Feeding by common heterotrophic protists on the mixotrophic dinoflagellate *Ansanella granifera* (Suessiaceae, Dinophyceae)

Hee Chang Kang[1], Hae Jin Jeong[1,2,*], An Suk Lim[3], Jin Hee Ok[1], Ji Hyun You[1], Sang Ah Park[1] and Se Hee Eom[1]

[1]*School of Earth and Environmental Sciences, College of Natural Sciences, Seoul National University, Seoul 08826, Korea*
[2]*Research Institute of Oceanography, Seoul National University, Seoul 08826, Korea*
[3]*Division of Life Science, Gyeongsang National University, Jinju 52828, Korea*

The mortality rate of red-tide dinoflagellates owing to predation is a major parameter that affects their population dynamics. The dinoflagellates *Ansanella granifera* and *Ansanella* sp. occasionally cause red tides. To understand the interactions between common heterotrophic protists and *A. granifera*, we explored the feeding occurrence of nine heterotrophic protists on *A. granifera* and the growth and ingestion rates of the heterotrophic dinoflagellate *Gyrodinium dominans* on *A. granifera* as a function of prey concentration and those of *Oxyrrhis marina* at a single high prey concentration. The heterotrophic dinoflagellates *Aduncodinium glandula*, *G. dominans*, *Gyrodinium moestrupii*, *Luciella masanensis*, *Oblea rotunda*, *O. marina*, *Polykrikos kofoidii*, and *Pfiesteria piscicida* and the naked ciliate *Strombidium* sp. were able to feed on *A. granifera*. With increasing mean prey concentrations, the growth and ingestion rates of *G. dominans* feeding on *A. granifera* rapidly increased and became saturated or slowly increased. The maximum growth and ingestion rates of *G. dominans* on *A. granifera* were 0.305 d^{-1} and 0.42 ng C predator^{-1} d^{-1} (3.8 cells predator^{-1} d^{-1}), respectively. Furthermore, the growth and ingestion rates of *O. marina* on *A. granifera* at 1,700 ng C mL^{-1} (15,454 cells mL^{-1}) were 0.037 d^{-1} and 0.19 ng C predator^{-1} d^{-1} (1.7 cells predator^{-1} d^{-1}), respectively. The growth and ingestion rates of *G. dominans* and *O. marina* feeding on *A. granifera* were almost the lowest among those on the dinoflagellate prey species. Therefore, *G. dominans* and *O. marina* may prefer *A. granifera* less than other dinoflagellate prey species. The low mortality rate of *A. granifera* may positively affect its bloom formation.

Keywords: bloom; ciliate; food web; heterotrophic dinoflagellate; predation; red tide; Suessiales

INTRODUCTION

Dinoflagellates are ubiquitous and one of the major components of marine ecosystems (Taylor et al. 2008, Stern et al. 2010, Kang et al. 2019b, Jeong et al. 2021, Lim and Jeong 2021, Ok et al. 2021). They play diverse ecological roles in marine food webs as primary producers, predators, prey, symbiotic partners, and parasites (Coats 1999, Jeong et al. 2010b, Hansen 2011, Stoecker et al. 2017, LaJeunesse et al. 2018, Eom et al. 2021, Lim and Jeong 2022). They have three trophic modes: autotrophy, mixotrophy (i.e., autotrophy + heterotrophy), and heterotrophy (Stoecker 1999, Jeong et al. 2010b). Many mixotrophic dinoflagellate species form red tides or harmful algal blooms (HABs), which often cause mass mortality in various marine organisms and significant economic

damage to the aquaculture industry (Hallegraeff 1995, Jeong et al. 2021, Sakamoto et al. 2021). Thus, to minimize economic losses owing to red tides or HABs by mixotrophic dinoflagellate species, the growth rate of the species under given conditions should be determined (Jeong et al. 2015). The growth of a species can be lowered if effective predators of the species are abundant (Yoo et al. 2013a, Lim et al. 2017, You et al. 2020). To understand and predict the outbreak of red tides or HABs by mixotrophic dinoflagellate species, the type of predators that are able to feed on the species as well as the growth and ingestion rates of predators on the prey species should be determined (Matsuyama et al. 1999, Jeong et al. 2017, Ok et al. 2017).

The dinoflagellate *Ansanella granifera* was formally described as a new species and genus in the order Suessiales in 2014 (Jeong et al. 2014a). Subsequently, *Ansanella natalensis* from South Africa and *A. catalana* from the NW Mediterranean Sea were formally described in 2018 and 2022, respectively (Dawut et al. 2018, Sampedro et al. 2022). All these species have a type E eyespot and small sizes with ranges of 9.6–15.5 μm in length and 7.3–12.4 μm in width (Jeong et al. 2014a, Dawut et al. 2018, Sampedro et al. 2022). These species have been found in many regions globally as vegetative cells or cysts (Jeong et al. 2014a, Belevich et al. 2021, Reñé et al. 2021, Liu et al. 2022, 2023, Pratomo et al. 2022, Sampedro et al. 2022). The presence of *A. granifera* has been reported in Korea, China, Indonesia, the Yellow Sea, and the Kara Sea (Jeong et al. 2014a, Belevich et al. 2021, Liu et al. 2022, 2023, Pratomo et al. 2022). Furthermore, *A. granifera* caused huge red tides in Manzanillo City, southeastern Cuba in August 2018, with a maximum concentration of 2.16×10^5 cells mL^{-1} (Moreira-González et al. 2021). Moreover, *Ansanella* sp. caused mixed blooms with the mixotrophic dinoflagellate *Karenia mikimotoi* within East Johor Straits, Singapore in January 2016, and the highest concentration of *Ansanella* sp. was 2.45×10^3 cells mL^{-1} (Kok and Leong 2019). *Ansanella granifera* has been revealed to be mixotrophic and its maximum growth rate is as high as 1.426 d^{-1} (Lee et al. 2014b). However, the type of predators that are able to feed on *A. granifera* and the growth and ingestion rates of the predators on *A. granifera* have not yet been explored.

Heterotrophic protists, such as heterotrophic dinoflagellates (HTDs) and ciliates, are major predators of mixotrophic dinoflagellates in marine ecosystems (Pierce and Turner 1992, Sherr and Sherr 2002, Kang et al. 2020). In general, the grazing impact of heterotrophic protists on populations of mixotrophic dinoflagellates is usually greater than that of metazoan predators because of the much higher abundance of heterotrophic protists than metazoan predators (Lee et al. 2017, Lim et al. 2017). The high grazing impact of heterotrophic protists sometimes prevents the outbreak of red tides or HABs by mixotrophic dinoflagellates (Yoo et al. 2013a, Lim et al. 2017, Kang et al. 2018). The HTDs *Aduncodinium glandula*, *Gyrodinium dominans*, *Gyrodinium moestrupii*, *Luciella masanensis*, *Oblea rotunda*, *Oxyrrhis marina*, *Polykrikos kofoidii*, and *Pfiesteria piscicida* and the naked ciliate *Strombidium* sp. are commonly found in many marine environments (Strom and Buskey 1993, Claessens et al. 2008, Taylor et al. 2008, Watts et al. 2010, Tillmann and Hoppenrath 2013, Lee et al. 2021). These potential heterotrophic protistan predators have different sizes, shapes, edible prey species, feeding mechanisms, and growth and ingestion rates on the same prey species (e.g., Mason et al. 2007, Jeong et al. 2010b, Lowe et al. 2011, Guo et al. 2013, Kang et al. 2015, 2020, Jang et al. 2016).

In the present study, the feeding occurrence of these eight HTDs and one naked ciliate on *A. granifera* was examined. Furthermore, the growth and ingestion rates of *G. dominans* feeding on *A. granifera* as a function of prey concentration and those of *O. marina* feeding on *A. granifera* at a single high prey concentration were measured because only these two predator species had positive growth rates in our preliminary tests. The growth and ingestion rates of *G. dominans* and *O. marina* feeding on *A. granifera* were compared with those of *G. dominans* and *O. marina* feeding on other dinoflagellate prey species. This study provides a better understanding of the interactions between *A. granifera* and common heterotrophic protists, as well as the population dynamics of *A. granifera* and its predators.

MATERIALS AND METHODS

Preparation of experimental organisms

Sediment samples were collected from Shiwha Bay, Korea, in September 2010, when the temperature and salinity of ambient waters were 21.3°C and 15.6, respectively (Table 1) (Jeong et al. 2014a). After germinating cysts in the samples, a clonal culture of *A. granifera* AGSW10 was established using two consecutive single-cell isolations. The culture of *A. granifera* with fresh f/2-Si medium in 500-mL bottles on a shelf was incubated at 20°C under an irradiance of 20 μE m^{-2} s^{-1} provided by cool white fluorescent lights and a 14 : 10 h light : dark (L : D) cycle.

For the isolation of the HTDs used in this study, plankton samples were collected off the coasts of Masan, Jeongok, Saemankeum, Jinhae, Kunsan, and Jangheung, Korea from 2001–2019 using water samplers (Table 1). The culture of *P. piscicida* was obtained from the National Center for Marine Algae and Microbiota. The naked ciliate *Strombidium* sp. was isolated from plankton samples collected using a 20-µm mesh net off the coasts of Kunsan in January 2023 (Table 1). To obtain clonal cultures of each HTD and ciliate species, two consecutive single-cell isolations were used.

