

## Interactions between common heterotrophic protists and the dinoflagellate *Triplos furca*: implication on the long duration of its red tides in the South Sea of Korea in 2020

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The mixotrophic dinoflagellate *Triplos furca* causes red tides in the waters of many countries. To understand its population dynamics, mortality due to predation as well as growth rate should be assessed. Prior to the present study, the heterotrophic dinoflagellates *Noctiluca scintillans*, *Polykrikos kofoidii*, *Protoperidinium steinii*, and mixotrophic dinoflagellate *Fragilidium subglobosum* were known to ingest *T. furca*. However, if other common heterotrophic protists are able to feed on *T. furca* has not been tested. We explored interactions between *T. furca* and nine heterotrophic dinoflagellates and one naked ciliate. Furthermore, we investigated the abundance of *T. furca* and common heterotrophic protists in coastal-offshore waters off Yeosu, southern Korea, on Jul 31, 2020, during its red tide. Among the tested heterotrophic protists, the heterotrophic dinoflagellates *Aduncodinium glandula*, *Luciella masanensis*, and *Pfiesteria piscicida* were able to feed on *T. furca*. However, the heterotrophic dinoflagellates *Gyrodiniellum shiwhaense*, *Gyrodinium dominans*, *Gyrodinium jinhaense*, *Gyrodinium moestrupii*, *Oblea rotunda*, *Oxyrrhis marina*, and the naked ciliate *Rimostrombidium* sp. were unable to feed on it. However, *T. furca* did not support the growth of *A. glandula*, *L. masanensis*, or *P. piscicida*. Red tides dominated by *T. furca* prevailed in the South Sea of Korea from Jun 30 to Sep 5, 2020. The maximum abundance of heterotrophic dinoflagellates in the waters off Yeosu on Jul 31, 2020, was as low as 5.0 cells mL<sup>-1</sup>, and *A. glandula*, *L. masanensis*, and *P. piscicida* were not detected. Furthermore, the abundances of the known predators *F. subglobosum*, *N. scintillans*, *P. kofoidii*, and *Protoperidinium* spp. were very low or negligible. Therefore, no or low abundance of effective predators might be partially responsible for the long duration of the *T. furca* red tides in the South Sea of Korea in 2020.

**Key Words:** ciliate; grazer; harmful algal bloom; heterotrophic dinoflagellate; red tide



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## INTRODUCTION

Red tides, which are discolorations due to plankton blooms, often cause large-scale morbidity and mortality of marine organisms such as fish, sea birds, and marine mammals (Landsberg 2002, Shumway et al. 2003, Flewelling et al. 2005, Jessup et al. 2009), as well as economic losses to aquaculture and tourism industries (Shumway 1990, Anderson 1997, Azanza et al. 2005, Jeong et al. 2021). To minimize financial losses, it is critical to understand and forecast the outbreak, persistence, and decline of red tides (Jeong et al. 2015). In models for predicting red tide dynamics, growth and mortality due to predation are the most important parameters.

The cosmopolitan dinoflagellate *Tripos furca* is renowned for causing red tides across the waters of many countries (Dodge and Marshall 1994, Horner et al. 1997, Tomas 1997). This dinoflagellate can grow autotrophically or mixotrophically (Smalley et al. 1999, 2003, Smalley and Coats 2002, Baek et al. 2008). *Tripos furca* is known to prey on the choreotrich ciliates *Strobilidium* spp., small tintinnids with sizes of 10–40 µm in diameter, and the mixotrophic ciliate *Mesodinium rubrum* (Bockstahler and Coats 1993, Smalley et al. 1999, Stoecker 1999, Johnson et al. 2013). Meanwhile, the heterotrophic dinoflagellates *Noctiluca scintillans*, *Polykrikos kofoidii*, *Protoperdinium steinii*, and mixotrophic dinoflagellate *Fragilidium subglobosum* are known to feed on this species (Hansen and Nielsen 1997, Jeong et al. 2001, Olseng et al. 2002, Drits et al. 2013). However, predation by many other common heterotrophic protists on *T. furca* has not been explored. To understand its red tide dynamics, feeding by common heterotrophic protists on *T. furca* should be investigated.

*Tripos furca* is one of the dinoflagellates that frequently cause red tides in Korean waters (Baek et al. 2011, Lee et al. 2013, Jeong et al. 2017). It usually causes red tides during spring and summer around the Korean coast, mainly at 24.6–25.1°C, although it has been recorded as being abundant at 17.5–28.4°C (Jeong et al. 2013). This species caused long-lasting red tides in the South Sea of Korea from Jun 30 to Sep 5, 2020 (NFRDI data; <http://www.nifs.go.kr/portal/redtideInfo>). It is worthwhile to explore the roles of potential predators in the long duration of *T. furca* red tides because high grazing impact by heterotrophic protists sometimes causes cessation of red tides (Watras et al. 1985, Nakamura et al. 1992, Jeong and Latz 1994, Turner 2006, Stoecker et al. 2008, Yoo et al. 2013, Yang et al. 2019). If there was a shortage of effective predators on this dinoflagellate, a low grazing im-

pact might be partially responsible for the long duration of these red tides. Therefore, whether there were effective predators on *T. furca* during its red tides of the year 2020 should be investigated.

