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Behavioral components of feeding selectivity of the heterotrophic dinoflagellate *Protoperidinium pellucidum*

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ABSTRACT: *Protoperidinium pellucidum* is a pallium feeding heterotrophic dinoflagellate that captures phytoplankton cells individually and digests them externally. In laboratory cultures, *P. pellucidum* feeds on a variety of diatom species and a limited number of dinoflagellate species, and grows more rapidly on diatoms than dinoflagellates. When offered food in mixed assemblages, it feeds selectively on diatoms over dinoflagellates, and selects between diatom species. Selectivity between different diatom species does not appear to be related to size, and size alone does not explain the low selectivity for dinoflagellates. Computerized motion analysis studies of swimming behavior reveal that *P. pellucidum* appears to use chemoreception as the major sensory mode to detect and locate food. When *P. pellucidum* passes near a food cell it circles around the cell several times before attaching to the food particle, apparently using chemoreception to judge the location of the cell. Detailed behavioral observations reveal that *P. pellucidum* sometimes loses contact with motile dinoflagellate cells before the capture occurs; such losses were not observed with diatoms. In addition, motile dinoflagellate prey often escape after initial capture, their swimming behavior causing the capture filament to break before the cell can be engulfed by the pallium of *P. pellucidum*; loss of a diatom after attachment was extremely rare. Feeding selectivity may be explained in part by the nature of the chemosensory signals given off by different prey types, and therefore the distance at which *P. pellucidum* can detect food, and in part by the lower capture success of *P. pellucidum* with motile prey.

KEY WORDS: Heterotrophic dinoflagellates · Selective feeding · Behavior

INTRODUCTION

Heterotrophic dinoflagellates are an important component of the marine microzooplankton, often approaching or exceeding the abundance of planktonic ciliates (Burkill et al. 1993, Verity et al. 1993), and they have been shown to be important grazers of diatoms (Hansen 1991, Tiselius & Kuylenstierna 1996). Due to morphological constraints (2 flagella compared to the numerous cilia of ciliates), heterotrophic dinoflagellates do not feed by filtering small particles from the water as some ciliates do (Fenchel 1986); instead they capture individual phytoplankton cells, sometimes nearly as large or larger than themselves, and either engulf the entire cell or transfer body fluids of the captured cell into themselves by way of a pallium or a peduncle (Gaines & Elbrächter 1987). *Protoperidinium pellucidum*, the subject of this study, is a pallium feeder, and captures and digests single phytoplankton cells (or chains of cells) externally (Jacobson & Anderson 1986).

Since larger phytoplankton cells are often less abundant than smaller-sized cells, heterotrophic dinoflagellates may not rely on random encounter with suitable food cells and therefore need some sensory modality to help them locate individual food particles. After passing near a potential food item, the *Protoperidinium* spp. circles around the food several times, usually without contacting the cell (Jacobson & Anderson 1986). This behavior suggests that chemoreception is used to recognize and locate a potential food item. Sev-

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eral previous studies have demonstrated the role of chemoreception in the feeding behavior of heterotrophic dinoflagellates (Hauser et al. 1975, Spero 1985) and other protozoans (Levandowsky et al. 1984, Verity 1988). Pallium feeding dinoflagellates of the genus *Protoperidinium* have been previously shown to feed mainly on diatoms and dinoflagellates (Jacobson & Anderson 1986, Hansen 1991, Buskey et al. 1994, Jeong & Latz 1994). Although there have been some studies of selective feeding in marine protozoans (e.g. Stoecker et al. 1981, Verity 1991), there has been little direct study of selective feeding in heterotrophic dinoflagellates, other than that based on prey size (Hansen 1992).

Although the trophic interaction between a pallium feeding heterotrophic dinoflagellate and a phytoplankton cell is most accurately described as a grazing interaction, since these grazers capture and consume their prey as individual targets (single cells or chains of cells), it can be constructive to examine this interaction in the context of a predator-prey interaction. Using the 'components of predation' framework of C. S. Holling (1959a, 1966), the behavioral components of this feeding interaction can be considered to include encounter, capture and ingestion. Since all aspects of this interaction can be easily observed and videotaped for more quantitative analysis with pallium feeders, it makes them excellent subjects for examining the behavioral components of selective feeding in marine protozoans. In the present study, the selective feeding of the pallium feeding heterotrophic dinoflagellate *Protoperidinium pellucidum* is investigated, and the behavioral components that affect selective feeding behavior are quantified.

MATERIALS AND METHODS

Plankton tows for culture of heterotrophic dinoflagellates were collected on the RV 'Gyre' during a LATEX (Louisiana-Texas Shelf Circulation Program) cruise in the Gulf of Mexico in May 1994. A 20 cm diameter, 20 µm mesh plankton net was gently pulled through the surface waters while the ship was on station (27° 23' N, 95° 37' W). Aliquots from these tows were then placed in 1 l polycarbonate centrifuge bottles filled with filtered seawater and enriched with a mixture of cultured diatoms and autotrophic dinoflagellates (*Ditylum brightwellii* and *Prorocentrum micans*). These bottles were then placed in a deck incubator and kept at ambient surface temperature with a flow of surface seawater until the ship returned to shore. The heterotrophic dinoflagellate *Protoperidinium pellucidum* was isolated from an enrichment and brought into culture using these same phytoplankton species as food with the addition of *Thalassiosira* sp. 1 and *Gonyaulax polyedra*.

Cultures of *Protoperidinium pellucidum* were maintained in 60 ml tissue culture flasks or 250 ml polycarbonate bottles in sterilized ciliate medium (Gifford 1985). Cultures were rotated within a translucent white PVC cylinder on a bottle roller at ca 2 rpm. Temperature was maintained at 20°C and cultures were held in subdued light (ca 1 µmol photons m^{-2} s^{-1}) on a 12 h light:12 h dark cycle. Phytoplankton species used as food in these studies were cultured using f/2 medium (Guillard & Ryther 1962), although silicate was omitted from the cultures of dinoflagellates. Phytoplankton were grown in polycarbonate 250 ml Erlenmeyer flasks at 20°C on a 12 h light:12 h dark cycle at ca 120 µmol photons m^{-2} s^{-1}. Only actively growing phytoplankton cultures (based on date of transfer) were used. Phytoplankton cells for elemental analysis were filtered onto precombusted GF/F filters, dried at 50°C, and combusted in a Carlo-Erba EA 1108 elemental analyzer.

Specific growth rate was measured by adding ca 3 *Protoperidinium pellucidum* per ml to 150 ml of ciliate culture medium in a 250 ml polycarbonate bottle and adding *Ditylum brightwellii*, *Thalassiosira* sp. 1, *Gonyaulax polyedra* or *Prorocentrum micans* at a range of food concentrations. A single bottle was inoculated at each food concentration, and the cultures were held at the same conditions as described above throughout the experiment. Triplicate 10 ml samples were taken from each bottle at the same time daily over a 4 d period, preserved with 6 drops of 10% glutaraldehyde and stained with 3 drops of a 10 g l^{-1} calcofluor solution and filtered onto 0.4 µm pore size polycarbonate filters. Slides were stored frozen in the dark until enumeration (usually only a few days). Specific growth rates were calculated as the slope of the linear portion of ln(*P. pellucidum* ml^{-1}) regressed against time.

