Ichthyotoxic *Cochlodinium polykrikoides* red tides offshore in the South Sea, Korea in 2014: II. Heterotrophic protists and their grazing impacts on red-tide organisms

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Occurrence of *Cochlodinium polykrikoides* red tides have resulted in considerable economic losses in the aquaculture industry in many countries, and thus predicting the process of *C. polykrikoides* red tides is a critical step toward minimizing those losses. Models predicting red tide dynamics define mortality due to predation as one of the most important parameters. To investigate the roles of heterotrophic protists in red tide dynamics in the South Sea of Korea, the abundances of heterotrophic dinoflagellates (HTDs), tintinnid ciliates (TCs), and naked ciliates (NCs) were measured over one- or two-week intervals from May to Nov 2014. In addition, the grazing impacts of dominant heterotrophic protists on each red tide species were estimated by combining field data on red tide species abundances and dominant heterotrophic protist grazers with data obtained from the literature concerning ingestion rates of the grazers on red tide species. The abundances of HTDs, TCs, and NCs over the course of this study were high during or after red tides, with maximum abundances of 82, 49, and 35 cells mL⁻¹, respectively. In general, the dominant heterotrophic protists differed when different species caused red tides. The HTDs *Polykrikos* spp. and NCs were abundant during or after *C. polykrikoides* red tides. The mean and maximum calculated grazing coefficients of *Polykrikos* spp. and NCs on populations of co-occurring *C. polykrikoides* were 1.63 d⁻¹ and 12.92 d⁻¹, respectively. Moreover, during or after red tides dominated by the phototrophic dinoflagellates *Prorocentrum donghaiense*, *Ceratium furca*, and *Alexandrium fraterculus*, which formed serial red tides prior to the occurrence of *C. polykrikoides* red tides, the HTDs *Gyrodinium* spp., *Polykrikos* spp., and *Gyrodinium* spp., respectively were abundant. The maximum calculated grazing coefficients attributable to dominant heterotrophic protists on co-occurring *P. donghaiense*, *C. furca*, and *A. fraterculus* were 13.12, 4.13, and 2.00 d⁻¹, respectively. Thus, heterotrophic protists may sometimes have considerable potential grazing impacts on populations of these four red tide species in the study area.

Key Words: ciliate; dinoflagellate; grazing impact; harmful algal bloom

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INTRODUCTION

Red tides, or harmful algal blooms, occur in coastal waters worldwide (Holmes et al. 1967, Eppley and Harrison 1975, Franks and Anderson 1992, Anderson 1995, Horner et al. 1997, Sordo et al. 2001, Imai et al. 2006, Seong et al. 2006, Jeong et al. 2015), and often result in large-scale fish and shellfish mortalities and substantial economic losses to the aquaculture and tourist industries (Smayda 1990, Glibert et al. 2005, Anderson et al. 2012, Fu et al. 2012, Park et al. 2013b). In particular, the ichthyotoxic dinoflagellate *Cochlodinium polykrikoides* forms red tides in the waters of many countries, and has been shown to cause large-scale mortality of finfish in both cages at sea and aqua-tanks on land (Whyte et al. 2001, Fukuyo et al. 2002, Gobler et al. 2008, Mulholland et al. 2009, Kudela and Gobler 2012, Park et al. 2013b, Lim et al. 2014a, 2017, Hong et al. 2016). Thus, to minimize the economic losses resulting from red tides, many countries attempt to predict and control such events. The growth rate of red tide species and its mortality rate due to predation are two critical parameters in prediction models (Jeong et al. 2015), but there is far less data available on the mortality rates of red tide species due to predation than on growth rates. Thus, to improve predictions of red tide outbreaks, persistence, and decline, it is useful to investigate the roles of heterotrophic protists in red tide dynamics, including the mortality rates of red tide species due to predation by heterotrophic protists.

Heterotrophic protists, such as heterotrophic dinoflagellates and ciliates, are often abundant during or after red tides (Hansen 1991, Nakamura et al. 1995, Yoo et al. 2013a). Moreover, several phytoplankton species belonging to various taxonomic groups sometimes form red tides simultaneously or in serial during a certain period of time (Jeong et al. 2013, 2017); for example, diatoms and the phototrophic dinoflagellates *Prorocentrum donghaiense*, *Ceratium furca*, *Alexandrium fraterculus*, and *C. polykrikoides* formed serial red tides in Korea's South Sea in 2014 (Jeong et al. 2017). This raises the question of whether the dominant heterotrophic protists also differ during different red tides. Furthermore, many heterotrophic protist species or groups are known to be effective grazers on red tide species, and grazing by heterotrophic protists often restricts the initial development of red tides and contributes to red tide termination (Lessard 1991, Montagnes and Lessard 1999, Calbet et al. 2003, Jeong et al. 2005, 2010, 2015, Turner 2006, Sherr and Sherr 2007, Yoo et al. 2013a, Jang et al. 2016). For instance, several heterotrophic protists, such as the ciliates *Strombidinop-*

sis spp., the heterotrophic dinoflagellate *Polykrikos kofoidii*, and the mixotrophic dinoflagellates *Alexandrium pohangense* and *Polykrikos hartmannii*, are known to feed on *C. polykrikoides* (Jeong et al. 1999, 2001, 2008, Kim 2004, Lee et al. 2015, Lim et al. 2015, 2017). However, a few studies have focused on the impacts of grazing by heterotrophic protists on populations of *C. polykrikoides* (Kim 2004, Yoo et al. 2013a), and none on populations of *P. donghaiense* and *A. fraterculus*. Thus, it is worthwhile to explore the impacts that grazing by heterotrophic protists have on these red tide species.

To investigate the roles of heterotrophic protists in red tide dynamics in the South Sea of Korea, the abundances of heterotrophic dinoflagellates (HTDs), tintinnid ciliates (TCs), and naked ciliates (NCs) in water samples collected from 2–5 different depths (depending on the overall water depth) at 60 stations (mostly offshore) weekly or every two weeks from May to Nov 2014 were measured. Environmental factors, such as water temperature, salinity, and chlorophyll-*a* (chl-*a*), and the abundances of dominant red-tide organisms, were simultaneously analyzed in a companion paper (Jeong et al. 2017). The grazing impacts by dominant heterotrophic protists on each red tide species were estimated by combining field data of red tide species and dominant heterotrophic protist grazer abundances with data obtained from the literature regarding grazer ingestion rates of the red tide species. The results of the present study provide a basis for understanding the role of heterotrophic protist grazers in red tide dynamics.

MATERIALS AND METHODS

Study area and sampling stations

The 60 stations used for sampling in the study area were located in the mid and eastern South Sea of Korea. Water depths at the sampling stations ranged between 4 and 53 m (Fig. 1). The depths of the stations in the western South Sea are shallower than those in the eastern South Sea at the same latitude (Fig. 1). One of the estuary stations was located ca 20 km south of the mouth of the Seumjin River, whereas the other estuary station was located 5 km southwest of Haechang Bay. Sixteen sampling time cruises were conducted at 1–2 week intervals from May to Nov 2014. Two days of sampling were undertaken during each cruise; on each day, two ships simultaneously collected water samples at half of the stations in the study area.

