



Mixotrophy in the newly described dinoflagellate *Alexandrium pohangense*: A specialist for feeding on the fast-swimming ichthyotoxic dinoflagellate *Cochlodinium polykrikoides*

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ABSTRACT

Newly described *Alexandrium pohangense* is a phototrophic dinoflagellate, and its trophic mode should be explored to understand its roles in marine ecosystems. To investigate feeding of *A. pohangense* and its ecological roles, its trophic mode, prey type, feeding mechanism, functional and numerical responses, and grazing impact were analyzed. Among diverse algal prey tested, it fed only on the fast swimming ichthyotoxic dinoflagellate *Cochlodinium polykrikoides*. *A. pohangense* ingested *C. polykrikoides* cells by engulfment, after immobilizing the prey cell using excreted materials. Thus, *A. pohangense* has an effective mechanism for feeding on fast-swimming prey through prey immobilization. With increasing mean prey concentrations, the specific growth and ingestion rates of *A. pohangense* increased rapidly before saturating at *C. polykrikoides* concentrations of 138 ng C ml⁻¹ (197 cells ml⁻¹) and 99 ng C ml⁻¹ (141 cells ml⁻¹), respectively. The maximum growth rate of *A. pohangense* fed with *C. polykrikoides* was 0.487 d⁻¹, while the growth rate of *A. pohangense* without added *C. polykrikoides* was 0.091 d⁻¹. The maximum ingestion rate of *A. pohangense* on *C. polykrikoides* was 4.99 ng C predator⁻¹ d⁻¹ (7.1 cells predator⁻¹ d⁻¹). The grazing coefficients attributable to *A. pohangense* on co-occurring *C. polykrikoides*, calculated by combining field data on abundance with the ingestion rates obtained in the present study, were 0.09–1.57 d⁻¹, which indicates that *A. pohangense* could have a considerable grazing impact on *C. polykrikoides* populations.

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1. Introduction

Trophic modes (i.e., exclusively autotrophic, mixotrophic, and heterotrophic) in dinoflagellates are important to understand their ecological roles in marine ecosystems (e.g., Jeong et al., 2010a). In the last two decades, many phototrophic dinoflagellates have been revealed as mixotrophic (Bockstahler and Coats, 1993; Jacobson and Anderson, 1996; Stoecker, 1999; Li et al., 2000; Skovgaard et al., 2000; Park et al., 2006; Berge et al., 2008; Burkholder et al., 2008; Jeong et al., 2010a, 2012; Kang et al., 2011). Mixotrophic dinoflagellates play diverse roles in food webs (Jeong et al., 1999a, 2010a; Glibert et al., 2009; Hansen, 2011; Sanders, 2011; Seong and Jeong, 2011); they are able to feed on diverse prey items such

as bacteria, algae, heterotrophic protists, and metazoans (for examples, see Jeong et al., 2010a). In turn, they serve as prey for various predators (Jeong et al., 1999b, 2008, 2015). The mixotrophic abilities of some dinoflagellates contribute considerably to their growth, and to the formation of red-tide patches (Jeong et al., 2010a, 2015; Lee et al., 2014a). Therefore, the mixotrophic abilities of newly described phototrophic dinoflagellate species should be explored.

Several *Alexandrium* species are toxic (Cembella et al., 2002; Anderson et al., 2012; Yoo et al., 2013), producing diverse phycotoxins such as saxitoxins, goniotoxins, and spirolides (Anderson et al., 2012). Saxitoxins cause paralytic shellfish poisoning and are related to the formation of harmful algal blooms causing large-scale mortality of finfish and shellfish; they also cause diseases in humans (Hallegraeff, 1993; Cembella et al., 2002; Anderson et al., 2012). Moreover, some *Alexandrium* species secrete lytic compounds that kill other protists (Tillmann et al., 2007; Blossom et al., 2012). Therefore, the growth and distribution of *Alexandrium* species are critical factors for scientists, government

