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Predation by a dinoflagellate on a red microalga with a cell wall modified by sulfate and nitrate starvation

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ABSTRACT: The dinoflagellate *Crypthecodinium cohnii* was found to prey specifically on the unicellular red alga *Porphyridium* sp. and to contain enzymes that degrade its cell wall. Cell wall production and composition of the alga are affected by nitrate and sulfate deprivation, the main changes being an increase in methylhexose and a decrease in glucose and xylose. When the dinoflagellate was fed with *Porphyridium* sp. having modified cell walls, fewer cells were ingested. Similarly, in chemosensory experiments it was found that the dinoflagellate was more attracted to the native polysaccharide than to polysaccharides extracted from deprived *Porphyridium* sp. Polysaccharide-degrading activity was higher when the dinoflagellate was fed with nondeprived algal cells than with deprived cells (82 to 86% and 45 to 53% reduction in viscosity, respectively). Although the dinoflagellate could not survive on polysaccharide alone, the induced enzymatic activity was similar irrespective of whether the polysaccharide was extracted from deprived or nondeprived cells. The results indicate that the process of predation is not linked to polysaccharide-degrading activity, which is affected by the cell-wall composition of the prey, i.e. algal cells.

KEY WORDS: *Crypthecodinium* · Dinoflagellate · *Porphyridium* · Rhodophyta · Sulfated polysaccharide · Cell wall · Starvation

INTRODUCTION

Heterotrophic microflagellates feed on a wide range of prey (Kimor 1979, Goldman et al. 1989). Some are selective, the selectivity being a function of size, structure, shape, or composition of the prey's cells and the morphology of the cytosome ('cell mouth') of the predator (Capriulo 1982, Lessard & Swift 1985, Andersson et al. 1986, Barlow et al. 1988). The phagocytic cell recognizes its prey before ingestion occurs. Recognition is manifested by cell-to-cell adhesion, which probably depends on the surface properties of the 2 cells. Ryter & De Chastellier (1983) proposed that during cellular recognition at least 3 properties of the cell surface must be considered: specific receptors, electrostatic charges, and hydrophobic properties. In many cases of phagocytic interaction, phagocytosis-specific molecules are indeed essential for adhesion and recognition (Wright & Silverstein 1986).

A heterotrophic dinoflagellate isolated by us from an outdoor cultivar of the red microalga *Porphyridium* sp. was originally thought to be *Gymnodinium* sp. (Ucko et al. 1989). It has, however, recently been identified as *Crypthecodinium cohnii*, a heterotrophic dinoflagellate that has been studied in some detail (Gold & Baren 1966, Hauser et al. 1975, Tuttle & Loeblich 1975, Beam & Himes 1982, 1987). This dinoflagellate was found to grow only on the cells of the red microalga *Porphyridium* sp., but not on other microalgae or on a medium alone (Ucko et al. 1989). We also found that the dinoflagellate contains enzymes that

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degrade the polysaccharide cell wall of *Porphyridium* sp. but not that of other red microalgae. The enzymatic activity of the dinoflagellate and the degradation products have previously been characterized (Simon et al. 1992, 1993).

The cells of the red microalgae are encapsulated within a sulfated polysaccharide (Ramus 1973). The polysaccharide is a sulfated heteropolymer made up of about 10 different sugars and a protein moiety (Geresh & Arad 1991).

It has previously been shown that nitrate and sulfate starvation affect the cell ultrastructure of the red microalgae (Köst et al. 1984, Wanner & Köst 1984). Nitrate starvation inhibits cell division and enhances cell wall polysaccharide production (Köst et al. 1984, Thepenier et al. 1985, Arad 1988, Arad et al. 1988). A similar response was found under sulfate starvation (Arad 1988, Arad et al. 1992). Cell recognition and adhesion events are known to be mediated by sulfated polysaccharides (Coombe et al. 1987).

The present study is based on the hypothesis that the dinoflagellate specifically recognizes the polysaccharide cell wall of its prey, the alga. Since nitrate and sulfate deprivation induce changes in the cell wall composition of *Porphyridium* sp. cells, we used these algae with altered cell walls to examine predation and growth in the dinoflagellate. The attraction between the dinoflagellate and algal polysaccharide was also studied.