The carbon contents of *A. granifera* and predator species were obtained from previous studies (Jeong et al. 2001*b*, 2007, 2008, Lee et al. 2014*b*, Jang et al. 2016, Ok et al. 2017, Kang et al. 2020). The carbon content of *Strombidium* sp. was estimated from cell volumes in this study using the equation suggested by Menden-Deuer and Lessard (2000).

Table 1. Information for the isolation and maintenance of the prey and predator species used in this study

Organisms (strain name)	Type	FM	Location	Date	T	S	Prey species	Feeding of Ag
Predators								
Aduncodinium glandula (AGMS1303)	HTD	PD	Masan, Korea	Mar 2013	8.1	30.3	As	Y
Gyrodinium dominans (GDJK1907)	HTD	EG	Jeongok, Korea	Jul 2019	25.2	31.9	Ac	Y
Gyrodinium moestrupii (GMSMK0910)	HTD	EG	Saemankeum, Korea	Oct 2009	21.2	31.0	Am	Y
Luciella masanensis (LMJH1607)	HTD	PD	Jinhae, Korea	Jul 2016	22.6	30.7	Api	Y
Oblea rotunda (ORJH1504)	HTD	PA	Jinhae, Korea	Apr 2015	12.6	31.2	Ac	Y
Oxyrrhis marina (OMKS0105)	HTD	EG	Kunsan, Korea	May 2001	16.0	27.7	Ac	Y
Polykrikos kofoidii (PKJH1607)	HTD	EG	Jangheung, Korea	Jul 2016	23.6	26.4	Al	Y
Pfiesteria piscicida (CCMP2091)	HTD	PD	Neuse River, USA	Jan 1998	NA	NA	Ac	Y
Strombidium sp. (SSKS2301)	NC	FF	Kunsan, Korea	Jan 2023	3.6	30.8	Pc	Y
Prey								
Ansanella granifera (AGSW10)	MTD	EG	Shiwha, Korea	Sep 2010	21.3	15.6	-	-

FM, feeding mechanism; T, temperature (°C); S, salinity; Ag, *Ansanella granifera*; HTD, heterotrophic dinoflagellate; PD, peduncle feeder; As, *Akashiwo sanguinea*; Y, feeding; EG, engulfment feeder; Ac, *Amphidinium carterae*; Am, *Alexandrium minutum* CCMP113; Api, *Apistonema* sp.; PA, pallium feeder; Al, *Alexandrium minutum* CCMP1888 (previously *A. lusitanicum*); NA, not available; NC, naked ciliate; FF, filter feeder; Pc, *Prorocentrum cordatum*; MTD, mixotrophic dinoflagellate.

Table 2. Experimental design

Experiment No.	Prey		Predator	
	Species	Density	Species	Density
1	*Ansanella granifera*	20,000	*Aduncodinium glandula*	1,000
			Gyrodinium dominans	1,000
			Gyrodinium moestrupii	500
			Luciella masanensis	4,000
			Oblea rotunda	800
			Oxyrrhis marina	4,000
			Polykrikos kofoidii	100
			Pfiesteria piscicida	2,000
			Strombidium sp.	20
2	*Ansanella granifera*	48, 179, 722, 1,312, 2,848, 4,765	*Gyrodinium dominans*	10, 15, 42, 87, 207, 444 (240)
3	*Ansanella granifera*	10,733	*Oxyrrhis marina*	951 (210)

The numbers in the prey and predator columns are the initial densities (cells mL^{-1}) of the prey and predator, respectively. Predator density in the control bottle is shown in parentheses.

Interactions between *Ansanella granifera* and heterotrophic protists

In experiment 1, feeding by each of the HTDs and ciliates on *A. granifera* was investigated (Table 2). Dense cultures of *A. granifera* (ca. 20,000 cells mL^{-1}) and each of the HTDs and ciliates (ca. 20–4,000 cells mL^{-1}) were added to each 42-mL PC bottle using an autopipette (Table 2). For each experiment, one experiment (mixtures of prey and predator), one prey control (only prey without predator), and one predator control (only predator without prey) bottle were set up. The bottles were placed on a 0.00017 g (0.9 rpm) rotating wheel, whereas those for the benthic species *A. glandula* were placed on a shelf. All bottles were incubated at 20°C under an illumination of 20 μE m^{-2} s^{-1} and a 14 : 10 h L : D cycle.

After 2, 24, and 48 h of incubation, 5 mL aliquots were taken from each bottle and transferred into the wells of a 6-well cell culture plate. To determine whether each predator could feed on *A. granifera*, each predator cell (n ≥ 30) was tracked for 2 min under a dissection microscope at 20–63× magnification. The feeding process of predators on *A. granifera* was photographed on a confocal dish with cover glasses at 200–1,000× magnification using a digital camera (Zeiss-AxioCam 506; Carl Zeiss Ltd., Göttingen, Germany) attached to an inverted light microscope (Zeiss-Axiovert 200 M; Carl Zeiss Ltd.).

Growth and ingestion rates of *Gyrodinium dominans* feeding on *Ansanella granifera* as a function of prey concentration

In experiment 2, the growth and ingestion rates of *G. dominans* feeding on *A. granifera* as a function of prey concentration were measured (Table 2). In preliminary tests, *A. granifera* supported only the growth of *G. dominans* and *O. marina* among the heterotrophic protists tested, and the growth rate of *G. dominans* on *A. granifera* was the highest.

Dense cultures of *G. dominans* grown on *Amphidinium carterae* were transferred into 250-mL PC bottles one day after cells of *A. carterae* were not observed. The bottles were filled with freshly filtered seawater, capped, placed on a 0.00017 g rotating plankton wheel, and incubated at 20°C under illumination of 20 μE m^{-2} s^{-1} and a 14 : 10 h L : D cycle. This was conducted to minimize possible residual growth from the ingested prey in their body. After one day, three 1 mL aliquots from each bottle were taken using an autopipette and enumerated using a compound microscope to determine the cell concentration. After determining that there was no residual growth, the cultures were used in further experiments.

The initial concentrations of *G. dominans* and *A. granifera* were established in six different combinations (Table 2). Triplicate 42-mL PC experimental bottles (mixtures of predator and prey) and triplicate control bottles (prey only) were set up for each of the six predator-prey combinations, and triplicate control bottles (predator only) were established at a single high predator concentration. Predetermined volumes of *G. dominans* and *A. granifera* were added to each bottle using autopipettes. To provide similar water conditions in experimental and control bottles, the predator culture was filtered through a 0.2-μm disposable syringe filter (DISMIC-25CS type, 25 mm; Advantec, Toyo Roshi Kaisha Ltd., Chiba, Japan), and then for each predator-prey combination, an amount equal to the amount of predator volume added to the experimental bottle was added to the prey control bottles. Similarly, the prey culture was filtered through a 0.2-μm disposable syringe filter, and then an amount equal to the prey volume added to the experimental bottles was added to the predator control bottles. To provide sufficient nutrients to *A. granifera*, 5 mL of f/2-Si medium was added to all bottles, which were then filled with freshly filtered seawater and capped. To determine the initial predator and prey densities at the beginning of the experiment, a 5 mL aliquot was taken from each bottle, fixed with 5% Lugol's solution, and counted in three 1-mL Sedgewick Rafter chambers (SRCs) using a microscope. The bottles were then filled to capacity with freshly filtered seawater, capped, and placed on 0.00017 g rotating wheels under the conditions described above. The dilution of the cultures in this process was considered when calculating the growth and ingestion rates. A 10 mL aliquot was taken from each bottle after 48 h and fixed with 5% Lugol's solution, and the abundances of predators and prey were then examined by counting all or >200 cells in three 1-mL SRCs.

The specific growth rate of the predator μ (d^{-1}) was calculated using the following equation:

$$\mu \, (d^{-1}) = [Ln \, (P_t / P_0)] / t \qquad (1)$$

, where P_0 and P_t represent the predator concentrations at 0 and 2 d, respectively.

Data for *G. dominans* growth rates were fitted to a modified Michaelis–Menten equation:

$$\mu \, (d^{-1}) = \mu_{max} \, (x - x') / [K_{GR} + (x - x')] \qquad (2)$$

, where μ_{max} is the maximum growth rate (d^{-1}), x is the prey concentration (cells mL^{-1} or ng C mL^{-1}), x' is the threshold of prey concentration (prey concentration where $\mu = 0$), and K$_{GR}$ is the prey concentration sustaining 1/2 μ_{max}. The data were iteratively fitted to the model using DeltaGraph (Red Rock Software Inc., Salt Lake, UT, USA).