Grazing rate estimates and functional response curves were made for 2 food items: *Ditylum brightwellii* which supported higher maximum growth rates and *Prorocentrum micans* which supported lower maximum growth rates. A similar approach to that used with growth rate determination was employed, except that higher concentrations of *Protoperidinium pellucidum* were used at higher food concentrations or with food species for which *P. pellucidum* exhibited a lower feeding rate (*P. micans*) and controls containing phytoplankton without grazers were also prepared for each food concentration. Grazing experiments were run for 24 h, and triplicate 10 ml samples were taken at the beginning and end of each experiment. Grazer and food cell counts were determined microscopically using the blue fluorescence of the calcofluor-stained dinoflagellates and the red autoflourescence of their phytoplankton food. Ingestion and clearance rates were determined using the equations of Heinbokel (1978).

Selective feeding experiments were conducted in polystyrene tissue culture plates with a total volume of ca 16 ml per well. Approximately 10 ml of ciliate culture media were added to each well and then 150 *Protoperidinium pellucidum* were transferred from cultures by pipet. The appropriate volume of phytoplankton culture was then added to result in the desired cell concentration. In the first experiment, 500 cells ml^{-1} of each of 4 food choices was used: *Ditylum brightwellii*, *Thalassiosira* sp. 1, *Prorocentrum micans* and *Gonyaulax polyedra*. Other experiments included 50 cells ml^{-1} of each of the same 4 phytoplankton cultures, 500 cells ml^{-1} of each of the 2 dinoflagellate species (*P. micans* and *G. polyedra*) and 100 cell ml^{-1} of each of 4 diatom species (*D. brightwellii*, *Thalassiosira* spp. 1 and 2, and *Biddulphia* sp.). The feeding behavior of the *P. pellucidum* was then observed under a stereomicroscope. The first 50 grazers seen dragging food cells were then picked out and their food choices noted. This procedure was repeated 12 times for each experimental condition.

The swimming behavior of *Protoperidinium pellucidum* was recorded on a video cassette recorder for dinoflagellates in clear plastic tissue culture flasks (60 ml volume) or clear plastic spectrophotometry cuvettes (4 ml volume) using a Cohu model 3315 monochrome CCD video camera mounted on an Olympus SH stereo microscope at 40× magnification. Images were recorded using dark field illumination to enhance contrast. Swimming behavior of *P. pellucidum* was quantified from videotapes using an Expertvision Cell-Trak video-computer motion analysis system. Videotaped images of the dinoflagellates were digitized using the Motion Analysis VP-110 video-to-digital processor, and digitized outlines of the dinoflagellates were sent to a host computer at a rate of 15 frames per second. These digitized images were processed to calculate the swimming speeds (mm s^{-1}) and the rate of change of direction (degrees s^{-1}) of the dinoflagellates' paths of travel (Buskey 1984).

A set of preliminary experiments to examine the behavioral responses of *Protoperidinium pellucidum* to sensory stimuli associated with the presence of food were performed on cells removed from actively growing and feeding cultures, and quite variable results were achieved. Since a short period of starvation might make these cells more receptive to stimuli associated with food, an experiment was performed to examine the effects of starvation on their swimming behavior. Three 50 ml tissue culture flasks were filled with filtered ciliate media and *P. pellucidum* were added at densities of approximately 10 ml^{-1}; the flasks were filmed 2 h after transfer, and after 24, 48, 72 and 96 h of starvation. Each flask was filmed for 10 min each day.

The chemosensory and mechanosensory responses of *Protoperidinium pellucidum* to its diatom prey *Ditylum brightwellii* was examined using an approach similar to that used by Buskey & Stoecker (1989) to examine the behavioral responses to the tintinnid *Favella* sp. to its phytoplankton prey. Ten replicate groups of 150 *P. pellucidum* were placed in 4 ml plastic spectrophotometry cuvettes with 3 ml of ciliate media, and were starved for ca 20 h. Each cuvette was then videotaped for 5 min. Then 1 ml of fresh filtrate from an actively growing *D. brightwellii* culture (filtered through a GF/F filter in a syringe holder) was added, and each cuvette was videotaped for an additional 5 min. Similar experiments were run to test the response of *P. pellucidum* to the presence of a 10^{-3} M solution of the amino acid glycine. To test the response of *P. pellucidum* to mechanosensory signals associated with its diatom food, behavioral responses to inert polystyrene beads (44 µm diameter) at a concentration of 500 beads ml^{-1} were recorded.

In order to estimate the distance at which *Protoperidinium pellucidum* can recognize a potential food particle, we videotaped as many initial encounters between *P. pellucidum* and its food as possible. A few *P. pellucidum* were placed in a 4 ml clear plastic spectrophotometry cuvette containing a suspension of a single species of phytoplankton, and the behavior of a single *P. pellucidum* was observed by moving the cuvette on the stage and adjusting the focus to keep the grazer in view. When a grazing interaction was observed, its location on the tape was noted for later analysis. When a *P. pellucidum* was swimming around a food cell before attaching to it, the maximum distance the *P. pellucidum* could move away from the cell without losing it was measured through frame-by-frame image analysis of the feeding encounter, using Bioscan Optimas image analysis software. Only interactions where a minimum of 5 orbits around the food cell were observed were included in the analysis.

The time required for *Protoperidinium pellucidum* to feed on a single cell of phytoplankton (*Ditylum brightwellii*, *Thalassiosira* sp. 1, *Gonyaulax polyedra* or *Prorocentrum micans*) was determined by direct observation under a stereomicroscope. A few *P. pellucidum* were placed in a petri dish with a suspension of a single species of phytoplankton. When *P. pellucidum* was observed to attach to a food cell, it was gently transferred to a cell well of a tissue culture plate and the time of capture was recorded. The feeding process was observed until *P. pellucidum* had dropped the remains of the food particle. A total of 50 feeding events were timed for each phytoplankton food species. A similar set of observations were made to determine the proportion of cells that were successfully captured. If a *P. pellucidum* attached to a phytoplankton cell, began

towing it around and then lost it within a few seconds of capture, this event was scored as an 'escape'. If a *P. pellucidum* swam around a cell with a characteristic pre-feeding motion but lost contact with the cell before attachment, this interaction was scored as a 'lost contact'. A minimum of 100 feeding interactions were observed between *P. pellucidum* and each of the following foods: *D. brightwellii*, *Thalassiosira* sp. 1, *G. polyedra* and *P. micans*.