The heterotrophic dinoflagellates *Gyrodinium dominans*, *Oblea rotunda*, *Oxyrrhis marina*, *Pfiesteria piscicida*, and naked ciliates are common heterotrophic protists in the waters of many countries, including Korea (Wood 1954, Hansen 1991, Jakobsen and Tang 2002, Mason et al. 2007, Lowe et al. 2010, Lim et al. 2017, Ok et al. 2017). Nevertheless, the worldwide distribution of these heterotrophic protists and whether they ingest *T. furca* has not been explored.

In the present study, we explored the interactions between *T. furca* and nine heterotrophic dinoflagellates (*Aduncodinium glandula*, *Gyrodiniellum shiwhaense*, *Gyrodinium dominans*, *Gyrodinium jinhaense*, *Gyrodinium moestrupii*, *Luciella masanensis*, *Oblea rotunda*, *Oxyrrhis marina*, and *Pfiesteria piscicida*), and one naked ciliate *Rimostrombidium* sp. These heterotrophic protists cover a wide range of size and feeding mechanisms (Hansen 1992, Strom and Buskey 1993, Sonntag et al. 2006, Jeong et al. 2007, 2011, Roberts et al. 2011, Jang et al. 2016, Kang et al. 2020). Furthermore, we investigated the abundance of *T. furca* and common heterotrophic protists in coastal-offshore waters off Yeosu in the South Sea of Korea on Jul 31, 2020, when huge *T. furca* red tides prevailed in the South Sea of Korea. The results of the present study will provide a better understanding of interactions between *T. furca* and heterotrophic protists and their population dynamics.

## MATERIALS AND METHODS

### Preparation of experimental organisms

*Tripos furca* was isolated from surface waters off the coast of Dundeok, Geoje, southern Korea (34°51'26" N, 128°28'34" E) using plankton samplers in August 2018, when the water temperature and salinity were 28.5°C and 32.5, respectively (Table 1). The collected samples were gently screened using a 100 µm sieve and 10 µm Nitex mesh. By conducting two consecutive single-cell isolations, a *T. furca* TFDD1808 clonal culture was established. When *T. furca* concentration had increased sufficiently, it was transferred into 32, 270, and 500-mL polycarbonate (PC) bottles filled with fresh half-diluted L1 medium. The bottles were placed at 20°C, under a 14 : 10 h light : dark cycle, on a shelf illuminated with cool white fluorescent

lights of 20  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ . Only cultures reaching the exponential growth stage were used in the study.

The heterotrophic dinoflagellates *A. glandula*, *G. shiwhaense*, *G. dominans*, *G. jinhaense*, *G. moestrupii*, *L. masanensis*, *O. rotunda*, *O. marina*, and *P. piscicida*, isolated from plankton samples collected from coastal waters off Geoje, Jeongok, Jinhae, Kunsan, Masan, Neuse River, and Saemankeum from 1998 to 2019, were used in this study (Table 1). Two consecutive single-cell isolations were conducted to establish each heterotrophic dinoflagellate species clonal culture, except for that of *P. piscicida* CCMP2091, which was acquired from the National Center for Marine Algae and Microbiota, USA. The naked ciliate *Rimostrombidium* sp. was isolated from plankton samples collected in a bucket from the coastal waters off Saemankeum, Korea, in July 2020, when the water temperature and salinity were 27.1°C and 18.8, respectively (Table 1). A clonal culture for *Rimostrombidium* sp. was also set up with two serial single-cell isolations, and its volume increased from 6-well plate chambers to 50 and 270-mL PC bottles, with a diet of *Heterocapsa rotundata* as prey (ca. 5,000 cells  $\text{mL}^{-1} \text{ d}^{-1}$ ).

The carbon content of *T. furca* TFDD1808 (1.7 ng C per cell) was estimated from the cell volume, according

to the equation proposed by Menden-Deuer and Lessard (2000). Using the same calculation, the carbon contents of all predator species in the present study were also evaluated from the cell volume. The cell volumes of the heterotrophic predators were assessed using the methods of Jang et al. (2016) for *A. glandula*; Ok et al. (2017) for *G. shiwhaense*; Kang et al. (2020) for *G. dominans*, *G. jinhaense*, and *G. moestrupii*; Jeong et al. (2007) for *L. masanensis* and *P. piscicida*; You et al. (2020) for *O. rotunda* and *O. marina*; and this study for *Rimostrombidium* sp. (Table 1).

### Interactions between *Triplos furca* and heterotrophic protists

This experiment was designed to examine whether each heterotrophic dinoflagellate or ciliate fed on *T. furca* TFDD1808, after mixing *T. furca* with potential predator species (Table 2). In this experiment, predation or other interactions between *T. furca* and the target heterotrophic protist were observed.

Dense cultures of *T. furca* (ca. 2,000 cells  $\text{mL}^{-1}$ ) and the target heterotrophic protist were added to individual 42-mL PC bottles (Table 2). One experiment bottle con-

**Table 1.** Information on the isolation and maintenance of the heterotrophic protists and *Triplos furca* used in the present study