Ingestion rate and mean prey concentration were calculated using the modified equations of Frost (1972) and Heinbokel (1978). Data for *G. dominans* ingestion rates (IR, cells predator^{-1} d^{-1} or ng C predator^{-1} d^{-1}) were fitted into a modified Michaelis–Menten equation:

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

, where I$_{max}$ is the maximum ingestion rate (cells predator^{-1} d^{-1} or ng C predator^{-1} d^{-1}), x is the prey concentration (cells mL^{-1} or ng C mL^{-1}), and K$_{IR}$ is the prey concentration that sustains 1/2 I$_{max}$.

Growth and ingestion rates of *Oxyrrhis marina* feeding on *Ansanella granifera* at a single prey concentration

Experiment 3 was designed to measure the growth and ingestion rates of *O. marina* feeding on *A. granifera* at a single high prey concentration at which the growth and ingestion rates of *G. dominans* on *A. granifera* were saturated. The growth and ingestion rates of *O. marina* feeding on *A. granifera* were determined as described above.

Statistical analysis

Pearson's correlation analysis was used to investigate the relationships between variables (i.e., the growth and ingestion rates of *G. dominans* or *O. marina* feeding on each prey species, and the equivalent spherical diameter and maximum swimming speed (MSS) of each prey species). All analyses were performed using SPSS version 25.0 (IBM-SPSS Inc., Armonk, NY, USA).

RESULTS AND DISCUSSION

Interactions between *Ansanella granifera* and heterotrophic protists

All tested HTDs, *A. glandula*, *G. dominans*, *G. moestrupii*, *O. marina*, *L. masanensis*, *P. piscicida*, *P. kofoidii*, *O. rotunda* and the ciliate *Strombidium* sp., were able to feed on *A. granifera* AGSW10 (Table 1). The cells of the engulf- ment feeders *G. dominans*, *G. moestrupii*, *O. marina*, *P. kofoidii*, and *Strombidium* sp. ingested *A. granifera* cells (Fig. 1), whereas the peduncle feeders *A. glandula*, *L. masanensis*, and *P. piscicida* fed on *A. granifera* cells using a peduncle (Fig. 2). A pallium feeder, *O. rotunda* ingested *A. granifera* cells using a pallium (feeding veil) after capturing the *A. granifera* cell using a tow filament.

Growth and ingestion rates of *Gyrodinium dominans* feeding on *Ansanella granifera* as a function of prey concentration

With increasing mean prey concentrations, the specific growth rate of *G. dominans* feeding on *A. granifera* AGSW10 increased at mean *A. granifera* concentrations <69 ng C mL^{-1} (631 cells mL^{-1}) but became saturated at higher mean prey concentrations (Fig. 3). When the data were fitted to Eq. (2), the maximum growth rate (μ_{max}) of *G. dominans* on *A. granifera* was 0.305 d^{-1}.

With increasing mean prey concentrations, the ingestion rate of *G. dominans* feeding on *A. granifera* increased rapidly with increasing mean prey concentrations < 69 ng C mL^{-1} (631 cells mL^{-1}) but slowly increased at higher concentrations (Fig. 4). When the data were fitted to Eq. (3), the maximum ingestion rate (I$_{max}$) of *G. dominans* on *A. granifera* was 0.42 ng C predator^{-1} d^{-1} (3.8 cells predator^{-1} d^{-1}).

Growth and ingestion rates of *Oxyrrhis marina* feeding on *Ansanella granifera* at a single prey concentration

At a single high mean prey concentration of 1,700 ng C mL^{-1} (15,454 cells mL^{-1}), the specific growth and ingestion rates of *O. marina* on *A. granifera* were 0.037 d^{-1} and 0.19 ng C predator^{-1} d^{-1} (1.7 cells predator^{-1} d^{-1}), respectively.

The present study clearly showed that all nine common heterotrophic protists tested were able to feed on *A. granifera* AGSW10, although they had diverse sizes, shapes, feeding mechanisms, and behaviors. The types of heterotrophic protist predators that can feed on *A. granifera* are similar to those on *Effrenium voratum* and *Biecheleria cincta* which belong to the same order (Table 3). Thus, heterotrophic protist predators may compete for *A. granifera*, *E. voratum*, or *B. cincta* in marine environments. However, in the order Suessiales, unlike *A. granifera*, only *O. marina*, *A. glandula*, and a naked ciliate can feed on *Yihiella yeosuensis* (Jeong et al. 2018a). Thus, *A. granifera* might be more vulnerable to common heterotrophic protist predators than *Y. yeosuensis*.
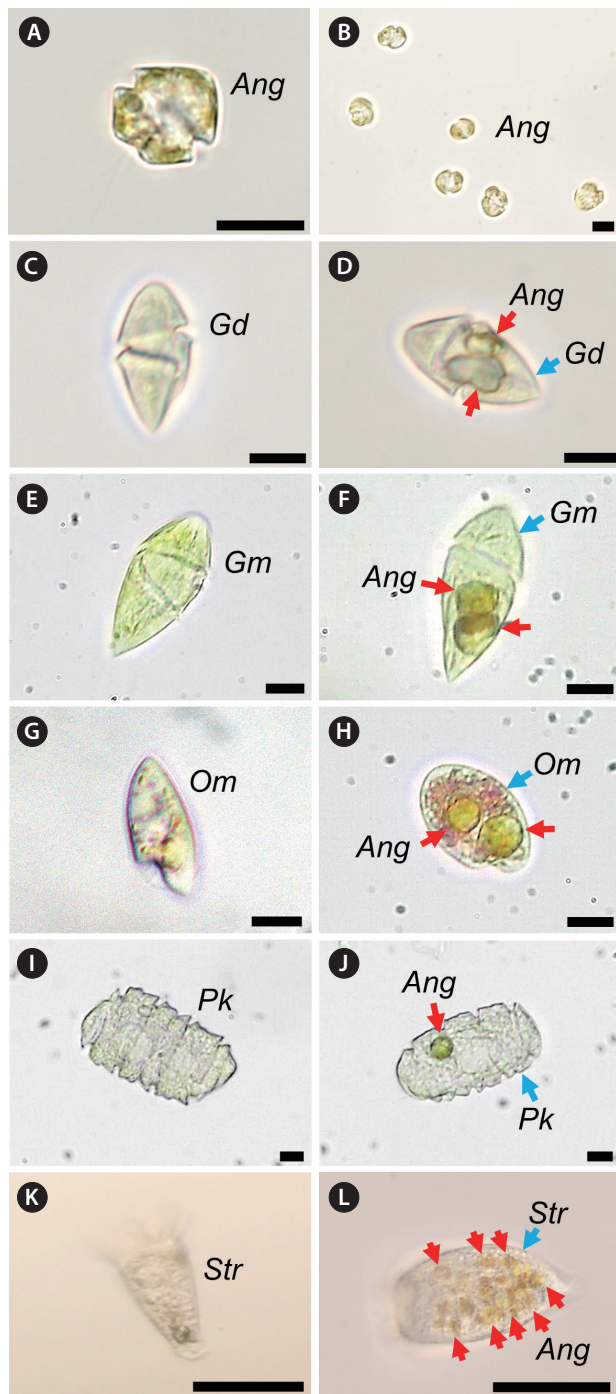
Fig. 1. Feeding by engulfment feeding heterotrophic dinoflagellates on *Ansanella granifera* (*Ang*). (A & B) Intact *Ang* cells. (C) Unfed *Gyrodinium dominans* (*Gd*). (D) *Gd* (blue arrow) with two ingested *Ang* cells (red arrows). (E) Unfed *Gyrodinium moestrupii* (*Gm*). (F) *Gm* (blue arrow) with two ingested *Ang* cells (red arrows). (G) Unfed *Oxyrrhis marina* (*Om*). (H) *Om* (blue arrow) with two ingested *Ang* cells (red arrows). (I) Unfed *Polykrikos kofoidii* (*Pk*). (J) *Pk* (blue arrow) with an ingested *Ang* cell (red arrow). (K) Unfed *Strombidium* sp. (*Str*). (L) *Str* (blue arrow) with several ingested *Ang* cells (red arrows). Scale bars represent: A–J, 10 μm; K & L, 50 μm.
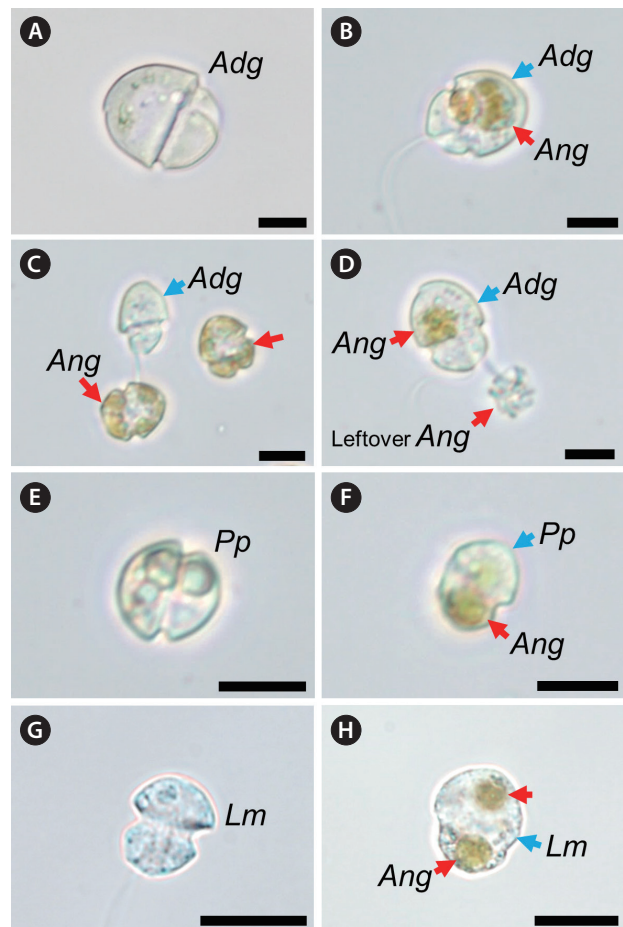

