Vol. 106: 173–185, 1994 | MARINE ECOLOGY PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published March 17

Growth and grazing rates of the heterotrophic dinoflagellates *Protoperidinium* spp. on red tide dinoflagellates

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ABSTRACT: Growth and ingestion rates of the heterotrophic dinoflagellates *Protoperidinium* cf. *divergens* and *P. crassipes* feeding on red tide dinoflagellates local to southern California, USA, were measured in the laboratory. Unialgal diets of the larger dinoflagellates *Gonyaulax polyedra* and *Gymnodinium sanguineum* supported population growth, while the smaller dinoflagellates *Prorocentrum* cf. *balticum* and *Scrippsiella trochoidea* did not; *G. polyedra* was the optimal diet. The maximum specific growth rates of *P.* cf. *divergens* and *P. crassipes* on a *G. polyedra* diet were 0.484 and 0.308 d^{-1}, respectively. Specific growth rate increased with mean prey concentration, with saturation at approximately 760 to 1500 cells ml^{-1}. Maximum ingestion and clearance rates of *P.* cf. *divergens* and *P. crassipes* fed on *G. polyedra* were 0.2 and 0.08 prey *Protoperidinium*$^{-1}$ h^{-1}, and 0.67 and 0.47 µl *Protoperidinium*$^{-1}$ h^{-1}, respectively. For a *G. sanguineum* diet, the pattern of specific growth rate as a function of mean prey concentration was quite different from that of *G. polyedra*. Maximum specific growth rates were 0.246 and 0.107 d^{-1} for *P.* cf. *divergens* and *P. crassipes* at mean prey concentrations of 530 to 1100 cells ml^{-1}. Growth was negative at higher *G. sanguineum* concentrations, and dead *Protoperidinium* were observed. *P.* cf. *divergens* selected *G. polyedra* over *G. sanguineum*. Cannibalism was observed in cultures mainly when *Protoperidinium* abundances were high, and may be a mechanism for withstanding prolonged starvation. The estimated ingestion rate of *Protoperidinium* during a *G. polyedra* red tide is ≤4800 prey ingested l^{-1} h^{-1}, so *Protoperidinium* may have a considerable grazing impact on some red tide dinoflagellate populations.

KEY WORDS: Dinoflagellate · Feeding · Microzooplankton · Plankton · Protozoa · Red tide

INTRODUCTION

Red tides, consisting of dense blooms of algae visible at the sea surface, can upset the balance of food webs and cause large-scale mortalities in fish and shellfish (e.g. Norris & Chew 1975). Red tides in the coastal waters of southern California have been monitored since the early 1900s (Allen 1941). *Gonyaulax polyedra* Stein, *Prorocentrum micans* Ehrenberg and *Gymnodinium sanguineum* Hirasaka are the most common local red tide dinoflagellates, with concentrations often reaching more than 10^6 cells l^{-1} (Clendenning 1958, Holmes et al. 1967, Eppley & Harrison 1975). Studies of red tide formation and persistence suggest that grazing pressure may sometimes play an important role in red tide dynamics (e.g. Watras et al. 1985). Some copepods and fish larvae are known to feed on some local red tide dinoflagellates (Lasker et al. 1970, Paffenhöfer 1976). Grazing by microzooplankton such as rotifers, tintinnids, and heterotrophic dinoflagellates is believed to contribute to the decline of blooms (Holmes et al. 1967, Eppley & Harrison 1975).

Historical evidence from the coastal waters of southern California (Torrey 1902, Allen 1949) reveals that the heterotrophic dinoflagellate genus *Protoperidinium* may be very abundant during dinoflagellate blooms, and much less abundant during diatom blooms. Recently, high numbers of *Protoperidinium*

were also associated with a red tide of *Gonyaulax polyedra* in La Jolla Bay during spring 1992 (Jeong unpubl. data). These observations suggest that *Protoperidinium* might have a considerable grazing impact on the populations of red tide dinoflagellates. *Protoperidinium* often dominates the protozoan biomass in coastal (Jacobson 1987) and oceanic waters of other regions (Lessard 1984).

Although most *Protoperidinium* species are known to feed on diatoms (Jacobson & Anderson 1986, 1992, Buskey et al. 1992) and bacteria (Lessard & Swift 1985, Lessard & Rivkin 1986), several species have been observed feeding on dinoflagellates (Jacobson & Anderson 1986, Hansen 1991). *Protoperidinium* does not engulf prey cells whole, but rather uses a tow filament to attach to a prey cell and then a pseudopod 'veil', called the pallium, to envelop the prey, with subsequent external digestion and pseudopod retraction (Gaines & Taylor 1984, Jacobson & Anderson 1986). This unique feeding mechanism suggests that prey selection by *Protoperidinium* may be different from that of grazers which swallow prey cells.

Pallium formation does not necessarily indicate that a prey type supports population growth of *Protoperidinium*. This is best determined by culturing on single algal prey species. Small species such as *P. hirobis* (23 µm diameter) and *P. pellucidum* (36 µm diameter) have been cultured on the diatoms *Leptocylindrus danicus* and *Skeletonema costatum*, respectively (Hansen 1992, Jacobson & Anderson 1993). There are no reports of *Protoperidinium* cultured on dinoflagellate species, although Hansen (1991) observed *P. divergens* and *P. pellucidum* feeding on dinoflagellates in short-term enrichment cultures.

This study is the first report on the growth and grazing rates, and prey selection, of *Protoperidinium* feeding on dinoflagellate prey. It describes feeding of *P.* cf. *divergens* (Ehrenberg) Balech and *P. crassipes* (Kofoid) Balech collected from the pier at Scripps Institution of Oceanography and successfully cultured on monospecific cultures of local red tide dinoflagellates, mainly *Gonyaulax polyedra*, *Gymnodinium sanguineum* and *Scrippsiella trochoidea* (Stein) Loeblich III. Both species exhibited maximal specific growth rates with *G. polyedra* as prey; *P.* cf. *divergens* offered mixed prey grazed preferentially on *G. polyedra*. This study provides a basis for understanding the interaction between *Protoperidinium* and red tide dinoflagellate prey.

MATERIALS AND METHODS

Culture of phytoplankton prey. Four species of autotrophic or mixotrophic dinoflagellates (Table 1) were grown in enriched f/4 seawater medium (Guillard & Ryther 1962) without silicate, at room temperature (20 to 23°C) with continuous illumination of 100 µE $m^{-2} s^{-1}$ of cool white fluorescent lights; cultures in exponential growth phase were used for feeding experiments. Cell size was measured with an Elzone model 280PC particle counter with a calibrated 120 µm orifice.