Fig. 1. Map of the study area (A & B) and sampling stations (black dots) (C) in the South Sea, Korea. (B) Section enlarged from map (A). (C) Section enlarged from map (B). The arrow in Goheung indicates Haechang Bay (HC Bay), the arrow between Goheung and Yeosu indicates Yeoja Bay (YJ Bay), and the arrow between Yeosu and Namhae indicates Seomjin River (SJ River).

Water temperatures and salinities throughout the water column were measured using 2 CTDs (YSI6600; YSI Inc., Yellow Springs, OH, USA; Ocean seven; Idronaut S.r.l., Milan, Italy). The data obtained using the CTDs were calibrated each cruise. In addition, when each water sample was taken, the temperature, salinity, pH, and dissolved oxygen (DO) in the sampling waters were measured using a YSI Professional Plus instrument (YSI Inc.). The chl-*a* concentration was measured in accordance with the protocol described in Eaton et al. (1995).

Abundances of heterotrophic protists

Water samples at each station were taken from 2-5 m depths depending on the depth with water samplers. Plankton samples were poured into 500-mL polyethylene bottles and preserved with acidic Lugol's solution for determination of heterotrophic protist abundances. To determine the abundances of HTDs, TCs, and NCs, the samples preserved in acidic Lugol's solution were concentrated by 1/5-1/10 using the settling and siphoning method (Welch 1948). After thorough mixing, all or a minimum of 100 cells of each protist species in one to ten

1-mL Sedgwick-Rafter counting chambers were counted under a compound microscope. Data on the abundances of phototrophic protists were obtained from Jeong et al. (2017).

The average and maximum values of the abundance of each protist group, water temperature, salinity, and concentration of chl-*a* on each sampling date were derived from all water samples collected on the sampling date.

The carbon content for each species of the red-tide dinoflagellates *A. fraterculus*, *C. polykrikoides*, *C. furca*, and *P. donghaiense* was obtained from the literature (Jeong et al. 1999, 2001, Yoo et al. 2013b, Zhang et al. 2015).

Pearson's correlation was used to calculate the correlation coefficients between heterotrophic protists and physical and red tide organisms (IBM SPSS statistics 23; IBM Corp., Armonk, NY, USA).

Grazing impacts

The grazing coefficients (*g*) attributable to a dominant heterotrophic protist feeding on a co-occurring red tide dinoflagellate were calculated by combining field data on the abundance of the dominant heterotrophic protist and red tide dinoflagellate with ingestion rates of the protist grazer on the red tide prey obtained from the literature (Jeong et al. 1999, 2001, Kim 2004, Kim and Jeong 2004, Yoo et al. 2013b, Zhang et al. 2015). The combination of a red tide dinoflagellate and dominant heterotrophic protist grazer in the study period was *C. polykrikoides* and NCs (>100 µm in cell length) and *P. kofoidii*, *C. furca* and *P. kofoidii*, *A. fraterculus* and *Gyrodinium dominans* / *G. moestrupii*, and *P. donghaiense* and *G. dominans* / *G. moestrupii*, *Noctiluca scintillans*, and NCs (>100 µm in cell length) (Jeong et al. 2017, this study). The ingestion rate of NCs (>100 µm) on *C. polykrikoides* was assumed to be the same as that of *Strombidinopsis* sp. on *C. polykrikoides* (Jeong et al. 1999). It was difficult to distinguish *G. moestrupii*, *G. dominans*, and other *Gyrodinium* spp. (<40 µm) from one another under a light microscope due to their morphological similarities (Yoo et al. 2013b). Thus, the ingestion rates of *G. moestrupii*, *G. dominans*, and other *Gyrodinium* spp. (<40 µm) on *P. donghaiense* were assumed to be the same as that of *G. dominans* on *Prorocentrum minimum*, because the cell size and shape of *P. minimum* and *P. donghaiense* are similar (Kim and Jeong 2004, Cai et al. 2006). The ingestion rate of NCs (>100 µm) on *P. donghaiense* was assumed to be the same as that of *Strombidinopsis* sp. on *P. minimum* (Jeong et al. 1999). Finally, the ingestion rate of *G. moestrupii*, *G. dominans*, and other *Gyrodinium* spp. (<40 µm) on *A. frater-*

culus was assumed to be the same as that of *G. moestrupii* on *Alexandrium minutum* (Yoo et al. 2013b).

The grazing coefficient (*g*, d⁻¹) was calculated as:

$$g = CR \times GC \times x \quad (1)$$

, where CR is the clearance rate (mL predator⁻¹ h⁻¹) for a predator of a red-tide organism at a given prey concentration and GC is the predator concentration (cells mL⁻¹). CR values were calculated as:

$$CR = IR / x \quad (2)$$

, where IR is the ingestion rate (cells eaten predator⁻¹ h⁻¹) of the predator on the prey and *x* is the prey concentration (cells mL⁻¹). CR values were corrected using *Q*₁₀ = 2.8 (Hansen et al. 1997) because the in situ water temperatures and the temperatures used in the laboratory for the experiment were different.

The percentage (%) of a red-tide organism population consumed by a predator population in 1 day was calculated as:

$$\text{Consumed percentage (\%)} = [1 - e^{(-g)}] \times 100 \quad (3)$$

RESULTS

Temporal variations in major environmental factors and heterotrophic protists

Average water temperatures ranged between 15.0–23.2°C during the study period, with a peak observed on Sep 28. Average salinity ranged between 32 from 34, with the lowest levels observed on Sep 1 (Fig. 2). Concentrations of chl-*a* ranged from 0.1–44.2 mg m⁻³, with averages ranging from 1.2–3.0 mg m⁻³ (Fig. 2). Peaks for both the maximum and average concentrations of chl-*a* were recorded on Sep 1 (Fig. 2). Three-dimensional distributions of water temperature, salinity, chl-*a* concentration, and heterotrophic protists in the study area are provided in Appendix 1.

Thirty-five TC taxa, several NC taxa, and 30 HTD taxa were found at all stations over the study period (Appendix 2). Although the maximum abundances of TCs (49.0 cells mL⁻¹), NCs (35.0 cells mL⁻¹), and HTDs (82.4 cells mL⁻¹) did not differ substantially from one another, the peak abundances of these 3 groups occurred at different times (Table 1, Fig. 2); TCs and NCs abundances were highest in May to Jun, whereas that of HTDs was highest in Sep. Maximal abundances of TCs and NCs were observed when the diatom or the dinoflagellate *P. donghaiense*

Fig. 2. Environmental factors and the abundances (cells mL⁻¹) of heterotrophic protists in the South Sea of Korea from May 7 to Nov 11, 2014. (A) Average water temperature (T, °C). (B) Average salinity (S). (C) Maximum (MChl-a, mg m⁻³) and average (AChl-a, mg m⁻³) chl-a concentrations. (D) The period of red tides dominated by diatoms (Dia), *Prorocentrum donghaiense* (Pd), *Ceratium furca* (Cf), *Alexandrium fraterculus* (Af), and *Cochlodinium polykrikoides* (Cp). (E) Maximum (MTCs) and average (ATCs) abundances of total tintinnid ciliates. (F) Maximum (MNCs) and average (ANCs) abundances of total naked ciliates. (G) Maximum (MTocil) and average (ATocil) abundances of total ciliates. (H) Maximum (MHTDs) and average (AHTDs) abundances of total heterotrophic dinoflagellates. Open circles represent average ± standard error.

formed red tides, whereas the maximal HTD abundance was observed following peak chl-*a* concentrations and *C. polykrikoides* red tides (Fig. 2). The abundance of total ciliates was 0-50.6 cells mL⁻¹ (Table 1, Fig. 2), and the maximum abundance of total ciliates was observed on May 7.