RESULTS

Cultures of *Protoperidinium pellucidum* actively grew when fed any of the diatom species offered in this study (Table 1). However, *P. pellucidum* would only feed and grow on 2 of the species of autotrophic dinoflagellates offered as food, *Gonyaulax polyedra* and *Prorocentrum micans*, and would not feed or grow on any of the other phytoplankton species used (Table 1). Of the foods found to support growth, 2 diatom species that supported good growth, *Ditylum brightwellii* and *Thalassiosira* sp. 1, and the 2 dinoflagellate species that supported growth, *G. polyedra* and *P. micans*, were selected for additional studies. These

Table 1 Foods fed to *Protoperidinium pellucidum* to test for consumption and growth. (+) *P. pellucidum* grew when fed this species, (–) no growth was observed. The volume of a *P. pellucidum* cell is approximately 24600 µm³

Food type	Growth	Approx. volume (µm³)
Diatoms		
Biddulphia sp.	+	6220
Corethron criophilum	+	7890
Ditylum brightwellii	+	9690
Nitzschia sp.	+	2860
Skeletonema sp.[a]	+	200
Thalassiosira sp. 1	+	1850
Thalassiosira sp. 2	+	3613
Dinoflagellates		
Gyrodinium dorsum	–	30560
Gonyaulax polyedra	+	17040
Gymnodinium simplex	–	240
Gymnodinium sp.	–	440
Heterocapsa niei	–	1250
Heterocapsa pygmaea	–	560
Prorocentrum micans	+	18350
Prorocentrum minimum	–	1530
Others		
Cryptomonas sp.	–	300
Dunaliella tertiolecta	–	120
Emiliana huxleyi	–	40
Isochrysis galbana	–	70
Pyrenomonas salina	–	210

[a]Forms chains up to 145 µm in length in culture; this volume is for a single cell

are the 4 food species that *P. pellucidum* had been grown on in culture since it was first isolated. CHN analysis of samples of the 4 phytoplankton foods used in the study revealed that *G. polyedra* had the largest biomass with 5024.6 ± 363.7 pg C cell^{-1}, followed by *P. micans* with 2308.5 ± 337.8 pg C cell^{-1}, *D. brightwellii* with 614.9 ± 30.9 pg C cell^{-1} and *Thalassiosira* sp. 1 with 223.2 ± 13.1 pg C cell^{-1}. The C:N ratio was greatest for the *Thalassiosira* sp. 1 cultures at 6.83 ± 0.09, followed by *G. polyedra* (6.68 ± 0.05), *P. micans* (6.50 ± 0.09) and *D. brightwellii* (6.01 ± 0.16). The cell volume of *P. pellucidum* was estimated to be 24600 µm³. This would yield an estimated biomass of 3444 pg C cell^{-1} using a carbon:cell volume ratio of 0.14 pg C µm^{-3} (measured for *Oblea rotunda* by Lessard, cited in Strom & Buskey 1993).

Protoperidinium pellucidum exhibited higher maximum specific growth rates on diets of the diatoms *Ditylum brightwellii* or *Thalassiosira* sp. 1 than on either of the dinoflagellate diets (Fig. 1). For both diatoms diets, maximum specific growth rates of ca 0.7 d^{-1} were achieved at food concentrations above 250 µg C l^{-1}. When offered diets of either *Gonyaulax polyedra* or *Prorocentrum micans*, maximum specific growth rates of only ca 0.4 d^{-1} were achieved at much higher food concentrations (above 750 µg C l^{-1}). *P. pellucidum* showed higher maximum ingestion rates on *D. brightwellii* than on *P. micans*, both in terms of cells consumed ind.$^{-1}$ h^{-1} and in terms of ng C ingested ind.$^{-1}$ h^{-1} (Fig. 2). *P. pellucidum* had a maximum ingestion rate for *D. brightwellii* of 0.48 ng C ind.$^{-1}$ h^{-1} (0.78 cells h^{-1}) at food concentrations above 350 µg C l^{-1}, but for *P. micans* the maximum ingestion rate was only 0.32 ng C ind.$^{-1}$ h^{-1} (0.14 cells h^{-1}) at food concentrations above 850 µg C l^{-1}.

When *Protoperidinium pellucidum* was allowed to choose between *Ditylum brightwellii*, *Thalassiosira* sp. 1, *Gonyaulax polyedra* or *Prorocentrum micans* at concentrations of 500 cells ml^{-1} of each food (2000 cells ml^{-1} total phytoplankton concentration), *P. pellucidum* showed a very strong preference for *D. brightwellii*, which was chosen 88% of the time (Fig. 3). *Thalassiosira* sp. 1 was chosen 8% of the time while *G. polyedra* was only chosen 1.3% of the time and *P. micans* only 2.7% of the time. When concentration of the 4 food species were lowered to 50 cells ml^{-1} of each food (200 cells ml^{-1} total), strong preference was still shown for diatoms, but *D. brightwellii* was chosen only 66.8% of the time. The number of times *Thalassiosira* sp. 1 was chosen increased to 27.8%, but the number of times dinoflagellate prey was chosen remained low at 2.7% for *G. polyedra* and 2.7% for *P. micans*. When concentrations of the 4 food species were lowered to 10 cells ml^{-1} of each food, too few feeding interactions were observed to complete the experiment. When *P.*

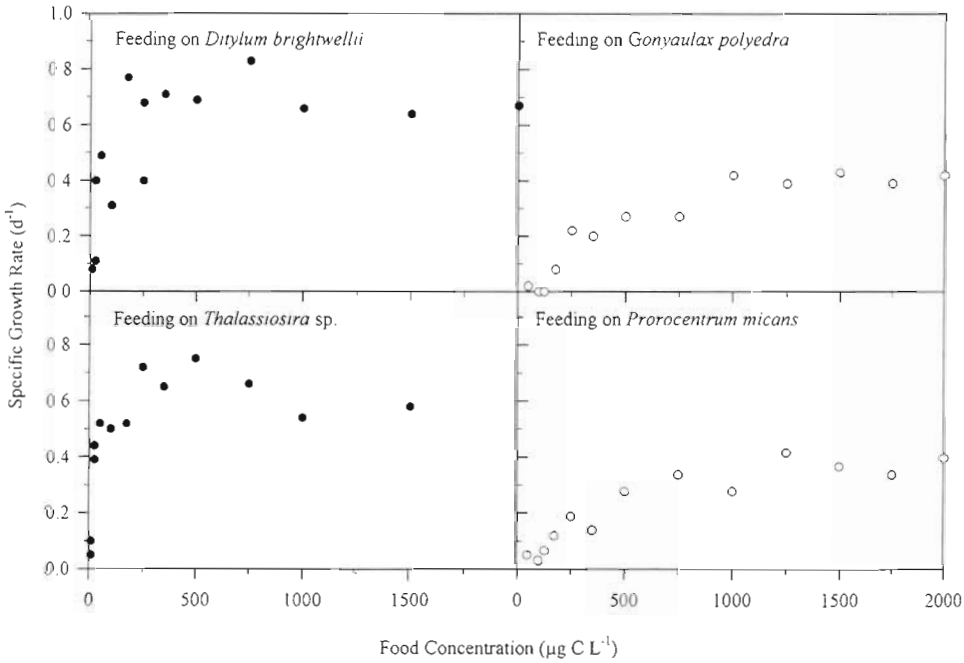

Fig. 1 *Protoperidinium pellucidum*. Specific growth rate as a function of mean food concentration over a 4 d experiment. Food species used were *Ditylum brightwellii*, *Thalassiosira* sp. 1, *Gonyaulax polyedra* and *Prorocentrum micans*