Fig. 2. Feeding by peduncle feeding heterotrophic dinoflagellates on *Ansanella granifera* (*Ang*). (A) Unfed *Aduncodinium glandula* (*Adg*). (B) *Adg* (blue arrow) with ingested *Ang* cells (red arrow). (C & D) *Adg* (blue arrows) feeding on an *Ang* cell (red arrows) using a peduncle. Each *Adg* cell in (A–D) is a different cell. (E) Unfed *Pfiesteria piscicida* (*Pp*). (F) *Pp* (blue arrow) with ingested *Ang* cells (red arrow). (G) Unfed *Luciella masanensis* (*Lm*). (H) *Lm* (blue arrow) with ingested *Ang* cells (red arrows). Scale bars represent: A–H, 10 μm.

When the μ_{max} and I_{max} of *G. dominans* on *A. granifera* AGSW10 were compared with those on the dinoflagellate prey species belonging to diverse orders, the μ_{max} and I_{max} of *G. dominans* on *A. granifera* were higher than those on the mixotrophic dinoflagellates *Paragymnodinium shiwhaense* and *B. cincta*, but lower than those on the mixotrophic dinoflagellates *Gymnodinium aureolum*, *Heterocapsa steinii*, *Prorocentrum cordatum*, *P. donghaiense*, and *E. voratum* belonging to the orders Gymnodiniales, Peridiniales, Prorocentrales, and Suessiales (Table 4). The smallest size and fastest swimming speed of *A. granifera* among the dinoflagellate prey species may be partially responsible for the low μ_{max} and I_{max} values of *G. dominans* on *A. granifera*. Therefore, if *A. granifera* is abundant in
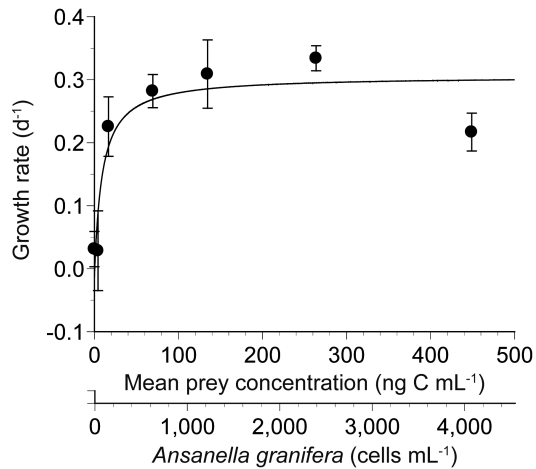
Fig. 3. Specific growth rates of the heterotrophic dinoflagellate *Gyrodinium dominans* on *Ansanella granifera* as a function of mean prey concentration (x, ng C mL^{-1}). The curves are fitted by a Michaelis-Menten equation [Eq. (2)] using all treatments in the experiment. Growth rate (d^{-1}) = 0.305 [(x – 1.12) / (9.48 + (x – 1.12)], r^2 = 0.726. Symbols represent treatment means ± standard error (n = 3).
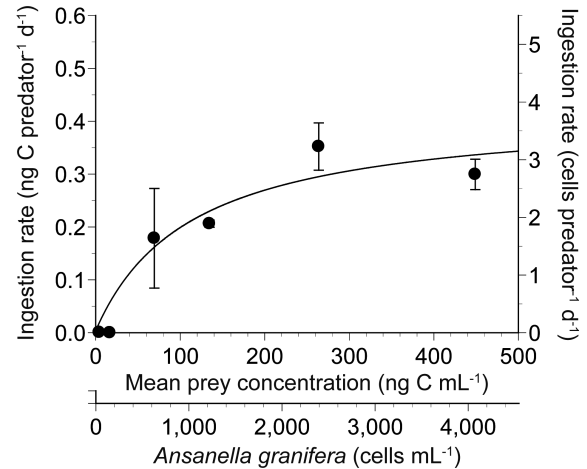

Fig. 4. Ingestion rates of the heterotrophic dinoflagellate *Gyrodinium dominans* on *Ansanella granifera* as a function of mean prey concentration (x, ng C mL^{-1}). The curves are fitted by a Michaelis-Menten equation [Eq. (3)] using all treatments in the experiment. Ingestion rate (ng C predator^{-1} d^{-1}) = 0.42 [x / (113 + x)], r^2 = 0.762. Symbols represent treatment means ± standard error (n = 3).

Table 3. Feeding occurrence of heterotrophic dinoflagellates and naked ciliates on five dinoflagellate prey species in the order Suessiales

Prey / Predators	ESD	Om	Gd	Gm	Pk	Pp	Lm	Ag	Or	NC	Reference
Yihiella yeosuensis	7.8	○	×	×	×	×	×	○	×	○	Jeong et al. (2018*a*)
Biecheleriopsis adriatica	10.1	○	○	○	×	○	○	○	○	○	Kang et al. (2019*a*)
Ansanella granifera	10.5	○	○	○	○	○	○	○	○	○	This study
Effrenium voratum	11.1	○	○	○	○	○	○	○	○	○	Jeong et al. (2014*b*), Kang et al. (2019*a*)
Biecheleria cincta	12.2	○	○	○	○	○	○	○	○	○	Yoo et al. (2013*b*), Kang et al. (2019*a*)

ESD, equivalent spherical diameter (μm); Om, *Oxyrrhis marina*; Gd, *Gyrodinium dominans*; Gm, *Gyrodinium moestrupii*; Pk, *Polykrikos kofoidii*; Pp, *Pfiesteria piscicida*; Lm, *Luciella masanensis*; Ag, *Aduncodinium glandula*; Or, *Oblea rotunda*; NC, naked ciliates.

Table 4. The maximum growth (μ$_{max}$, d^{-1}) and ingestion (I$_{max}$, ng C predator^{-1} d^{-1}) rates of *Gyrodinium dominans* on dinoflagellate prey species

Prey order / Species	ESD	μ$_{max}$	I$_{max}$	MSS	Reference
Gymnodiniales					
Paragymnodinium shiwhaense	13.0	0.18[a]	0.0	863	Yoo et al. (2010*b*), Jeong et al. (2017)
Gymnodinium aureolum	19.5	0.92	2.0	576	Jeong et al. (2010*a*), Yoo et al. (2010*a*)
Peridiniales					
Heterocapsa steinii	15.3	0.54[b]	2.9[b]	496	Nakamura et al. (1995), Jeong et al. (2002)
Prorocentrales					
Prorocentrum cordatum	12.1	1.13	1.2	194	Jeong et al. (1999), Kim and Jeong (2004)
Prorocentrum donghaiense	13.3	1.62	1.5	280	You et al. (2020)
Suessiales					
Ansanella granifera	10.5	0.31	0.4	1,603	Lee et al. (2014*b*), this study
Effrenium voratum	11.1	0.61	1.9	340	Jeong et al. (2014*b*), Kang et al. (2019*a*)
Biecheleria cincta	12.2	0.07[c]	0.1[c]	378	Kang et al. (2011), Yoo et al. (2013*b*)

ESD, equivalent spherical diameter (μm); MSS, maximum swimming speed (μm s^{-1}).
[a]The highest growth rate.
[b]Corrected values to 20°C using Q10 = 2.8 (Hansen et al. 1997).
[c]Growth and ingestion rates at a single high prey concentration.

natural marine environments, *G. dominans* will possibly be less abundant than when *G. aureolum*, *H. steinii*, *P. cordatum*, *P. donghaiense*, or *E. voratum* is abundant. In contrast, *G. dominans* may be more abundant when *A. granifera* is abundant than when *P. shiwhaense* or *B. cincta* is abundant. Therefore, *A. granifera* may not be the preferred prey for *G. dominans* except for *P. shiwhaense* and *B. cincta*. The μ_{max} or I_{max} of *G. dominans* on dinoflagellate prey species was not significantly correlated with prey size (Pearson's correlation test, p > 0.1) (Fig. 5A & B). The μ_{max} of *G. dominans* on dinoflagellate prey species

was not significantly correlated with the I_{max} (Pearson's correlation test, p > 0.1) (Fig. 5C). This suggests that factors other than prey size affected the μ_{max} and I_{max} of *G. dominans* on dinoflagellate prey species, and that there was a difference in the nutritional values of prey species. The μ_{max} or I_{max} of *G. dominans* on dinoflagellate prey species was also not correlated with the MSS of the prey species.