Spatial variations in major heterotrophic protists

When considering locations where high abundances were observed, the spatial distributions of TCs, NCs, and HTDs differed from one another at all sampling times with the exception of the period Jun 12 to Jul 1, 2014 (Fig. 3). High abundances of TCs was observed in the western part of the study area at most sampling times; high abundances of NCs was observed in the western or middle parts of the study area at most sampling times; and high abundances of HTDs was observed in the eastern part of the study area from May 7-Jun 5 and Aug 6-Sep 15, but in the western or middle parts of the study area from Jun 12-Jul 1.

Temporal and spatial variations in the abundance of dominant HTDs during red tides

Diatoms, *P. donghaiense*, *C. furca*, *A. fraterculus*, and *C. polykrikoides* formed serial red tides in the study area from May 7 to Nov 11 in 2014 (Fig. 4, redrawn from Jeong et al. 2017). In general, the dominant HTD genera during

Table 1. Range of abundances for each group of heterotrophic protists and the major heterotrophic protist taxon, and the water temperature and salinity where each taxon was found in the South Sea of Korea from May to Nov 2014

	Temperature (°C)	Salinity	Abundance (cells mL ⁻¹)
Major group			
Total heterotrophic dinoflagellates	13.6-26.6	23.5-35.8	0-82.4
Total tintinnid ciliates	13.6-26.6	25.9-35.8	0-49.0
Total naked ciliates	13.6-26.6	23.5-35.8	0-35.0
Total ciliates	13.6-26.6	23.5-35.8	0-50.6
Total heterotrophic protists	13.6-26.6	23.5-35.8	0-87.8
Major heterotrophic taxon			
<i>Gyrodinium dominans</i> / <i>G. moestrupii</i>	13.6-25.6	31.4-34.4	0-13.1
<i>Polykrikos kofoidii</i>	14.7-34.4	31.4-34.1	0-27.0
<i>Polykrikos schwarzii</i>	14.7-25.9	30.8-34.5	0-51.8
<i>Noctiluca scintillans</i>	13.9-26.6	23.5-34.3	0-30.7
<i>Tintinnopsis sufflata</i>	14.0-21.1	33.6-34.3	0-45.7
<i>Tiarina fusus</i>	13.6-24.1	31.4-34.5	0-20.0

Fig. 3. Three-dimensional distributions (cells mL⁻¹) of tintinnid ciliates (TCs), naked ciliates (NCs), total ciliates (ToCil), and total heterotrophic dinoflagellates (HTDs) in the study area for each cruise from May 7 to Nov 11, 2014 drawn using Voxler software (Golden software, LLC, Golden, CO, USA).

Fig. 3. Continued.

Fig. 4. The abundances (cells mL⁻¹) of dominant heterotrophic dinoflagellates in the South Sea of Korea from May 7 to Nov 11, 2014. (A) The period of red tides dominated by diatoms (Dia), *Prorocentrum donghaiense* (Pd), *Ceratium furca* (Cf), *Alexandrium fraterculus* (Af), and *Cochlodinium polykrikoides* (Cp). (B) Maximum (MAGyr) and average (AAGyr) abundances of *Gyrodinium* spp. (C) Maximum (MAPro) and average (AAPro) abundances of *Protoperidinium* spp. (D) Maximum (MANoc) and average (AANoc) abundances of *Noctiluca scintillans*. (E) Maximum (MAPol) and average (AAPol) abundances of *Polykrikos* spp. Open circles represent average $\pm$ standard error.

Table 2. Correlations between the abundances (cells mL⁻¹) of heterotrophic dinoflagellates (HTDs), tintinnid ciliates (TCs), naked ciliates (NCs), and the major HTDs and physical and biological properties, and the red tide species in the South Sea, Korea from May to Nov 2014

Organism	T	S	Chl- <i>a</i>	PHY	DIA	PTD	Pd	Cf	Af	Cp
TCs	0.071**	-	0.031*	0.047*	0.032*	0.045**	0.086**	0.042*	-	-
NCs	-0.149**	0.089**	-	0.072**	0.033*	0.087**	0.107**	-	-	-
HTDs	-	-	0.041**	0.115**	0.080**	0.104**	-	-	-	-
<i>Gyrodinium</i> spp.	-	-	-	-	-	-	0.050**	-	-	-
<i>Protoperidinium</i> spp.	-	-	-	-	0.097**	-	0.099**	-	-	-
<i>Noctiluca scintillans</i>	-	-	-	-	0.127**	-	0.046**	0.043**	-	-
<i>Polykrikos</i> spp.	-	-	-	-	-	-	-	-	-	0.039*

T, temperature (°C); S, salinity; Chl-*a*, chlorophyll-*a* (mg m⁻³); PHY, total phytoplankton; DIA, diatom; PTD, total phototrophic dinoflagellates; Pd, *Prorocentrum donghaiense*; Cf, *Ceratium furca*; Af, *Alexandrium fraterculus*; Cp, *Cochlodinium polykrikoides*.

p* < 0.05, *p* < 0.01.

or after each red tide changed (Fig. 4); *Gyrodinium* spp. were abundant during the red tide dominated by *P. donghaiense* from Jun 23-Jul 1, *Protoperidinium* spp. during the *C. furca*, and *C. polykrikoides* red tide on Aug 6 and Sep 1, and *N. scintillans* and *Polykrikos* spp. during the *C. polykrikoides* red tide on Sep 15. The maximum abundances of *Gyrodinium* spp., *Protoperidinium* spp., *N. scintillans*, and *Polykrikos* spp. were 41.9, 11.0, 30.7, and 78.8 cells mL⁻¹, respectively.

The spatial distributions of *Gyrodinium* spp., *Protoperidinium* spp., *N. scintillans*, and *Polykrikos* spp. differed from one another at most sampling times (Fig. 5); *Gyrodinium* spp. were highly abundant in all three parts of the study area (i.e., the eastern part from May 7 to Jun 5, the western part from Jun 12 to 23, and the middle part on Jul 1); *Protoperidinium* spp. were highly abundant in the western or middle parts at most sampling times; *N. scintillans* was most abundant in the middle part of the study area; and *Polykrikos* spp. were abundant in all three sections (from Jun 12-Jul 1 in the western part, from Jul 11-Aug 6 in the middle part, and on Sep 15 in the eastern part) of the study area.

Correlations between major heterotrophic groups and physical and biological properties

There was a significantly positive correlation between TCs abundance and water temperature (T), whereas NCs abundance was significantly negatively correlated with T (Table 2) but significantly positively correlated with salinity (S) (Table 2). No correlations were found between HTDs abundance and T or S (Table 2).

The abundances of TCs, NCs, and HTDs were significantly and positively correlated with total phytoplankton, diatom, and phototrophic dinoflagellate abundances (Table 2). Furthermore, *Polykrikos* spp. abundances were significantly positively correlated with *C. polykrikoides*

Fig. 5. Three-dimensional distributions (cells mL⁻¹) of *Gyrodinium* spp., *Polykrikos* spp., *Proto-peridinium* spp., and *Noctiluca scintillans* in the study area for each cruise from May 7 to Nov 11, 2014.