MATERIALS AND METHODS

Organisms and growth conditions. *Porphyridium* sp. (UTEX 637) was grown in artificial seawater (ASW) according to Jones et al. (1963) in 1 l columns (6 cm in diameter) at 24 ± 1 °C. The cultures were illuminated continuously with fluorescent light lamps at an irradiance of 150 $\mu E\ m^{-2}\ s^{-1}$. The cultures were aerated with sterile air containing 3 to 4 % CO_2.

In the nitrogen starvation experiments, *Porphyridium* sp. cells were inoculated into nitrate-free ASW. Sulfate starvation was achieved by growing the algal cells 3 cycles prior to the experiment in ASW supplemented with $MgCl_2 \cdot 6H_2O$ (10.24 g l^{-1}) and Na_2SO_4 (0.0623 g l^{-1}) instead of $MgSO_4$.

The dinoflagellate (formerly reported to be *Gymnodinium* sp.) was isolated from outdoor ponds of *Porphyridium* sp. with a micropipette. Recently, the dinoflagellate was identified as *Crypthecodinium cohnii* by M. Elbrächter & E. Schnepf (pers. comm). Cultures of the dinoflagellate were maintained at 20 ± 1 °C in 3 l Erlenmeyer flasks containing 1.5 l of ASW supplemented with cells of *Porphyridium* sp. cultivated on ASW from the stationary phase of growth. For certain experiments the dinoflagellates were fed with *Porphyridium* sp. starved of nitrogen or sulfate (as described in the previous paragraph). The cultures were aerated with sterile air, and illumination was supplied from the side at an intensity of 50 $\mu E\ m^{-2}\ s^{-1}$. During the experiments the cultures were grown in 40 ml test tubes containing 5 ml of medium. Growth was followed by periodic monitoring of cell numbers with a light microscope by means of a hemocytometer. The movement of dinoflagellate cells was arrested with 4 % formaldehyde. Predation was measured by counting the number of algal cells in a *C. cohnii* cell with the aid of an epifluorescence microscope.

The effect of different treatments on the ingestion of *Porphyridium* sp. was analyzed by ANOVA and Duncan's multiple range test-SAS (Sokal & Rohlf 1969). Variance was tested for normality and homogeneity (Hartley's *F*-max test; Sokal & Rohlf 1969). (The critical level of significance for testing the hypothesis was $p < 0.005$.)

Chemosensory experiments. In order to maximize the motility and the chemosensory response of *C. cohnii* the dinoflagellate cells were starved by growing them in ASW 48 to 72 h before the experiment. In the chemosensory response assays, micropipettes (10 µl ± 0.25 % Brand Cat. No. 708709) were filled with the following polysaccharides (0.1 %) and then sealed with a tube sealer: *Porphyridium* sp. (native, starved of nitrate, or starved of sulfate); *Rhodella reticulata*; and carrageenan (Type J, The Copenhagen Pectin Factory Ltd, Denmark). The control was ASW. The chemosensory response assays were conducted as follows: starved dinoflagellates (1.5 to 2×10^4 cells ml^{-1}) were added to a plastic petri dish in which 15 or 16 micropipettes filled with the various polysaccharides had been placed. After 2 h at 20 ± 1 °C the number of dinoflagellates in the capillary tubes was determined by means of a hemocytometer. The chemosensory ratio was the number of dinoflagellates entering the polysaccharide-containing pipettes divided by the number of dinoflagellates entering the control (Verity 1988).

Dinoflagellate enzymatic extract. Dinoflagellate cultures (total of 2×10^8 cells), 14 h old, were centrifuged for 10 min at 11 000 × *g*. The pellet was suspended in 15 ml Tris-maleate buffer (0.1 M, pH 6.7), and the cells were broken by freezing in liquid nitrogen and thawing thereafter (5 times). The crude extract was centrifuged for 30 min at 18 000 × *g*, and the supernatant was used as the enzyme preparation.

Preparation of algal cell wall polysaccharides. Cultures of *Porphyridium* sp. grown in ASW or in ASW without nitrate or sulfate were centrifuged (20 min at 27 500 × *g*) to separate the cells from the growth medium containing the soluble fraction of the cell wall polysaccharide. The supernatant was dialyzed against doubly distilled water (until the conductivity of the

water reached 25 to 30 mΩ). The supernatant was then frozen and lyophilized.

