



Differential feeding by common heterotrophic protists on 12 different *Alexandrium* species

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ABSTRACT

The genus *Alexandrium* often forms harmful algal blooms causing human illness and large-scale mortality of fish and shellfish. Thus, *Alexandrium* bloom dynamics are primary concerns for scientists, government officials, aquaculture farmers, and the public. To understand bloom dynamics, mortality due to predation needs to be assessed; however, interactions between many *Alexandrium* species and their potential predators have not previously been reported. Thus, feeding by five common heterotrophic dinoflagellates (*Oxyrrhis marina*, *Gyrodinium dominans*, *Polykrikos kofoidii*, *Pfiesteria piscicida*, and *Oblea rotunda*) and a naked ciliate (*Strombidinopsis* sp.) on 12 *Alexandrium* species was examined. Furthermore, the growth and ingestion rates of *P. kofoidii* on *A. minutum* CCMP 1888 (previously *A. lusitanicum*), *A. minutum* CCMP 113, and *A. tamarensis* were measured as a function of prey concentration. The growth rates of *P. kofoidii* on the other *Alexandrium* species at single high prey concentrations were measured, at which the growth rates on *A. minutum* CCMP 1888 and *A. tamarensis* were saturated. Feeding occurrence by these predators on 12 *Alexandrium* species could be categorized into 6 different prey groups. Each *Alexandrium* species was consumed by at least one predator; however, there was no *Alexandrium* species that was eaten by all six predators. Cells of *A. minutum* CCMP 1888, *A. minutum* CCMP 113, and *A. tamarensis* were fed upon by four predators, but *A. affine* and *A. pacificum* by only one predator species, *P. kofoidii* or *Strombidinopsis* sp. Furthermore, *A. minutum* CCMP 1888 and *A. tamarensis* supported high growth rates of *P. kofoidii*, but the other *Alexandrium* species did not support, but rather inhibited *P. kofoidii* growth. With increasing prey concentrations, the growth and ingestion rates of *P. kofoidii* on *A. minutum* CCMP 1888 and *A. tamarensis* increased and became saturated, whereas those on *A. minutum* CCMP 113 continuously decreased. The maximum growth rates of *P. kofoidii* on *A. tamarensis* and *A. minutum* CCMP 1888 were 1.010 and 0.765 d⁻¹, respectively, and *P. kofoidii* maximum ingestion rates were 26.2 and 11.1 ng C predator⁻¹d⁻¹, respectively. In contrast, the growth rates of *P. kofoidii* on the other *Alexandrium* species at single high prey concentrations were almost zero (*A. pacificum*) or negative. Based on the feeding occurrence and growth and ingestion rates of predators on 12 *Alexandrium* species, it is suggested that common heterotrophic protistan predators respond differently to different *Alexandrium* species, and thus ecological niches of the *Alexandrium* species may be different from each other. These results may provide an insight into the roles of protistan predators in bloom dynamics of *Alexandrium* species.

1. Introduction

The species in the dinoflagellate genus *Alexandrium* occasionally form red tides or harmful algal blooms which cause human illness and large-scale mortality of fish and shellfish (Anderson, 1997; Cembella et al., 2000; Grattan et al., 2016). Some *Alexandrium* species produce paralytic shellfish poisoning (PSP) toxins or unidentified allelochemicals (Cembella et al., 2000; Ma et al., 2011; Anderson et al., 2012; Tillmann et al., 2016). These toxins are sometimes transferred to higher

trophic level organisms, where they are accumulated (Turner et al., 2005; Sephton et al., 2007). Thus, *Alexandrium* bloom dynamics are primary concerns for scientists, government officials, aquaculture farmers, and the public. Many countries monitor PSP toxins (Kudela et al., 2015; Penna et al., 2015; Davidson et al., 2016). To minimize damage owing to *Alexandrium* blooms, predicting the outbreak, persistence, and decline of the blooms is fundamental. To predict the bloom processes, the population dynamics of these species should be understood. To determine the population dynamics, initial

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concentrations of the species, growth rates, and mortality rates due to predation need to be assessed (Jeong et al., 2015).