Fig. 5. Continued.

Fig. 6. Calculated grazing coefficients (g, d^{-1}) attributable to the heterotrophic dinoflagellate *Polykrikos kofoidii* on co-occurring *Cochlodinium polykrikoides*, based on assumption (see text) in the study area at each cruise from May 7 to Nov 11, 2014.

abundance, whereas *Gyrodinium* spp. abundances were significantly positively correlated with *P. donghaiense* abundance. In addition, the abundances of *Protoperdinium* spp., *N. scintillans*, TCs, and NCs were significantly positively correlated with total diatom and *P. donghaiense* abundances (Table 2).

Grazing impacts on red-tide organisms

When the abundances of *C. polykrikoides* and *P. kofoidii* were $0.1\text{--}2,989.3 \text{ cells mL}^{-1}$ and $0.0\text{--}27.0 \text{ cells mL}^{-1}$, respectively, the calculated g attributable to *P. kofoidii* on co-occurring *C. polykrikoides* were up to 7.02 d^{-1} (i.e., up to 99% of the population *C. polykrikoides* were consumed in 1 d) (mean $\pm$ SE = $0.06 \pm 0.01 \text{ d}^{-1}$, $n = 1,682$) (Table 3, Fig. 6). In addition, when the abundances of *C. polykrikoides* and NCs ($>100 \mu\text{m}$) were $0.1\text{--}2,989.3 \text{ cells mL}^{-1}$ and $0.0\text{--}7.4 \text{ cells mL}^{-1}$, respectively, the g attributable to NCs ($>100 \mu\text{m}$) on co-occurring *C. polykrikoides* were up to 12.92 d^{-1}

(i.e., up to 99% of the population *C. polykrikoides* were consumed in 1 d) (mean $\pm$ SE = $0.21 \pm 0.02 \text{ d}^{-1}$, $n = 1,682$) (Table 3, Fig. 7).

When the abundances of *P. donghaiense* and *G. dominans* / *G. moestrupii* were $0.1\text{--}4,369.1 \text{ cells mL}^{-1}$ and $0.0\text{--}15.0 \text{ cells mL}^{-1}$, respectively, the g attributable to *G. dominans* / *G. moestrupii* on co-occurring *P. donghaiense* were up to 0.58 d^{-1} (i.e., up to 44% of the population *P. donghaiense* were consumed in 1 d) (mean $\pm$ SE = $0.02 \pm 0.00 \text{ d}^{-1}$, $n = 868$) (Table 4). When the abundances of *P. donghaiense* and *N. scintillans* were $0.1\text{--}4,369.1 \text{ cells mL}^{-1}$ and $0.0\text{--}30.7 \text{ cells mL}^{-1}$, respectively, the g attributable to *N. scintillans* on co-occurring *P. donghaiense* were up to 1.70 d^{-1} (i.e., up to 82% of the population *P. donghaiense* were consumed in 1 d) (mean $\pm$ SE = $0.02 \pm 0.01 \text{ d}^{-1}$, $n = 868$) (Table 4). Furthermore, when the abundances of *P. donghaiense* and NCs ($>100 \mu\text{m}$) were $0.1\text{--}4,369.1 \text{ cells mL}^{-1}$ and $0.0\text{--}7.2 \text{ cells mL}^{-1}$, respectively, the g attributable to NCs ($>100 \mu\text{m}$) on co-occurring *P. donghaiense* were up to

Fig. 7. Calculated grazing coefficients (g, d^{-1}) attributable to the naked ciliates ($>100 \mu\text{m}$) on co-occurring *Cochlodinium polykrikoides*, based on assumption (see text) in the study area for each cruise from May 7 to Nov 11, 2014.

Table 3. Calculated grazing coefficient (g, d^{-1}) of the heterotrophic protists, *Polykrikos kofoidii* (Pk) and naked ciliates (NCs $> 100 \mu\text{m}$) on *Cochlodinium polykrikoides* (Cp) observed in the South Sea of Korea from May to Nov in 2014

Sampling date	Abundance (cells mL^{-1})		g	Abundance (cells mL^{-1})		g
	Cp	Pk		Cp	NCs	
May 7-8	0.1-10.4	0.0	0.00	0.1-10.4	0.0-7.4	0.00-8.75 (1.35)
May 21-22	0.1-24.3	0.0-0.6	0.00-0.13 (0.00)	0.1-24.3	0.0-1.0	0.00-1.54 (0.21)
Jun 5-6	0.1-4.1	0.0-0.8	0.00-0.22 (0.01)	0.1-4.1	0.0-2.0	0.00-3.12 (0.17)
Jun 12-13	0.1-5.0	0.0-0.8	0.00-0.24 (0.00)	0.1-5.0	0.0-5.0	0.00-12.92 (0.60)
Jun 23-24	0.1-1.4	0.0	0.00	0.1-1.4	0.0-3.0	0.00-7.46 (0.67)
Jul 1-2	0.1-0.7	0.0-0.1	0.00-0.40 (0.01)	0.1-0.7	0.0-0.9	0.00-2.35 (0.08)
Jul 11-12	0.1-3.1	0.0-7.0	0.00-3.11 (0.05)	0.1-3.1	0.0-0.8	0.00-2.33 (0.08)
Jul 22-23	0.1-1.8	0.0-0.7	0.00-0.25 (0.01)	0.1-1.8	0.0-1.0	0.00-3.45 (0.09)
Aug 6-7	0.1-5.7	0.0-1.0	0.00-0.39 (0.01)	0.1-5.7	0.0-1.0	0.00-2.88 (0.05)
Aug 13-14	0.1-32.3	0.0	0.00	0.1-32.3	0.0-1.1	0.00-3.20 (0.21)
Aug 21-22	0.1-1,767.0	0.0-0.7	0.00-0.32 (0.00)	0.1-1,767.0	0.0-1.2	0.00-4.06 (0.20)
Sep 1-2	0.2-2,989.3	0.0-1.6	0.00-0.40 (0.01)	0.2-2,989.3	0.0-2.0	0.00-4.24 (0.05)
Sep 15-16	0.1-334.9	0.0-27.0	0.00-7.02 (0.40)	0.1-334.9	0.0-1.8	0.00-5.27 (0.14)
Sep 28-29	0.1-438.0	0.0-1.0	0.00-0.37 (0.00)	0.1-438.0	0.0-0.9	0.00-2.75 (0.08)
Oct 9-10	0.1-521.3	0.0-0.8	0.00-0.28 (0.01)	0.1-521.3	0.0-0.9	0.00-2.34 (0.05)
Nov 10-11	0.1-6.0	0.0	0.00	0.1-6.0	0.0-1.1	0.00-2.03 (0.09)

Numbers in parentheses are mean g values. See text for calculation.

13.12 d⁻¹ (i.e., up to 99% of the population *P. donghaiense* were consumed in 1 d) (mean ± SE = 0.40 ± 0.04 d⁻¹, n = 868) (Table 4).