When the growth and ingestion rates of *O. marina* feeding on *A. granifera* at a single high prey concentration were compared with μ_{max} and I_{max} of *O. marina* feed-

Table 5. The maximum growth (μ_{max}, d^{-1}) and ingestion (I_{max}, ng C predator^{-1} d^{-1}) rates of *Oxyrrhis marina* on dinoflagellate prey species

Prey order / Species	ESD	μ_{max}	I_{max}	MSS	Reference
Amphidiniales					
Amphidinium carterae	9.7	1.17	2.8	199	Kamykowski and McCollum (1986), Jeong et al. (2001*a*)
Gymnodiniales					
*Karlodinium veneficum*_NTX	9.1	0.85	6.4	NA	Adolf et al. (2007)
Shimiella gracilenta	9.3	0.65	0.1	500	Park et al. (2021)
*Karlodinium veneficum*_TX	10.5	0.25	2.4	NA	Adolf et al. (2007)
Gymnodinium smadyae	10.5	0.41	0.3	707	Lee et al. (2014*a*), Jeong et al. (2018*b*)
Paragymnodinium shiwhaense	13.0	-	0.0	863	Yoo et al. (2010*b*), Jeong et al. (2017)
Gymnodinium aureolum	19.5	0.71	0.5	576	Jeong et al. (2010*a*), Yoo et al. (2010*a*)
Dinophyceae ordo incertae sedis					
Azadinium cf. *poporum*	10.0	0.50	5.0	550	Potvin et al. (2013)
Suessiales					
Yihiella yeosuensis	7.8	-	0.1[a]	1,572	Jang et al. (2017), Jeong et al. (2018*a*)
Biecheleriopsis adriatica	10.1	0.16	0.2	1,119	Jang et al. (2015), Kang et al. (2019*a*)
Ansanella granifera	10.5	0.04[b]	0.2[b]	1,603	Lee et al. (2014*b*), this study
Effrenium voratum	11.1	0.87	2.1	340	Jeong et al. (2014*b*), Kang et al. (2019*a*)
Biecheleria cincta	12.2	0.49	0.4	378	Kang et al. (2011), Yoo et al. (2013*b*)
Thoracosphaerales					
Pfiesteria piscicida	13.5	0.66	0.3	670	Jeong et al. (2007), Jang et al. (2016)
Stoeckeria algicida	13.9	0.22	0.1	549	Jeong et al. (2007), Jang et al. (2016)

ESD, equivalent spherical diameter (μm); MSS, maximum swimming speed (μm s^{-1}); NTX, non-toxic; NA, not available; TX, toxic; -, negative growth rate.
[a]Highest ingestion rate.
[b]Growth and ingestion rates at a single high prey concentration.

Table 6. The reported abundances of *Ansanella granifera* or *Ansanella* sp. and *Gyrodinium dominans* or *Gyrodinium* spp. in the global ocean and calculated growth and ingestion rates of *G. dominans* or *Gyrodinium* spp. on *A. granifera* or *Ansanella* sp.

Prey	Conc	CGR	CIR	Predator	Conc	Prey consumed daily (cells mL^{-1})	Prey consumed daily (%)	Reference
Caribbean Sea								
A. granifera	216,000	0.3	3.8	*Gyrodinium* spp.	0.2	0.6[a]	0.0003	Moreira-González et al. (2021), Ayala-Galván et al. (2022)
Singapore								
Ansanella sp.	1–2,450	0–0.3[b]	0–2.7[b]	*G. dominans*	0.3–2.0	0–5.4	0–0.7	Li et al. (2012), Kok and Leong (2019)
NW Mediterranean Sea								
Ansanella sp.	49	0.1[b]	0.2[b]	*G. dominans*	0.1	0.02	0.04	Reñé et al. (2015, 2021)

Conc, concentration (cells mL^{-1}); CGR, calculated growth rate (d^{-1}) using the equation in Fig. 3; CIR, calculated ingestion rate (cells predator^{-1} d^{-1}) using the equation in Fig. 4.
[a]Assuming that all cells of *Gyrodinium* spp. feed on *A. granifera* at the same rate as *G. dominans* feeds on *A. granifera*.
[b]Assuming that the growth and ingestion rates of *G. dominans* on *Ansanella* sp. are the same as those on *A. granifera*.
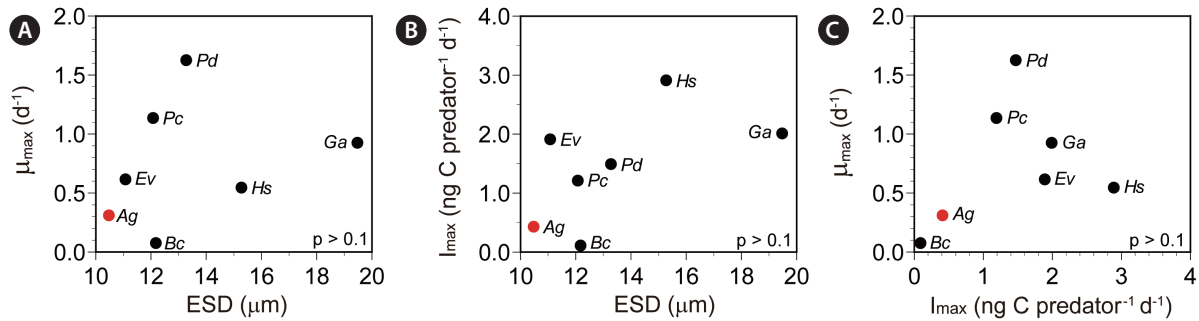
Fig. 5. Maximum growth (μ_{max}) and ingestion (I_{max}) rates of *Gyrodinium dominans* on the dinoflagellate prey species. (A) μ_{max} as a function of equivalent spherical diameter (ESD, μm) of prey species. (B) I_{max} as a function of ESD of prey species. (C) μ_{max} as a function of I_{max}. *Ag, Ansanella granifera; Bc, Biecheleria cincta; Ev, Effrenium voratum; Ga, Gymnodinium aureolum; Hs, Heterocapsa steinii; Pc, Prorocentrum cordatum; Pd, Prorocentrum donghaiense.* See Table 4 for details. Only positive values of μ_{max} and I_{max} were included in this figure.
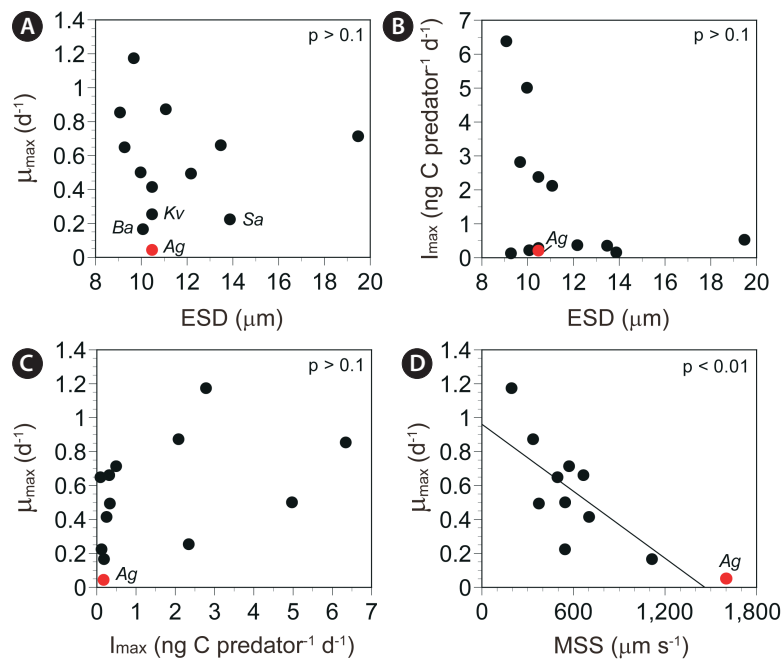

Fig. 6. Maximum growth (μ_{max}) and ingestion (I_{max}) rates of *Oxyrrhis marina* on the dinoflagellate prey species. (A) μ_{max} as a function of equivalent spherical diameter (ESD, μm) of prey species. (B) I_{max} as a function of ESD of prey species. (C) μ_{max} as a function of I_{max}. (D) μ_{max} as a function of maximum swimming speed (MSS, x) of prey species. Maximum growth (μ_{max}, d^{-1}) = -0.0007x + 0.96, r^2 = 0.627. *Ag, Ansanella granifera; Ba, Biecheleriopsis adriatica; Kv,* non-toxic *Karlodinium veneficum; Sa, Stoeckeria algicida.* See Table for details. Only positive values of μ_{max} and I_{max} were included in this figure.

ing on other dinoflagellate prey species belonging to diverse orders, the growth and ingestion rates of *O. marina* feeding on *A. granifera* were higher than the μ_{max} and I_{max} of *O. marina* feeding on *P. shiwhaense* and *Y. yeosuensis*, but lower than those of *O. marina* feeding on most other dinoflagellate prey (Table 5). The μ_{max} or I_{max} of *O. marina* on dinoflagellate prey species was not significantly correlated with prey size (Pearson's correlation test, $p > 0.1$) (Fig. 6A & B). Furthermore, the μ_{max} of *O. marina* on dinoflagellate prey species was not significantly correlated

with I_{max} (Pearson's correlation test, $p > 0.1$) (Fig. 6C). However, the μ_{max} of *O. marina* was significantly and negatively correlated with the MSS of dinoflagellate prey species (Pearson's correlation test, $p < 0.01$) (Fig. 6D). This suggests that the μ_{max} of *O. marina* is likely to be affected by the MSS of dinoflagellate prey species, but not by prey species. Cells of *O. marina* may spend more energy to catch and ingest faster-swimming prey species such as *A. granifera* than slow-swimming prey species (Table 5).