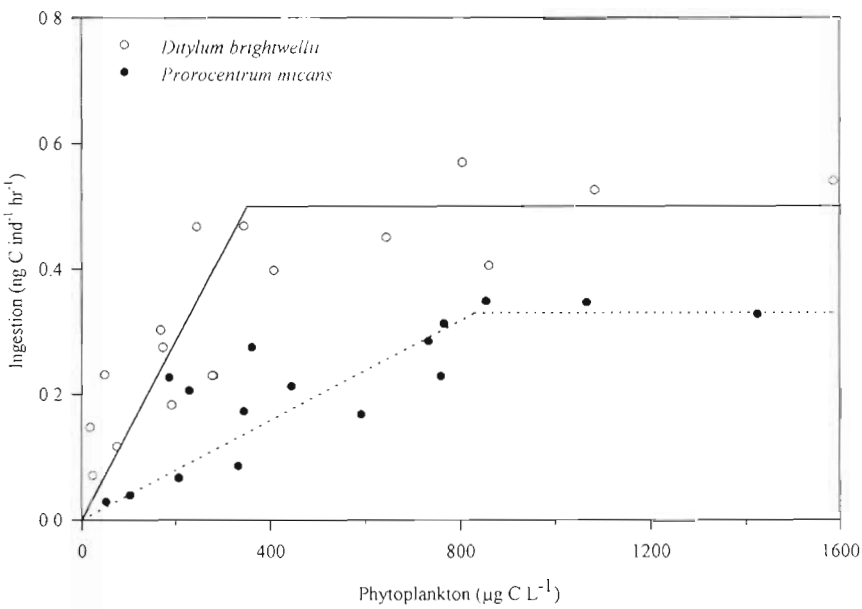

Fig. 2. *Protoperidinium pellucidum*. Ingestion rate over a range of concentrations of *Ditylum brightwellii* and *Prorocentrum micans*

pellucidum were allowed to choose only between the 2 dinoflagellate species at 500 cells ml^{-1} of each food, there was a slight preference for *P. micans* (58.6 ± 18.4%) over *G. polyedra* (41.4 ± 18.4%). A final selective feeding experiment was performed using 4 different species of diatom (*D. brightwellii*, *Thalassiosira* sp. 1, *Biddulphia* sp., and *Thalassiosira* sp. 2). In this experiment, the 2 largest diatom species, *D. brightwellii* and *Thalassiosira* sp. 2 were chosen approximately equally over the 2 smaller species. *Thalassiosira* sp. 2 was chosen 49 ± 9.2% and *D. brightwellii* 39 ± 18.5% of the time; *Thalassiosira* sp. 1 was chosen 4 ± 2% and *Biddulphia* sp. 8 ± 1.9% of the time.

Starvation affected the behavior of *Protoperidinium pellucidum* by causing a decrease in swimming speed over the first 48 h of starvation (Fig. 4). After 48 h of starvation, there appeared to be little additional change in swimming speed until the experiment was ended at 96 h. Measures of rate of change of direction showed more variability, although mean rate of change of direction did decrease over the first 48 h. When exposed to a filtrate from a fresh *Ditylum bright-*

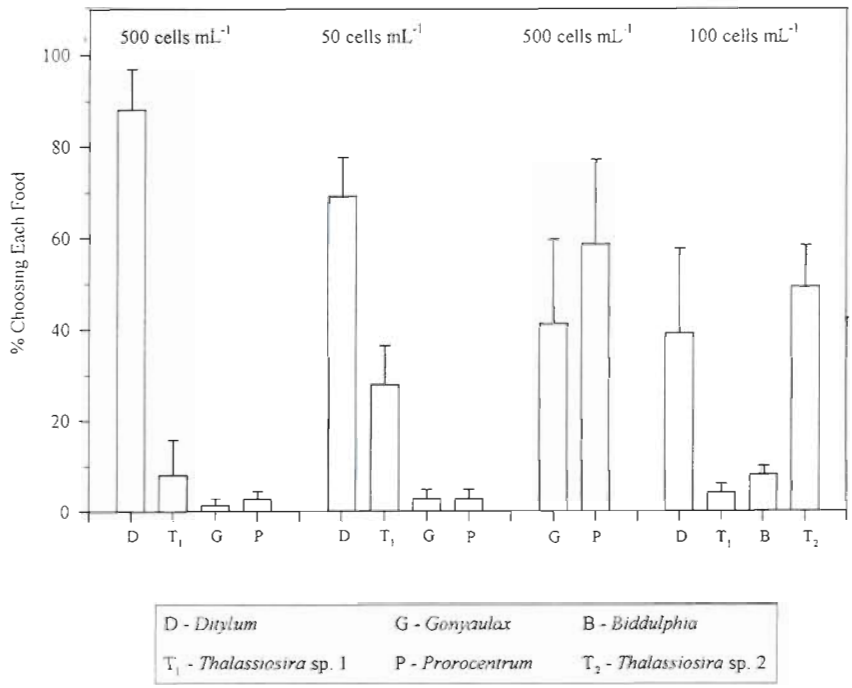

Fig. 3. *Protoperidinium pellucidum*. Feeding selectivity studies. Percent of the time that each of 4 phytoplankton foods (*Ditylum brightwellii, Thalassiosira* sp. 1, *Gonyaulax polyedra* or *Prorocentrum micans*) were chosen at food concentrations of 500 cells ml^{-1} or 50 cells ml^{-1} of each food, that each of 2 dinoflagellate species were chosen at 500 cells ml^{-1}, or that each of 4 diatom species (*Ditylum brightwellii, Thalassiosira* sp. 1, *Biddulphia* sp. or *Thalassiosira* sp. 2) were chosen at 100 cells ml^{-1}

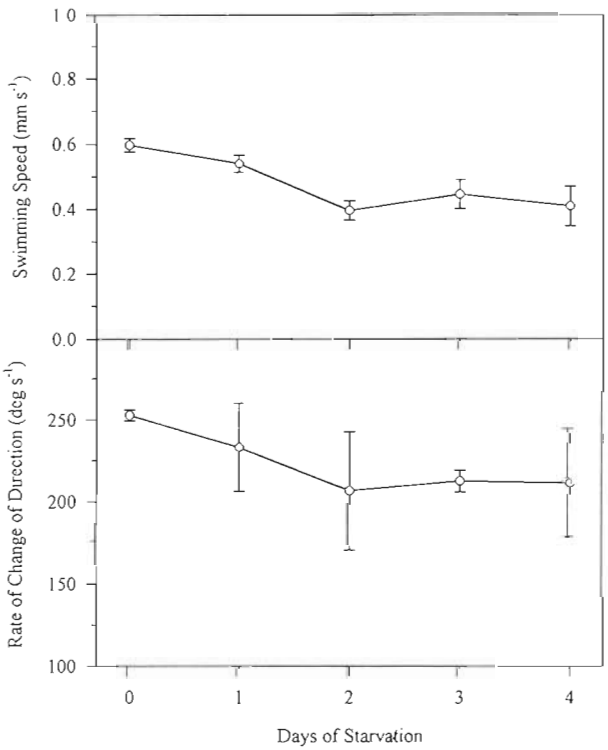

Fig. 4. *Protoperidinium pellucidum* Effects of starvation on the swimming behavior. Changes in swimming speed and rate of change of direction over a 96 h period of starvation

wellii culture, *P. pellucidum* that had been starved 24 h showed an increase in swimming speed (Fig. 5) and a decrease in turning rate. Before addition of the filtrate, the starved *P. pellucidum* had an average swimming speed of 0.48 ± 0.04 mm s^{-1} (grand mean of 10 replicates ± 1 SD) and an average turning rate of 249° s^{-1}. After addition of filtrate from the phytoplankton culture, there was a significant increase in swimming speed to 0.57 ± 0.06 mm s^{-1} (Student's *t*-test with paired design, $\alpha = 0.05$) and a significant decrease in turning rate to 203° s^{-1} (Student's *t*-test with paired design, $\alpha = 0.05$). *P. pellucidum* showed a similar behavioral response when exposed to 10^{-3} M seawater solution of the amino acid glycine (Fig. 6). These behavioral responses to chemosensory stimuli observed in the first 5 min of exposure were transient; swimming speeds and turning rates returned to previous values within an hour, probably due to adaptation of sensory systems. *P. pellucidum* showed no significant changes in swimming speed or turning rate when inert polystyrene beads (44 µm diameter) were added at a concentration of 500 beads ml^{-1}.