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officials, and the aquaculture industry. Approximately 30 *Alexandrium* species have been described so far, of which only five species (i.e., *A. minutum*, *A. tamarense*, *A. catenella*, *A. ostenfeldii*, and *A. pseudogonyaulax*) are known to be mixotrophic (Nygaard and Tobiesen, 1993; Jacobson and Anderson, 1996; Gribble et al., 2005; Jeong et al., 2005a,b; Yoo et al., 2009; Blossom et al., 2012). Therefore, to understand the ecological roles and the bloom dynamics of newly described *Alexandrium* species, it is necessary to investigate their mixotrophic ability.

Cochlodinium polykrikoides is a bloom-forming dinoflagellate found in the coastal waters of many countries (Jeong et al., 2008; Mulholland et al., 2009; Tang and Gobler, 2010; Park et al., 2013a). This dinoflagellate is known to kill fish in aqua-cages by clogging their gills using mucus, thus sometimes causing great losses in the aquaculture industry (Park et al., 2013b). Therefore, many countries spend considerable budgets to minimize the loss due to *C. polykrikoides*. Owing to these efforts, the mixotrophic ability, optimal temperature, salinity, light intensity, and interactions with competing species of *C. polykrikoides* have been well documented (Park et al., 2001; Jeong et al., 2004; Kim et al., 2004; Tang and Gobler, 2010; Gobler et al., 2012; Lim et al., 2014a). However, information on effective predators of this dinoflagellate is still lacking. The chain-forming *C. polykrikoides* is one of the fastest swimming phototrophic dinoflagellates and may not be easy for potential predators to capture (maximum swimming speed = $\sim 1450 \mu\text{m s}^{-1}$; Jeong et al., 1999a). Large ciliates, *Strombidinopsis* spp., are effective protistan predators of *C. polykrikoides* (Jeong et al., 1999b, 2008). To better understand *C. polykrikoides* bloom dynamics and harmful effects, its mortality rate due to predation should be explored.

Recently, *Alexandrium* sp. was isolated from the waters off Pohang, Korea, during a *Cochlodinium polykrikoides* red tide, and a clonal culture was established. Based on morphological and genetic analyses, it was revealed as a new species and described as *Alexandrium pohangense* (Lim et al., 2015a). In the present study using this culture, mixotrophic ability, prey type, and feeding mechanisms of this dinoflagellate were investigated. Additionally, the growth and ingestion rates of *A. pohangense* on *C. polykrikoides*, the only prey, as a function of prey concentration, were determined. Furthermore, grazing impact of *A. pohangense* on *C. polykrikoides* populations was estimated using data on the abundance of these two species in the field, and ingestion rates obtained in this study. The results of the present study provided a basis for understanding the interactions between *A. pohangense* and *C. polykrikoides* and their ecological roles in marine ecosystems.

2. Materials and methods

2.1. Preparation of experimental organisms

Phytoplankton species used in this study were grown at 20 °C in enriched f/2 seawater media (Guillard and Ryther, 1962) under continuous illumination of $100 \mu\text{E m}^{-2} \text{s}^{-1}$ provided by cool white fluorescent lights (Table 1). The mean equivalent spherical diameter (ESD) \pm standard deviation was measured using an electronic particle counter (Coulter Multisizer II, Coulter Corporation, Miami, FL, USA). The carbon content of phytoplankton was estimated from the cell volume according to Strathmann (1967).

Alexandrium pohangense was isolated from plankton samples collected from waters off Pohang, Korea, in September 2014, when the water temperature and salinity were 23.3 °C and 31.1, respectively (Lim et al., 2015a). Only cultures in the exponential growth phase were used.