To estimate the grazing impact of *G. dominans* on

populations of *A. granifera*, data on the abundance of *G. dominans* and *A. granifera* in the same water parcel are needed. However, there are no data on the abundances of *G. dominans* and *A. granifera* that co-occur yet. There are data on the abundance of *A. granifera* and *Ansanella* sp. in the waters of the three regions in which there are data on the abundance of *G. dominans* or *Gyrodinium* spp., but they are not in the same water parcels (Table 6). The highest abundance of *A. granifera* in the Caribbean Sea was 216,000 cells mL^{-1} (Moreira-González et al. 2021). When using the equation in Figs 3 & 4 and the abundance of *A. granifera* in Caribbean Sea, the calculated growth and ingestion rates of *G. dominans* on *A. granifera* were 0.3 d^{-1} and 3.8 cells predator^{-1} d^{-1}, respectively (Table 6). If all cells of *Gyrodinium* spp. feed on *A. granifera* at the same rate that *G. dominans* feeds on *A. granifera*, the population of *Gyrodinium* spp. (0.2 cells mL^{-1}) in the Caribbean Sea is calculated to eliminate 0.6 *Ansanella* cells in a day. Similarly, the highest abundance of *Ansanella* sp. in the waters off Singapore was 2,450 cells mL^{-1} (Kok and Leong 2019). When using the equation in Figs 3 & 4 and the abundance of *Ansanella* sp. in the waters off Singapore and assuming that the ingestion rate of *G. dominans* on *Ansanella* sp. is the same as that on *A. granifera*, the calculated growth and ingestion rates of *G. dominans* on *Ansanella* sp. were 0.3 d^{-1} and 2.7 cells predator^{-1} d^{-1}, respectively (Table 6). The population of *G. dominans* (2.0 cells mL^{-1}) in the waters off Singapore is calculated to eliminate 5.4 *Ansanella* cells in a day. Furthermore, the highest abundance of *Ansanella* sp. in the NW Mediterranean Sea was 49 cells mL^{-1} (Reñé et al. 2021). When using the equation in Fig. 3 & 4 and the abundance of *Ansanella* sp. in the NW Mediterranean Sea and assuming that the ingestion rate of *G. dominans* on *Ansanella* sp. is the same as that on *A. granifera*, the calculated growth and ingestion rates of *G. dominans* on *Ansanella* sp. were 0.1 d^{-1} and 0.2 cells predator^{-1} d^{-1}, respectively (Table 6). The population of *G. dominans* (0.1 cells mL^{-1}) in the NW Mediterranean Sea is calculated to eliminate 0.02 *Ansanella* cells in a day. Data on the abundance of co-occurring prey and predators should be obtained to better estimate the grazing impact of heterotrophic protist predators on the *Ansanella* spp.

CONCLUSION

The growth and ingestion rates of *G. dominans* and *O. marina* feeding on *A. granifera* were almost the lowest among those on the dinoflagellate prey species. There-fore, *G. dominans* and *O. marina* may prefer *A. granifera* less than other dinoflagellate prey species. The low mortality rate of *A. granifera* may be helpful in forming blooms, and *A. granifera* may have an advantage over other competing prey species regarding survival.

ACKNOWLEDGEMENTS

CONFLICTS OF INTEREST

The authors declare that they have no potential conflicts of interest.

REFERENCES

Adolf, J. E., Krupatkina, D., Bachvaroff, T. & Place, A. R. 2007. Karlotoxin mediates grazing by *Oxyrrhis marina* on strains of *Karlodinium veneficum*. Harmful Algae 6:400–412.

Ayala-Galván, K., Gutiérrez-Salcedo, J. M. & Montoya-Cadavid, E. 2022. Phytoplankton from the oceanic province of the Colombian Caribbean Sea: ten years of history. Biota Colomb. 23:e401.

Belevich, T. A., Milyutina, I. A. & Troitsky, A. V. 2021. Seasonal variability of photosynthetic microbial eukaryotes (<3 μm) in the Kara Sea revealed by 18S rDNA metabarcoding of sediment trap fluxes. Plants 10:2394.

Claessens, M., Wickham, S. A., Post, A. F. & Reuter, M. 2008. Ciliate community in the oligotrophic Gulf of Aqaba, Red Sea. Aquat. Microb. Ecol. 53:181–190.

Coats, D. W. 1999. Parasitic life styles of marine dinoflagellates. J. Eukaryot. Microbiol. 46:402–409.

Dawut, M., Sym, S. D. & Horiguchi, T. 2018. Re-investigation of *Gymnodinium natalense* (Dinophyceae), a tidal pool dinoflagellate from South Africa and the proposal of a new combination *Ansanella natalensis*. Phycol. Res. 66:300–309.

Eom, S. H., Jeong, H. J., Ok, J. H., Park, S. A., Kang, H. C., You, J. H., Lee, S. Y., Yoo, Y. D., Lim, A. S. & Lee, M. J. 2021. Interactions between common heterotrophic protists

and the dinoflagellate *Tripos furca*: implication on the long duration of its red tides in the South Sea of Korea in 2020. Algae 36:25–36.

Frost, B. W. 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnol. Oceanogr. 17:805–815.

Guo, Z., Zhang, H., Liu, S. & Lin, S. 2013. Biology of the marine heterotrophic dinoflagellate *Oxyrrhis marina*: current status and future directions. Microorganisms 1:33–57.

Hallegraeff, G. M. 1995. Harmful algal blooms: a global overview. *In* Hallegraeff, G. M., Anderson, D. M. & Cembella, A. D. (Eds.) *Manual on Harmful Marine Microalgae*. UNESCO, Paris, pp. 1–22.

Hansen, P. J. 2011. The role of photosynthesis and food uptake for the growth of marine mixotrophic dinoflagellates. J. Eukaryot. Microbiol. 58:203–214.

Hansen, P. J., Bjørnsen, P. K. & Hansen, B. W. 1997. Zooplankton grazing and growth: scaling within the 2–2,000-μm body size range. Limnol. Oceanogr. 42:687–704.

Heinbokel, J. F. 1978. Studies on the functional role of tintinnids in the Southern California Bight. I. Grazing and growth rates in laboratory cultures. Mar. Biol. 47:177–189.

Jang, S. H., Jeong, H. J., Kwon, J. E. & Lee, K. H. 2017. Mixotrophy in the newly described dinoflagellate *Yihiella yeosuensis*: a small, fast dinoflagellate predator that grows mixotrophically, but not autotrophically. Harmful Algae 62:94–103.

Jang, S. H., Jeong, H. J., Lim, A. S., Kwon, J. E. & Kang, N. S. 2016. Feeding by the newly described heterotrophic dinoflagellate *Aduncodinium glandula*: having the most diverse prey species in the family Pfiesteriaceae. Algae 31:17–31.

Jang, S. H., Jeong, H. J., Moestrup, Ø., Kang, N. S., Lee, S. Y., Lee, K. H., Lee, M. J. & Noh, J. H. 2015. Morphological, molecular and ecophysiological characterization of the phototrophic dinoflagellate *Biecheleriopsis adriatica* from Korean coastal waters. Eur. J. Phycol. 50:301–317.

Jeong, H. J., Jang, S. H., Moestrup, Ø., Kang, N. S., Lee, S. Y., Potvin, É. & Noh, J. H. 2014a. *Ansanella granifera* gen. et sp. nov. (Dinophyceae), a new dinoflagellate from the coastal waters of Korea. Algae 29:75–99.

Jeong, H. J., Kang, H. C., Lim, A. S., Jang, S. H., Lee, K., Lee, S. Y., Ok, J. H., You, J. H., Kim, J. H., Lee, K. H., Park, S. A., Eom, S. H., Yoo, Y. D. & Kim, K. Y. 2021. Feeding diverse prey as an excellent strategy of mixotrophic dinoflagellates for global dominance. Sci. Adv. 7:eabe4214.

Jeong, H. J., Kang, H., Shim, J. H., Park, J. K., Kim, J. S., Song,

J. Y. & Choi, H. -J. 2001a. Interactions among the toxic dinoflagellate *Amphidinium carterae*, the heterotrophic dinoflagellate *Oxyrrhis marina*, and the calanoid copepods *Acartia* spp. Mar. Ecol. Prog. Ser. 218:77–86.