Image analysis of the stereotypical pre-feeding behavior of circling around a prey cell before attaching to it, revealed only small differences in the maximum distance between *Protoperidinium pellucidum* and its prey for all 4 phytoplankton species tested. For fifty measures of the maximum distance measured, the mean distance (± 1 SD) was 123 ± 35 µm for *Ditylum brightwellii*, 108 ± 28 µm for *Thalassiosira* sp. 1,

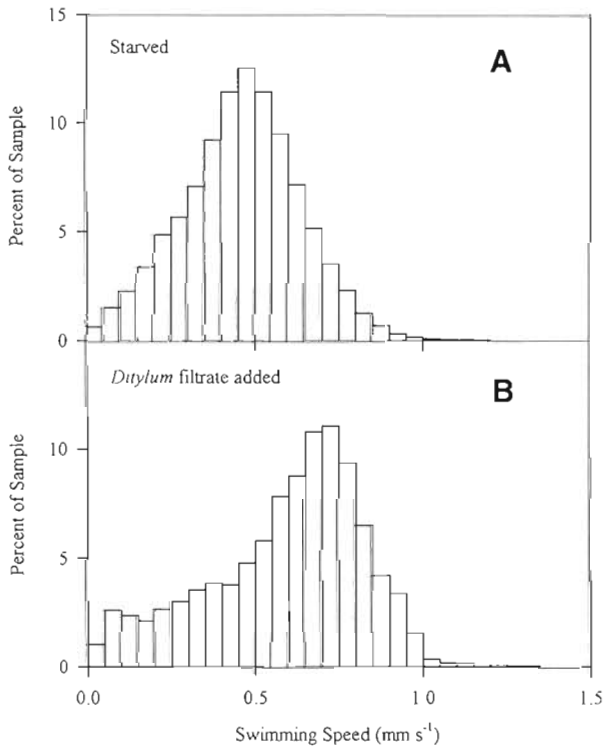

Fig. 5. *Protoperidinium pellicidum*. Distribution of swimming speeds (A) after ca 20 h of starvation and (B) after having been exposed to a fresh filtrate from a culture of actively growing *Ditylum brightwellii*

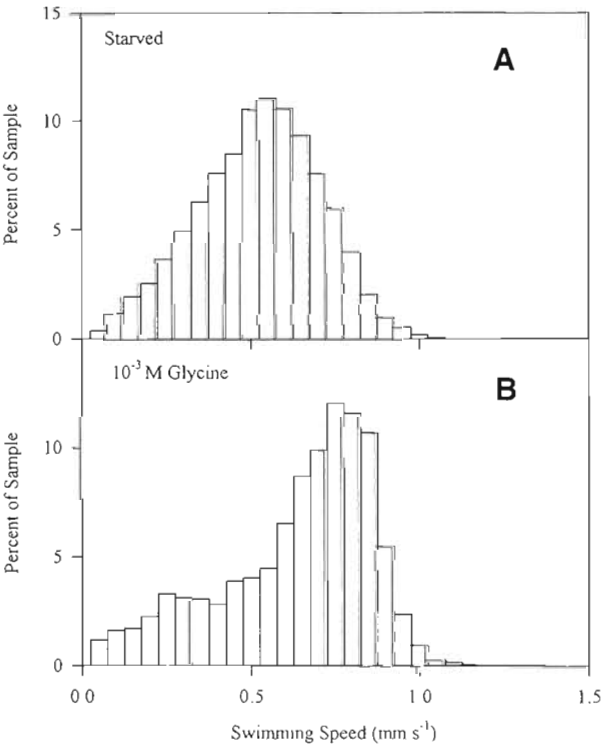

Fig. 6. *Protoperidinium pellucidum*. Distribution of swimming speeds (A) after ca 20 h of starvation and (B) after having been exposed to seawater containing 10^{-3} M solution of the amino acid glycine

97 ± 23 µm for *Gonyaulax polyedra* and 94 ± 22 µm for *Prorocentrum micans*.

The capture phase of the feeding interaction between *Protoperidinium pellucidum* and its phytoplankton food was quantified for the frequency of successful captures, lost contacts and escapes after attachment for each of 4 different food types. This type of behavioral analysis is made possible by the stereotyped circling behavior which precedes the attachment phase of feeding, and the ability to directly observe the initial attachment of a *P. pellucidum* to its food cell. Feeding interactions between *P. pellucidum* and diatoms were nearly always successful. In over 100 observed feeding interactions, an interaction where a *Ditylum brightwellii* cell was not successfully captured was never observed. In only 2 instances were cells lost after attachment during over 100 feeding interactions observed between *P. pellucidum* and *Thalassiosira* sp. 1. In contrast, over 20% of *Gonyaulax polyhedra* and over 40% of *Prorocentrum micans* were able to break the tow thread and escape after initial capture by *P. pellucidum* (Table 2). Clearly, *P. pellucidum* has a higher success rate capturing non-motile cells (diatoms) than motile cells (autotrophic dinoflagellates). It is unclear why there was a higher escape rate for the slower swimming species (*P. micans*, 0.1 mm s^{-1}) compared to the faster swimming species (*G. polyedra*, 0.4 mm s^{-1}). *P. pellucidum* also tended to lose contact with motile dinoflagellate prey in over 10% of the interactions observed, but this was not observed in feeding interactions with diatoms (Table 2).

Table 2. Observed feeding interactions between *Protoperidinium pellucidum* and 4 potential food types: *Ditylum brightwellii*, *Thalassiosira* sp. 1, *Gonyaulax polyedra* and *Prorocentrum micans*. If *P. pellicudum* formed a pallium around its food cell, it was scored as a successful capture. If the cell was lost after the tow thread was attached, it was scored as an escape. If *P. pellucidum* circled the cell in a stereotypical feeding behavior, but failed to attach a tow thread, it was scored as a lost contact. n = no. of observations

Prey	Prey speed (mm s^{-1})	Successful capture	Escape	Lost contact	n
Ditylum brightwellii	0	100%	0	0	115
Thalassiosira sp. 1	0	98.3%	1.7%	0	116
Gonyaulax polyedra	0.4	61.9%	21.2%	16.9%	118
Prorocentrum micans	0.1	46%	43%	11%	100

The time required for *Protoperidinium pellucidum* to ingest a phytoplankton cell varied with the food species, although it was similar for the dinoflagellate species (Table 3). Feeding time increased proportionally with the biomass of the phytoplankton cell consumed for *Thalassiosira* sp. 1, *Ditylum brightwellii* and *Prorocentrum micans*, but did not significantly increase for the larger *Gonyaulax polyedra* cells (Fig. 7). It is possible that there may be a maximum average feeding time for *P. pellucidum* of about 70 min; this may represent the time required for *P. pellucidum* to ingest the maximum amount of carbon it can assimilate, or it might simply represent the maximum average time for a single pallium feeding event. There is quite a bit of variability in our measured digestion times for different foods; this may be due in part to release of the pallium before the food cell is completely digested. It is suspected that this may occur for a number of reasons, and that a more accurate estimate of time required to ingest the entire cell may be given by the 'most probable value', which is defined as the mean of the upper half of measurements (Fig. 7, Table 3).