When the abundances of *C. furca* and *P. kofoidii* were 0.1–400.4 cells mL⁻¹ and 0.0–15.4 cells mL⁻¹, respectively, the g attributable to *P. kofoidii* on co-occurring *C. furca* were up to 4.13 d⁻¹ (i.e., up to 98% of the population *C. furca* were consumed in 1 d) (mean ± SE = 0.02 ± 0.00 d⁻¹,

n = 1,304) (Table 5).

When the abundances of *A. fraterculus* and co-occurring *G. dominans* / *G. moestrupii* were 0.1–1,276.0 cells mL⁻¹ and 0.0–15.0 cells mL⁻¹, respectively, the g attributable to the HTD *G. dominans* / *G. moestrupii* on co-occurring *A. fraterculus* were up to 2.00 d⁻¹ (i.e., up to 87% of the population *A. fraterculus* were consumed in 1 d) (mean ± SE = 0.06 ± 0.01 d⁻¹, n = 732) (Table 6).

Table 4. Calculated grazing coefficient (g, d⁻¹) of the heterotrophic protists, *Gyrodinium dominans* / *G. moestrupii* (Gd / Gm), *Noctiluca scintillans* (Ns), and naked ciliates (NCs > 100 µm) on *Prorocentrum donghaiense* (Pd) observed in the South Sea of Korea from May to Nov in 2014

Sampling date	Abundance (cells mL ⁻¹)		g	Abundance of Ns (cells mL ⁻¹)		g	Abundance of NCs (cells mL ⁻¹)		g
	Pd	Gd / Gm							
May 7-8	0.3-117.0	0.0-13.8	0.00-0.33 (0.03)	0.0-1.1	0.00-0.04 (0.01)		0.0-7.2		0.00-13.12 (2.10)
May 21-22	0.5-235.9	0.0-9.9	0.00-0.26 (0.02)	0.0-4.6	0.00-0.23 (0.02)		0.0-1.2		0.00-2.825 (0.24)
Jun 5-6	0.2-233.6	0.0-10.1	0.00-0.28 (0.01)	0.0-30.7	0.00-1.70 (0.03)		0.0-2.0		0.00-3.941 (0.12)
Jun 12-13	0.2-2,725.0	0.0-15.0	0.00-0.58 (0.02)	0.0-15.0	0.00-0.95 (0.02)		0.0-5.0		0.00-4.506 (0.35)
Jun 23-24	0.1-948.8	0.0-3.1	0.00-0.10 (0.01)	0.0-3.8	0.00-0.24 (0.01)		0.0-2.0		0.00-7.456 (0.80)
Jul 1-2	0.2-4,369.1	0.0-13.2	0.00-0.47 (0.03)	0.0-4.4	0.00-0.27 (0.03)		0.0-1.3		0.00-4.414 (0.19)
Jul 11-12	0.5-463.6	0.0-4.5	0.00-0.21 (0.02)	0.0-0.9	0.00-0.07 (0.01)		0.0-0.9		0.00-3.858 (0.13)
Jul 22-23	0.7-1.0	0.0-3.2	0.00-0.21 (0.06)	0.0	0.00		0.0		0.00
Aug 6-7	0.8-2.1	0.0-1.0	0.00-0.06 (0.03)	0.0-1.1	0.00-0.08 (0.02)		0.0		0.00
Aug 13-14	-	-	-	-	-		-		-
Aug 21-22	-	-	-	-	-		-		-
Sep 1-2	-	-	-	-	-		-		-
Sep 15-16	-	-	-	-	-		-		-
Sep 28-29	1.0	0.0	0.00	0.0	0.00		0.0		0.00
Oct 9-10	0.4	0.0	0.00	0.0	0.00		0.0		0.00
Nov 10-11	0.5	0.0	0.00	0.0	0.00		0.0		0.00

Numbers in parentheses are mean g values.

Table 5. Calculated grazing coefficient (g, d⁻¹) of the heterotrophic protist, *Polykrikos kofoidii* (Pk) on *Ceratium furca* (Cf) observed in the South Sea of Korea from May to Nov in 2014

Sampling date	Abundance (cells mL ⁻¹)		g
	Cf	Pk	
May 7-8	0.1-1.0	0.0	0.00
May 21-22	0.1-1.5	0.0	0.00
Jun 5-6	0.2-4.0	0.0	0.00
Jun 12-13	0.5-9.9	0.0-0.8	0.00-0.13 (0.00)
Jun 23-24	0.2-13.8	0.0	0.00
Jul 1-2	0.8-1.8	0.0	0.00
Jul 11-12	0.1-94.5	0.0-7.0	0.00-1.76 (0.02)
Jul 22-23	0.3-131.2	0.0-2.1	0.00-0.56 (0.00)
Aug 6-7	0.1-400.4	0.0-1.1	0.00-0.21 (0.00)
Aug 13-14	0.1-100.0	0.0-1.0	0.00-0.23 (0.00)
Aug 21-22	0.7-220.0	0.0-0.7	0.00-0.19 (0.00)
Sep 1-2	0.7-11.7	0.0-1.0	0.00-0.25 (0.01)
Sep 15-16	0.5-5.6	0.0-15.4	0.00-4.13 (0.27)
Sep 28-29	0.1-3.0	0.0-0.5	0.00-0.12 (0.00)
Oct 9-10	0.1-3.3	0.0-0.7	0.00-0.16 (0.01)
Nov 10-11	0.1-3.0	0.0	0.00

Numbers in parentheses are mean g values.

Table 6. Calculated grazing coefficient (g, d⁻¹) of the heterotrophic protist, *Gyrodinium dominans* / *G. moestrupii* (Gd / Gm) on *Alexandrium fraterculus* (Af) observed in the South Sea of Korea from May to Nov in 2014

Sampling date	Abundance (cells mL ⁻¹)		g
	Af	Gd / Gm	
May 7-8	0.2-15.5	0.0-13.8	0.00-1.06 (0.12)
May 21-22	0.1-20.4	0.0-10.9	0.00-1.10 (0.11)
Jun 5-6	0.1-2.2	0.0-4.8	0.00-0.48 (0.05)
Jun 12-13	0.5-17.5	0.0-15.0	0.00-2.00 (0.13)
Jun 23-24	0.2-3.5	0.0-0.8	0.00-0.10 (0.02)
Jul 1-2	0.7-3.8	0.0-10.9	0.00-1.49 (0.15)
Jul 11-12	0.1-2.3	0.0-2.5	0.00-0.38 (0.05)
Jul 22-23	0.5-1.0	0.0-1.0	0.00-0.19 (0.05)
Aug 6-7	0.2-1.5	0.0-1.1	0.00-0.20 (0.02)
Aug 13-14	0.1-9.5	0.0-3.0	0.00-0.57 (0.08)
Aug 21-22	0.5-1,276.0	0.0-4.0	0.00-0.38 (0.02)
Sep 1-2	0.2-49.5	0.0-15.0	0.00-1.34 (0.02)
Sep 15-16	0.5-3.4	0.0-3.0	0.00-0.54 (0.03)
Sep 28-29	0.5-8.9	0.0-2.0	0.00-0.35 (0.04)
Oct 9-10	0.3-8.3	0.0-0.7	0.00-0.11 (0.01)
Nov 10-11	0.1-12.0	0.0-0.7	0.00-0.07 (0.00)

Numbers in parentheses are mean g values.