Enzyme assay. Dinoflagellate enzymatic extract (2 ml) was added to 0.2% of polysaccharides (substrate) dissolved in 6 ml of Tris-maleate buffer (0.1 M, pH 6.7), supplemented with 0.1% sodium azide. The mixture was incubated at 30°C in a shaker bath for 24 h. Enzyme(s) activity was determined by measuring the decrease in viscosity of the solution by means of a Brookfield Digital Viscometer (spindle 18, sample volume 8 ml, speed 30 rpm).

GC analysis of sugar composition. The polysaccharides were hydrolyzed in 2 N trifluoroacetic acid for 2 h at 100°C, and derivatized to the corresponding alditol acetates. The monosaccharides were identified with a Varian GC equipped with a methylsilicon column (Supelco sp. 2100, 30 m, d = 0.25 µm) and a flame ionization detector (myoinositol was used as the internal standard; Albersheim et al. 1967).

RESULTS

The composition of polysaccharides extracted from *Porphyridium* sp. starved of nitrate and sulfate is shown in Table 1. The main differences were found in the amounts of 2,4-O-MeO-hexose, xylose, and glucose. Methylhexose increased from 1.3% in the native polysaccharide to >20%; xylose was reduced from 40.9 to ≤18%; and glucose was reduced from 14.5 to ≤8% in both nitrate and sulfate starvation. The best growth of the dinoflagellate was observed when it was fed with nondeprived *Porphyridium* sp. cells. The poorest growth was found for dinoflagellates fed with algal cells deprived of nitrate or sulfate before and during the experiment (Fig. 1). The ingestion by the dinoflagellate of nondeprived *Porphyridium* sp. (Table 2) was significantly different ($p < 0.005$) from that of deprived (of sulfate or nitrate) cells. This finding was particularly marked in the group containing 10 to 17 algal cells per dinoflagellate cell.

Table 1 Sugar composition of the *Porphyridium* sp. polysaccharide deprived of nitrate or sulfate. Data represent the % of each sugar of total sugars in each polysaccharide. Bold values indicate sugars with major differences in composition. Results are the average of 2 different batches of polysaccharide. Sugars were identified by GC according to the alditol acetate method (Albersheim et al. 1967). Carbohydrate content of the native polysaccharide was 67% and that of the nitrate- and sulfate-deprived polysaccharide was 77% and 67%, respectively

Sugar	Native polysaccharide	Polysaccharide from cultures deprived of: Nitrate	Sulfate
3-O-MeO-pentose	0.06	0.50	0.50
Rhamnose	0.49	3.20	3.04
Arabinose	0.52	1.7	1.30
Xylose	**40.9**	**9.8**	**18.07**
Mannose	10.01	0.40	6.19
Glucose	**14.5**	**4.20**	**8.14**
Galactose	23.8	40.75	29.7
2,4-O-MeO-hexose	**1.3**	**27.18**	**20.88**
Glucuronic acid	7.02	11.3	11.6
Methyl galactose	1.4	–	–

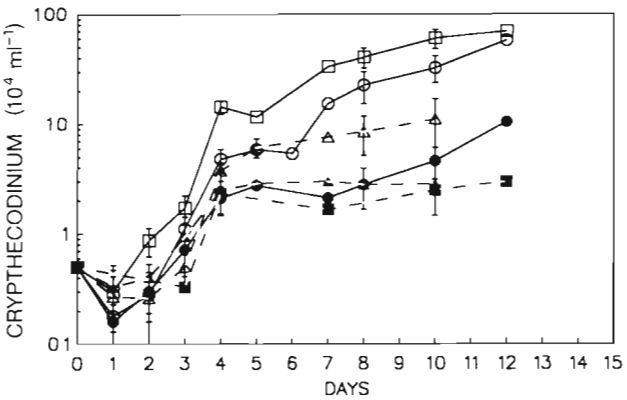

Fig. 1. Effect of nitrate or sulfate deprivation of *Porphyridium* sp. on the growth of dinoflagellate cells. Dinoflagellate cells (0.5×10^4 cells ml^{-1}) were inoculated into *Porphyridium* sp. cultures (3×10^6 cells ml^{-1}) that were: (□) grown on ASW before and during the experiment, (▲) starved of nitrate before and during the experiment, (△) starved of nitrate before but not during the experiment, (●) deprived of sulfate before and during the experiment, (○) starved of sulfate before but not during the experiment. (■) Dinoflagellate cells inoculated into a growth medium without algae. Bars = SE

The chemotactic response of the dinoflagellates to the native polysaccharide (55 to 30%) was greater than that to nitrate- or sulfate-deprived polysaccharides (Table 3). Polysaccharides from another species of red microalga *Rhodella reticulata* and from a red seaweed were also found to be less attractive than the native polysaccharide.