Isolation and culture of *Protoperidinium*. Specimens of *Protoperidinium* were collected from the Scripps pier during October 1992 using a 35 cm diameter, 25 µm mesh plankton net. Plankton samples were screened gently through 154 µm Nitex mesh and placed in 1 l glass bottles. After 2 h the upper three fourths of the volume was gently discarded and the remaining volume transferred into 250 ml polycarbonate (PC) bottles. A mixture of *Gonyaulax polyedra*, *Gymnodinium sanguineum* and *Scrippsiella trochoidea* was added along with 50 ml of f/4 medium. Bottles were placed on wheels rotating at 0.9 rpm under a 12:12 h light:dark cycle of illumination with 50 µE $m^{-2} s^{-1}$ of cool white fluorescent light in a 19°C culture room. Five days later, aliquots of the enriched water were transferred into multi-well tissue culture plates containing freshly filtered seawater. Several large species of *Protoperidinium* were

Table 1 Species of heterotrophic dinoflagellates (last 2 taxa) and autotrophic or mixotrophic prey used in the present study, listed in order of size. Mean equivalent spherical diameter (ESD) ± standard deviation of the mean for phytoplankton was measured by the Elzone 280PC particle counter, and for heterotrophic dinoflagellates by the equation: ESD = $(l\ w\ h)^{1/3}$ where l refers to cell length, w = width, and h = height. Volume (to the nearest 100 μm^3) was calculated according to the equation: volume = $4/3\,\pi\,(ESD/2)^3$. The number of cells measured was >5000 for phytoplankton and >50 for *Protoperidinium*

Species	ESD (µm)	Volume (μm^3)
Prorocentrum cf. *balticum*	11.2 ± 1.2	700
Scrippsiella trochoidea	19.1 ± 2.0	3600
Gymnodinium sanguineum	31.7 ± 3.2	16700
Gonyaulax polyedra	36.7 ± 3.0	25700
Protoperidinium cf. *divergens*	61.0 ± 2.8	119000
Protoperidinium crassipes	73.0 ± 4.9	204000

abundant. Of these *P.* cf. *divergens* (73 × 61 × 52 µm; 61 µm equivalent spherical diameter, ESD) and *P. crassipes* (86 × 80 × 56 µm, 73 µm ESD) were selected for experimental work.

Taxonomic authorities used to identify specimens were Balech (1988), Dodge (1982, 1985) and Taylor (1976) For identification, plate patterns and thecate forms of living, but motionless *Protoperidinium* on a slide were examined under a microscope. *P.* cf. *divergens* may be either *P. divergens* or *P. brochii* (Kofoid & Swezy) Balech. The only difference between these 2 species is that the epitheca of *P. divergens* is more concave than in *P. brochii*.

Approximately 20 actively swimming individuals of each species were transferred into 32 ml PC centrifuge bottles. A mixture of *Gonyaulax polyedra*, *Gymnodinium sanguineum* and *Scrippsiella trochoidea* was added to each bottle as food. Alternatively, several diatom species, including *Chaetoceros gracilis* Schutt (10 µm ESD), *C. decipiens* Cleve (13 µm ESD for each cell of the chain), *Leptocylindrus danicus* Cleve (17 µm ESD for each cell of the chain), *Skeletonema costatum* (Greville) Cleve (17 µm ESD for each cell of the chain), and *Thalassiosira weissflogii* Grun (14 µm ESD) were provided as food. However, the diatom diet did not support growth of either *Protoperidinium* species, even though the presence of diatom cells within a pallium indicated that feeding was occurring.

Bottles were placed on rotating wheels, maintained under controlled conditions as described above, and observed daily under a dissecting microscope to examine the swimming pattern and condition of *Protoperidinium* as well as food abundance. For the first 3 wk, actively swimming cells were individually transferred into new bottles containing freshly filtered seawater and algal mixture every 4 or 5 d. After 3 wk, one-third of the bottle volume was transferred into new bottles. Once dense cultures of *Protoperidinium* were obtained they were maintained in 43 and 250 ml PC bottles.

Feeding process. To observe the feeding process, a dense culture of *Protoperidinium* cf. *divergens* was placed in multi-well tissue culture plates containing *Gonyaulax polyedra* cells. Many *P.* cf. *divergens* were observed under a dissecting microscope to immediately catch prey. Eight *P.* cf. *divergens* which had just made a pallium were individually transferred by a Pasteur micropipette into each well of multi-well tissue culture plates containing only freshly filtered seawater. The duration of the feeding process was recorded.

Growth of *Protoperidinium* cf. *divergens* and *P. crassipes* on red tide dinoflagellates. These experiments were designed to determine the species and concentration of local red tide dinoflagellates that would support maximum growth of *Protoperidinium* in culture. One predator species and one algal prey species were used in each experiment. More than 1 wk prior to an experiment, high numbers of *Protoperidinium* cells from actively growing cultures were transferred into 43 ml PC bottles containing the test prey. During the preincubation period, *Gonyaulax polyedra* or *Gymnodinium sanguineum* at prey concentrations of approximately 500 and 1200 cells ml^{-1} were used. The former concentration was used for experiments using ≤500 cells ml^{-1}, while the latter concentration was for experiments with >500 cells ml^{-1}. Preincubations with *Prorocentrum* cf. *balticum* (Lohmann) Loeblich or *Scrippsiella trochoidea* were at a prey concentration of approximately 5000 cells ml^{-1}. There was evidence of no residual growth after preincubation because the growth rates of *P.* cf. *divergens* and *P. crassipes* were zero or less at low prey concentrations of *G. polyedra* and *G. sanguineum* and all tested concentrations of *P.* cf. *balticum* and *S. trochoidea*.

After a series of rinses by micropipette, large, fast-swimming *Protoperidinium* (1 grazer ml^{-1}, Expt 1, or 7 to 10 grazers ml^{-1}, Expt 2) were added to 32 ml PC bottles containing freshly filtered seawater and different concentrations of algae. Each treatment was performed in duplicate or triplicate. Experiments in duplicate were repeated under identical conditions. Based on preliminary tests, the initial concentration series of *Gonyaulax polyedra* ranged from 50 to 3000 cells ml^{-1} for *P.* cf. *divergens* experiments and 50 to 2000 cells ml^{-1} for *P. crassipes*. Initial concentrations of *Gymnodinium sanguineum* for both *Protoperidinium* species ranged from 50 to 2500 cells ml^{-1}, and *Prorocentrum* cf. *balticum* and *Scrippsiella trochoidea* had initial concentrations of 500 to 12000 cells ml^{-1}. In addition, 1.5 to 2.0 ml of f/4 medium was added because preliminary tests indicated that this maintained final cell concentrations of *G. polyedra* and *G. sanguineum* in control bottles within 20% of initial concentrations. Once algal prey, medium, and *Protoperidinium* cells had been added, bottles were filled to capacity with filtered seawater using a Pasteur micropipette to minimize the bubble size that remained inside bottles after capping. Bottles were incubated for 4 d at 19°C as described above. This incubation period was chosen based on *P.* cf. *divergens* growth rate vs incubation time data, which will be detailed below.

Following incubation, final concentrations of prey cells in 1 ml aliquots from experimental bottles were counted in triplicate using a Sedgwick-Rafter counting chamber. The remaining contents were transferred to multi-well tissue culture plates and the number of *Protoperidinium* counted under a dissecting microscope by removal with a Pasteur micropipette. Instantaneous feeding frequency was determined by counts of *Protoperidinium* cells with and without a pallium.

The specific growth rate of *Protoperidinium*, μ (d^{-1}), was calculated as:

$$\mu = \frac{\ln\left(\frac{P_t}{P_0}\right)}{t}$$

where P_0 = the initial concentration of *Protoperidinium*; and P_t = the final concentration after time t.

In order to determine the relationship between estimated population growth rate and incubation time, 32 *Protoperidinium* cf. *divergens* cells (1 grazer ml^{-1}) were added to 32 ml PC bottles containing freshly filtered seawater, 2 ml f/4 medium, and 1400 cells ml^{-1} of *Gonyaulax polyedra*. Two or three replicates for each day were incubated for 1 to 5 d. Growth rate was calculated as described above.