DISCUSSION

Our results clearly demonstrated that (1) the type and abundance of red tide species affect the type and abundance of the dominant heterotrophic protists and (2) some heterotrophic protists had considerable grazing impacts on populations of the red tide species inhabiting the South Sea during the study period.

Effects of red tide species on the distributions of major heterotrophic protist groups

Significantly positive correlations between HTDs, TCs, and NCs and total phytoplankton abundance suggest that the abundances of these heterotrophic protists are affected by total phytoplankton abundance in the study area. However, the dominant heterotrophic protist genera or taxa differed when the red tide causative species changed; TCs and / or NCs were dominant during or after diatom red tides; *Gyrodinium* spp. were dominant during or after *P. donghaiense* red tides; *Protoberidinium* spp. were dominant during or after *C. furca*, *A. fraterculus*, and / or *C. polykrikoides* red tides; and *N. scintillans* and *Polykrikos* spp. were dominant during or after *C. polykrikoides* red tides. High abundances of TCs and / or NCs during or after diatom red tides, *Protoberidinium* spp. during or after *C. furca* red tides, and *N. scintillans* and *Polykrikos* spp. during or after *C. polykrikoides* red tides have been previously reported to occur in Korea, India, and Norway (Jeong et al. 2000, Olseng et al. 2002, Biswas et al. 2013, Yoo et al. 2013a, National Fisheries Research & Development Institute 2014). Here, however, we report for the first time that *Gyrodinium* spp. are abundant during or after *P. donghaiense* red tides and that *Protoberidinium* spp. are abundant during or after *A. fraterculus* and / or *C. polykrikoides* red tides. Although *Gyrodinium* spp. and *Protoberidinium* spp. are known to feed on *P. donghaiense* and *C. polykrikoides*, respectively (Cho 2006, Gu et al. 2014), no study of *Protoberidinium* spp. feeding on *A. fraterculus* has yet been published. It is worthwhile to explore feeding by *Protoberidinium* spp. on *A. fraterculus* because field data suggest the existence of potential predator-prey relationships between heterotrophic and phototrophic dinoflagellates.

There was a 2-week time lag between the peak abundances of *C. polykrikoides* (Sep 1) and *Polykrikos* spp. (Sep 15). *C. polykrikoides* abundance was 3,000 cells mL⁻¹ on Sep 1 and 335 cells mL⁻¹ on Sep 15 (Jeong et al. 2017), whereas that of *Polykrikos* spp. on the same dates was 2.5 and 78.8 cells mL⁻¹, respectively. In a laboratory feeding

experiment in which concentrations of *C. polykrikoides* were increased, *P. kofoidii* grew rapidly at mean prey concentrations $\leq$ ca. 300 cells mL⁻¹ but became saturated at higher prey concentrations (Kim 2004). Thus, theoretically, the abundance of *C. polykrikoides* from Sep 1 to 15 was likely to support positive growth of *Polykrikos* spp. The growth rate of *Polykrikos* spp. feeding on *C. polykrikoides* from Sep 1 to 15 was estimated to be 0.25 d⁻¹, which is 23% of the maximum growth rate of *P. kofoidii* on *C. polykrikoides* obtained in the laboratory by Kim (2004). Many environmental factors, such as water temperature, turbulence, predators, and competition, may lower the growth rate. However, our results suggest that high *C. polykrikoides* abundance may result in increasing abundances of *Polykrikos* spp. during *C. polykrikoides* red tides.

Abundance of dominant heterotrophic protist groups

The maximum abundance of all HTDs observed during the study period was 82 cells mL⁻¹, a level comparable to or higher than that measured in Sandsfjord (Norway), the Seto Inland Sea (Japan), Gyeonggi Bay (Korea), Chesapeake Bay (USA), Chile, and the Pearl River Estuary (Hong Kong, China) (Table 7). The maximum chl-*a* concentration observed during the study period (44.2 µg L⁻¹) was also comparable to or higher than those in other regions of the world (Table 7). In general, the growth rate of HTDs rapidly increased with increasing concentrations of suitable algal prey species before becoming saturated (i.e., Lim et al. 2014b). Thus, high chl-*a* concentrations during red tides dominated by suitable prey species in this region may be partially responsible for the comparable or higher maximum abundance of total HTDs. However, the maximum abundance of total HTDs in this area was found to be considerably lower than in Masan Bay (Korea) and Albemarle-Pamlico Estuary (USA), as was the maximum concentration of chl-*a* (Table 7). Thus, lower levels of chl-*a* during red tides may be partially responsible for the lower maximum abundance of total HTDs in the South Sea. Although maximum abundances differed substantially between the study area and Masan Bay and Albemarle-Pamlico Estuary, the differences between the maximum biomasses may be much smaller. The dominant HTDs in Masan Bay and Albemarle-Pamlico Estuary during periods of maximal HTD abundance were *Pfiesteria* and *Pfiesteria*-like dinoflagellates (PLDs, including species in the genera *Luciella*, *Stoeckeria*, and *Cryptoperidiniopsis*) (Glasgow et al. 2001, Yoo et al. 2013a), whereas

the dominant HTDs in the study area were *Polykrikos* spp. The maximum biomass of *Polykrikos* spp. (3.6 ng C cell⁻¹) in the study area was estimated to be 280 ng C mL⁻¹, which is ~15% of the maximum biomass of HTDs in Masan Bay (1,916 ng C mL⁻¹) (Yoo et al. 2013a). The equivalent spherical diameter of *Polykrikos* spp. (ca. 44 µm) is much larger than that of PLDs (~13-14 µm) (Jeong et al. 2010). Furthermore, the types of prey species that *Polykrikos* spp. feed on differ from those consumed by PLDs; engulfment-feeding *Polykrikos* spp. are known to consume large algal prey like the phototrophic dinoflagellates *Lingulodinium polyedrum*, *Scrippsiella trochoidea*, *C. furca*, *C. polykrikoides*, *Gymnodinium catenatum*, *Gymnodinium impudicum*, and *Prorocentrum micans* (Jeong et al. 2001, Kim 2004), whereas peduncle-feeding PLDs prefer smaller algal prey such as the raphidophyte *Heterosigma akashiwo*, the cryptophytic *Teleaulax* sp.,

Rhodomonas salina, and *Rhodomonas* sp., and the phototrophic dinoflagellate *Amphidinium carterae* (Jeong et al. 2005, 2006, 2007, Baek et al. 2010, Lim et al. 2014b). Therefore, the causative species of red tides in these waters may support different dominant HTDs, resulting in differences in maximum abundances.