Organism (strain name)	Location	Time	T	S	Type	FM	ESD	PS	PC
Predator									
<i>Aduncodinium glandula</i> (AGMS1303)	Masan, Korea	Mar 2013	8.1	30.3	HTD	PE	21.0	As	1,000–2,000
<i>Gyrodiniellum shiwhaense</i> (GSGJ1408)	Geoje, Korea	Aug 2014	26.5	33.4	HTD	PE	10.5	Ac	~20,000
<i>Gyrodinium dominans</i> (GDJK1907)	Jeongok, Korea	Jul 2019	25.2	31.9	HTD	EG	11.6	Ac	10,000–20,000
<i>Gyrodinium jinhaense</i> (GSJH1710)	Jinhae, Korea	Oct 2017	21.6	32.5	HTD	EG	10.2	Heat-killed Ds	10,000–20,000
<i>Gyrodinium moestrupii</i> (GMSMK0910)	Saemankeum, Korea	Oct 2009	21.2	31.0	HTD	EG	16.0	Am	10,000–20,000
<i>Luciella masanensis</i> (LMJH1607)	Jinhae, Korea	Jul 2016	22.6	30.7	HTD	PE	13.5	Api	~20,000
<i>Oblea rotunda</i> (ORJH1504)	Jinhae, Korea	Apr 2015	12.6	31.2	HTD	PA	21.6	Ac	~10,000
<i>Oxyrrhis marina</i> (OMKS0105)	Kunsan, Korea	May 2001	16.0	27.7	HTD	EG	15.6	Ac	10,000–20,000
<i>Pfiesteria piscicida</i> (CCMP2091)	Neuse River, USA	Jan 1998	-	-	HTD	PE	13.5	Ac	~5,000
<i>Rimostrombidium</i> sp. (RSSMK2007)	Saemankeum, Korea	Jul 2020	27.1	18.8	NC	FF	29.8	Hr	~5,000
Prey									
<i>Triplos furca</i> (TFDD1808)	Dundeok, Geoje, Korea	Aug 2018	28.5	32.5	MTD	EG	28.9	-	-

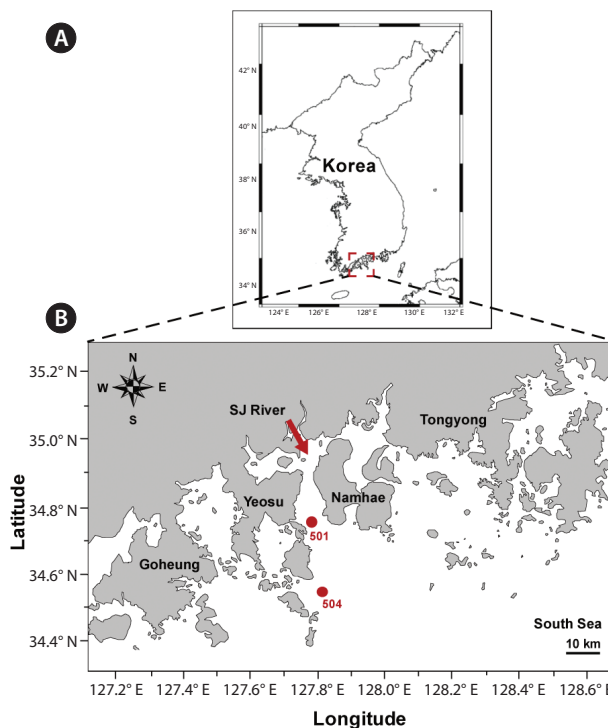
T, temperature (°C); S, salinity; FM, feeding mechanism; ESD, equivalent spherical diameter ( $\mu\text{m}$ ); PS, prey species; PC, prey concentration (cells  $\text{mL}^{-1}$ ); HTD, heterotrophic dinoflagellate; PE, peduncle feeder; As, *Akashiwo sanguinea*; Ac, *Amphidinium carterae*; EG, engulfment feeder; Ds, *Dunaliella salina*; Am, *Alexandrium minutum* (CCMP113); Api, *Apistonema*-like sp. (CCMP3085); PA, pallium feeder; -, not available; NC, naked ciliate; FF, filter feeder; Hr, *Heterocapsa rotundata*; MTD, mixotrophic dinoflagellate.

taining prey and predator, one prey control, and one predator control bottle were set up for the target heterotrophic protist. All the bottles, except for the ones with the *A. glandula* predator, were placed on a rotating wheel at 0.00017 g (0.9 rpm), while those for the *A. glandula* predator were placed on a shelf. All the bottles were incubated at 20°C, under a 14 : 10 h light : dark cycle, and illuminated with cool white fluorescent light of 20 μmol photons m<sup>-2</sup> s<sup>-1</sup>.

Aliquots of 3 mL were taken from each bottle after 2, 24, and 48 h of incubation period, and placed into separate wells of 6-well plate chambers. More than 30 cells of each predator species were transferred into plate chambers and tracked for a minimum of 2 min under a dissecting microscope at 20–63× magnification to test whether the target predator fed on *T. furca* or not. The predator cells with and without ingested *T. furca* cells in their protoplasts were photographed on confocal dishes with cover glasses at 200–630× 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.). The feeding process of the heterotrophic protists that successfully ingested *T. furca* cells was recorded and captured using an identical digital camera.

**Abundance of *Triplos furca* and common heterotrophic protists in the waters off Yeosu**

The two stations (Stations 501 and 504) were located in the nearshore and offshore regions off Yeosu in the South Sea of Korea (Fig. 1). The water depth for both sampling stations was approximately 20 m. Station 501 was located approximately 20 km south of the Seumjin River; thus, the salinity at this station sometimes reduced due to freshwater input (Jeong et al. 2017). Water temperature, salinity, dissolved oxygen (DO), and pH for each sam-



**Fig. 1.** Maps of the study region and the sampling stations (A & B). The arrow between Yeosu and Namhae indicates Seomjin (SJ) River.

pling depth were measured using a YSI Professional Plus instrument (YSI Inc., Yellow Springs, OH, USA).

