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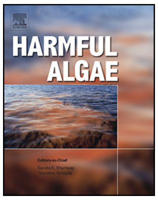

Feeding by the harmful phototrophic dinoflagellate *Takayama tasmanica* (Family Kareniaceae)

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ABSTRACT

The trophic mode of a phototrophic dinoflagellate is a critical factor in the dynamics of its harmful algal bloom. Recent discoveries of the mixotrophic capabilities of phototrophic dinoflagellates have changed the traditional view of bloom dynamics and prediction models. Here, mixotrophy in the harmful phototrophic dinoflagellate *Takayama tasmanica* was examined. Moreover, growth and ingestion rates of *T. tasmanica* on each of *Alexandrium minutum* CCMP1888 and *Alexandrium tamarense* CCMP1493, suitable prey, were determined as a function of prey concentration. This study reported for the first time that *T. tasmanica* is a mixotrophic species. Among the phytoplankton species offered as prey, *T. tasmanica* fed on all prey species whose equivalent spherical diameter (ESD) was greater than 30 μm, but also *A. minutum* whose ESD was 19 μm. In contrast, *T. tasmanica* did not feed on the phototrophic dinoflagellates *Heterocapsa triquetra*, *Gymnodinium aureolum*, *Scrippsiella acuminata* (previously *S. trochoidea*), *Cochlodinium polykrikoides*, *Alexandrium affine*, *Alexandrium insuetum*, and *Alexandrium pacificum* that its sister species *Takayama helix* is able to feed on. With increasing mean prey concentration, ingestion rates of *T. tasmanica* on *A. minutum* increased, but became saturated at the prey concentrations of >2130 cells mL^{-1} (1070 ng C mL^{-1}). The maximum ingestion rate (MIR) of *T. tasmanica* on *A. minutum* was 0.5 ng C $predator^{-1}$ d^{-1} (1.0 cells $predator^{-1}$ d^{-1}) which is only 64% of the body carbon of a *T. tasmanica* cell. Growth rates of *T. tasmanica* on *A. minutum* were not affected by prey concentrations. Thus, the low maximum ingestion rate is likely to be responsible for the small increases of its growth rate through mixotrophy. In addition, neither growth nor ingestion rates of *T. tasmanica* feeding on *Alexandrium tamarense* were affected by prey concentrations. The maximum ingestion rate of *T. tasmanica* on *A. minutum* was considerably lower than that of *T. helix* on the same prey species. Therefore, the mixotrophic ability of *T. tasmanica* is weaker than that of *T. helix*, and also *T. tasmanica* may have an ecological niche different from that of *T. helix* in marine ecosystems.

1. Introduction

Dinoflagellates are ubiquitous in marine ecosystems, and play diverse roles as primary producers, prey, and predators (Hansen, 2011; Berge et al., 2012; Stoecker et al., 2017). Many species can cause harmful algal blooms, which often result in economic losses, ecological disturbances, and even human illness (Smayda, 1997; Jeong et al., 2004; Jessup et al., 2009; Anderson et al., 2012; Park et al., 2013a,b). As such, research focusing on the physiological and ecological characteristics of dinoflagellates has increased dramatically in recent decades (Jeong et al., 2004, 2005a, 2010a; Moorthi et al., 2006; Lee et al., 2014a, 2017; Johnson, 2015; Menden-Deuer and Montalbano, 2015; Anderson and Menden-Deuer, 2017).

The trophic mode (i.e., autotrophic, heterotrophic, and mixotrophic) of a phototrophic dinoflagellate is a critical factor influencing the dynamics of harmful algal blooms. Over the past 30 years, many dinoflagellate species that were thought to be exclusively phototrophic have been shown to be mixotrophic (i.e., they have been observed to feed on live prey) (Stoecker et al., 1997; Li et al., 2000; Jeong et al., 2004, 2005b, c, 2010a, b, 2015; Seong et al., 2006; Burkholder et al., 2008; Zhang et al., 2013). The discovery of mixotrophism in phototrophic dinoflagellates has altered conventional perspectives of bloom dynamics and

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prediction models (Stoecker, 1998, 1999; Jeong et al., 2010a, 2015; Mitra and Flynn, 2010; Caron, 2016; Berge et al., 2017). Mixotrophic behavior improves the growth rates of some dinoflagellates, and reduces the abundance of potential competitors via reductions in prey populations (Stoecker et al., 1997; Li et al., 2000; Jeong et al., 2015). Moreover, some phototrophic dinoflagellates are in fact obligate mixotrophic species, because they do not grow in the absence of prey (Yoo et al., 2010; Lee et al., 2014b; Jang et al., 2017). Thus, it is necessary to examine mixotrophism in phototrophic dinoflagellates in order to more fully understand their ecological roles.