The type species *A. minutum* was established in 1960 and since then 33 *Alexandrium* species have been established (Halim, 1960; Balech, 1989; Steidinger and Tangen, 1996; John et al., 2014; Lim et al., 2015). Although there have been many studies on the allelochemical effects of *Alexandrium* species on heterotrophic protists (Tillmann and John, 2002; Fistarol et al., 2004; Tillmann et al., 2007, 2008, 2016), there have been limited studies on feeding by heterotrophic protistan predators on *Alexandrium* species (Matsuoka et al., 2000; Kamiyama et al., 2005; Yoo et al., 2013b). Moreover, there have been limited studies on quantifying the growth and/or ingestion rates or grazing impacts of heterotrophic protistan predators on *Alexandrium* species (Balech, 1995; Kamiyama et al., 2005; Yoo et al., 2013b). A lack of data on these rates has limited the establishment of models for predicting *Alexandrium* bloom dynamics. So far, there have been only some *Alexandrium* species whose protistan predators have been discovered (Hansen, 1992; Matsuoka et al., 2000; Kamiyama et al., 2005; Yoo et al., 2013b); the heterotrophic dinoflagellate (HTD) *Gyrodinium moestrupii* is known to feed on *A. minutum* CCMP 113 and both toxic and non-toxic strains of *A. tamarensis* (Yoo et al., 2013b), the HTD *Gyrodinium spirale* feeds on *A. tamarensis* (Hansen, 1992), the HTD *Polykrikos kofoidii* on *A. tamarensis* and *A. affine* (Matsuoka et al., 2000), the mixotrophic dinoflagellate *Takayama helix* on *A. tamarensis* and *A. minutum* CCMP 1888 (= *A. lusitanicum*) (Jeong et al., 2016), and the tintinnid ciliates *Favella* spp. on *A. tamarensis* (Stoecker et al., 1981; Hansen, 1989; Kamiyama et al., 2005). In general, the grazing impact by heterotrophic protistan predators on red-tide dinoflagellates is much greater than that by metazoan predators (Turner and Borkman, 2005; Kim et al., 2013; Yoo et al., 2013a; Lee et al., 2017; Lim et al., 2017). Thus, to understand the population dynamics of an *Alexandrium* species, the types of heterotrophic protistan predators that can feed on *Alexandrium* species and growth and ingestion rates of the heterotrophic protistan predators on the *Alexandrium* species need to be measured.

The HTDs *Gyrodinium dominans*, *Oblea rotunda*, *Oxyrrhis marina*, *Pfiesteria piscicida*, and *P. kofoidii* are common HTDs in many marine environments (Chomérat et al., 2004; Watts et al., 2010; Tillmann and Hoppenrath, 2013; Yoo et al., 2013a). In addition, naked ciliates, *Strombidinopsis* spp., are also common in diverse marine environments (Doherty et al., 2007; Xu et al., 2013), and have been found to grow well on suitable prey (Strom and Buskey, 1993; Jeong et al., 2010; Roberts et al., 2010), and can sometimes control prey populations with high grazing coefficients in natural environments (e.g., Yoo et al., 2013a). Thus, whether any of these protistan predators can feed on *Alexandrium* species may be critical in prey population dynamics. These five HTDs have diverse sizes, shapes, and feeding mechanisms (e.g., Hansen and Calado, 1999), and can feed on a wide range of diverse algal prey items, including *Alexandrium* species.

In this study, feeding by these five common heterotrophic dinoflagellates and the naked ciliate on each of the 12 *Alexandrium* species [*A. affine*, *A. andersonii*, *A. catenella*, *A. fraterculus*, *A. insuetum*, *A. margalefii*, *A. mediterraneum*, *A. minutum* CCMP 113, *A. minutum* CCMP 1888, *A. pacificum*, *A. tamarensis*, and *A. tamutum*] was examined. Furthermore, the growth and ingestion rates of *P. kofoidii* on *A. minutum* CCMP 113, *A. minutum* CCMP 1888, and *A. tamarensis* were measured as a function of prey concentration, and the growth rates of *P. kofoidii* on the other *Alexandrium* species were also measured at single high prey concentrations at which the rates on *A. minutum* CCMP 1888 and *A. tamarensis* were saturated. The largest dinoflagellate predator, *P. kofoidii*, was selected because theoretically it is large enough to engulf all the *Alexandrium* species, and thus, prey size may not affect its feeding. The results of the present study provided a basis for understanding the interactions between *Alexandrium* species and common heterotrophic protists and the roles of protistan predators in bloom dynamics of *Alexandrium* species.