The maximum abundance of total TCs in the South Sea during the study period (49 cells mL⁻¹) was higher than in the Seto Inland Sea (Japan), North Irish Sea (Ireland), Buzzards Bay, Long Island Sound, and Chesapeake Bay (USA), Sandsfjord (Norway), and the Gulf of Naples (Italy) (Table 7). The maximum concentration of chl-*a* in the study area was also higher than in other regions of the world (Table 7). On the other hand, the maximum abundance of total TCs in the study area was lower than in the Coastal North Sea and Masan Bay, and the maximum concentration of chl-*a* in the South Sea was also lower than in the Coastal

Table 7. Comparison of the abundances of total heterotrophic dinoflagellates (HTDs), tintinnid ciliates (TCs), and naked ciliates (NCs), and chl-*a* concentrations at each sampling site in estuarine and coastal regions

Study area	Abundance (cell mL ⁻¹)	Chl- <i>a</i> (µg L ⁻¹)	Reference
Total HTDs			
South Sea, Korea	0-82	0.1-44.2	This study
Sandsfjord system, Norway	7.5-19	~6	Nielsen and Andersen (2002)
Seto Inland, Japan	4-90	~8	Nakamura et al. (1995)
Gyenggi Bay, Korea	0.4-95	1.0-66.4	Yang et al. (2008)
Chesapeake Bay, USA	0-99	4.8-24.1	Johnson et al. (2003)
Coast of Chile, Chile	59-104	~3	Claustre et al. (2008), Masquelier and Vaulot (2008)
Pearl River Estuary, China Sea	10-142	>1.0	Lan et al. (2009)
Masan Bay, Korea	1-10,289	0.02-514.7	Yoo et al. (2013a)
Albemarle-Pamlico Estuary, USA	300-1,200,000	10-112	Glasgow et al. (2001)
Total TCs			
South Sea, Korea	0-49	0.1-44.2	This study
Seto Inland Sea, Japan	<0.1-0.2	~8	Nakamura et al. (1995)
North Irish Sea, Ireland	0-1.5	~12	Graziano (1989)
Buzzards Bay, USA	0-3.3	-	Pierce and Turner (1994)
Sandsfjord system, Norway	0.7-5.5	~6	Nielsen and Anderson (2002)
Seto Inland Sea, Japan	0.02-5.7	0.4-8.0	Kamiyama and Tsujino (1996)
Long Island Sound, USA	0.3-12.6	-	Capriulo and Carpenter (1983)
Chesapeake Bay, USA	0-13	4.8-24.1	Johnson et al. (2003)
Gulf of Naples, Italy	0-30.5	0.1-7.5	Modigh and Castaldo (2002)
Coastal North Sea, Netherlands	118 ^a	50 ^a	Admiraal and Venekamp (1986), Admiraal et al. (1985)
Narragansett Bay, Rhode Island	270 ^a	20 ^a	Verity (1987)
Masan Bay, Korea	1-216	0.02-514.7	Yoo et al. (2013a)
Flødevigen Bay, Norway	729 ^a	0.5-4.6	Dale and Dahl (1987)
Total NCs			
South Sea, Korea	0-35	0.1-44.2	This study
Long Island Sound, USA	0.02-6.4	-	Capriulo and Carpenter (1983)
Sandsfjord system, Norway	5-18	~6	Nielsen and Andersen (2002)
Seto Inland Sea, Japan	2-22	~8	Nakamura et al. (1995)
Chesapeake Bay, USA	1.7-22	4.8-24.1	Johnson et al. (2003)
Masan Bay, Korea	1-1,113	0.02-514.7	Yoo et al. (2013a)

^aMaximum abundance.

North Sea and Masan Bay (Table 7). Thus, higher or lower chl-*a* concentrations during or after red tides in the study area may be also partially responsible for the higher or lower maximum abundance of total TCs.

The maximum abundance of total NCs (35 cells mL⁻¹) was higher in the South Sea than in Long Island Sound and Chesapeake Bay (USA), Sandsfjord (Norway), and the Seto Inland Sea (Japan) (Table 7), as was the maximum chl-*a* concentration (Table 7). However, the maximum abundance of total NCs was considerably lower in the study region than in Masan Bay (Korea) (Table 7). Moreover, the maximum concentration of chl-*a* and the maximum abundance of diatoms in the study area (44.2 µg L⁻¹ and 13,020 cells mL⁻¹, respectively) (Jeong et al. 2017) were also much lower than in Masan Bay (514.7 µg L⁻¹ and 71,538 cells mL⁻¹, respectively) (Jeong et al. 2013). According to Yoo et al. (2013a), total NC biomass was significantly positively correlated with diatom abundance in Masan Bay. Thus, the lower maximum abundance of diatoms in the study area may explain why the maximum abundance of total NCs was lower in the South Sea than in Masan Bay.

Grazing impacts by major heterotrophic protist groups on populations of red tide organisms

The maximum *g* by dominant heterotrophic protists on *A. fraterculus*, *C. furca*, *C. polykrikoides*, and *P. donghaiense* mostly exceeded 2.0 d⁻¹ (i.e., ~87% of the population of a given red tide species was consumed in 1 d), but the mean *g* were <0.4 d⁻¹ (i.e., ~33% of the population of a given red tide species was consumed in 1 d). Therefore, the dominant heterotrophic protists may at times have considerable grazing impacts on populations of these red tide species. The very high *g* (i.e., >5 d⁻¹) may be caused by a combination of low red tide species abundance and high dominant heterotrophic protist abundance during the declining stages of red tides.

The maximum *g* attributable to dominant hetero-

trophic protists on co-occurring *C. polykrikoides* and *C. furca* estimated in this study were higher than those on the same prey species in other regions (Table 8); for instance, the maximum *g* of *P. kofoidii* on *C. polykrikoides* in the present study (7.02 d⁻¹) was higher than reported for Tongyeong and Masan Bay, Korea (1.21–2.64 d⁻¹) (Kim 2004, Yoo et al. 2013a). In addition, the maximum *g* for *P. kofoidii* on *C. furca* in the present study (4.13 d⁻¹) was much higher than observed in Masan Bay (1.20 d⁻¹) (Yoo et al. 2013a). The abundances of *P. kofoidii* during *C. polykrikoides* and *C. furca* red tides in the study region were higher than those in Tongyeong and Masan Bay. Therefore, higher abundances of *P. kofoidii* during *C. polykrikoides* or *C. furca* red tides may be partially responsible for the higher maximum *g*'s of *P. kofoidii* on co-occurring *C. polykrikoides* and *C. furca* in the South Sea than in Tongyeong and Masan Bay.

To the best of our knowledge, no studies have presented data on the grazing impacts of heterotrophic protists on *P. donghaiense* and *A. fraterculus* in other regions despite their having caused red tides in the waters of many countries (Moncheva et al. 2001, MacKenzie et al. 2004, Tang et al. 2006, Omachi et al. 2007, Nagai et al. 2009, Hu et al. 2012, Park et al. 2013a). Thus, it is difficult to compare *g*'s by heterotrophic protists on *P. donghaiense* and *A. fraterculus* in the South Sea to those in other waters. The maximum *g*'s of *G. dominans* / *G. moestrupii*, *N. scintillans*, and NCs (>100 µm) on *P. donghaiense* and *A. fraterculus* in our study were high, as mentioned above. Thus, it would be useful to explore the *g*'s of heterotrophic protists on *P. donghaiense* and *A. fraterculus* in other regions of the world.