The enzymatic activities of the dinoflagellates in degrading the polysaccharide are shown in Table 4. The highest activities (82 to 86% decrease in viscosity) were observed in enzymes from dinoflagellate cells fed with algae cultivated in ASW, the source of the substrate — the polysaccharide — having almost no effect. However, when the dinoflagellates were fed with starved (of nitrate or sulfate) *Porphyridium* sp., their enzymatic activity was significantly lower (only 45 to 53% decrease in viscosity).

Addition of polysaccharide extracted from *Porphyridium* sp. to the dinoflagellate induced its enzymatic activities (results not shown). The source of the polysaccharide (native or deprived of nitrate or sulfate) did not affect the activity (92 to 97% decrease in viscosity after 14 h of growth).

Table 2. Effect of nitrate or sulfate starvation on ingestion of *Porphyridium* sp. cells by the dinoflagellate. Results are taken from Day 2 to 3 of growth. ASW: growth medium containing NO_3^- and SO_4^{2-}; $-SO_4^{2-}$: ASW without sulfate; $-NO_3^-$: ASW without nitrate

Growth medium for *Porphyridium*		No. of dinoflagellates counted[a]	% of dinoflagellates containing the following no. of algal cells				Statistical difference[b]
Before expt	During expt		0-1	2-5	6-9	10-17	
ASW	ASW	181	35	29	20	16	A
$-SO_4^{2-}$	ASW	75	35	45	16	4	B
$-SO_4^{2-}$	$-SO_4^{2-}$	91	67	27	5	0	B
$-NO_3^-$	ASW	53	53	22	11	13	B
$-NO_3^-$	$-NO_3^-$	67	88	9	1.5	1.5	B

[a]The number of dinoflagellate cells counted is considered as 100%
[b]Rows of values having the same letter are not significantly different from one another ($p < 0.005$)

Table 3. *Crypthecodinium cohnii*. Chemotactic response to various polysaccharides. In all cases 0.1% (w/v) of polysaccharides were used. The number of dinoflagellates in the pipet was determined after 2 h. Data are the means (± SD) of 3 different experiments; in each one 15 or 16 capillaries were used for each different polysaccharide. Chemosensory ratio: no. of dinoflagellate cells in capillary with attractant/no. of dinoflagellate cells in capillary filled with ASW

Attractant	No. of cells in pipets (± SD)	Chemosensory ratio (± SD)	Statistical difference[a]
ASW (control)	4088 ± 4088	-	D
Native *Porphyridium* polysaccharide	25166 ± 12500	5.7 ± 1.2	A
NO_3^--deprived *Porphyridium* polysaccharide	11722 ± 6222	2.6 ± 0.4	C
SO_4^{2-}-deprived *Porphyridium* polysaccharide	17461 ± 7333	4.1 ± 0.8	B
Rhodella reticulata polysaccharide	13288 ± 7833	3.7 ± 0.7	BC
Carrageenan	13016 ± 6722	2.7 ± 1.1	BC

[a]Rows of values having the same letter are not significantly different from one another ($p < 0.005$)

Table 4. Degradation of *Porphyridium* sp. polysaccharide by dinoflagellate enzymes. Dinoflagellates were fed with algae starved of nitrate or sulfate, and enzymatic activity was measured by changes in the viscosity. Carbohydrate percentages in the polysaccharide are as presented in Table 1

Enzyme source[a]	Source of polysaccharide substrate[b]	% decrease in viscosity[c]
-	ASW	10.5 ± 0.75
-	$-NO_3^-$	7.5 ± 0.5
-	$-SO_4^{2-}$	8.6 ± 3.2
ASW	ASW	84.5 ± 3.2
ASW	$-NO_3^-$	86.5 ± 8.5
ASW	$-SO_4^{2}$	82 ± 6
$-NO_3^-$	ASW	45.5 ± 1.5
$-NO_3^-$	$-NO_3^-$	51.5 ± 8.5
$-NO_3^-$	$-SO_4^{2-}$	48.5 ± 2.5
$-SO_4^{2-}$	ASW	46 ± 3
$-SO_4^{2-}$	$-NO_3^-$	53.5 ± 6.5
$-SO_4^{2-}$	$-SO_4^{2-}$	50.5 ± 4.5