Table 3. *Protoperidinium pellucidum*. Time (min) required to consume a single cell of each of the experimental foods used in this study. A total of 50 feeding times were measured for each phytoplankton food species. The most probable value (MPV) is the mean of the 25 longest feeding interactions

Food	Mean (SD)	MPV (SD)	Minimum	Maximum
Ditylum brightwellii	24.2 (7.9)	30.4 (5.2)	10	43
Thalassiosira sp. 1	10.7 (4.1)	13.9 (2.8)	3	22
Gonyaulax polyedra	53.7 (19.7)	68.9 (13.1)	17	101
Prorocentrum micans	52.3 (26.5)	72.9 (19.3)	15	109

DISCUSSION

The survey of potential foods indicates that *Protoperidinium pellucidum* will grow on a wide range of diatom species (Table 1). This is in agreement with previous studies indicating that some species of *Protoperidinium* appear to prefer diatoms as food (Jacobson & Anderson 1986, Buskey et al. 1994). *P. pellucidum* would grow on only 2 of the 8 monospecific dinoflagellate diets offered, suggesting that autotrophic dinoflagellates as a group were somehow less suitable as food items. However, it is interesting to note that all foods that supported growth of *P. pellucidum* fell between the approximate volumes of 1850 and 18350 μm^3, while all the phytoplankton species that did not support growth fell outside this size range (total volume of chains of the smaller *Skeletonema* sp. cells also fall within this range). This indicates that size plays an important role in suitability of food for *P. pellucidum*.

A comparison of growth rates of *P. pellucidum* on 2 species of diatom (*Ditylum brightwellii*, *Thalassiosira* sp. 1) and 2 species of dinoflagellate (*Gonyaulax polyedra*, *Prorocentrum micans*) show that *P. pellucidum* has a higher specific growth rate when fed diatoms (0.7 d^{-1}) compared to a dinoflagellate diet (0.4 d^{-1}) (Fig. 1). Based on the limited evidence available, there may be a general trend of higher growth rates for *Protoperidinium* species fed diatoms compared to those

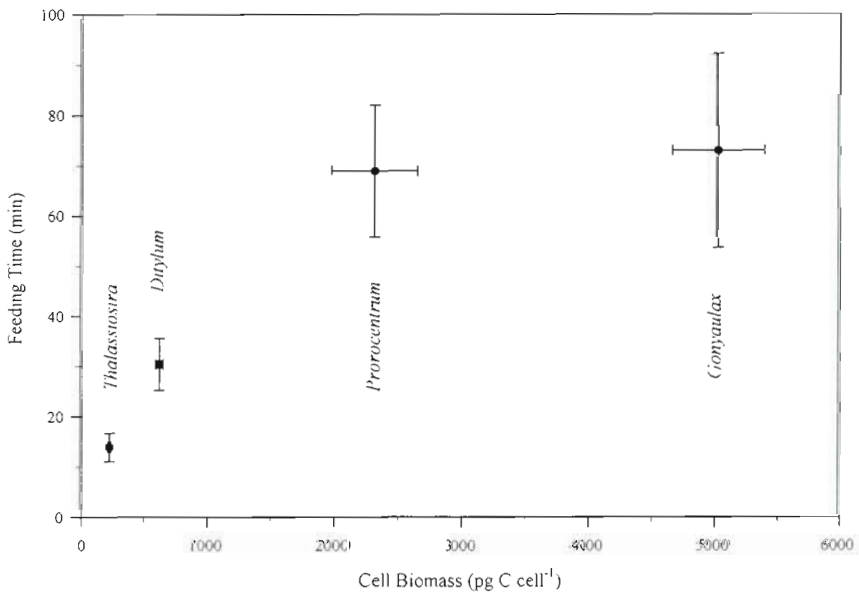

Fig. 7 *Protoperidinium pellucidum*. Time required to feed on a single cell of *Ditylum brightwellii*, *Thalassiosira* sp., *Gonyaulax polyedra* or *Prorocentrum micans* as a function of the biomass of the food cell. Most probable value (MPV) ± 1 SD, n = 25

fed autotrophic dinoflagellates. Jacobson & Anderson (1993) and Buskey et al. (1994) found maximum specific growth rates of 1.23 d^{-1} and 0.72 d^{-1}, respectively, for *Protoperidinium* species fed diatoms, whereas Jeong & Latz (1994) found maximum specific growth rates of 0.48 and 0.31 d^{-1} for 2 species of *Protoperidinium* fed dinoflagellates. However, it should be noted that the *Protoperidinium* species with the higher growth rates were also smaller in size, and an alternative explanation might be that smaller species have greater maximum growth rates than larger species. *P. pellucidum* also exhibited higher maximum ingestion rates when fed the diatom *Ditylum brightwellii* compared to the autotrophic dinoflagellate *Prorocentrum micans* (Fig 2). A previous study suggested that *Protoperidinium* species (*P.* cf. *divergens* and *P. crassipes*) might play important roles as grazers of dinoflagellates in red tide blooms when high concentrations of dinoflagellates existed (Jeong & Latz 1994). Other species of *Protoperidinium* appear to feed preferentially on diatoms and, along with other species of heterotrophic dinoflagellates, may play an important role in grazing diatom blooms (Hansen 1991, Tiselius & Kuylenstierna 1996). Selective feeding by rapidly growing heterotrophic dinoflagellate species may play a role in determining phytoplankton community structure.

In feeding selectivity studies, *Protoperidinium pellucidum* showed strong preference for diatoms over dinoflagellates (Fig. 3). Pallium feeding heterotrophic dinoflagellates are particularly amenable to studies of feeding selectivity, since each organism selects a single food cell and remains attached to it for periods of up to an hour, allowing for easy visual determination of the food species chosen. It would seem that this feeding selectivity is not a result simply of the size or shape of the food cell, since there usually appears to be no contact between the *P. pellucidum* and the food cell until the tow thread is attached and the selection has been made. Although the role of prey size and shape in food selection has not been specifically investigated for pallium feeding heterotrophic dinoflagellates, these protists show remarkable range in the sizes of individual phytoplankton cells they can capture and consume, from 1% to over 500% of their own cell volume (Strom & Buskey 1993, Buskey et al. 1994). When food selectivity was tested amoung 4 species of diatoms, selection was not directly related to size. *Thalassiosira* sp. 2 (cell volume of 3613 μm^3) was chosen 48% of the time, *Ditylum brightwellii* (cell volume 9690 μm^3) was chosen 39% of the time, *Biddulphia* sp. (cell volume 6220 μm^3) was chosen 8% of the time, and *Thalassiosira* sp. 1 (cell volume 1850 μm^3) was chosen 4% of the time. However, there is indirect evidence that chemosensory perception may play a role in feeding selectivity. *P. pellucidum* shows a clear behavioral response to chemosensory signals associated with its phytoplankton prey (Fig. 5) and to a solution of a single amino acid (Fig 6), indicating that it is capable of remote perception of chemosensory signals associated with the phytoplankton it feeds on. Several previous studies have demonstrated chemosensory capabilities in heterotrophic dinoflagellates and indicated a potential role of free amino acids in chemosensory responses of heterotrophic dinoflagellates and other protozoa (Hauser et al. 1975, Fitt 1985, Spero 1985). It seems likely that initial food choice by *P. pellucidum* is made by means of remotely detected chemosensory signals that stimulate the stereotypical pre-feeding behavior. More study is needed to determine the extent to which *P. pellucidum* can distinguish between chemosensory signals associated with specific phytoplankton species.

