Predation effects of the calanoid copepod *Acartia tonsa* on a population of the heterotrophic dinoflagellate *Protoperidinium* cf. *divergens* in the presence of co-occurring red-tide dinoflagellate prey

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ABSTRACT: This study investigated feeding rates and selective feeding of the common copepod *Acartia tonsa* on mixtures of the heterotrophic dinoflagellate *Protoperidinium* cf. *divergens* and the co-occurring red-tide dinoflagellate *Gonyaulax polyedra* and predation effects of *A. tonsa* on the population growth of *P.* cf. *divergens* during simulated red-tide and non-red-tide periods. Ingestion and clearance rates of *A. tonsa* on *P.* cf. *divergens* were similar to those on ciliates of similar cell volumes measured in other studies, when each heterotrophic protist was offered as the only prey and similar prey densities were used. In general, in mixed prey experiments, there was no evidence of a strong preference by *A. tonsa* for *P.* cf. *divergens* over *G. polyedra*. However, there may be a weak preference at low total prey concentrations or low ratios of prey availability (*G. polyedra*:*P.* cf. *divergens*). *A. tonsa* ingested similar amounts of carbon from *P.* cf. *divergens* and *G. polyedra* at a *G. polyedra*:*P.* cf. *divergens* carbon biomass ratio of about 1.8. The maximum clearance rate of *A. tonsa* on *P.* cf. *divergens* (5.5 ml *Acartia*$^{-1}$ h^{-1}) was higher than that on *G. polyedra* (3.1 ml *Acartia*$^{-1}$ h^{-1}). The effect of *A. tonsa* predation on the population growth of *P.* cf. *divergens* decreased with increasing *G. polyedra* concentrations and was negligible at 2200 cells ml^{-1}. At low *G. polyedra* concentrations, high mortality rates of *P.* cf. *divergens* due to *A. tonsa* predation may enable *A. tonsa* to limit the population growth of *P.* cf. *divergens*. However, a dense layer of *G. polyedra* may provide *P.* cf. *divergens* a 'refuge' from *A. tonsa* predation during red tides.

KEY WORDS: Copepod · Dinoflagellates · Microzooplankton · Protozoa · Predation · Red tides

INTRODUCTION

Heterotrophic protists are a significant component of the nanoplankton and microplankton in marine environments (Porter et al. 1985, Stoecker & Capuzzo 1990). Many are important potential prey for zooplankton and some fish larvae (Sherr et al. 1986, Gifford & Dagg 1988, 1991, Ohman et al. 1991). It has been suggested that the predation by crustacean zooplankton on heterotrophic protists such as ciliates and heterotrophic dinoflagellates can affect prey population dynamics (Smetacek 1981, Sheldon et al. 1986, Stoecker & Capuzzo 1990). So far, most studies of the predation by copepods on heterotrophic protists have focused on ciliates, emphasizing their importance as a food source for copepods (Stoecker & Egloff 1987, Gifford & Dagg 1988, 1991, Ohman & Runge 1994). Heterotrophic dinoflagellates are often among the most abundant heterotrophic protists (Lessard 1984, Jacobson 1987, Jeong unpubl.), and the heterotrophic dinoflagellate *Oxyrrhis marina* has proved suitable food for continuously breeding and culturing some copepods (Klein Breteler 1980, Klein Breteler & Gonzalez 1986, 1988). However, there are a few studies (Klein Breteler et al. 1990, Gifford & Dagg 1991, Hansen et al. 1993) quantifying the predation rates of copepods on heterotrophic dinoflagellates and the predation effect of copepods on dynamics of both heterotrophic dinoflagellates and their phytoplankton prey.

Species in the genus *Protoperidinium* often dominate the biomass of heterotrophic protists ≥ 20 µm in size in coastal (Jacobson 1987) and oceanic waters (Lessard 1984). They are present all year in the coastal waters of southern California, USA (Allen 1949, Reid et al. 1970) and are often particularly abundant (up to 26.5 cells ml^{-1}) during red tides of autotrophic dinoflagellates (Allen 1949, Jeong unpubl. data) or during diatom blooms (Jacobson 1987). Jeong & Latz (1994) showed that some species of *Protoperidinium* grew well on some southern Californian red-tide dinoflagellates in laboratory cultures, and suggested that *Protoperidinium* might have a considerable grazing impact on their populations.

Co-occurring algal prey for *Protoperidinium* may significantly reduce the predation by copepods on *Protoperidinium*. Under some conditions, the presence of algae reduces the ingestion and clearance rates of microzooplankton by copepods (Anraku & Omori 1963, Landry 1981, Stoecker & Sanders 1985), but not under others (Lonsdale et al. 1979, Paffenhöfer & Knowles 1980).