Water samples at Stations 501 and 504 were collected using water samplers at depths of 0, 5, 10, 15, and 20 m. The sampling time was 13:00 at Station 501 and 13:40 at Station 504. Plankton samples for counting were collected into 500-mL polyethylene bottles and preserved with acidic Lugol’s solution. To clarify the abundance of *T. furca* and heterotrophic protists, the fixed samples were concentrated by 1/5–1/10, using the settling and siphoning method (Welch 1948). After thorough mixing, all or a

**Table 2.** Experimental design

Prey species	Prey density	Predator species	Predator density
<i>Triplos furca</i>	800–1,100	<i>Aduncodinium glandula</i>	650
		<i>Gyrodiniellum shiwhaense</i>	3,600
		<i>Gyrodinium dominans</i>	800
		<i>Gyrodinium jinhaense</i>	400
		<i>Gyrodinium moestrupii</i>	900
		<i>Luciella masanensis</i>	2,000
		<i>Oblea rotunda</i>	700
		<i>Oxyrrhis marina</i>	1,500
		<i>Pfiesteria piscicida</i>	2,000
		<i>Rimostrombidium</i> sp.	280

The numbers in the prey and predator density columns are the initial densities (cells mL<sup>-1</sup>).

minimum of 100 cells of *T. furca* and each heterotrophic protist species in one to ten 1-mL Sedgwick-Rafter chambers were enumerated under a light microscope.

## RESULTS

### Interactions between *Triplos furca* and heterotrophic protists

The heterotrophic dinoflagellates *A. glandula*, *L. masa-*

*nensis*, and *P. piscicida* were able to feed on *T. furca*. However, the heterotrophic dinoflagellates *G. shiwhaense*, *G. dominans*, *G. jinhaense*, *G. moestrupii*, *O. rotunda*, *O. marina*, and the naked ciliate *Rimostrombidium* sp. were unable to feed on the prey (Table 3, Figs 2 & 3). Cells of *A. glandula*, *L. masanensis*, and *P. piscicida* successfully ingested *T. furca* using peduncles (Fig. 2). Multiple cells of *L. masanensis* or *P. piscicida* attacked a *T. furca* cell together (Fig. 2). However, *G. jinhaense*, *G. moestrupii*, *O. rotunda*, and *O. marina* attempted to capture *T. furca*, but failed to do so (Table 3, Fig. 3). Moreover, *G. shiwhaense*,

**Table 3.** Taxa, size, and response of potential heterotrophic dinoflagellate and naked ciliate predators offered to *Triplos furca* (TFDD1808)

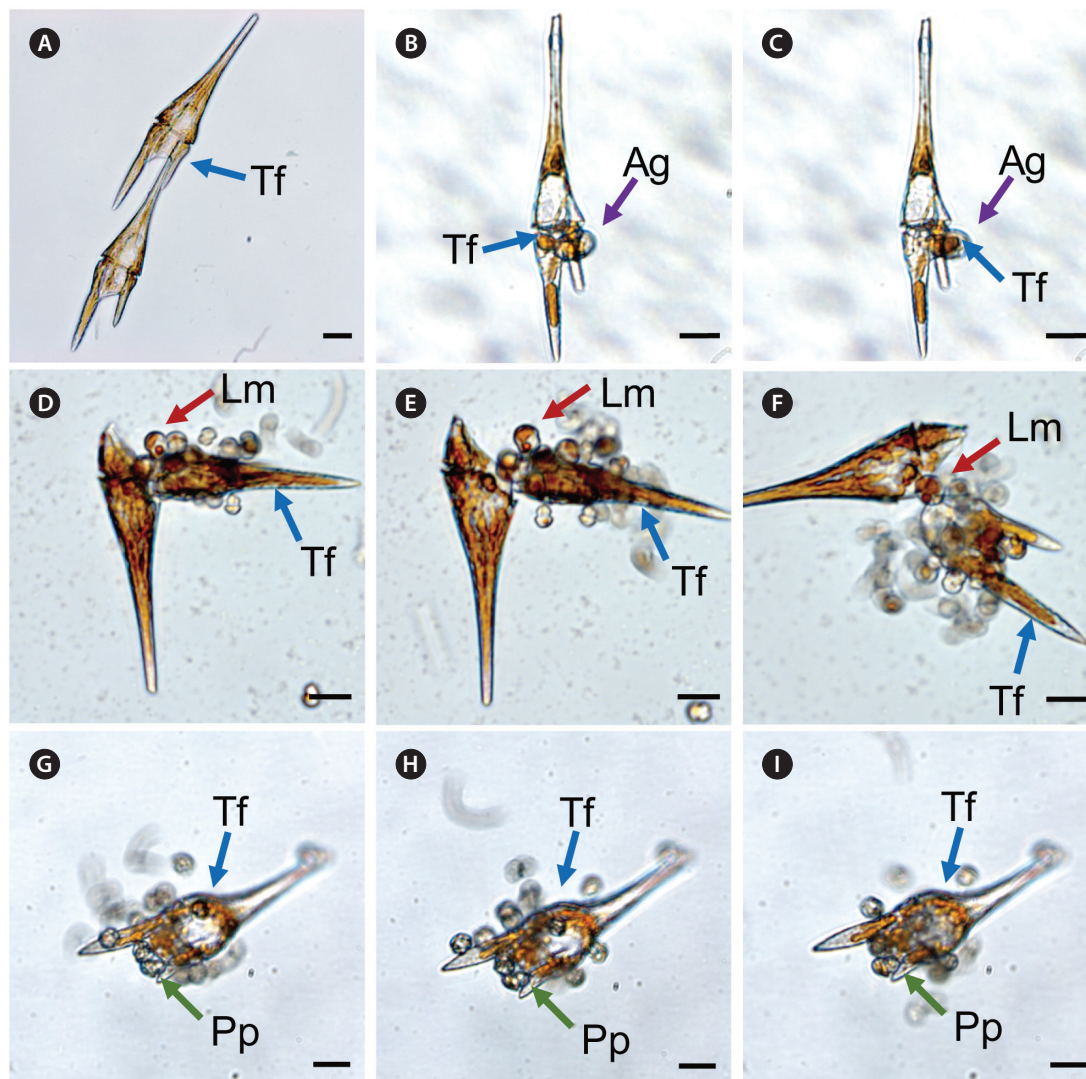
	FM	ESD (µm)	Physical attack	Successful capture	Growth
Heterotrophic dinoflagellate					
<i>Gyrodinium jinhaense</i>	EG	10.2	○	×	N
<i>Gyrodiniellum shiwhaense</i>	PE	10.5	×	×	N
<i>Gyrodinium dominans</i>	EG	11.6	×	×	N
<i>Luciella masanensis</i>	PE	13.5	○	○	N
<i>Pfiesteria piscicida</i>	PE	13.5	○	○	N
<i>Oxyrrhis marina</i>	EG	15.6	○	×	N
<i>Gyrodinium moestrupii</i>	EG	16.0	○	×	N
<i>Aduncodinium glandula</i>	PE	21.0	○	○	N
<i>Oblea rotunda</i>	PA	21.6	○	×	N
Naked ciliate					
<i>Rimostrombidium</i> sp.	FF	29.8	×	×	N