Ingestion and prey selection. Because the highest specific growth rates of *Protoperidinium* were obtained with a diet of *Gonyaulax polyedra*, the ingestion rates of *P.* cf. *divergens* and *P. crassipes* fed on *G. polyedra* were measured. Initial concentrations of *G. polyedra* based on the results of the growth experiments were 100, 300, 700, 1400, 2000, and 3000 cells ml^{-1} for *P.* cf. *divergens* ingestion studies, and 100, 500, 1000, 1500, and 2000 cells ml^{-1} for *P. crassipes*. Two initial concentrations of *Protoperidinium* were used, obtained by individually transferring cells by micropipette into triplicate 32 ml PC test bottles. At all but the lowest prey concentrations, 320 grazers (10 grazers ml^{-1}) were added. At prey concentrations of 100 and 300 cells ml^{-1}, only 224 grazers (7 grazers ml^{-1}) were used, to minimize the depletion of prey. Control bottles contained only *G. polyedra*. In addition, 1.5 to 2.0 ml f/4 medium was added to each bottle. Bottles were incubated at 19°C for 4 d as described above. After incubation, the contents in experimental and control bottles were fixed with acidic Lugol's solution.

Ingestion rates were calculated using 2 different methods, one based on prey concentration, the other based on the abundance of round fecal aggregations of undigested compacted materials of prey. The conventional method (Method 1) compared final concentrations of prey in control and grazing bottles, measured by counting 1 ml aliquots using a Sedgwick-Rafter counting chamber. More than 300 cells were counted in experiments with initial prey concentrations of 100 and 300 cells ml^{-1}, and more than 500 cells at the other prey concentrations. The final concentration of *Protoperidinium* was obtained from counting the number of cells in a 6 ml aliquot. Cell size of 20 grazers in each bottle was measured under an inverted microscope using an ocular micrometer. Using the equations of Frost (1972), the ingestion rate I (prey ingested $grazer^{-1}\ d^{-1}$) was calculated as:

$$I = \bar{c}\,F \times 24$$

where $\bar{c}$ = the mean prey concentration; and F = the clearance rate (volume $grazer^{-1}\ h^{-1}$), calculated as:

$$F = V g \bar{P}^{-1}$$

where V = the bottle volume; g = the grazing constant (h^{-1}; see below); and $\bar{P}$ = the mean *Protoperidinium* number in the experimental bottles. The volume-specific clearance rate (h^{-1}), defined as volume cleared (body volume)$^{-1}$ h^{-1}, was also calculated. The mean prey concentration $\bar{c}$ is:

$$\bar{c} = \frac{C_0(e^{t(k-g)} - 1)}{t(k-g)}$$

where C_0 = the initial prey concentration in the experimental bottles; and k = the prey growth constant [$k = \ln(C_t/C_0)/t$, where C_t = the final prey concentration in control bottles as a result of growth]. The grazing constant is calculated as:

$$g = k - \frac{\ln\left(\frac{C_t^{\bullet}}{C_0}\right)}{t}$$

where the final prey concentration in the experimental bottles ($C_t^{\bullet}$) is the result of effects of grazing and growth:

$$C_t^{\bullet} = C_0 e^{t(k-g)}$$

Based on Heinbokel (1978), the mean number of *Protoperidinium* in the experimental bottles, $\bar{P}$, was calculated as:

$$\bar{P} = \frac{P_0\,(e^{\mu t} - 1)}{\mu t}$$

where P_0 = the initial number of *Protoperidinium*.

Method 2, used to calculate ingestion rate, was based on the abundance of fecal aggregations produced following feeding, similar to the method of Jacobson & Anderson (1993) to determine ingestion rates by counting empty diatom frustules after incubation. They observed that pallium formation resulted in frustules persisting during the incubation period. At the end of the feeding process the pallium detached, and only a round fecal aggregation of undigested compacted material, 15 to 20 µm in diameter, remained. One prey ingested resulted in one fecal aggregation. Round fecal aggregations persisted due to the stickiness of the pallium and were readily distinguished from intact prey cells or other detritus. For experimental bottles, more than 50 fecal aggregations for prey concentrations of 100 and 300 cells ml^{-1} were counted, and more than 100 for the other prey concentrations. For *Protoperidinium crassipes*, ingestion rates were calculated by the second method only, because the low specific growth rate of *P. crassipes* did not result in significant changes in the final concentrations of prey between control and grazing bottles at high prey concentrations.

Gross growth efficiency (GGE), defined as grazer biomass produced per prey biomass ingested, was calculated from estimates of carbon content per cell based on cell volume (Strathmann 1967). Ohman & Snyder (1991) point out the bias that results if GGE is estimated directly from biovolumes.

Prey selectivity of *Protoperidinium* cf. *divergens* was investigated using a mixture of 2 algal species as food. 320 individuals of *P.* cf. *divergens* were added to 32 ml PC bottles (10 grazers ml^{-1}) containing different ratios of *Gonyaulax polyedra* and *Gymnodinium sanguineum*. Initial prey concentrations (cells ml^{-1}) of *G. polyedra* and *G. sanguineum* (and the corresponding ratios of *G. polyedra* to total prey) were 333/1000 (0.25), 500/500 (0.50), 1000/1000 (0.50) and 1000/333 (0.75). The concentrations of *G. sanguineum* chosen supported optimal growth of *P.* cf. *divergens* populations based on unialgal studies. In addition to grazer and prey cells, 1.5 to 2.0 ml of f/4 medium was added to each bottle. Bottles were incubated at 19 °C for 4 d as described above. Ratios of ingestion rates of *P.* cf. *divergens* feeding on *G. polyedra* and *G. sanguineum* were calculated based on the difference in the final concentrations of prey in control and experimental bottles.

To determine the effect of prolonged starvation on survival and cell size of *Protoperidinium*, cultures were sieved though 54 µm mesh to retain large cells, and transferred to a 250 ml PC bottle containing filtered seawater without prey. Initial cell concentration was approximately 40 cells ml^{-1} and cell size was measured using the particle counter. Bottles were examined every 2 d under a dissecting microscope, and cell size was measured again after 12 d using the particle counter.

RESULTS

Feeding process

Protoperidinium were observed to feed on red tide dinoflagellates according to the mechanism described by Jacobson & Anderson (1986), which involved deployment of a pallium which enveloped the prey cell. Once a *Protoperidinium* cell detected a suitable prey cell, it spun around the prey several times and caught the cell by deploying a tow filament. Two minutes later the length of the tow filament was shortened and the prey was attached to the posterior flagellar pore of *Protoperidinium*. Within 5 min a pallium had been deployed to envelop the prey; at this moment it was strong enough to resist detachment even when the *Protoperidinium* cell was transferred with a micropipette. Soon after the pallium formed the enveloped prey cell appeared to collapse as the cytoplasm was digested. At the end of the feeding process the pallium detached from the grazer and only a round fecal aggregation of undigested compacted thecate material from the prey cell remained. These round fecal aggregations were readily distinguished from intact prey cells or other detritus. For *Gonyaulax polyedra* and *Gymnodinium sanguineum* prey, the diameters of the fecal aggregations were approximately ½ and ⅓, respectively, of the original size of the pallium. The duration of the entire feeding process was usually 38 to 60 min, but could last more than 90 min. During this time the *Protoperidinium* cell continued to swim; this behavior differed from that of *Protoperidinium* feeding on large chain-forming diatoms, where grazers often remained motionless and were unable to swim with the prey (Jacobson & Anderson 1986). In many cases, a pallium containing a fecal aggregation was observed to detach prior to pallium retraction due to the swimming activities of the *Protoperidinium*. Fecal aggregations accumulated within the culture bottles.

Growth of *Protoperidinium* cf. *divergens*

Populations of *Protoperidinium* cf. *divergens* fed on *Gonyaulax polyedra* exhibited constant exponential growth for incubation periods as long as 4 d (Fig. 1A). There was a 1 d phase with reduced growth rate. This is similar to population growth of the heterotrophic dinoflagellate *Oblea rotunda* (Strom & Buskey 1993), which shows constant exponential growth for 5 d. In the present study, prey swimming activity did not change after the 4 d incubation, implying a healthy condition, but after 5 d this was observed to diminish. The growth rates calculated between time zero and either Day 3 or Day 4 (0.405 to 0.411 d^{-1}) (Fig. 1B) compared favorably with the growth rate obtained from regression of ln-transformed cell abundance vs time for Days 1 to 4 (0.477 d^{-1}).