Table 1

Taxa, size, and concentration of algal prey species offered to *Alexandrium pohangense*. Mean equivalent spherical diameter (ESD, μm) \pm standard deviation (SD) of the mean for algae were measured by an electronic particle counter (Coulter Multisizer II, Coulter Corporation, Miami, FL, USA). The numbers of counted cells were >2000 cells for each algal species. Y: Feeding by *A. pohangense*, N: Not fed on by *A. pohangense*, L: the prey cell was lysed with added *A. pohangense* cultures, I: the prey cells were immobilized with added *A. pohangense* cultures, T: Toxic, NT: non-toxic dinoflagellate. The initial concentration of *A. pohangense* was ca. 300 cell mL^{-1} .

Prey species	ESD (SD)	Initial prey concentration cell mL^{-1}	Effects	Feeding by <i>A. pohangense</i>
Diatom				
<i>Skeletonema costatum</i>	5.9 (1.1)	150,000	N	N
Prymnesiophytes				
<i>Isochrysis galbana</i>	4.8 (0.2)	150,000	I	N
Cryptophytes				
<i>Teleaulax</i> sp.	5.6 (1.5)	100,000	L	N
<i>Stoerataula major</i>	6.0 (1.7)	50,000	L	N
<i>Rhodomonas salina</i>	8.8 (1.5)	50,000	L	N
Rhaphidophytes				
<i>Heterosigma akashiwo</i>	11.5 (1.9)	30,000	I	N
Mixotrophic dinoflagellates				
<i>Heterocapsa rotundata</i> (T)	5.8 (0.4)	100,000	I	N
<i>Amphidinium carterae</i> (NT)	9.7 (1.6)	30,000	I	N
<i>Prorocentrum minimum</i> (T)	12.1 (2.5)	20,000	I	N
<i>Heterocapsa triquetra</i> (T)	15.0 (1.3)	30,000	I	N
<i>Gymnodinium aureolum</i> (NT)	19.5 (4.9)	3000	I	N
<i>Scrippsiella trochoidea</i> (T)	22.8 (2.7)	15,000	I	N
<i>Cochlodinium polykrikoides</i> (NT)	25.9 (2.9)	2000	I	Y
<i>Prorocentrum micans</i> (T)	26.6 (2.8)	3000	I	N
<i>Akashiwo sanguinea</i> (NT)	30.8 (3.5)	1000	I	N
<i>Gymnodinium catenatum</i> (T)	33.9 (1.6)	1000–3000	I	N
Naked ciliate				
<i>Mesodinium rubrum</i>	22 (0.04)	2000	L	N

2.2. Prey type

Experiment 1 was designed to investigate whether *Alexandrium pohangense* was able to feed on potential prey when unialgal diets of diverse microalgal species were provided (Table 1). The initial concentrations of each algal species were similar in terms of carbon biomass.

A dense culture of *Alexandrium pohangense* growing photosynthetically in f/2 media at 20 °C and under a 14:10 h light-dark (LD) cycle at $100 \mu\text{E m}^{-2} \text{s}^{-1}$ was transferred to a 2-L PC bottle containing f/2 medium. The culture was maintained in f/2 media for 2 d under the same conditions described above. Three 1-ml aliquots were then removed from the bottle and *A. pohangense* densities were determined using a compound light microscope.

To observe the ingestion of eukaryotic algal prey under a light microscope and/or an epifluorescence microscope, the target initial concentrations of *Alexandrium pohangense* and each algal prey species were established as described below (Table 1). Triplicate 42-ml PC experimental bottles and predator control bottles were set up for each target algal species. The bottles were filled to capacity with freshly filtered seawater, capped, and then placed on a shelf and incubated at 20 °C under a 14:10 h LD cycle of cool white fluorescent light at $100 \mu\text{E m}^{-2} \text{s}^{-1}$. After 6, 12, 24, and 48 h of incubation, a 5-ml aliquot was subsampled from each bottle. Two tenths to one ml aliquots of the subsample were placed on slides with cover glasses. The protoplasm of >200 *A. pohangense* cells was carefully examined using a light microscope and/or epifluorescence microscope at a magnification of 100–400 \times to

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