FM, feeding mechanism; ESD, equivalent spherical diameter (µm); EG, engulfment feeder; ○, observed; ×, not observed; N, no growth; PE, peduncle feeder; PA, pallium feeder; FF, filter feeder.

**Table 4.** The abundances (cells mL<sup>-1</sup>) of *Triplos furca*, heterotrophic dinoflagellates, and tintinnid and naked ciliates in five depths of Stations 501 and 504 located off Yeosu in South Sea of Korea on Jul 31, 2020

Taxon	Station 501					Station 504				
	0 m	5 m	10 m	15 m	20 m	0 m	5 m	10 m	15 m	20 m
Mixotrophic dinoflagellate										
<i>Triplos furca</i>	23.7	130.8	19.4	0.9	22.2	59.2	41.4	3.0	1.5	-
Heterotrophic dinoflagellate										
<i>Gyrodinium</i> sp. (ca. 60–80 µm)	-	-	-	-	-	-	2.0	-	-	-
<i>Gyrodinium</i> sp. (>80 µm)	-	0.3	-	-	-	-	2.0	0.6	-	-
<i>Noctiluca scintillans</i>	-	-	-	-	-	-	-	0.6	-	-
<i>Protoperdinium</i> spp.	-	-	0.5	-	-	0.8	1.0	-	-	-
Tintinnid ciliate										
<i>Leprotintinnus nordqvistii</i>	-	-	-	-	-	-	2.0	1.2	-	0.7
<i>Tintinnopsis akkeshiensis</i>	-	-	-	-	-	0.8	-	-	-	-
<i>Tintinnopsis kofoidii</i>	-	-	-	-	-	0.8	-	-	-	-
<i>Tintinnopsis lohmanni</i>	-	-	-	0.9	-	-	-	-	-	-
<i>Tintinnopsis radix</i>	-	-	0.5	-	-	-	-	-	-	-
<i>Tintinnopsis tubulosoides</i>	-	-	-	-	-	-	-	-	-	1.4
Naked ciliate										
Naked ciliates (>50 µm)	-	-	-	-	-	1.7	-	1.8	-	-
T	25.6	22.4	21.5	20.6	20.0	26.7	23.5	21.4	19.9	17.1
S	14.26	28.01	31.87	32.96	33.17	23.05	29.90	31.51	32.70	34.42
DO	7.22	6.32	6.11	6.30	6.15	8.95	7.22	5.65	6.36	8.09
pH	8.44	8.23	8.24	8.14	8.14	8.74	8.47	8.36	8.33	8.38

-, not detected; T, temperature (°C); S, salinity; DO, dissolved oxygen (mg L<sup>-1</sup>).