Jeong, H. J., Kang, H. C., You, J. H. & Jang, S. H. 2018a. Interactions between the newly described small- and fast-swimming mixotrophic dinoflagellate *Yihiella yeosuensis* and common heterotrophic protists. J. Eukaryot. Microbiol. 65:612–626.

Jeong, H. J., Kim, J. S., Lee, K. H., Seong, K. A., Yoo, Y. D., Kang, N. S., Kim, T. H., Song, J. Y. & Kwon, J. E. 2017. Differential interactions between the nematocyst-bearing mixotrophic dinoflagellate *Paragymnodinium shiwhaense* and common heterotrophic protists and copepods: killer or prey. Harmful Algae 62:37–51.

Jeong, H. J., Kim, J. S., Song, J. Y., Kim, J. H., Kim, T. H., Kim, S. K. & Kang, N. S. 2007. Feeding by heterotrophic protists and copepods on the heterotrophic dinoflagellates *Pfiesteria piscicida*, *Stoeckeria algicida*, and *Luciella masanensis*. Mar. Ecol. Prog. Ser. 349:199–211.

Jeong, H. J., Kim, S. K., Kim, J. S., Kim, S. T., Yoo, Y. D. & Yoon, J. Y. 2001b. Growth and grazing rates of the heterotrophic dinoflagellate *Polykrikos kofoidii* on red-tide and toxic dinoflagellates. J. Eukaryot. Microbiol. 48:298–308.

Jeong, H. J., Lim, A. S., Franks, P. J. S., Lee, K. H., Kim, J. H., Kang, N. S., Lee, M. J., Jang, S. H., Lee, S. Y., Yoon, E. Y., Park, J. Y., Yoo, Y. D., Seong, K. A., Kwon, J. E. & Jang, T. Y. 2015. A hierarchy of conceptual models of red-tide generation: nutrition, behavior, and biological interactions. Harmful Algae 47:97–115.

Jeong, H. J., Lim, A. S., Yoo, Y. D., Lee, M. J., Lee, K. H., Jang, T. Y. & Lee, K. 2014b. Feeding by heterotrophic dinoflagellates and ciliates on the free-living dinoflagellate *Symbiodinium* sp. (Clade E). J. Eukaryot. Microbiol. 61:27–41.

Jeong, H. J., Seong, K. A., Yoo, Y. D., Kim, T. H., Kang, N. S., Kim, S., Park, J. Y., Kim, J. S., Kim, G. H. & Song, J. Y. 2008. Feeding and grazing impact by small marine heterotrophic dinoflagellates on hetertrophic bacteria. J. Eukaryot. Microbiol. 55:271–288.

Jeong, H. J., Shim, J. H., Kim, J. S., Park, J. Y., Lee, C. W. & Lee, Y. 1999. Feeding by the mixotrophic thecate dinoflagellate *Fragilidium* cf. *mexicanum* on red-tide and toxic dinoflagellates. Mar. Ecol. Prog. Ser. 176:263–277.

Jeong, H. J., Yoo, Y. D., Kang, N. S., Rho, J. R., Seong, K. A., Park, J. W., Nam, G. S. & Yih, W. 2010a. Ecology of *Gymnodinium aureolum*. I. Feeding in western Korean waters. Aquat. Microb. Ecol. 59:239–255.

Jeong, H. J., Yoo, Y. D., Kim, J. S., Seong, K. A., Kang, N. S. & Kim, T. H. 2010b. Growth, feeding, and ecological roles of the mixotrophic and heterotrophic dinoflagellates in

marine planktonic food webs. Ocean Sci. J. 45:65–91.

Jeong, H. J., Yoon, J. Y., Kim, J. S., Yoo, Y. D. & Seong, K. A. 2002. Growth and grazing rates of the prostomatid ciliate *Tiarina fusus* on red-tide and toxic algae. Aquat. Microb. Ecol. 28:289–297.

Jeong, H. J., You, J. H., Lee, K. H., Kim, S. J. & Lee, S. Y. 2018*b*. Feeding by common heterotrophic protists on the mixotrophic alga *Gymnodinium smaydae* (Dinophyceae), one of the fastest growing dinoflagellates. J. Phycol. 54:734–743.

Kamykowski, D. & McCollum, S. A. 1986. The temperature acclimatized swimming speed of selected marine dinoflagellates. J. Plankton Res. 8:275–287.

Kang, H. C., Jeong, H. J., Jang, S. H. & Lee, K. H. 2019*a*. Feeding by common heterotrophic protists on the phototrophic dinoflagellate *Biecheleriopsis adriatica* (Suessiaceae) compared to that of other suessioid dinoflagellates. Algae 34:127–140.

Kang, H. C., Jeong, H. J., Kim, S. J., You, J. H. & Ok, J. H. 2018. Differential feeding by common heterotrophic protists on 12 different *Alexandrium* species. Harmful Algae 78:106–117.

Kang, H. C., Jeong, H. J., Ok, J. H., You, J. H., Jang, S. H., Lee, S. Y., Lee, K. H., Park, J. Y. & Rho, J. -R. 2019*b*. Spatial and seasonal distributions of the phototrophic dinoflagellate *Biecheleriopsis adriatica* (Suessiaceae) in Korea: quantification using qPCR. Algae 34:111–126.

Kang, H. C., Jeong, H. J., Park, S. A., Eom, S. H., Ok, J. H., You, J. H., Jang, S. H. & Lee, S. Y. 2020. Feeding by the newly described heterotrophic dinoflagellate *Gyrodinium jinhaense*: comparison with *G. dominans* and *G. moestrupii*. Mar. Biol. 167:156.

Kang, N. S., Jeong, H. J., Moestrup, Ø., Jang, T. Y., Lee, S. Y. & Lee, M. J. 2015. *Aduncodinium* gen. nov. and *A. glandula* comb. nov. (Dinophyceae, Pfiesteriaceae), from coastal waters off Korea: morphology and molecular characterization. Harmful Algae 41:25–37.

Kang, N. S., Jeong, H. J., Yoo, Y. D., Yoon, E. Y., Lee, K. H., Lee, K. & Kim, G. 2011. Mixotrophy in the newly described phototrophic dinoflagellate *Woloszynskia cincta* from western Korean waters: feeding mechanism, prey species and effect of prey concentration. J. Eukaryot. Microbiol. 58:152–170.

Kim, J. S. & Jeong, H. J. 2004. Feeding by the heterotrophic dinoflagellates *Gyrodinium dominans* and *G. spirale* on the red-tide dinoflagellate *Prorocentrum minimum*. Mar. Ecol. Prog. Ser. 280:85–94.

Kok, J. W. K. & Leong, S. C. Y. 2019. Nutrient conditions and the occurrence of a *Karenia mikimotoi* (Kareniaceae) bloom within East Johor Straits, Singapore. Reg. Stud. Mar. Sci. 27:100514.

LaJeunesse, T. C., Parkinson, J. E., Gabrielson, P. W., Jeong, H. J., Reimer, J. D., Voolstra, C. R. & Santos, S. R. 2018. Systematic revision of Symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. Curr. Biol. 28:2570–2580.

Lee, K. H., Jeong, H. J., Jang, T. Y., Lim, A. S., Kang, N. S., Kim, J. -H., Kim, K. Y., Park, K. -T. & Lee, K. 2014*a*. Feeding by the newly described mixotrophic dinoflagellate *Gymnodinium smaydae*: feeding mechanism, prey species, and effect of prey concentration. J. Exp. Mar. Biol. Ecol. 459:114–125.

Lee, M. J., Jeong, H. J., Kim, J. S., Jang, K. K., Kang, N. S., Jang, S. H., Lee, H. B., Lee, S. B., Kim, H. S. & Choi, C. H. 2017. Ichthyotoxic *Cochlodinium polykrikoides* red tides offshore in the South Sea, Korea in 2014: III. Metazooplankton and their grazing impacts on red-tide organisms and heterotrophic protists. Algae 32:285–308.

Lee, S. K., Jeong, H. J., Jang, S. H., Lee, K. H., Kang, N. S., Lee, M. J. & Potvin, É. 2014*b*. Mixotrophy in the newly described dinoflagellate *Ansanella granifera*: feeding mechanism, prey species, and effect of prey concentration. Algae 29:137–152.

Lee, S. Y., Jeong, H. J., Kang, H. C., Ok, J. H., You, J. H., Park, S. A. & Eom, S. H. 2021. Comparison of the spatial-temporal distributions of the heterotrophic dinoflagellates *Gyrodinium dominans*, *G. jinhaense*, and *G. moestrupii* in Korean coastal waters. Algae 36:37–50.

Li, G., Huang, L., Liu, H., Ke, Z., Lin, Q., Ni, G., Yin, J., Li, K., Song, X., Shen, P. & Tan, Y. 2012. Latitudinal variability (6°S–20°N) of early summer phytoplankton species compositions and size-fractioned productivity from Java Sea to South China Sea. Mar. Biol. Res. 8:163–171.

Lim, A. S. & Jeong, H. J. 2021. Benthic dinoflagellates in Korean waters. Algae 36:91–109.