The specific growth rate of *Protoperidinium* cf. *divergens* fed on *Gonyaulax polyedra* was dependent on mean prey concentration and perhaps influenced by initial grazer concentration (Fig. 2A). In general, specific growth rates increased with increasing mean prey concentration. The maximum specific growth rate at the lower initial grazer density (1 grazer ml^{-1}; Expt 1) averaged 0.484 d^{-1}, obtained at a mean prey concentration of 1500 cells ml^{-1}. At higher grazer concentrations (7 to 10 grazers ml^{-1}; Expt 2), maximal specific growth rate was 0.363 d^{-1} at a mean prey concentration of 1100 cells ml^{-1}. Specific growth rates for Expt 1 decreased at the highest mean prey concentration, while for Expt 2 they remained nearly saturated at mean prey concentrations above 1100 cells ml^{-1}. The

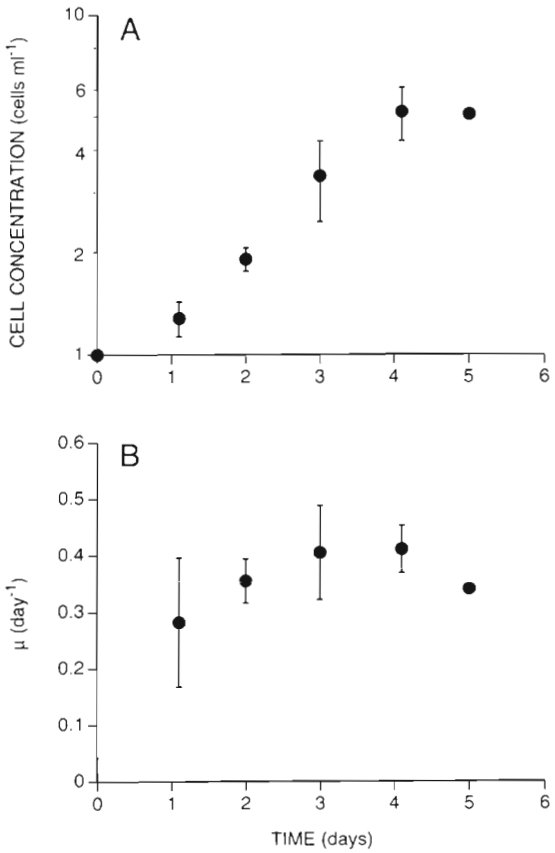

Fig. 1. Growth of *Protoperidinium* cf. *divergens* feeding on *Gonyaulax polyedra* at a prey concentration of 1400 cells ml^{-1} as a function of incubation time. Data are treatment means ±1 SE. (A) *P.* cf. *divergens* cell concentration over time. (B) Calculated *P.* cf. *divergens* population growth rates for corresponding incubation times

threshold mean prey concentration for population growth of *P.* cf. *divergens* in Expt 1 was approximately 70 to 100 cells ml^{-1}.

Cannibalism occurred mainly at high grazer concentrations. Under these conditions, *P.* cf. *divergens* were observed with a pallium containing similarly sized cells of *P.* cf. *divergens*. The rate of cannibalism, and its effect on nutrition and growth, were not quantified in this study.

The specific growth rate of *Protoperidinium* cf. *divergens* feeding on *Gymnodinium sanguineum* exhibited a different pattern (Fig. 2B) from that for *Gonyaulax polyedra*. The threshold mean prey concentration for population growth of *P.* cf. *divergens* feeding on *G. sanguineum* was 70 cells ml^{-1}, and maximum specific growth rate was 0.246 d^{-1} at a mean prey concentration of only 530 cells ml^{-1}. At mean prey concentrations higher than 1000 cells ml^{-1} the specific growth rate declined, with negative values at mean prey concentrations greater than 2000 cells ml^{-1}. An identical result was obtained in an additional experiment at the initial prey concentration of 2000 cells ml^{-1}. Microscopic examination at the highest mean prey concentration confirmed the presence of dead *P.* cf. *divergens* cells.

The instantaneous feeding frequency was the proportion of the grazer population observed feeding at any one time, determined from the presence of prey within the pallium. The maximum instantaneous feeding frequency rather than mean instantaneous feeding frequency was tabulated because evidence for diel feeding periodicity was found at the conclusion of these experiments, and sampling was conducted at different times of day for the 2 species (Table 2). The maximum instantaneous feeding frequency was diet dependent. Up to 27% of *Protoperidinium* cf. *divergens* cells were observed feeding on *Gonyaulax polyedra*, while a maximum frequency of 20% was obtained with a *Gymnodinium sanguineum* diet.

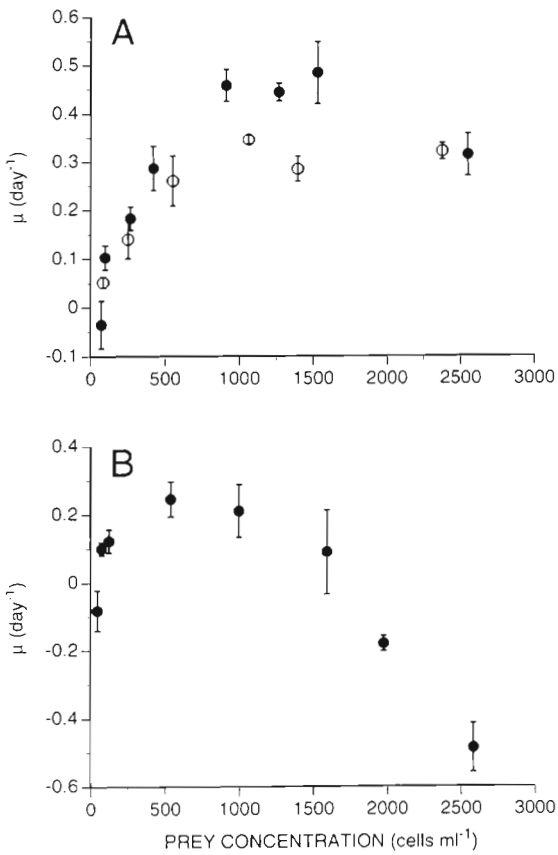

Fig. 2. *Protoperidinium* cf. *divergens*. Specific growth rate as a function of mean prey concentration. Data are treatment means ±1 SE. (A) *Gonyaulax polyedra* prey. (●) Expt 1 (initially 1 grazer ml^{-1}); (○) Expt 2 (initially 7 grazers ml^{-1} at initial prey concentrations ≤300 cells ml^{-1} and 10 grazers ml^{-1} at other initial prey concentrations). (B) *Gymnodinium sanguineum* prey. Initial grazer concentration was 1 grazer ml^{-1}

Table 2. *Protoperidinium* cf. *divergens*, *P. crassipes*. Maximum instantaneous feeding frequencies (MIFF), based on the percent ratio of *Protoperidinium* with a pallium to total grazers, for a variety of dinoflagellate prey. n: number of *Protoperidinium* observed

Prey	*P.* cf. *divergens*		*P. crassipes*	
	MIFF	n	MIFF	n
Gonyaulax polyedra	27	7086	17	2474
Gymnodinium sanguineum	20	1782	5	734
Scrippsiella trochoidea	25	621	10	673
Prorocentrum cf. *balticum*	0	552	0	537

Gonyaulax polyedra and *Gymnodinium sanguineum* were the only dinoflagellate prey tested that supported population growth of *Protoperidinium* cf. *divergens*. Other prey species tested were *Scrippsiella trochoidea* and *Prorocentrum* cf. *balticum*. Although *P.* cf. *divergens* were observed to feed on *S. trochoidea*, based on the presence of grazers with a pallium containing prey cells, the specific growth rate of *P.* cf. *divergens* fed on *S. trochoidea* was zero at prey concentrations between 1000 and 6000 cells ml^{-1}, and were negative for prey concentrations of 500 and ≥8000 cells ml^{-1}. The maximum instantaneous feeding frequency of *P.* cf. *divergens* feeding on *S. trochoidea* was similar to that for *G. polyedra* (Table 2), even though the specific growth rate for the former diet was zero. There were no observed differences in the size or swimming pattern of *P.* cf. *divergens* after feeding experiments with *G. polyedra* and *S. trochoidea*.