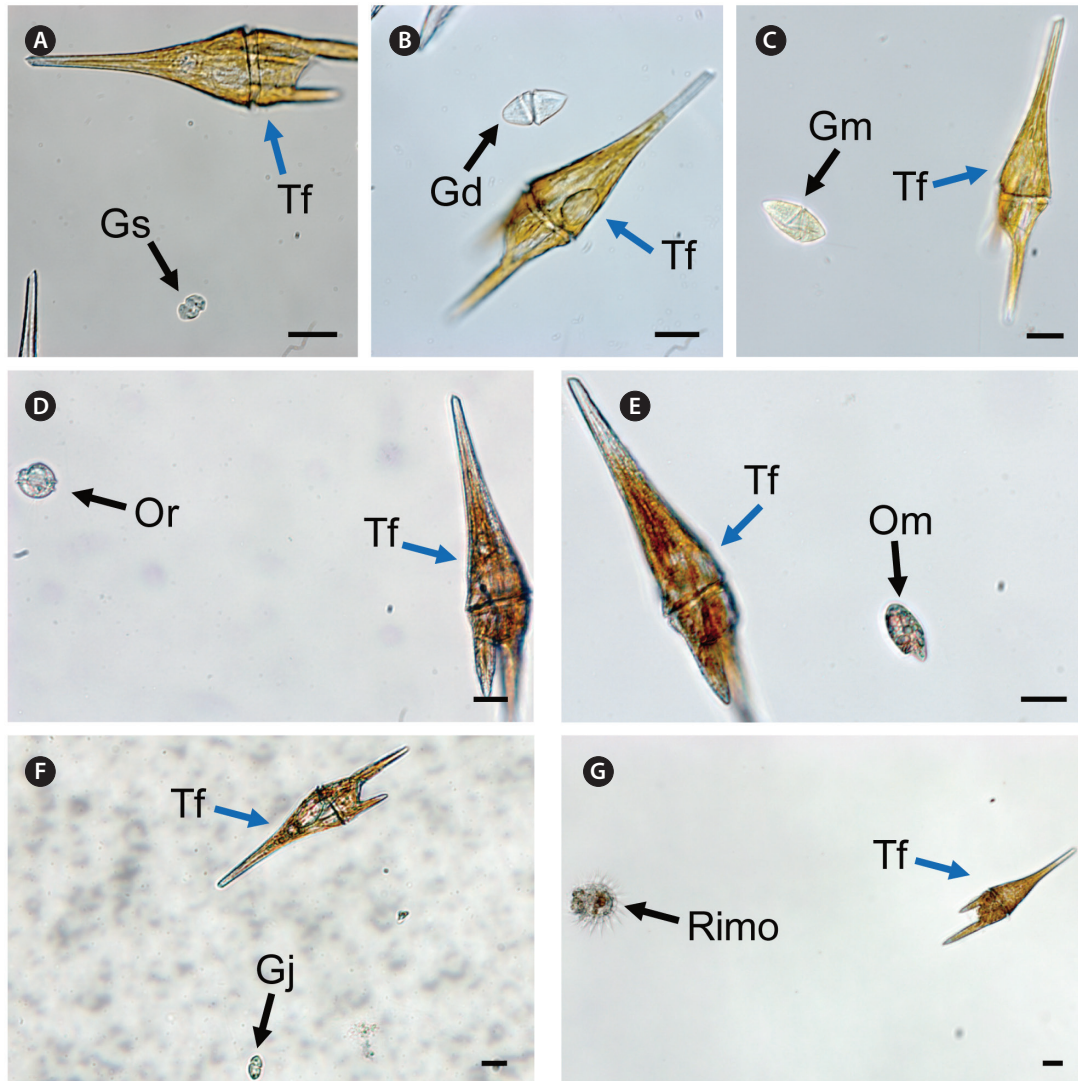
**Fig. 2.** Successful feeding process of heterotrophic protists on *Tripos furca* (Tf) recorded using a digital camera attached to an inverted light microscope. (A) Two Tf cells as prey control. (B & C) Feeding by *Aduncodinium glandula* (Ag) on a Tf cell. An Ag cell fed on a Tf cell using peduncle. (D–F) Feeding by *Luciella masanensis* (Lm) on a Tf cell. Multiple Lm cells fed on a Tf cell using peduncles. (G–I) Feeding by *Pfiesteria piscicida* (Pp) on a Tf cell. Multiple Pp cells fed on a Tf cell using peduncles. Scale bars represent: A–I, 20  $\mu\text{m}$ .

*G. dominans*, and *Rimostrombidium* sp. did not attack *T. furca* (Table 3, Fig. 3). Regardless of capture by potential predators, *T. furca* did not support positive growth of any of the heterotrophic protists tested in the present study; thus, *T. furca* may be an undesirable food source for the common heterotrophic protists (Table 3).

#### Abundance of *Tripos furca* and common heterotrophic protists in the waters off Yeosu on Jul 31, 2020

*Tripos furca* caused huge red tides in the South Sea of

Korea from Jun 30 to Sep 5, 2020 (NFRDI data; <http://www.nifs.go.kr/portal/redtideInfo>). The water temperature and salinity at Station 501 on Jul 31, 2020, ranged from 20.0 to 25.6°C and 14.26 to 33.17, respectively, while those at Station 504 ranged from 17.1 to 26.7°C and 23.05 to 34.42, respectively (Table 4). The DO and pH at Station 501 on Jul 31, 2020, ranged from 6.11 to 7.22 mg L<sup>-1</sup> and 8.14 to 8.44, respectively, while those at Station 504 ranged from 5.65 to 8.95 mg L<sup>-1</sup> and 8.33 to 8.74, respectively (Table 4). The abundance of *T. furca* at Station 501 was 0.9 to 130.8 cells mL<sup>-1</sup>, but that at Station 504 was 0 to 59.2 cells mL<sup>-1</sup> (Table 4). The abundance of the hetero-



**Fig. 3.** Unsuccessful feeding process of heterotrophic dinoflagellates on *Triplos furca* (Tf) recorded using a digital camera attached to an inverted light microscope. (A) *Gyrodiniellum shiwhaense* (Gs) did not feed on Tf. (B) *Gyrodinium dominans* (Gd) did not feed on Tf. (C) *Gyrodinium moestrupii* (Gm) did not feed on Tf. (D) *Oblea rotunda* (Or) did not feed on Tf. (E) *Oxyrrhis marina* (Om) did not feed on Tf. (F) *Gyrodinium jinhaense* (Gj) did not feed on Tf. (G) *Rimostrombidium* sp. (Rimo) did not feed on Tf. Scale bars represent: A–G, 20  $\mu\text{m}$ .