Optimal foraging theory predicts that predators should selectively feed on the largest prey they can handle and that feeding selectivity should be greater when the food is more abundant (Pyke et al. 1977). If size were the only factor determining which food species would be most 'profitable' to consume, one would predict that *Protoperidinium pellucidum* should select the 2 dinoflagellates over the 2 diatom species offered as food. Not only were the 2 dinoflagellates larger than the 2 diatoms, but when handling times were factored in, carbon ingested per minute was about twice as high for dinoflagellates compared to diatoms. There must be other factors affecting the nutritional quality and attractiveness of diatoms as food. Studies of the chemical composition of phytoplankton (e.g. Parsons et al. 1961, Moal et al. 1987) do not reveal general patterns that help explain the higher maximum growth rates of *P. pellucidum* when fed diatoms. However, it is interesting to note that *P. pellucidum* demonstrated a stronger preference for *Ditylum brightwellii* at high food concentrations (500 cells ml^{-1} of each of 4 foods) than at lower food concentrations (50 cells ml^{-1} of each of 4 foods) (Fig 3), supporting the idea of increased selectivity for preferred foods at high concentrations predicted by optimal foraging theory.

In order to understand the factors contributing to this apparent selection for diatom prey over dinoflagellate prey, it is useful to examine the feeding behavior of *Protoperidinium pellucidum* using the 'components of predation' framework of Holling (1959a, 1966). Thus we can consider separately the factors affecting encounter, capture and ingestion of different prey types by *P. pellucidum*. The encounter rates between *P. pellucidum* and its food can be predicted based on the encounter model of Gerritsen & Strickler (1977) The behavioral parameters needed for this model include the swimming speeds of the 'predator' (*P. pellucidum*) and its 'prey' (diatoms or autotrophic dino-

flagellates), prey density and the distance at which prey can be detected by the sensory systems of the predator (the 'encounter radius') All of these parameters can be measured for interactions between *P. pellucidum* and its phytoplankton food.

The most difficult parameter to estimate for encounter models is the encounter radius, the distance at which a predator detects its prey. Error in estimating this parameter will have a much larger effect on estimates of encounter rate than errors in measuring swimming speeds or prey density, since the term is squared in the encounter model equation of Gerritsen & Strickler (1977). Previous studies using encounter models to estimate encounter frequencies have sometimes simply guessed at an appropriate value (e.g Buskey & Swift 1990). The size of the 'encounter radius' for *Protoperidinium pellucidum* feeding on 4 different species of phytoplankton was estimated by measuring the maximum distances that *P. pellucidum* could move away from its food without losing contact with it during *P. pellucidum*'s stereotypical pre-feeding behavior, in which it circles the cell before attaching to it. This may underestimate the maximum distance at which a food cell can be detected, but it should be proportional to the size of the 'active space' (Bossert & Wilson 1963, Andrews 1983) around the food cell containing chemosensory signals recognizable to *P. pellucidum*. It seems reasonable that this encounter distance should be greater for larger-sized cells which might release more dissolved organic substances that could be used as chemosensory cues. It also seems intuitive that motile dinoflagellates would have differently shaped 'active spaces' surrounding their cells; they would tend to leave a trail of scent behind in addition to a small sphere of dissolved chemicals in the waters trapped in a boundary layer around them. This should make dinoflagellates more difficult to detect at low concentrations compared to non-motile diatoms, which should produce larger and more symmetrically shaped 'active spaces' around each cell. Our results show that the active spaces are slightly larger for larger diatoms compared to smaller diatoms (*Ditylum brightwellii* vs *Thalassiosira* sp. 1), and are larger for diatoms compared to dinoflagellates per unit cell volume. However, the empirically estimated encounter radii were highly variable and not significantly different for the species we tested. The method used to estimate this distance (the maximum distance measured between cells during stereotypical pre-feeding behavior) may not accurately reflect the distance at which initial perception of the cell was made.

Estimates of swimming speeds of *Protoperidinium pellucidum* and its food cells are also needed to predict encounter frequencies. The average swimming speed for well-fed *P. pellucidum* is ca 0.6 mm s^{-1}. This is similar to but slightly higher than speeds measured for 2 other species of *Protoperidinium* (*P. depressum*, *P. pacificum*) using the same method (Buskey et al. 1993). Swimming speeds of the 2 motile autotrophic dinoflagellates used as food in this study were 0.4 mm s^{-1} for *Gonyaulax polyedra* and 0.1 mm s^{-1} for *Prorocentrum micans*. Diatoms are non-motile, and were considered to have a 'swimming speed' of zero, although they may sink slowly through the water column.

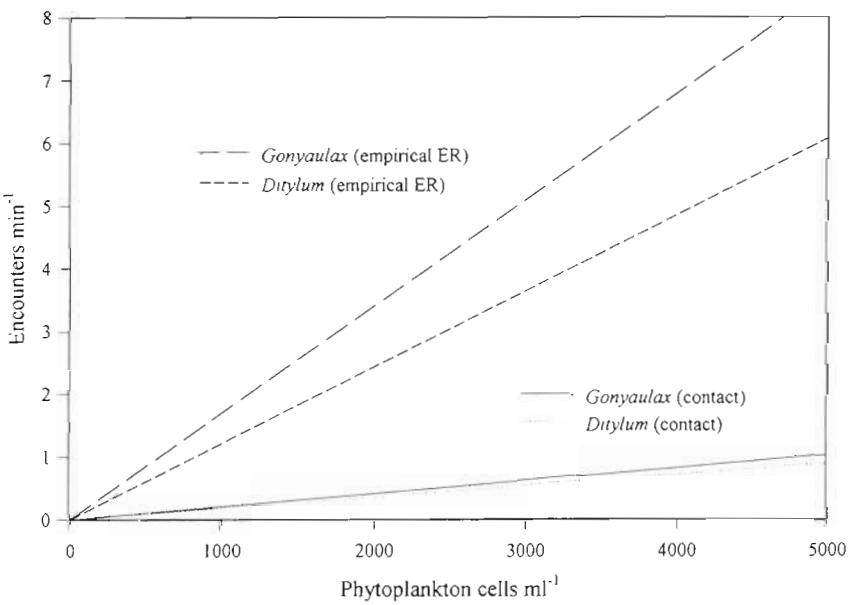

Fig. 8. Predicted encounter rates between *Protoperidinium pellucidum* and 2 phytoplankton species, *Gonyaulax polyedra* and *Ditylum brightwellii*. Encounter rates are predicted from the encounter model of Gerritsen & Strickler (1977) based on the assumption that cells must physically collide to encounter one another (contact) or that *P. pellucidum* can remotely detect phytoplankton prey at a distance equivalent to an empirically determined encounter radius (empirical ER)

Using these estimates of encounter radius, and our measures of swimming speed for *Protoperidinium pellucidum* and its motile autotrophic dinoflagellate prey (e.g. *Gonyaulax polyedra*) the encounter model of Gerritsen & Strickler (1977) can be used to predict encounter rates between *P. pellucidum* and its prey at different prey densities (Fig 8). Comparing encounter rates with the motile *G. polyedra* (0.4 mm s^{-1}) and non-motile diatom *Ditylum brightwellii* (0 mm s^{-1}), if we assume that *P. pellucidum* must physically run into

and contact its food to detect it (i.e. encounter radius is equivalent to the distance between the centers of the 2 cells when they contact (ca 40 µm), it is clear that encounter rates are very low, and only slightly higher for the motile prey compared to the non-motile prey (Fig. 8). In both cases, encounter rates only approach 1 min^{-1} at cell densities of 5000 cells ml^{-1}. However, if we use our empirically determined estimates of encounter radius and recalculate the changes in encounter rate with food density, it is clear that these small increases in encounter radius have an enormous effect on encounter rate. Now encounter rates of 1 encounter min^{-1} occur at cell densities <1000 cells ml^{-1} It is also apparent that the effects of a slightly larger encounter radius for detecting *D. brightwellii* increase encounter rate more than the motility of *G. polyedra*.