The specific growth rate of *Protoperidinium* cf. *divergens* fed on *Prorocentrum* cf. *balticum* was negative, and *P.* cf. *divergens* with a pallium were not observed in this treatment.

Growth of *Protoperidinium crassipes*

Generally, the pattern of specific growth rate as a function of mean prey concentration for *Protoperidinium crassipes* was similar to that of *P.* cf. *divergens* for each diet, although the rates were lower.

Protoperidinium crassipes fed *Gonyaulax polyedra* grew maximally at a mean prey concentration of 760 cells ml^{-1} (Fig. 3A). At higher mean prey concentrations the specific growth rate decreased. At all mean prey concentrations >75 cells ml^{-1}, specific growth rates at the lower initial grazer concentration of 1 grazer ml^{-1} (Expt 3) were higher than those at the higher concentration of 7 to 10 grazers ml^{-1} (Expt 4). The maximum specific growth rate for Expt 3 was 0.308 d^{-1}, while for Expt 4 it was 0.155 d^{-1} The threshold mean prey concentration for the population growth of *P. crassipes* for Expt 3 was approximately 70 to 90 cells ml^{-1}, similar to that of *P.* cf. *divergens*. Mainly at high grazer concentrations, cannibalism by *P. crassipes* on similar-sized cells was observed.

The specific growth rate of *Protoperidinium crassipes* fed on *Gymnodinium sanguineum* (Fig. 3B) exhibited a maximum of 0.107 d^{-1} at a mean prey concentration of 1050 cells ml^{-1}, with a decrease at greater

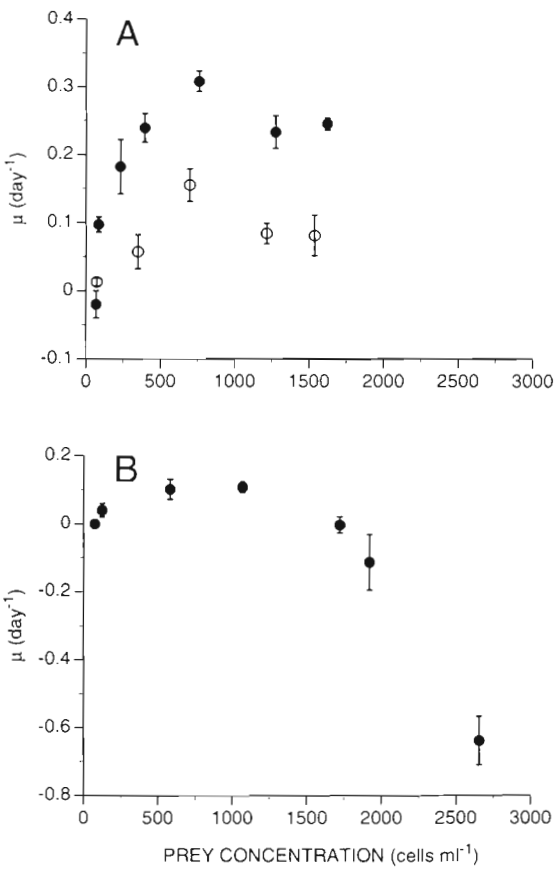

Fig. 3. *Protoperidinium crassipes*. Specific growth rate as a function of mean prey concentration. As in Fig. 2. (A) *Gonyaulax polyedra* prey. (●) Expt 3 (initially 1 grazer ml^{-1}); (○) Expt 4 (initially 7 grazers ml^{-1} at an initial prey concentration of 100 cells ml^{-1} and 10 grazers ml^{-1} at the other initial prey concentrations). (B) *Gymnodinium sanguineum* prey. Initial grazer concentration was 1 grazer ml^{-1}

concentrations. Specific growth rates were negative at mean prey concentrations ≥2000 cells ml^{-1}.

The maximum feeding frequencies of *Protoperidinium crassipes* on *Gonyaulax polyedra*, *Gymnodinium sanguineum*, and *Scrippsiella trochoidea* were lower than those of *P.* cf. *divergens* (Table 2). Even though *P. crassipes* fed on *S. trochoidea*, based on the presence of a pallium containing prey cells, specific growth rate was zero for this diet. A *Prorocentrum* cf. *balticum* diet did not support population growth of *P. crassipes*, nor did grazers make a pallium.

Ingestion and clearance rates

Ingestion rates calculated from final concentrations of prey in control and experimental bottles (Method 1) were consistently higher than those determined by enumerating fecal aggregations (Method 2). How long fecal aggregations persist is not known, although the evidence of Jacobson & Anderson (1993) suggested that no degradation occurs due to the surrounding pallium. However, if some degrade during the incubation period then lower counts of fecal aggregations would be obtained. In any case, the pattern of ingestion rates as a function of mean prey concentration with both methods was similar (Fig. 4A). The ingestion rate of *Protoperidinium* cf. *divergens* feeding on *Gonyaulax polyedra* increased with increasing mean prey concentration to a maximum of 4.8 prey $grazer^{-1}$ d^{-1} for Method 1 and 3.5 prey $grazer^{-1}$ d^{-1} for Method 2. Ingestion rates saturated at mean prey concentrations ≥1100 cells ml^{-1} for both methods within the range tested. No threshold significantly different from 0 was found for either curve ($p > 0.05$) using nonlinear regression (NLIN procedure; SAS 1990). Clearance rates determined by both methods decreased with increasing mean prey concentration (Fig. 4B). Maximum clearance rate for Method 1 was 0.67 µl $grazer^{-1}$ h^{-1} and for Method 2 was 0.38 µl $grazer^{-1}$ h^{-1}. Maximum volume-specific clearance rate for Method 1 was 5.6×10^3 h^{-1} and for Method 2 was 3.2×10^3 h^{-1}. The gross growth efficiency of *P.* cf. *divergens* fed on *G. polyedra* was 13.8 to 37% for Method 1 and 21.7 to 41.3% for Method 2.

Ingestion and clearance rates of *Protoperidinium crassipes* feeding on *Gonyaulax polyedra* as functions of mean prey concentration were based on Method 2 only. Because of the low specific growth rate of *P. crassipes*, differences in the final concentrations of prey between control and grazing bottles at high mean prey concentrations were not significant. Ingestion rate increased with mean prey concentration to a maximum of 2.1 prey $grazer^{-1}$ d^{-1}, reached at a mean prey concentration of 700 cells ml^{-1} (Fig. 5A). At higher mean prey concentrations there was a slight decrease in ingestion rate. Clearance rate decreased with mean prey concentration (Fig. 5B). Maximum clearance rate was 0.47 µl $grazer^{-1}$ h^{-1}. Maximum volume-specific clearance rate was 2.3×10^3 h^{-1}. The gross growth efficiency of *P. crassipes* feeding on *G. polyedra* was 8.7 to 47.2%.