Seven species in the dinoflagellate genus *Takayama*, family Kareniaceae, have been reported since the genus was first established in 2003 (de Salas et al., 2003, 2008; Gu et al., 2013). Of these seven species, however, only the trophic mode of *Takayama helix* has been determined (Jeong et al., 2016). Blooms of several *Takayama* species, including *Takayama tasmanica*, are known to cause fish kills in the waters of many countries (Steidinger et al., 1998; de Salas et al., 2005). Thus, establishing the trophic modes of each *Takayama* species would be a critical step toward gaining a better understanding of the species' population dynamics and the outbreak of harmful algal blooms. To the best of our knowledge, of the *Takayama* species, only cultures of *T. tasmanica* and *T. helix* are currently available; as such, examining the mixotrophic ability of *T. tasmanica* and comparing the result to that of *T. helix* is possible. The morphology, chloroplast pigment, and large subunit (LSU) ribosomal (r) DNA sequences of *T. tasmanica* are considerably different from those of *T. helix* (de Salas et al., 2003); for instance, the cell size of *T. tasmanica* is smaller than that of *T. helix*; the shape of the apical groove on the epitheca, the shape and location of the nucleus, and the distribution of pyrenoids differ (de Salas et al., 2003); *T. tasmanica* has gyroxanthin-diester and gyroxanthin-like accessory pigments, which are absent in *T. helix* (de Salas et al., 2003); the sequence of LSU rDNA sequences differ by ca. 4% between the two species (de Salas et al., 2003); and finally, the species differ in their global distributions, in that *T. tasmanica* occurs in Australia, the Gulf of Mexico, China, and New Zealand, whereas *T. helix* occurs in Australia, Spain, South Africa, New Zealand, Japan, and Korea (de Salas et al., 2003; Mooney et al., 2009; Siano et al., 2009; Gu et al., 2013; McCarthy, 2013; our unpublished data).

In the present study, first, whether *Takayama tasmanica* (CAWD115) is mixotrophic or not was explored. Next, the kind of prey species that *T. tasmanica* is able to feed on and feeding mechanism were investigated. Furthermore, the growth and ingestion rates of *T. tasmanica* on the dinoflagellates *Alexandrium minutum* and *Alexandrium tamarense*, suitable prey, were determined as a function of prey concentration. Moreover, the results of these experiments on the mixotrophic ability of *T. tasmanica* were compared to those of *T. helix*. The results of this study provide a basis for better understanding the ecological roles of *T. tasmanica* in the marine planktonic community, and differences in mixotrophic activities among the species in the same genus.

2. Materials and methods

2.1. Preparation of experimental organisms

Diverse algal species that ranged widely in morphological and biochemical traits were provided as potential prey items (Table 1).

Table 1
Taxa, size, and concentration of algal prey species offered to *Takayama tasmanica*. Mean equivalent spherical diameter (ESD, µm) for algae. The initial concentrations of *T. tasmanica* were 500–2000 cells mL^{-1}. IPC: initial prey concentration (cell mL^{-1}); Y: consumed by *T. tasmanica*; N: Not consumed by *T. tasmanica*.

Prey species	ESD (µm)	IPC (cell mL^{-1})	Attack	Feeding occurrence
Diatom				
Skeletonema costatum	5.9	15,000	N	N
Prymnesiophyte				
Isochrysis galbana	4.8	150,000	N	N
Cryptophytes				
Teleaulax sp.	5.6	100,000	N	N
Storeatula major	6.0	15,000	N	N
Rhodomonas salina	8.8	50,000	N	N
Raphidophyte				
Heterosigma akashiwo	11.5	30,000	N	N
Phototrophic dinoflagellates				
Heterocapsa rotundata	5.8	9000	N	N
Amphidinium carterae	9.7	30,000	Y	N
Prorocentrum cordatum (= *P. minimum*)	12.1	15,000	N	N
Alexandrium andersonii	14.9	2000	N	N
Heterocapsa triquetra	15.0	10,000	N	N
Alexandrium minutum (CCMP113)	18.1	2500–7000	Y	N
Gymnodinium aureolum	19.5	3000	N	N
Alexandrium minutum (CCMP 1888, previously *A. lusitanicum*)	20.4	5000	Y	**Y**
Karenia mikimotoi (NIES 2411)	21.3	2000	Y	N
Scrippsiella acuminata (=*S. trochoidea*)	22.8	5000–8000	Y	N
Alexandrium affine	25.8	1000–3000	N	N
Cochlodinium polykrikoides	25.9	1000–2000	N	N
Alexandrium insuetum (CCMP2082)	26.4	3000–5000	N	N
Prorocentrum micans	26.6	2000–3000	N	N
Alexandrium pacificum (CCMP3434)	29.4	3000–5000	N	N
Coolia malayensis	30.4	2000	Y	**Y**
Akashiwo sanguinea	30.8	1000	Y	**Y**
Alexandrium tamarense (CCMP1493)	31.2	2000	Y	**Y**
Levanderina fissa (previously *Gymnodinium instriatum*)	31.2	200	Y	**Y**
Coolia canariensis	32.8	2000	Y	**Y**
Gymnodinium catenatum	33.9	1000	Y	**Y**
Lingulodinium polyedra	38.2	2000	Y	**Y**
Gambierdiscus caribaeus	67.4	100	Y	**Y**