trophic dinoflagellates *Gyrodinium* sp. (approximately 60–80  $\mu\text{m}$  in cell length) and *Gyrodinium* sp. (>80  $\mu\text{m}$  in cell length), both 2.0 cells  $\text{mL}^{-1}$ , were observed at 5 m of Station 504, where an abundance of the heterotrophic dinoflagellates *Protoperidinium* spp., 1.0 cells  $\text{mL}^{-1}$ , was found (Table 4). The maximum abundance of the heterotrophic dinoflagellates was 5.0 cells  $\text{mL}^{-1}$ . The highest abundance of total tintinnids, 2.1 cells  $\text{mL}^{-1}$ , was found at 20 m at Station 504, and *Leprotintinnus nordqvistii* was the most dominant tintinnid (Table 4). Naked ciliates >50  $\mu\text{m}$  were found within 10 m at Station 504, with a maximum abundance of 1.8 cells  $\text{mL}^{-1}$  (Table 4).

## DISCUSSION

Prior to the present study, the mixotrophic dinoflagellate *Fragilidium subglobosum* and heterotrophic dinoflagellates *Noctiluca scintillans*, *Polykrikos kofoidii*, and *Protoperidinium steinii* were reported to feed on *T. furca* (Hansen and Nielsen 1997, Jeong et al. 2001, Olseng et al. 2002, Drits et al. 2013). *Fragilidium* spp. are known to engulf whole prey through the sulcal area, *N. scintillans* engulf prey cell using mucus attached to the tentacle, and *Polykrikos* spp. engulf prey cells after anchoring the prey with a nematocyst-taeniocyst complex (Kjørboe

and Titelman 1998, Hansen and Calado 1999, Tillmann and Hoppenrath 2013). However, *Proto-peridinium* spp. feed on prey cells wrapped in pallium after anchoring prey using a tow filament (Jacobson and Anderson 1992, Hansen and Calado 1999). Interestingly, the results of the present study clearly showed that among the common heterotrophic protist predators tested, only peduncle-feeders *Aduncodinium glandula*, *Luciella masanensis*, and *Pfiesteria piscicida* ingested *T. furca* TFDD1808. In contrast, the engulfment feeders *Gyrodinium dominans*, *G. jinhaense*, *G. moestrupii*, and *Oxyrrhis marina*, the filter feeder *Rimostrombidium* sp., and the pallium feeder *Oblea rotunda* did not consume *T. furca*. However, not all peduncle feeders were successful at feeding on *T. furca*; one of the peduncle feeders, *Gyrodiniellum shiwhaense*, failed to ingest *T. furca*. Therefore, feeding mechanisms may not be primarily responsible for the ability and inclination of these common heterotrophic protists to feed on *T. furca*. Cells of *A. glandula* are known to feed on diverse prey items, including perch blood cells and many algal prey species (Jang et al. 2016). The results of the present study extend the prey species of *A. glandula* to *T. furca*. Cells of *L. masanensis* and *P. piscicida* are known to feed on dinoflagellate prey species of  $\leq 9.7 \mu\text{m}$  in the equivalent spherical diameter (ESD) and athecate dinoflagellates such as *Margalefidinium polykrikoides*, *Akashiwo sanguinea*, and *Gymnodinium catenatum*, but they did not feed on thecate dinoflagellates  $\geq 12.1 \mu\text{m}$  (Jeong et al. 2007). You et al. (2020) reported that *P. piscicida* fed on larger sized thecate dinoflagellates, but only on motionless cells. Thus, the present study is the first to report that *L. masanensis* and *P. piscicida* are able to feed on a moving thecate dinoflagellate  $\geq 12.1 \mu\text{m}$  because the ESD of *T. furca* is approximately  $29 \mu\text{m}$  (Jeong et al. 2001). Cells of *L. masanensis* and *P. piscicida* swarmed to feed on a *T.*

*furca* cell. Other peduncle feeding heterotrophic dinoflagellates *Stoeckeria algicida* and *Stoeckeria changwonensis* are known to swarm to feed on a prey cell (Jeong et al. 2005, Lim et al. 2014). Their distinctive swarming behaviors may be triggered by the chemosensory signals from prey (Burkholder and Glasgow 1995, Lewitus et al. 1999).

Among the heterotrophic protists that did not predate *T. furca* in the present study, *G. shiwhaense*, *G. dominans*, and *Rimostrombidium* sp. did not attempt to attack *T. furca*, whereas the other heterotrophic protists attempted to feed on *T. furca* cells. Thus, *G. shiwhaense*, *G. dominans*, and *Rimostrombidium* sp. may not have enzymes related to the detection of *T. furca* cells. Cells of *G. jinhaense* are known not to feed on microalgae  $> 26 \mu\text{m}$  in ESD, except the dinoflagellate *Lingulodinium polyedra*, where ESD is approximately  $38 \mu\text{m}$  (Kang et al. 2020). Thus, *G. jinhaense* may have difficulty engulfing *T. furca* cells. Furthermore, *G. moestrupii* cells were also observed to have difficulty in utilizing long *T. furca* cells as prey, although *G. moestrupii* is known to feed on *L. polyedra* (Kang et al. 2020). Cells of *O. rotunda* and *O. marina* successfully target dinoflagellate prey species  $< 27 \mu\text{m}$  in ESD, respectively (Strom and Buskey 1993, Kang et al. 2019, Kim et al. 2019, You et al. 2020). Therefore, the elongated horns, and large size of *T. furca* may be partially responsible for non-feeding by these heterotrophic dinoflagellates.