Selective feeding of copepods on heterotrophic protists over co-occurring phytoplankton may be very important in the population dynamics of both prey, especially if the phytoplankton are also prey for the heterotrophic protists. Several studies (Stoecker & Egloff 1987, Wiadnyana & Rassoulzadegan 1989, Ohman & Runge 1994) showed that the clearance rates of copepods on ciliates were markedly higher than those on phytoplankton, and copepods sometimes fed on ciliates preferentially to phytoplankton in mixtures.

Protoperidinium feeds on prey cells by using a pseudopod 'veil', called the pallium, to envelop the prey, with subsequent external digestion (Gaines & Taylor 1984, Jacobson & Anderson 1986). This unique feeding mechanism enables *Protoperidinium* to feed on prey larger than itself. Jeong & Latz (1994) suggest that *Protoperidinium* requires dinoflagellate prey larger than one-third of its own size for its population growth, and can achieve higher growth rates on larger prey. Therefore, size or motility differences between *Protoperidinium* and their dinoflagellate prey during red tides may be less than those for most ciliates and their prey.

The objectives of this study were to test the following hypotheses:

H$_0$1: the presence of co-occurring red-tide dinoflagellate prey does not significantly affect the ingestion and clearance rates of copepods on *Protoperidinium*.

H$_0$2: copepods do not distinguish between (i.e. do not have a preference for) the heterotrophic dinoflagellate *Protoperidinium* and co-occurring red-tide dinoflagellate prey.

H$_0$3: copepod predation does not significantly affect the population growth of *Protoperidinium* during either simulated red-tide or non-red-tide periods.

In order to explore whether copepods might encounter *Protoperidinium* at rates similar to encounter rates with ciliates or large autotrophic dinoflagellates, the swimming speed of *Protoperidinium* cf. *divergens* was measured. This study provides a basis for understanding the interactions among these 3 important components of the plankton community, especially during red tides.

MATERIALS AND METHODS

Preparation of experimental organisms. *Gonyaulax polyedra* Stein, *Protoperidinium* cf. *divergens* (Ehrenberg) Balech, and *Acartia tonsa* Dana were chosen for these experiments. *G. polyedra* is one of the most common red-tide dinoflagellates in the coastal waters off southern California (Eppley & Harrison 1975). Several species of *Protoperidinium* have been abundant during the red tides dominated by *G. polyedra* (Allen 1949), which is a preferred prey for *P.* cf. *divergens* (Jeong & Latz 1994). *A. tonsa* is one of the most common copepods in the coastal zone and often abundant during red tides of *G. polyedra* (Morey-Gaines 1980). The ratio of the diameter of *P.* cf. *divergens* (61 µm in equivalent spherical diameter) to *G. polyedra* (36 µm) is about 1.7.

Gonyaulax polyedra was 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.

A dense population of cultured *Protoperidinium* cf. *divergens*, originally collected from the Scripps Institution of Oceanography pier, California, USA, during October, 1992, was used for these experiments. Details of culturing this species are described by Jeong & Latz (1994).

Adult female *Acartia tonsa* were collected from the coastal waters off La Jolla Bay, California, using a 303 µm mesh net, and acclimated for 20 to 24 h in a 19 °C room in the presence of *Gonyaulax polyedra* and *Protoperidinium* cf. *divergens*.

Experimental designs. The initial densities of the predator and prey are given in Table 1. Expts 1 and 2 were designed to measure the ingestion and clearance rates of copepods on *Protoperidinium* cf. *divergens* without additional prey. Expts 3, 4, and 5, where the concentration of *P.* cf. *divergens* was fixed, while that of *Gonyaulax polyedra* varied in each experiment, were designed to test the hypotheses stated previously.