The second 'component of predation' to be considered in the interaction between *Protoperidinium pellucidum* and its phytoplankton prey is capture probability. Very little is known about the factors affecting food capture success in pallium feeding heterotrophic dinoflagellates. In other planktonic predator-prey interactions, prey escape may play an important role in predator selectivity (Drenner et al. 1978, Landry 1978, Greene & Landry 1985). The selection of *P. pellucidum* for diatoms over dinoflagellates may relate at least in part to the motility of the autotrophic dinoflagellates, compared to the lack of motility in diatoms. *P. pellucidum* was never observed to 'lose contact' with a non-motile diatom once it began its stereotypical circling behavior, but it was observed to lose contact with *Gonyaulax polyedra* in 17% of interactions and with *Prorocentrum micans* in 11% of interactions. Even though the motility was not in direct response to the approach of the heterotrophic dinoflagellate, the motility of the autotrophic dinoflagellates appears to have aided in their escape, perhaps due to the lower ability of *P. pellucidum* to locate and remain near a moving cell. Similarly, once *P. pellucidum* had attached a tow thread to a diatom, failure to engulf the cell in its pallium was never observed when *Ditylum brightwellii* was the food, and was observed in only 2 instances with *Thalassiosira* sp. 1 (Table 2). Failure to capture *Thalassiosira* sp. 1 cells in these rare instances may have been related to the presence of extensive marginal threads of *Thalassiosira* that have been demonstrated to interfere with the feeding of tintinnid ciliates (Verity & Villareal 1986); these threads may have interfered with the ability of *P. pellucidum* to securely attach the tow thread to the frustule. The loss of motile dinoflagellate cells after attachment of the tow thread seemed to be the result of detachment or breakage of the thread when the 2 cells swam in different directions. It did not appear that the feeding attempt by *P. pellucidum* elicited a specific escape response in the autotrophic dinoflagellates, but the normal swimming behavior of the dinoflagellates did appear to aid in their escape.

The final 'component of predation' to be considered for the feeding behavior of *Protoperidinium pellucidum* is ingestion. The fact that *P. pellucidum* and other pallium feeding heterotrophic dinoflagellates digest their prey externally allows us to accurately measure the time required for digestion of different food types. The *P. pellucidum* cell engulfs its food in a pallium and remains attached to it until apparently only non-digestible materials remain (e.g. diatom frustule, dinoflagellate thecal plates). There appears to be a relationship between MPV digestion time and the carbon content of the cells consumed up to a maximum average ingestion time of about 70 min (Fig. 7). However, when the values for carbon content per cell for each prey type are divided by the time required to consume them, the average carbon ingested per minute is 25.4 pg C min^{-1} for *Ditylum brightwellii*, 21.7 pg C min^{-1} for *Thalassiosira* sp. 1, 93.5 pg C min^{-1} for *Gonyaulax polyedra* and 44.1 pg C min^{-1} for *Prorocentrum micans*. For the dinoflagellates, however, some of the carbon measured for each cell is in the form in indigestible material in the theca which would be left behind in the pallium, and this may cause an overestimation of carbon consumed per unit time. Also, since the feeding time on the larger *G. polyhedra* is not significantly different from the smaller *P. micans*, *P. pellucidum* may not be capable of ingesting all the carbon from the larger prey.

The behavioral components of feeding by *Protoperidinium pellucidum* measured in this study may help us to understand the differences in functional response (ingestion vs food concentration) observed with diatom and dinoflagellate foods (Fig. 2). For a type I functional response curve (Holling 1959b), as is often found for heterotrophic dinoflagellates feeding individually on phytoplankton cells (e.g. Strom & Buskey 1993, Buskey et al. 1994; Fig. 2), the maximum ingestion rate should be a function of capture success by the predator for that prey type and the time required to handle and digest that food type. Therefore we would predict lower maximum ingestion rates on food types with lower proportions of successful capture and for food types that require longer handling and ingestion times. The higher maximum ingestion rate on *Ditylum brightwellii* compared to *Prorocentrum micans* (Fig. 2) is probably due mainly to higher capture success, since *P. pellucidum* appears to acquire more carbon per unit time when feeding on dinoflagellates. At its maximum ingestion rate, *P. pellucidum* spends more time feeding on *D. brightwellii* than on *P. micans*. Based on the average time required for feeding (Table 3), at maximum ingestion rates *P. pellucidum* spends only 31.4% of its time consuming *D. brightwellii* (to consume ca

18.7 cells d^{-1}) or 12.3% of its time consuming *P. micans* (3.4 cells d^{-1}). *P. pellucidum* must spend more of its time with unsuccessful feeding interactions with motile dinoflagellate prey. The steepness of the slope of the functional response curve in the region where ingestion increases linearly with food concentration may be determined in part by the distance at which *P. pellucidum* can detect its food (Fig. 8); as expected the slope of the functional response curve with *D. brightwellii* as food is steeper than with *P. micans* as food (Fig 2). Using Gerritsen & Strickler's (1977) encounter model, the number of encounters between *P. pellucidum* and *D. brightwellii* or *P. micans* can be predicted at food concentrations that produce maximum ingestion rates. The encounter rate between *P. pellucidum* and *D. brightwellii* would be 0.97 encounters min^{-1} at 350 µg C l^{-1} (569 cells ml^{-1}); the encounter rate with *P. micans* would be 0.6 encounters min^{-1} at 830 µg C l^{-1} (360 cells ml^{-1}). It seems surprising that feeding rates were encounter limited at encounter rates only slightly lower than these.

Protozooplankters such as heterotrophic dinoflagellates play a central role in marine food webs by serving as an important link between phytoplankton primary production and higher trophic levels. Although there may be a tendency to consider small, unicellular organisms as lacking in complex sensory capabilities and behavioral adaptations, there is a growing body of evidence that many protozoa have sophisticated behavioral and sensory capabilities and are capable of selectively feeding on specific types of food using criteria other than size. In this study, the ability of a pallium feeding heterotrophic dinoflagellate to feed selectively in mixtures of food has been demonstrated, and the behaviors contributing to this feeding selectivity have been explored. Although feeding selectivity was found not to be a simple function of phytoplankton size, the precise factors affecting prey selection, especially within a single taxonomic group such as the diatoms, remain unknown. Future studies need to examine the chemosensory capabilities of the protozoa in more detail, and to examine the roles of feeding prehistory and adaptation in prey selectivity.

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