The preference of *Protoperidinium* cf. *divergens* for a particular diet was determined from the ratio of ingestion rates for *Gonyaulax polyedra* and *Gymnodinium sanguineum* as a function of the ratio of the mean prey concentrations (Fig. 6A). All data points but one were above the 1:1 line, indicating that *P.* cf. *divergens* preferred *G. polyedra* to *G. sanguineum*. In these experiments the specific growth rate of *P.* cf. *divergens* was strongly correlated with the absolute concentration of *G. polyedra* (Fig. 6B).

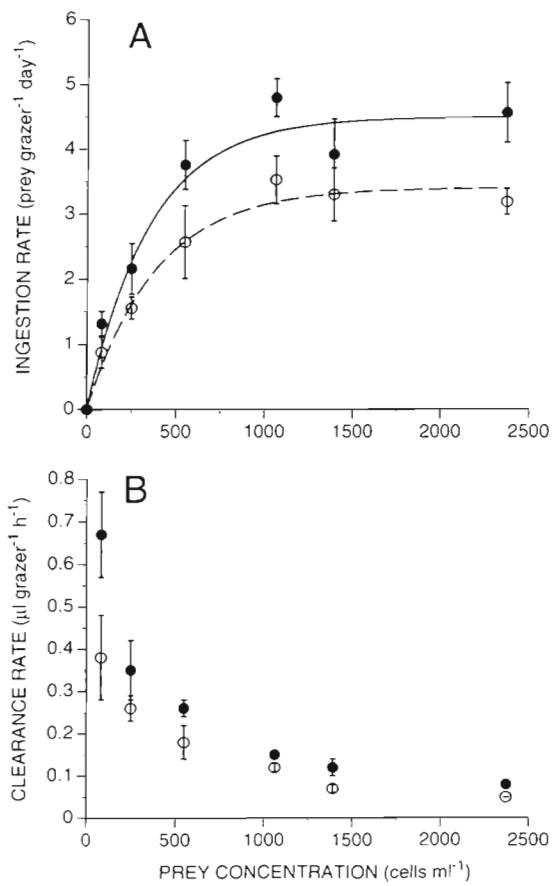

Fig. 4. *Protoperidinium* cf. *divergens* feeding on *Gonyaulax polyedra*. Data are treatment means ± 1 SE. (A) Ingestion rate as function of mean prey concentration). (●) Method 1 (see text); (○) Method 2. Both curves are fitted by the Ivlev model. Method 1: ingestion rate (IR, prey $grazer^{-1}$ d^{-1}) = $4.5(1 - e^{-0.00282\bar{c}})$, $R^2 = 0.967$; Method 2: IR = $3.4(1 - e^{-0.00259\bar{c}})$, $R^2 = 0.964$; where $\bar{c}$ = mean prey concentration. (B) Clearance rate as a function of mean prey concentration. (●) Method 1; (○) Method 2

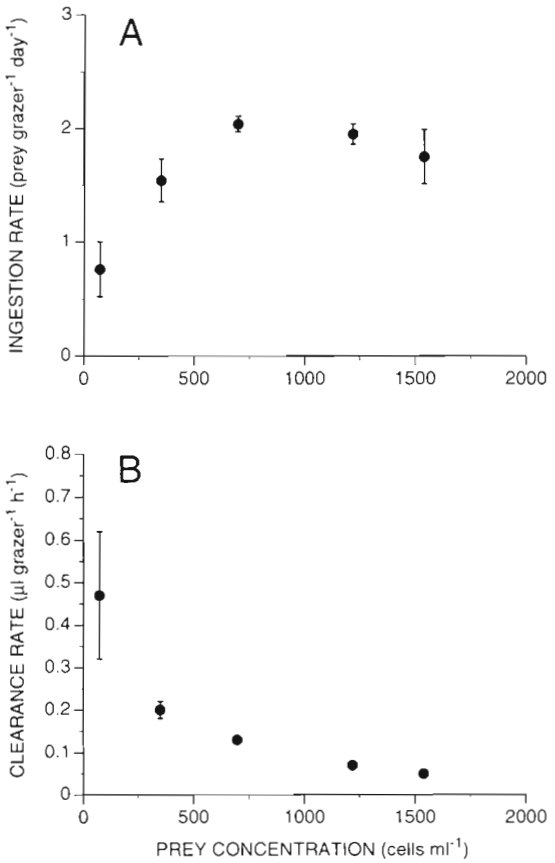

Fig. 5. *Protoperidinium crassipes* feeding on *Gonyaulax polyedra*. As in Fig. 4. (A) Ingestion rate as a function of mean prey concentration, based on enumeration of round fecal aggregations. (B) Clearance rate as a function of mean prey concentration, based on enumeration of round fecal aggregations

The size distribution of *Protoperidinium* cf. *divergens* changed from an initial range of 55.4–73.6 µm ESD (median 64.1 µm) to 11.2–75.4 µm (median 14.93 µm) after 12 d without added prey. Some cells were observed swimming even after 15 d without added prey.

DISCUSSION

Populations of *Protoperidinium* cf. *divergens* and *P. crassipes* grow well in culture when maintained on unialgal diets of some local red tide dinoflagellates. This was expected because *Protoperidinium* has been observed to be very abundant during some local red tides (Torrey 1902, Allen 1949, Jeong unpubl. data). To date only *P. pyriforme*, *P. divergens*, and *P. pellucidum* have been described as feeding on dinoflagellates (Jacobson & Anderson 1986, Hansen 1991). Most *Protoperidinium* species have been reported to feed on diatoms (Jacobson & Anderson 1986, 1992, Buskey et al. 1992, Hansen 1992) and bacteria (Lessard & Swift 1985, Lessard & Rivkin 1986), even though the entire dietary range of any species has yet to be determined. During initial enrichment experiments, cells of other *Protoperidinium* species similar in size to and also smaller than the species tested were observed to produce a pallium and feed on the local red tide dinoflagellates *Gonyaulax polyedra*, *Gymnodinium sanguineum*, and *Scrippsiella trochoidea*.