Lim, A. S. & Jeong, H. J. 2022. Primary production by phytoplankton in the territorial seas of the Republic of Korea. Algae 37:265–279.

Lim, A. S., Jeong, H. J., Seong, K. A., Lee, M. J., Kang, N. S., Jang, S. H., Lee, K. H., Park, J. Y., Jang, T. Y. & Yoo, Y. D. 2017. Ichthyotoxic *Cochlodinium polykrikoides* red tides offshore in the South Sea, Korea in 2014: II. Heterotrophic protists and their grazing impacts on red-tide organisms. Algae 32:199–222.

Liu, X., Liu, Y., Chai, Z., Hu, Z. & Tang, Y. Z. 2023. A combined approach detected novel species diversity and distribution of dinoflagellate cysts in the Yellow Sea, China. Mar. Pollut. Bull. 187:114567.

Liu, Y., Song, L., Song, G., Wu, J., Wang, K., Wang, Z. & Liu, S. 2022. Spatiotemporal distribution of size-fractioned

phytoplankton in the Yalu River Estuary, China. Ecosyst. Health Sustain. 8:2133637.

Lowe, C. D., Keeling, P. J., Martin, L. E., Slamovits, C. H., Watts, P. C. & Montagnes, D. J. S. 2011. Who is *Oxyrrhis marina*? Morphological and phylogenetic studies on an unusual dinoflagellate. J. Plankton Res. 33:555–567.

Mason, P. L., Litaker, R. W., Jeong, H. J., Ha, J. H., Reece, K. S., Stokes, N. A., Park, J. Y., Steidinger, K. A., Vandersea, M. W., Kibler, S, Tester, P. A. & Vogelbein, W. K. 2007. Description of a new genus of *Pfiesteria*-like dinoflagellate, *Luciella* gen. nov. (Dinophyceae), including two new species: *Luciella masanensis* sp. nov. and *Luciella atlantis* sp. nov. J. Phycol. 43:799–810.

Matsuyama, Y., Miyamoto, M. & Kotani, Y. 1999. Grazing impacts of the heterotrophic dinoflagellate *Polykrikos kofoidii* on a bloom of *Gymnodinium catenatum*. Aquat. Microb. Ecol. 17:91–98.

Menden-Deuer, S. & Lessard, E. J. 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. Limnol. Oceanogr. 45:569–579.

Moreira-González, A. R., Alonso-Hernández, C. M., Arencibia-Carballo, G., Betanzos-Vega, A., Morton, S. L. & Richlen, M. L. 2021. First report of an *Ansanella granifera* bloom associated with eutrophication in Cuban waters, Caribbean region. Harmful Algae News 67:10–11.

Nakamura, Y., Suzuki, S. -Y. & Hiromi, J. 1995. Growth and grazing of a naked heterotrophic dinoflagellate, *Gyrodinium dominans*. Aquat. Microb. Ecol. 9:157–164.

Ok, J. H., Jeong, H. J., Kang, H. C., Park, S. A., Eom, S. H., You, J. H. & Lee, S. Y. 2021. Ecophysiology of the kleptoplastidic dinoflagellate *Shimiella gracilenta*: I. spatiotemporal distribution in Korean coastal waters and growth and ingestion rates. Algae 36:263–283.

Ok, J. H., Jeong, H. J., Lim, A. S. & Lee, K. H. 2017. Interactions between the mixotrophic dinoflagellate *Takayama helix* and common heterotrophic protists. Harmful Algae 68:178–191.

Park, S. A., Jeong, H. J., Ok, J. H., Kang, H. C., You, J. H., Eom, S. H. & Park, E. C. 2021. Interactions between the kleptoplastidic dinoflagellate *Shimiella gracilenta* and several common heterotrophic protists. Front. Mar. Sci. 8:738547.

Pierce, R. W. & Turner, J. T. 1992. Ecology of planktonic ciliates in marine food webs. Rev. Aquat. Sci. 6:139–181.

Potvin, É., Hwang, Y. J., Yoo, Y. D., Kim, J. S. & Jeong, H. J. 2013. Feeding by heterotrophic protists and copepods on the photosynthetic dinoflagellate *Azadinium* cf. *poporum* from western Korean waters. Aquat. Microb. Ecol. 68:143–158.

Pratomo, A., Bengen, D. G., Zamani, N. P., Lane, C.,

Humphries, A. T., Borbee, E., Subhan, B. & Madduppa, H. 2022. Diversity and distribution of Symbiodiniaceae detected on coral reefs of Lombok, Indonesia using environmental DNA metabarcoding. PeerJ 10:e14006.

Reñé, A., Camp, J. & Garcés, E. 2015. Diversity and phylogeny of Gymnodiniales (Dinophyceae) from the NW Mediterranean Sea revealed by a morphological and molecular approach. Protist 166:234–263.

Reñé, A., Timoneda, N., Sampedro, N., Alacid, E., Gallisai, R., Gordi, J., Fernández-Valero, A. D., Pernice, M. C., Flo, E. & Garcés, E. 2021. Host preferences of coexisting Perkinsea parasitoids during coastal dinoflagellate blooms. Mol. Ecol. 30:2417–2433.

Sakamoto, S., Lim, W. A., Lu, D., Dai, X., Orlova, T. & Iwataki, M. 2021. Harmful algal blooms and associated fisheries damage in East Asia: current status and trends in China, Japan, Korea and Russia. Harmful Algae 102:101787.

Sampedro, N., Reñé, A., Matos, J., Fortuño, J. -M. & Garcés, E. 2022. Detection of the widespread presence of the genus *Ansanella* along the Catalan coast (NW Mediterranean Sea) and the description of *Ansanella catalana* sp. nov. (Dinophyceae). Eur. J. Phycol. 57:125–142.

Sherr, E. B. & Sherr, B. F. 2002. Significance of predation by protists in aquatic microbial food webs. Antonie Van Leeuwenhoek 81:293–308.

Stern, R. F., Horak, A., Andrew, R. L., Coffroth, M. -A., Andersen, R. A., Küpper, F. C., Jameson, I., Hoppenrath, M., Véron, B., Kasai, F., Brand, J., James, E. R. & Keeling, P. J. 2010. Environmental barcoding reveals massive dinoflagellate diversity in marine environments. PLoS ONE 5:e13991.

Stoecker, D. K. 1999. Mixotrophy among dinoflagellates. J. Eukaryot. Microbiol. 46:397–401.

Stoecker, D. K., Hansen, P. J., Caron, D. A. & Mitra, A. 2017. Mixotrophy in the marine plankton. Ann. Rev. Mar. Sci. 9:311–335.

Strom, S. L. & Buskey, E. J. 1993. Feeding, growth, and behavior of the thecate heterotrophic dinoflagellate *Oblea rotunda*. Limnol. Oceanogr. 38:965–977.

Taylor, F. J. R., Hoppenrath, M. & Saldarriaga, J. F. 2008. Dinoflagellate diversity and distribution. Biodivers. Conserv. 17:407–418.

Tillmann, U. & Hoppenrath, M. 2013. Life cycle of the pseudocolonial dinoflagellate *Polykrikos kofoidii* (Gymnodiniales, Dinoflagellata). J. Phycol. 49:298–317.

Watts, P. C., Martin, L. E., Kimmance, S. A., Montagnes, D. J. S. & Lowe, C. D. 2010. The distribution of *Oxyrrhis marina*: a global disperser or poorly characterized endemic? J. Plankton Res. 33:579–589.

Yoo, Y. D., Jeong, H. J., Kang, N. S., Kim, J. S., Kim, T. H. &

Yoon, E. Y. 2010*a*. Ecology of *Gymnodinium aureolum*. II. Predation by common heterotrophic dinoflagellates and a ciliate. Aquat. Microb. Ecol. 59:257–272.

Yoo, Y. D., Jeong, H. J., Kang, N. S., Song, J. Y., Kim, K. Y., Lee, G. & Kim, J. 2010*b*. Feeding by the newly described mixotrophic dinoflagellate *Paragymnodinium shiwhaense*: feeding mechanism, prey species, and effect of prey concentration. J. Eukaryot. Microbiol. 57:145–158.

Yoo, Y. D., Jeong, H. J., Kim, J. S., Kim, T. H., Kim, J. H., Seong, K. A., Lee, S. H., Kang, N. S., Park, J. W., Park, J., Yoon, E. Y. & Yih, W. H. 2013*a*. Red tides in Masan Bay, Korea in 2004–2005: II. daily variations in the abundance of heterotrophic protists and their grazing impact on red-tide organisms. Harmful Algae 30(Suppl. 1):S89–S101.

Yoo, Y. D., Yoon, E. Y., Lee, K. H., Kang, N. S. & Jeong, H. J. 2013*b*. Growth and ingestion rates of heterotrophic dinoflagellates and a ciliate on the mixotrophic dinoflagellate *Biecheleria cincta*. Algae 28:343–354.

You, J. H., Jeong, H. J., Kang, H. C., Ok, J. H., Park, S. A. & Lim, A. S. 2020. Feeding by common heterotrophic protist predators on seven *Prorocentrum* species. Algae 35:61–78.