[a]Enzymes extracted from dinoflagellates (after 14 h, 2×10^6 cells) fed with algae grown on ASW (ASW), ASW without sulfate ($-SO_4^{2-}$), or ASW without nitrate ($-NO_3^-$)
[b]Polysaccharides (0.2%) extracted from *Porphyridium* sp. grown on ASW (ASW), ASW without nitrate ($-NO_3^-$) or ASW without sulfate ($-SO_4^{2-}$)
[c]The decrease after 17 h of incubation versus the value at zero time

DISCUSSION

The inferior growth and predation of the dinoflagellate fed with starved algal cells (nitrate or sulfate) probably results from changes in the cell wall polysaccharide, e.g. in the sequence of the sugars or in the proteins that might affect its physical characteristics, such as charge. In addition to its effect on the algal cell wall, removal of nitrate or sulfate from the medium might also affect the ability of the dinoflagellate to ingest algal cells. Thus, nitrate or sulfate deprivation might have a specific effect on the dinoflagellate, such as on its mobility, that will in turn affect its predation ability. It is also possible that the different physiological conditions to which the algal cells were exposed during deprivation influenced some other characteristics of cell content and appearance. Indeed, Cowles et al. (1988) and Butler et al. (1989) showed that the physiological conditions of growing cells is a critical factor in the food detection/selection process of zooplankton.

It has previously been shown that nitrate and sulfate deprivation affects the production of the cell wall polysaccharide of *Porphyridium* sp. and its distribution between bound and dissolved fractions (Köst et al.

1984, Wanner & Köst 1984, Thepenier et al. 1985, Arad 1988, Arad et al. 1988). In this study we show for the first time that the sugar composition of the deprived polysaccharide was also modified. It is interesting to note that the pattern of change in cell wall composition was similar for nitrate and sulfate deprivation, the main changes being an increase in methylhexose accompanied by a decrease in glucose and xylose. We thus assume that the hexose in the methylhexose is glucose. This has to be further confirmed. It is likely that the protein in the cell wall was also modified, which in turn might affect the overall properties of the cell wall. Moreover, this change might be the main factor affecting the attraction to the algal cell.

The differences in the chemosensory responses of the dinoflagellate cells to the various polysaccharides support our hypothesis that the recognition between the predator and its prey is based on the cell wall composition of the prey. These results are also in accordance with the growth and predation experiments. *Crypthecodinium cohnii* has previously been shown to be attracted to a variety of chemical compounds, such as sugars and amino acids (Hauser et al. 1975, Spero 1985), and a more detailed study of the chemosensory attractants of our isolate of *C. cohnii* is under way.

The dinoflagellate enzymatic activity was measured in a crude extract preparation by measuring the changes in viscosity. The fact that we have used a crude preparation and the means we used to measure enzyme activity did not allow us to determine specific activity. We did, however, use identical numbers of cells in each enzymatic preparation so that the effect of starvation on growth of the dinoflagellates was not involved in this measurement.

We have previously shown (Ucko et al. 1989) that the dinoflagellate cannot grow solely on the polysaccharide extracted from *Porphyridium* sp. but requires whole algal cells. However, under these conditions polysaccharide-degrading activity is induced (Simon et al. 1992), even when the polysaccharides are modified by starvation. Thus, it seems to us that predation is not necessarily related to digestion, for which polysaccharide-degrading activity is essential.

The reason why the dinoflagellate ingests *Porphyridium* sp., i.e. whether the dinoflagellate requires the cell-wall polysaccharide or the intracellular matter, is becoming clearer Based on the results obtained here, it seems to us that the induction of polysaccharide-degrading enzymes enables the dinoflagellate to peel off the algal cell wall so that it can digest the intracellular matter. As a result, within the dinoflagellate cells there appeared protoplasts of *Porphyridium* sp. that had been ingested by the dinoflagellate cells. This preliminary observation has to be studied further.

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