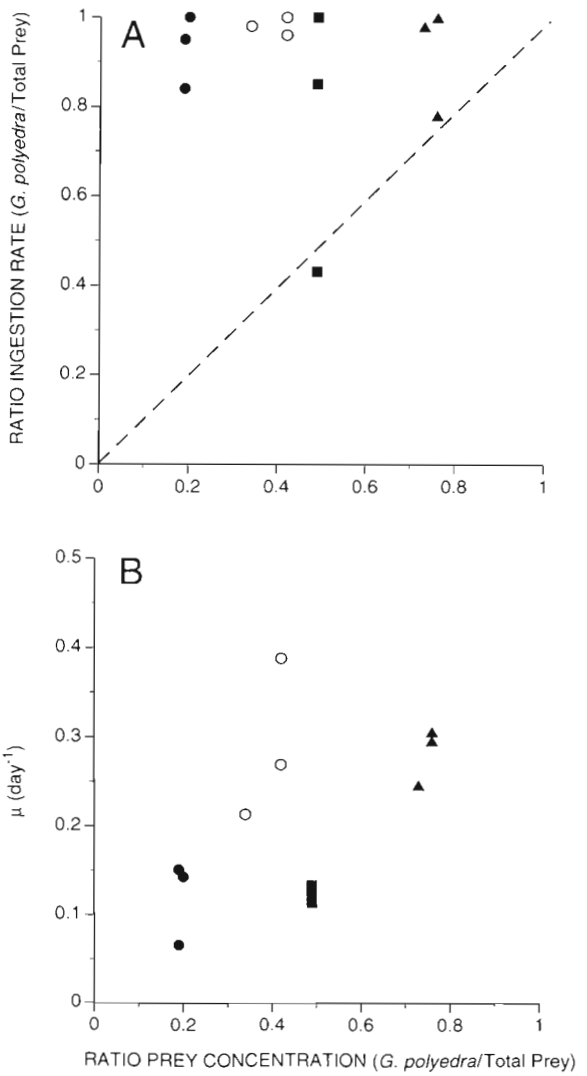

Fig. 6. Prey selection of *Protoperidinium* cf. *divergens* on a mixed diet of *Gonyaulax polyedra* and *Gymnodinium sanguineum*. Each symbol represents the result of a single incubation bottle. (A) Ingestion of *G. polyedra* relative to ingestion of total prey (*G. polyedra* and *G. sanguineum*), compared to relative availability of *G. polyedra*. Initial prey concentrations of *G. polyedra* and *G. sanguineum*, respectively, were 333 and 1000 cells ml^{-1} (●), 500 and 500 cells ml^{-1} (■), 1000 and 1000 cells ml^{-1} (○), and 1000 and 333 cells ml^{-1} (▲). (B) Specific growth rate of *P.* cf. *divergens* as a function of the ratio of *G. polyedra* to total mean prey concentration. Symbols as in (A)

The larger dinoflagellates *Gonyaulax polyedra* and *Gymnodinium sanguineum* supported population growth of *Protoperidinium* cf. *divergens* and *P. crassipes*, while the smaller dinoflagellates *Prorocentrum* cf. *balticum* and *Scrippsiella trochoidea* did not. On the basis of growth rates and prey selection, for both grazer species *G. polyedra* was the optimal prey tested.

The maximum specific growth rates (μ_{max}) of *Protoperidinium* cf. *divergens* and *P. crassipes* were 0.484 and 0.308 d^{-1} at 19°C, respectively, approximately 50 and 33% of those for ciliates of equivalent cell volumes at 20°C (Banse 1982, Fenchel & Finlay 1983), and 40% and 25% of that for the tintinnid ciliate *Favella* at 19°C, which grows well on red tide dinoflagellates such as *Gonyaulax polyedra*, *Gymnodinium sanguineum*, and *Scrippsiella trochoidea* (Stoecker et al. 1981, Jeong unpubl. data). Hansen (1992) found a linear relationship between maximum growth rate and cell volume [$\log \mu\ (h^{-1}) = -0.513 - 0.244 \log V\ (\mu m^3)$, where V = cell volume] for some heterotrophic dinoflagellates with $< 3 \times 10^4$ μm^3 cell volume. The μ_{max} values for *P.* cf. *divergens* and *P. crassipes* (1.2×10^5 and 2×10^5 μm^3 in cell volume, respectively) obtained in the present study are similar to values calculated from this equation. Therefore the constant relationship of maximum growth rate to cell volume also is valid for much larger heterotrophic dinoflagellates.

The μ_{max} values obtained for *Protoperidinium* cf. *divergens* and *P. crassipes* feeding on *Gonyaulax polyedra* and *Gymnodinium sanguineum* are similar to or larger than those of the prey populations (Thomas et al. 1973, Prézelin & Sweeney 1978), as is true for small heterotrophic dinoflagellates and their prey (Goldman et al. 1989).

The specific growth rates of *Protoperidinium* cf. *divergens* and *P. crassipes* fed on *Gymnodinium sanguineum* were lower than for a *Gonyaulax polyedra* diet. This may be due to the lower carbon content of *G. sanguineum* compared to that of *G. polyedra* (Fernández 1979), and the lower maximum feeding frequencies on *G. sanguineum* compared to those of *G. polyedra*. The ratio of surface area to volume of *G. sanguineum* is 60% larger than for *G. polyedra* (Kamykowski et al. 1992). Therefore, *Protoperidinium* might spend more energy in pallium deployment on *G. sanguineum* than *G. polyedra* to gain the same carbon content for their growth.

For both grazers negative growth occurred at mean *Gymnodinium sanguineum* concentrations >2000 cells ml^{-1}, and dead *Protoperidinium* were observed. Because high concentrations of *Gonyaulax polyedra* did not result in negative population growth, mechanical interference from the high number of prey cells may not be responsible. *G. sanguineum* has been demonstrated to be mixotrophic (Hellebust 1970, cited in Gaines & Elbrächter 1987; Bockstahler & Coats 1993), so perhaps when in high numbers *G. sanguineum* attacks the grazers, although *P.* cf. *divergens* and *P. crassipes* are much larger than the prey found inside vacuoles of *G. sanguineum* (Bockstahler & Coats 1993). Alternatively, the toxicity of *G. sanguineum* may affect the growth of *Protoperidinium*. *G. sanguineum* has been reported to excrete toxic substances which inhibit the growth of fungi (Nagai et al. 1990). Additional experiments are needed to determine the mechanism responsible. In the field, *Protoperidinium* may avoid dense layers of *G. sanguineum* by regulating its vertical distribution, as do some copepods (Fiedler 1982).

The smaller dinoflagellate *Scrippsiella trochoidea* did not support population growth of *Protoperidinium* cf. *divergens* and *P. crassipes*, even though it was actively grazed by these species and was an excellent food for an unidentified small *Protoperidinium* species (slightly larger than *Gonyaulax polyedra*). This suggests, at least for this prey species, that feeding frequency was not an accurate indicator of prey suitability for long-term culturing. An *S. trochoidea* diet appears to fulfill routine energy requirements, but is insufficient to support population growth. There were no observed differences in size and swimming pattern of *P.* cf. *divergens* fed on *G. polyedra* and *S. trochoidea* after 4 d or 1 wk incubations, and the bioluminescence of *P.* cf. *divergens* following a 4 d incubation with *S. trochoidea* was not significantly different from that after being maintained on a *G. polyedra* diet (Latz & Jeong unpubl. data). This suggests that an *S. trochoidea* diet can maintain *P.* cf. *divergens* populations in a healthy condition with no net energy gain or loss.

The smallest prey used in this study, *Prorocentrum* cf. *balticum*, did not support population growth nor was there evidence of feeding based on pallium formation. However, Lessard & Swift (1985) found evidence for ingestion of bacteria by *Protoperidinium* species similar in size to *Protoperidinium* cf. *divergens* and *P. crassipes*, although it is not known whether this was sufficient to support population growth.

Some studies have suggested that the most efficient feeding mechanism and maximum specific clearance are a function of predator-to-prey size ratio in flagellates and ciliates (Fenchel 1986, Goldman & Dennett 1990). An optimal ratio for maximum growth rate may also be important in predator and prey population dynamics. *Protoperidinium* is a raptorial feeder and can feed on prey larger than itself. The growth rate of this heterotrophic dinoflagellate varied greatly depending on prey size. Based on data from this study, the maximum growth rate, μ_{max}, is negatively corre-

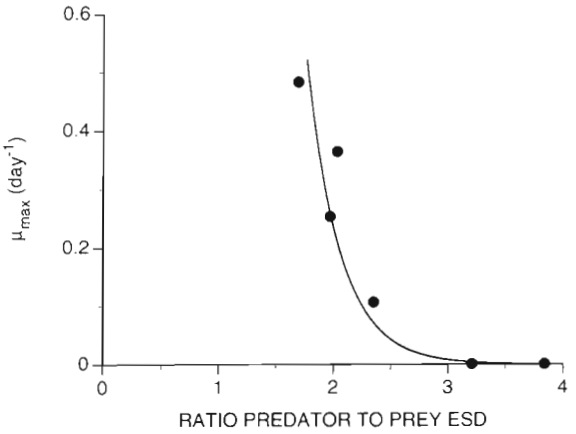

Fig. 7. Maximum growth rate, μ_{max}, of *Protoperidinium* cf. *divergens* and *P. crassipes* feeding on red tide dinoflagellate prey as a function of the ratio of predator-to-prey ESD. The least squares exponential regression is given as $\mu_{max} = 200.89\,e^{-3.378x}$ ($R^2 = 0.93$) for $x \geq 1.69$, where x is the ratio of predator-to-prey ESD

lated with the ratio of predator-to-prey ESD for ratios ≥1.69 (Fig. 7). Population growth of *Protoperidinium* occurs for a predator-to-prey size ratio ≤3. The correlation between the maximum growth rate and ratio of predator-to-prey ESD suggests that the growth rates and feeding frequencies of *P. crassipes* might have been greater if it had fed on larger prey than those tested in this study. In preliminary tests, populations of *P. depressum* (Bailey) Balech (125 µm ESD), larger than *P. crassipes*, did not grow when fed on *Gonyaulax polyedra*, suggesting that they may require much larger sized prey.