2. Materials and methods

2.1. Preparation of experimental organisms

Cells of *A. affine*, *A. andersonii*, *A. catenella*, *A. fraterculus* and *A. tamutum* were isolated from Korean coastal waters and then clonal cultures were established using two serial single isolations (Table 1). Cultures of the other *Alexandrium* species used in this study were obtained from the National Center for Marine Algae and Microbiota (NCMA), USA and Cawthron Institute Culture Collection of Micro-algae (CICCM), New Zealand (Table 1). All cultures were maintained in 500 ml polycarbonate (PC) bottles containing f/2-Si or L1-Si medium (Guillard and Rytter, 1962; Guillard and Hargraves, 1993) placed on the shelf at 20 °C under illumination of 20 $\mu\text{E m}^{-2} \text{s}^{-1}$ provided by cool-white fluorescent light in a 14 h:10 h light/dark cycle. The carbon content of each *Alexandrium* species was estimated from the cell volume according to Strathmann (1967).

For the isolation and culture of the HTDs *G. dominans*, *O. rotunda*, *O. marina*, and *P. kofoidii*, plankton samples were collected using water samplers from Korean coastal waters during 2001–2016 (Table 2). A clonal culture of each species was also established by two serial single-cell isolations. The culture of *P. piscicida* was obtained from NCMA. Moreover, for the isolation and culture of the ciliate *Strombidinopsis* sp. (ca. 90 μm in cell length), plankton samples were collected using a 10- μm mesh net from the waters of Masan Bay, Korea, in January 2018, when the water temperature and salinity were 5.6 °C and 33.0, respectively (Table 2). The cell volumes of the predators were estimated using the methods of Kim and Jeong (2004) for *G. dominans*, Ok et al. (2017) for *O. rotunda*, Jeong et al.

Table 1

Conditions for the isolation and maintenance of 12 *Alexandrium* species, the potential prey provided. ESD, equivalent spherical diameter (μm); T, temperature (°C); S, salinity; TC, toxicity.

Organisms	Strain name	ESD	Location	Time	T	S	TC
<i>Alexandrium andersonii</i>	AJH1505	14.9	Jinhae, Korea	May 2015	22.0	32.2	
<i>Alexandrium minutum</i> A (= <i>A. lusitanicum</i>)	CCMP1888	20.4	Laguna Obidos, Portugal				O ^[1]
<i>Alexandrium minutum</i> B	CCMP113	20.5	Ria de vigo, Spain	Sep 1987			O ^[1]
<i>Alexandrium tamutum</i>	ATSH1609	22.5	Shiwha, Korea	Sep 2016	25.9	32.6	
<i>Alexandrium insuetum</i>	CCMP2082	26.8	Uchiumi Bay, Japan	Jun 1985			X ^[1]
<i>Alexandrium catenella</i>	ACBS1309	30.0	Busan, Korea	Sep 2013	24.7	26.4	
<i>Alexandrium margalefii</i>	CAWD10	30.0	Bream Bay, New Zealand	1993			X ^[2]
<i>Alexandrium pacificum</i>	CCMP3434	30.3	Port Phillip Bay, Australia	Mar 1988			O ^[3]
<i>Alexandrium tamarensis</i>	CCMP1493	31.2	Bay west of Hong Kong Island	Jan 1991			O ^[1]
<i>Alexandrium affine</i>	AATA1308	31.4	Taeon, Korea	Aug 2013	21.5	32.2	
<i>Alexandrium fraterculus</i>	AFYS1309	32.3	Yeosu, Korea	Sep 2013	23.4	32.8	
<i>Alexandrium mediterraneum</i>	CCMP3433	33.0	Gulf of Naples, Italy	Jul 1999			X ^[3]

[1] Orr et al. (2011), [2] Mackenzie, (2004) [3] John et al. (2014).

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