Overall, the dominant heterotrophic protist groups and their abundances in Korea's South Sea varied considerably both spatially and temporally over the course of the study period; such variability was associated with changes in the dominant red tide species or groups. Furthermore, the maximum *g*'s of the dominant heterotrophic protists on the red tide species or groups were extremely

Table 8. Comparison of the measured or calculated grazing coefficient (*g*, d⁻¹) of heterotrophic protists on each red-tide organism

Red-tide organism	Predator	Area	<i>g</i> (d ⁻¹)	Reference
<i>Ceratium furca</i>	<i>Polykrikos kofoidii</i>	South Sea, Korea	0.00–4.13	This study
	<i>Polykrikos kofoidii</i>	Masan Bay, Korea	0.24–1.20	Yoo et al. (2013a)
<i>Cochlodinium polykrikoides</i>	<i>Polykrikos kofoidii</i>	South Sea, Korea	0.00–7.02	This study
	Ciliates (>100 µm)	South Sea, Korea	0.00–12.92	This study
	<i>Polykrikos kofoidii</i>	Masan Bay, Korea	0.07–2.64	Yoo et al. (2013a)
	<i>Polykrikos kofoidii</i>	Tongyeong, Korea	0.01–1.21	Kim (2004)
	<i>Strombidinopsis</i> sp.	Tongyeong, Korea	0.01–0.79	Kim (2004)

high. Thus, red tide species, as prey, play important roles in the dynamics of the dominant heterotrophic protists, and in turn the dominant heterotrophic protists, as predators, play important roles in the dynamics of red tide organisms in marine ecosystems.

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Appendix 1. Three-dimensional distributions of water temperature (T), salinity (S), chl-*a* (mg m^{-3}), and heterotrophic protists (HTP, cells mL^{-1}) in the study area for each cruise from May 7 to Nov 11, 2014. T, S, and chl-*a* were redrawn from Jeong et al. (2017).

Appendix 1. Continued.

Appendix 2. List of heterotrophic protists and their presence / absence on each sampling date in the South Sea, Korea, from May to Nov 2014

	May 7	May 21	Jun 5	Jun 12	Jun 23	Jul 1	Jul 11	Jul 22	Aug 6	Aug 13	Aug 21	Sep 1	Sep 15	Sep 28	Oct 9	Nov 10
Heterotrophic dinoflagellate																
<i>Amphidiniopsis kofoidii</i>	+	+														
<i>Gyrodinium dominans</i> / <i>G. moestrupii</i> (<40 µm)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Gyrodinium spirale</i>					+								+			
<i>Gyrodinium</i> sp. A (41-60 µm)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Gyrodinium</i> sp. B (61-69 µm)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Gyrodinium</i> sp. C (70-89 µm)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
<i>Gyrodinium</i> sp. D (90-99 µm)				+												
<i>Gyrodinium</i> sp. E (>100 µm)	+	+	+	+	+	+	+	+	+	+				+	+	+
<i>Katodinium glaucum</i>	+	+		+	+		+			+		+			+	
<i>Nematodinium</i> spp.	+	+	+	+	+	+	+	+	+	+			+	+	+	
<i>Noctiluca scintillans</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Oxyphysis oxytoxoides</i>							+				+					
<i>Podolampas palmipes</i>	+								+	+				+	+	+
<i>Polykrikos kofoidii</i>		+	+	+	+	+	+	+	+	+	+	+	+	+	+	
<i>Polykrikos schwarzii</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Protoperidinium bipes</i>	+	+	+	+		+	+	+		+						
<i>Protoperidinium brevipes</i>	+	+	+	+	+	+	+	+	+	+						+
<i>Protoperidinium crassipes</i>							+		+		+				+	
<i>Protoperidinium cruciferum</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Protoperidinium depressum</i>	+	+		+	+	+	+	+	+	+	+	+	+	+	+	
<i>Protoperidinium divergens</i>					+		+	+	+	+	+	+	+		+	+
<i>Protoperidinium excentricum</i>	+		+													
<i>Protoperidinium hirobis</i>	+	+			+	+	+			+					+	
<i>Protoperidinium leonis</i>	+	+	+							+		+				
<i>Protoperidinium oceanicum</i>	+	+	+	+		+		+		+	+	+	+	+	+	
<i>Protoperidinium pallidum</i>		+	+	+	+	+		+	+		+				+	+
<i>Protoperidinium pentagonum</i>	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+
<i>Protoperidinium pyriforme</i>	+	+	+	+	+	+	+	+	+	+		+	+	+	+	
<i>Protoperidinium subinerme</i>		+		+		+	+		+					+		+
<i>Protoperidinium</i> sp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Tintinnid ciliate																
<i>Amphorellopsis acuta</i>	+							+		+	+	+		+	+	
<i>Codonellopsis frigida</i>												+	+			
<i>Codonellopsis nipponica</i>	+	+						+			+	+	+	+	+	+
<i>Codonellopsis</i> sp.										+	+	+	+			
<i>Dadayiella ganymedes</i>				+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Eutintinnus lusus-undae</i>	+															
<i>Eutintinnus</i> sp.		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Favella ehrenbergii</i>	+		+	+		+	+		+	+	+	+	+	+	+	
<i>Favella</i> sp.	+	+	+			+	+	+	+	+	+	+	+	+	+	
<i>Helicostomella longa</i>	+		+	+	+	+	+	+	+	+		+	+			+
<i>Helicostomella subulata</i>													+			
<i>Leptotintinnus bottnicus</i>		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Leptotintinnus nordquisti</i>	+		+	+	+	+	+	+	+		+		+			+
<i>Leptotintinnus pellucides</i>													+			
<i>Steestrupella steenstrupii</i>							+									
<i>Stenosemella nivalis</i>		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Stenosemella</i> sp.	+															

Appendix 2. Continued

	May 7	May 21	Jun 5	Jun 12	Jun 23	Jul 1	Jul 11	Jul 22	Aug 6	Aug 13	Aug 21	Sep 1	Sep 15	Sep 28	Oct 9	Nov 10
<i>Tintinnidium mucicola</i>		+	+	+	+	+	+	+	+	+			+	+	+	+
<i>Tintinnopsis akkeshiensis</i>	+		+	+	+	+	+	+	+	+	+	+		+	+	+
<i>Tintinnopsis angustior</i>	+															
<i>Tintinnopsis beroidea</i>	+	+							+							
<i>Tintinnopsis brevicollis</i>		+	+						+	+				+	+	
<i>Tintinnopsis directa</i>	+					+		+	+				+		+	
<i>Tintinnopsis gracilis</i>		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Tintinnopsis kofoidii</i>	+		+	+	+	+	+	+	+	+	+	+	+		+	+
<i>Tintinnopsis lohmanni</i>	+	+				+								+		
<i>Tintinnopsis mortensenii</i>			+	+		+	+	+	+	+	+	+	+	+	+	
<i>Tintinnopsis nana</i>	+	+		+	+	+		+	+	+			+		+	+
<i>Tintinnopsis radix</i>				+	+	+	+	+	+	+	+	+	+	+		+
<i>Tintinnopsis rapa</i>	+		+					+	+						+	
<i>Tintinnopsis sufflata</i>	+					+										
<i>Tintinnopsis tubulosa</i>		+	+	+	+	+	+	+	+	+	+		+	+	+	+
<i>Tintinnopsis tubulosoides</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Tintinnopsis</i> sp.		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Undella</i> sp.	+		+	+	+	+	+	+	+	+	+	+	+	+		+
Naked ciliate																
<i>Didinium</i> sp.						+	+	+	+	+						
<i>Tiarina fusus</i>	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+
Ciliate (≤ 50 μm)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Ciliate (51-99 μm)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Ciliate (>100 μm)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+