Protoperidinium cf. *divergens* and *P. crassipes* fed on conspecific cells of similar size. Cannibalism was observed in cultures mainly when grazer populations were high. Cannibalism may be responsible for the maintenance of some large (ca 75 µm) cells of *P.* cf. *divergens* without added prey, even though median cell size decreases. Cannibalism may also be responsible for decreased growth rates obtained for higher initial grazer concentrations of 7 to 10 grazers ml^{-1}. If this is true then the measured grazing rate may be overestimated.

The maximal instantaneous feeding frequency was 27% for a *Gonyaulax polyedra* diet, similar to the value of 30% obtained for *Protoperidinium hirobis* feeding on the diatom *Leptocylindrus danicus* (Jacobson & Anderson 1993). Because the maximal instantaneous feeding frequency was not higher for smaller prey such as *Scrippsiella trochoidea*, these values may represent a maximal potential feeding frequency. Differences in specific growth rates for the various diets were not due to differences in feeding frequency.

There are few data on prey selection of heterotrophic dinoflagellates in mixtures of prey (Strom 1991). *Protoperidinium* were expected to exhibit prey selection due to their precapture behavior, which involves spinning around a target prey cell (Jacobson & Anderson 1986). *P.* cf. *divergens* clearly preferred *Gonyaulax polyedra* over *Gymnodinium sanguineum* in mixed diets. Microscope observations confirmed that *P.* cf. *divergens* produced a pallium much more frequently with *G. polyedra* cells than with *G. sanguineum*. Even though the prey concentrations of *G. sanguineum* in these experiments were optimal for the growth of *P.* cf. *divergens*, the specific growth rate of *P.* cf. *divergens* on mixtures of *G. polyedra* and *G. sanguineum* was strongly correlated with an absolute concentration of *G. polyedra*. Ciliates also exhibit differential ingestion of prey not according to relative abundance, when a mixture of acceptable prey and less preferred prey is offered (Verity 1991).

Other microzooplankton have higher ingestion rates than *Protoperidinium*. The maximum ingestion rates of *P.* cf. *divergens* and *P. crassipes* fed on *Gonyaulax polyedra*, 0.2 and 0.08 prey *Protoperidinium*$^{-1}$ h^{-1}, respectively, were only 10 and 4%, respectively, of that of the tintinnid ciliate *Favella*, which is approximately 2 prey *Favella*$^{-1}$ h^{-1} (Jeong unpubl. data). Maximum clearance rates were slightly higher than that of *P. hirobis* feeding on *Leptocylindrus danicus* (Jacobson & Anderson 1993), but much lower than the values for freshly collected *P. divergens* feeding on natural particles including bacteria (Lessard & Swift 1985). Ingestion of bacteria may occur by a different feeding strategy not involving production of a pallium. Alternatively, differences in experimental methodology may explain differences in clearance rate, as suggested by Jacobson (1987).

The maximum grazing impact of microzooplankton during local red tides can be estimated based on the product of ingestion rate and grazer abundance. The ciliates *Favella* and *Tiarina*, as well as *Protoperidinium*, are associated with dinoflagellate red tides in the La Jolla area (Beers 1986, Jeong unpubl. data), and grow well feeding on the dinoflagellates *Gonyaulax polyedra*, *Scrippsiella trochoidea*, and *Gymnodinium sanguineum* (Stoecker et al. 1981, Jeong unpubl. data). The maximum growth rates of these ciliates are some 4 times higher than for *Protoperidinium*. However, the maximum abundances of *Favella* and *Tiarina* during local red tides (approximately 500 to 1000 ind. l^{-1} for each genus; Jeong unpubl. data), are much less than that for *Protoperidinium*. For an ingestion rate of 0.2 prey grazer^{-1} h^{-1} and a grazer abundance of 24000 ind. l^{-1} (Allen 1949), the estimated impact on *G. polyedra*, 4800 prey ingested l^{-1} h^{-1}, is more than double that of *Favella*, which has an ingestion rate of 2 prey grazer^{-1} h^{-1}, an

abundance of 1000 ind. l^{-1}, and a calculated impact of 2000 prey ingested l^{-1} h^{-1}.

In the Southern California Bight, *Protoperidinium* is present in the plankton throughout the year (Allen 1949, Reid et al. 1970, Beers 1986). Several mechanisms may contribute to its maintenance during unfavorable prey conditions (Jacobson & Anderson 1986, present study):

(1) Populations can be maintained on a suboptimal diet even if it results in no net population growth. During initial tests, *P.* cf. *divergens* and *P. crassipes* were maintained on diatoms even though population growth did not occur. The maximum abundance of *Protoperidinium* during local diatom blooms is approximately 1200 ind. l^{-1} (Allen 1949), less than that during dinoflagellate red tides. In contrast, ciliates which feed on red tide dinoflagellates have a more limited dietary range and do not feed on diatoms (Stoecker et al. 1981).

(2) *Protoperidinium*, as well as other heterotrophic dinoflagellates, is able to resist starvation (Goodman 1987, Buskey et al. 1992, Hansen 1992, present study). In 2 experiments, *P.* cf. *divergens* was observed alive and swimming after 12 d without added prey. *Favella* is unable to resist starvation and dies within 3 d without food (Jeong pers. obs.), even though some ciliates can resist long starvation (Jackson & Berger 1984).

(3) *Protoperidinium* feeds on conspecific cells in order to survive prolonged starvation as mentioned above. Cells presumably cannibalize unhealthy cells with impaired motility.

Cyst formation may be another mechanism used by dinoflagellates to survive periods of starvation (Goodman 1987). However, it is unknown if *Protoperidinium* uses cyst formation as a strategy for resisting starvation because at no time during the present study were cysts of *Protoperidinium* observed.

The ability to prey on a variety of food, including conspecific cells, and resistance to prolonged starvation, may allow *Protoperidinium* to maintain baseline populations at higher levels between blooms than do other microzooplankton grazers. This ability, coupled with population growth when suitable dinoflagellates are abundant, may explain the high abundance of *Protoperidinium* during red tides. *Protoperidinium* grazing may be important in regulating the populations of some red tide dinoflagellates, especially during the peak and decline of red tides.

Acknowledgements. We thank Michael Mullin, Mark Ohman, and Elizabeth Venrick for providing facilities and for comments on the manuscript. This paper was funded by a grant from California Sea Grant Graduate Fellowship Program, NOAA, U.S. Department of Commerce, (grant number NA89AA-D-SG138, project number E/G-10-6A) to H.J.J. and a grant from the Office of Naval Research (N00014-92-J-1475) to M.I.L.

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This article was presented by D. K. Stoecker, Cambridge, Maryland, USA

Manuscript first received: June 29, 1993
Revised version accepted: November 16, 1993