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Feeding preferences and grazing rates of *Pfiesteria piscicida* and a cryptoperidiniopsoid preying on fish blood cells and algal prey

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Abstract

The grazing rates and feeding preferences of the dinoflagellates *Pfiesteria piscicida* and a cryptoperidiniopsoid on the alga *Rhodomonas* sp. and fish blood cells were calculated at different ratios of the two food types and at different total food densities. Data from 6 h grazing periods within microcosms were used to calculate grazing rates. Grazing rates of both dinoflagellates increased linearly with an increased ratio of blood cells to *Rhodomonas*, and *P. piscicida* had a higher maximum grazing rate than the cryptoperidiniopsoid. The grazing rate of *P. piscicida* on *Rhodomonas* also increased with increased *Rhodomonas* densities relative to the blood cells, but increased densities of *Rhodomonas* did not increase the grazing rate of the cryptoperidiniopsoid, suggesting a lower feeding threshold for this species. Both dinoflagellates demonstrated a preference for fish blood cells over *Rhodomonas* cells, with no significant difference in the index of preference between the two species. Total food abundance affected the degree of preference differently for each dinoflagellate species. A higher index of feeding preference was attained by *P. piscicida* when resource levels were high, while the cryptoperidiniopsoid did not show this response. A preference for fish blood cells occurred at all food ratios for both dinoflagellates, including when blood cells were scarce relative to the alternate food type (15% of total available food). These results suggest that these strains of *P. piscicida* and the cryptoperidiniopsoid share similar feeding preferences for the prey types tested, although cryptoperidiniopsoids have not been associated with fish kills.

Keywords: Cryptoperidiniopsoid; Feeding preference; Heterotrophic dinoflagellates; *Pfiesteria piscicida*

1. Introduction

Optimal foraging theory assumes that a predator will preferentially consume the resource which will maximize its fitness through maximum net energetic intake (MacArthur and Pianka, 1966; McNamara and Houston, 1985). Differences in resource availability will favor certain foraging behaviors (e.g. generalist, specialist and facultative). When a predator encounters changing levels of prey, a facultative strategy should provide maximal energy uptake (Glasser, 1984). Facultative predators would specialize on the most profitable food items when they are abundant, and expand their diet to less profitable prey when resources are scarce (Glasser, 1984). Feeding preference experiments of protists are relatively rare, although selective predation has been identified (Stoecker et al., 1981; Jacobson and Anderson, 1986; Šimek et al., 1995). Dinoflagellates have life histories with different stages that can respond to changing environmental situations (Rengefors and Anderson, 1998) and react to stimuli that include light, temperature, gravity, chemical and mechanical cues (Levandowsky and Kaneta, 1987; Cancellieri et al., 2001), making dinoflagellates a reasonable model to study a behavioral response to varying food resources.

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Due to toxin production and associated fish kills, *Pfiesteria piscicida* Steidinger et Burkholder and *Pfiesteria shumwayae* Glasgow et Burkholder (Marshall et al., 2006) have been studied extensively since their identification (Burkholder and Glasgow, 1997; Glasgow et al., 2001; Gordon et al., 2002; Vogelbein et al., 2002; Burkholder et al., 2005; Gordon and Dyer, 2005). Cryptoperidiniopsoids (Seaborn et al., 1999, 2001; Burkholder et al., 2001; Parrow and Burkholder, 2003) are closely related to *Pfiesteria* spp. based on morphological, ecological and genetic similarities (Marshall, 1999; Parrow and Burkholder, 2003; Seaborn et al., 2006). Both *P. piscicida* and cryptoperidiniopsoids feed by means of myzocytosis (Seaborn et al., 2001), a process where the predatory dinoflagellate inserts a feeding tube (peduncle) into the interior of the prey cell and ingests the cell contents (Schnepf and Deichgräber, 1984). *Pfiesteria* spp. and cryptoperidiniopsoids can feed on a diverse assemblage of algae (Seaborn et al., 2001), bacteria (Burkholder and Glasgow, 1995), finfish (Burkholder and Glasgow, 1997; Gordon et al., 2002), shellfish (Burkholder and Glasgow, 1997) and mammalian red blood cells (Glasgow et al., 2001).

In systems that include multiple omnivorous predators and multiple prey items, it is likely that competing predators have different feeding preferences both to maximize energy intake and avoid competitive exclusion. This may be the scenario with heterotrophic dinoflagellates, in particular *P. piscicida* and cryptoperidiniopsoid taxa due to the broad food selection available to these species. Previous studies to identify the optimal food source for these dinoflagellates relied on comparing growth curves (e.g. Seaborn et al., 1999) and did not measure food preference when given multiple food types. The objectives of this study were to determine whether a preference is shown by *P. piscicida* and a cryptoperidiniopsoid between fish blood cells and an algal food source, and if preference is influenced by the total and relative abundance of these resources.

2. Materials and methods

2.1. Culturing

The clone of *P. piscicida* used in this study was obtained from the Provasoli-Guillard National Center for Culture of Marine Phytoplankton (CCMP1834), West Boothbay Harbor, ME. A cryptoperidiniopsoid dinoflagellate (00DEQ029; with identical SSU rRNA sequence as that submitted to GenBank as cryptoperidiniopsoid sp. *brodyi* AF080097 by Litaker et al. (1999), and informally named as '*Cryptoperidiniopsis brodyi*', e.g. Litaker et al., 2000) was established from samples collected from Nomini Creek, a tributary of the Potomac River, VA, USA. These dinoflagellates were identified with scanning electron microscope analysis following the suture swelling technique of Glasgow et al. (2001). Real-time PCR analysis was used to verify their species identification and test for cross-contamination (Bowers et al., 2000).

The algal food source for the dinoflagellate cultures was the cryptophyte *Rhodomonas* sp. (CCMP 768). Cultures were grown in 200 ml Falcon tissue flasks using F/2-Si medium (Guillard, 1975) at 20 °C in a Precision incubator on a 12-h light:12-h dark cycle. The medium was made using filtered (0.2 μm pore size) Atlantic Ocean seawater diluted to 15 ppt. A 1 ml aliquot of *Rhodomonas* ($\sim 10^3$ cells ml^{-1}) was added to each flask at 2–3 day intervals, with media changes made monthly.

2.2. Prey preparation

The *Rhodomonas* sp. in the study was the same strain used in maintaining the dinoflagellate cultures. Fish blood cells were obtained from freshly caught Atlantic croaker (*Micropogonias undulatus*), George's Seafood, Norfolk, VA, USA. Fish blood cells were collected by dissecting the fish along the ventral section of the body and removing the internal organs. Blood was taken from the dorsal aorta with a syringe and filtered through a 100 μm aperture mesh. The blood was then mixed with F/2-Si medium at 9 ppt and diluted as necessary to obtain the desired cell density.

2.3. Grazing experiments

The grazing experiments consisted of seven food treatments, each with a different ratio of fish blood cells to *Rhodomonas* cells. Total prey density in each treatment was ~300 cells (Table 1). Additionally, one treatment consisted of equal densities of the two food types (1:1) with a total abundance of ~100 cells. Dinoflagellate densities were determined by light microscopy using a Palmer–Maloney chamber and reduced as needed by dilution with F/2-Si medium to obtain equal initial cell densities (100 cells $well^{-1}$) in all treatments. Dinoflagellates and food treatments were added to a Nunclon© Microwell cell culture plate by micropipetting. The volume of each well was brought to 150 μl using F/2-Si medium. There were three well replicates per treatment for each species and three controls that contained no dinoflagellates. Three