*Aduncodinium glandula*, *L. masanensis*, and *P. piscicida* were not found in the water samples collected from two stations on Jul 31, 2020. In the present study, *T. furca* did not support the positive growth of these three heterotrophic dinoflagellates. Therefore, the results of the feeding experiments in the present study may provide an explanation for the non-detection of these three heterotrophic dinoflagellates in the water samples. The heterotrophic dinoflagellates *Gyrodinium* sp. ( $> 80 \mu\text{m}$ ) and *Pro-*

**Table 5.** The lorical oral diameter (LOD) of the tintinnids<sup>a</sup>, the maximum ingestible prey size (MIP)<sup>b</sup> of each tintinnid, and the dimension of *Tripos furca*

	LOD or length ( $\mu\text{m}$ )	MIP or width ( $\mu\text{m}$ )	Reference
Tintinnid ciliate species			
<i>Tintinnopsis akkeshiensis</i>	24–34	10.3–14.6	Hada (1937)
<i>Leptotintinnus nordqvistii</i>	30–38	12.9–16.3	Abou Zaid and Hellal (2012)
<i>Tintinnopsis tubulosoides</i>	32–36	13.8–15.5	Feng et al. (2018)
<i>Tintinnopsis kofoidi</i>	33–35	14.2–15.1	Hada (1937)
<i>Tintinnopsis lohmanni</i>	35–52	15.1–22.4	Hada (1937)
<i>Tintinnopsis radix</i>	45	19.4	Hada (1937)
Mixotrophic flagellate			
<i>Tripos furca</i>	100–200	30–50	Baek et al. (2008)

<sup>a</sup>Species observed in the study region on Jul 31, 2020.

<sup>b</sup>Maximum ingestible prey size was calculated according to Heinbokel (1978).



*toperidinium* spp. and two tintinnid ciliates were found in the water samples collected from Station 501, at which the maximum abundance of *T. furca* was 130.8 cells mL<sup>-1</sup>. Meanwhile, *Gyrodinium* spp. ( $\geq 60 \mu\text{m}$ ), *Noctiluca scintillans*, *Protoperidinium* spp., and several tintinnid species were found in the water samples collected from Station 504, at which the maximum abundance of *T. furca* was 59.2 cells mL<sup>-1</sup>. Furthermore, the abundances of *Gyrodinium* spp. ( $\geq 60 \mu\text{m}$ ), *N. scintillans*, *Protoperidinium* spp., and several tintinnid species at Station 504 were as low as 0.6–2.0 cells mL<sup>-1</sup>. In contrast, *Polykrikos kofoidii* was not found in these water samples. Jeong et al. (2001) reported that *P. kofoidii* grew on *T. furca* with a maximum growth rate of 0.35 d<sup>-1</sup>, and half-saturation constant (the prey concentration sustaining 1/2 maximum growth rate) and the threshold prey concentration of *P. kofoidii* feeding on *T. furca* was 128 ng C mL<sup>-1</sup> (102 cells mL<sup>-1</sup>) and 113 ng C mL<sup>-1</sup> (90 cells mL<sup>-1</sup>), respectively. When the abundance of *T. furca* was 59.2 and 130.8 cells mL<sup>-1</sup>, the growth rates of *P. kofoidii* feeding on *T. furca*, calculated using the equation of Jeong et al. (2001), were -0.153 and 0.101 d<sup>-1</sup>, respectively. Therefore, low abundances of *T. furca* during the study period may be partially responsible for the lack of detection of *Polykrikos* spp.

The naked ciliate *Rimostrombidium* sp. (oral diameter = 29.4  $\mu\text{m}$ , n = 6) did not consume *T. furca*. The large tintinnid ciliates *Favella philippinensis* and *Favella ehrenbergii* (lorical oral diameter [LOD] = 69–144  $\mu\text{m}$ ) are known to engulf *Tripus* sp., while the small tintinnid ciliate *Tintinnopsis uruguayensis* (LOD = 37–42  $\mu\text{m}$ ) is unable to feed on *T. furca* (Godhantaraman and Krishnamurthy 1997, Sivasankar et al. 2017). The LOD of tintinnids is known to strongly correlate with the maximum and optimal prey size (Dolan 2010). In general, tintinnids are known to ingest maximum prey size up to roughly 43% of their LOD (Heinbokel 1978). To ingest whole *T. furca* cells, the LOD of tintinnids should be wider than approximately 70  $\mu\text{m}$ . However, the tintinnids found in the sample waters (LOD = 24–52  $\mu\text{m}$ ) may not be large enough to feed on *T. furca* (Table 5). Thus, in the collected waters, the tintinnid ciliates may not be large enough to engulf *T. furca*. Therefore, *T. furca* was unlikely to support the rapid growth of the tintinnids at Stations 501 and 504 on Jul 31, 2020.

Conclusively, among the nine common heterotrophic dinoflagellates and one naked ciliate tested in the present study, only *A. glandula*, *L. masanensis*, and *P. piscicida* were found to feed on *T. furca*. However, *T. furca* did not support the positive growth of any of these predator species. Furthermore, the abundances of the heterotrophic protists that were able to feed on *T. furca* were low at

Stations 501 and 504 on Jul 31, 2020. Therefore, predators may not significantly reduce the abundance of *T. furca*, which may be partially responsible for the prevalence of *T. furca* on the coast of the South Sea from June to September 2020.

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## CONFLICTS OF INTEREST

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

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