2007a,b, 2011, 2014, 2018a,b), Tillmann and Reckermann (2002), Strom et al. (2003), Kimmance et al. (2006), Adolf et al. (2007), Yoo et al. (2010, 2013b,c), Potvin et al. (2013), Anderson and Menden-Deuer (2017), and Kang et al. (2019).

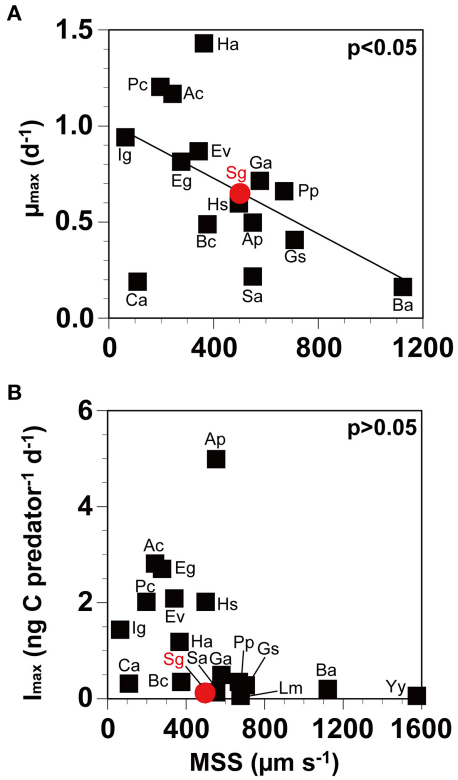

FIGURE 4 | The maximum growth rate (μ_{max}) and the ingestion rate (I_{max}) of *Oxyrrhis marina* on prey as a function of maximum swimming speed (MSS), as described in **Supplementary Table 2**. The μ_{max} (**A**; $r = -0.51$, $p = 0.04$) and the I_{max} (**B**; $r = -0.37$, $p = 0.13$) of *Oxyrrhis marina* on prey (black square) and *Shimiella gracilenta* (red circle), as a function of MSS. Ac, *Amphidinium carterae*; Ap, *Azadinium* cf. *poporum*; Ba, *Biecheleriopsis adriatica*; Bc, *Biecheleria cincta*; Ca, *Cafeteria* sp.; Eg, *Eutreptiella gymnastica*; Ev, *Effrenium voratum*; Ga, *Gymnodinium aureolum*; Gs, *Gymnodinium smaydae*; Ha, *Heterosigma akashiwo*; Hs, *Heterocapsa steinii*; Ig, *Isochrysis galbana*; Lm, *Luciella masanensis*; Pc, *Prorocentrum cordatum*; Pp, *Pfiesteria piscicida*; Sa, *Stoeckeria algicida*; Sg, *Shimiella gracilenta*; Yy, *Yihiella yeosuensis*. Data were obtained from Throndsen (1973), Kamykowski and McCollum (1986), Lee (1998), Jeong et al. (1999, 2001a, 2002, 2003, 2007a,b, 2010a, 2011, 2014, 2018a,b), Kimmance et al. (2006), Yoo et al. (2010, 2013b,c), Kang et al. (2011, 2019), Potvin et al. (2013), Lee et al. (2014a), Jang et al. (2015, 2016, 2017), Anderson and Menden-Deuer (2017), and Lim et al. (2018).

species, except for *Yihiella yeosuensis* and *Luciella masanensis* (**Supplementary Table 2**). The fast swimming speed and quick jumping behavior of *Y. yeosuensis* might be responsible for the lack of predation (Jeong et al., 2018a). Therefore, the quick jumping behavior of *S. gracilenta* may lower the I_{max} of *O. marina* on itself. However, the jumping speed of *S. gracilenta* is lower than that of *Y. yeosuensis*, and this may partially be responsible for the higher I_{max} of *O. marina* on *S. gracilenta*. Cells of *L. masanensis* do not have the quick jumping behavior, but it was suggested that they excrete chemicals to protect themselves from predation (Jeong et al., 2007a).

This study clearly showed that *S. gracilenta* supported the positive growth of only *O. marina* and *Rimostrombidium* sp. among the potential predator species tested. Notably, these two predators have cosmopolitan distributions (Agatha, 2011; Watts et al., 2011). *Shimiella gracilenta* has been found in the regions where *O. marina* and *Rimostrombidium* sp. have been found: the

east coast of the United States (Campbell, 1973; Johnson et al., 2003; Tucker et al., 2017), the Baltic Sea (Pedersen and Hansen, 2003; Hällfors, 2004; Watts et al., 2011), and Jinhae Bay, Korea (Choi et al., 2016; Yoon, 2018; Ok et al., 2021). Therefore, *O. marina* and *Rimostrombidium* sp. may grow on *S. gracilenta* if both predators and prey coexist in the regions.

To investigate the impact of predation by *O. marina* or *Rimostrombidium* sp. on the populations of *S. gracilenta*, ingestion rates of *O. marina* or *Rimostrombidium* sp. on *S. gracilenta* and their abundances should be quantified. The results of the present study provided the ingestion rates of *O. marina* and *Rimostrombidium* sp. on *S. gracilenta* as a function of the prey concentration. Thus, if the abundances of *S. gracilenta* and co-occurring *O. marina* or *Rimostrombidium* sp. are available, the predation impact by *O. marina* or *Rimostrombidium* sp. on the populations of *S. gracilenta* can be estimated at any prey concentration. Depending on the degree of predation impact by *O. marina* or *Rimostrombidium* sp. on the populations of *S. gracilenta*, the ecological roles of *S. gracilenta* as prey for the predator can be evaluated. Moreover, the results of the present study provide the threshold *S. gracilenta* concentration for the growth of *O. marina* or *Rimostrombidium* sp. and also, growth rates of the predators as a function of the prey concentration. Thus, the ecological roles of *S. gracilenta* as prey for *O. marina* or *Rimostrombidium* sp. can be determined. This study suggested that *S. gracilenta* may have an advantage for survival due to only a few common heterotrophic protist predators and low ingestion rates of the predators in marine ecosystems.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

SP and HJ designed the study conception and drafted the manuscript. SP, HJ, JO, HK, JY, SE, and EP obtained the data and conducted the experiments. SP, HJ, and JO performed data analyses. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.738547/full#supplementary-material

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