Table 1. Design of experiments. Numbers in prey and predator columns are initial densities

Expt no.	Prey		Predator
	Gonyaulax polyedra (cells ml^{-1})	*Protoperidinium* cf. *divergens* (cells ml^{-1})	*Acartia tonsa* (ind. l^{-1})
1	0	1, 5, 15, 60	12, 16, 20
2	0	1, 3, 5, 10, 20	12, 16, 20
3	1.5, 5, 30, 100, 200	3	12, 16, 20
4	10, 30, 50, 300, 700	7	20
5	20, 60, 500, 1000, 2500	10	20

Dense cultures of *Protoperidinium* cf. *divergens* were sieved though 54 µm mesh; the large cells retained were transferred to a 270 ml polycarbonate (PC) bottle. Most *P.* cf. *divergens* sieved recovered their normal swimming ability within 30 min. Three 1 ml aliquots from the bottle were counted to determine density. In Expts 1 and 2, the concentration of 1 *P.* cf. *divergens* ml^{-1} was obtained by individually transferring cells by a micropipette into triplicate 500 ml PC bottles, and other *P.* cf. *divergens* concentrations by volume conversion with an autopipette. The variation in *P.* cf. *divergens* concentrations among control bottles after incubation (for 17 to 20 h) was $\leq 7.3\%$, further suggesting that this method is precise. To minimize the depletion of prey, only 6 female *Acartia tonsa* (12 *Acartia* l^{-1}) for 1 *Protoperidinium* ml^{-1}, 8 (16 *Acartia* l^{-1}) for 3 and 5 *Protoperidinium* ml^{-1}, and 10 (20 *Acartia* l^{-1}) for other prey concentrations were added to the 500 ml PC bottles. Triplicate control bottles contained only *P.* cf. *divergens*. In Expts 3, 4, and 5, mixtures of *Gonyaulax polyedra* and *P.* cf. *divergens*, and 6 female *A. tonsa* (12 *Acartia* l^{-1}) for 1.5 *Gonyaulax* ml^{-1}, 8 (16 *Acartia* l^{-1}) for 5 *Gonyaulax* ml^{-1}, and 10 (20 *Acartia* l^{-1}) for other prey concentrations were added to 500 ml PC bottles. Triplicate control bottles containing only *G. polyedra* and *P.* cf. *divergens* at all prey concentration combinations were set up.

Experimental and control bottles were placed on rotating wheels at 0.9 rpm under dim light at 19°C for 17 to 20 h. After incubation, *Acartia tonsa* were sieved through a 101 µm net and counted. The remaining contents in experimental and control bottles were fixed with acidic Lugol's solution.

Ingestion rates were calculated by comparing final concentrations of prey in experimental and control bottles. The final concentrations of *Protoperidinium* cf. *divergens* were measured by counting more than 100 cells in multiwell chambers by removal with a micropipette. The final concentrations of *Gonyaulax polyedra* were measured by counting 200 to 500 cells in multiwell chambers by removal for low *G. polyedra*

concentrations and in 1 ml Sedgewick-Rafter counting chambers for high concentrations.

Using the equations of Frost (1972), ingestion (prey ingested *Acartia*$^{-1}$ h^{-1}) and clearance rates (ml *Acartia*$^{-1}$ h^{-1}) of *A. tonsa* on *Protoperidinium* cf. *divergens* or *Gonyaulax polyedra* were calculated. When the initial prey concentrations in the control (C_0) and experimental bottles ($C_0^\bullet$) are equal, the mortality rate of prey due to *A. tonsa* predation (predation coefficient g, h^{-1}) can be calculated from

$$g = \frac{1}{t}\ln\left(\frac{C_t}{C_t^\bullet}\right)$$

where C_t and $C_t^\bullet$ are the final prey concentrations in the control and experimental bottles, respectively. In Expts 3, 4, and 5, control bottles contained *G. polyedra* and *P.* cf. *divergens*, while experimental bottles contained *A. tonsa* in addition to these 2 prey. In control bottles, *G. polyedra* cells were ingested only by *P.* cf. *divergens* (I_P, the cell number of *G. polyedra* ingested by *P.* cf. *divergens* population during incubation time), while in experimental bottles, by both *P.* cf. *divergens* and *A. tonsa* ($I_P^\bullet$ and $I_A^\bullet$, the cell number of *G. polyedra* ingested by *P.* cf. *divergens* and *A. tonsa* populations, respectively). Assuming the values of I_P and $I_P^\bullet$ were equal at the same initial *G. polyedra* concentrations, $I_A^\bullet$ was calculated from the difference in final *G. polyedra* concentrations between control and experimental bottles. In fact, the values of $I_P^\bullet$ could have been slightly lower than those of I_P due to lower mean *P.* cf. *divergens* concentrations caused by *A. tonsa* predation in experimental bottles. However, the difference between calculated values of I_P and $I_P^\bullet$ [based on the data of Jeong & Latz (1994) on ingestion rates of *P.* cf. *divergens* as a function of *G. polyedra* concentration, averaging the values from Methods 1 and 2] was $\leq 7\%$ of the total ingested *G. polyedra* at all mean *G. polyedra* concentrations, except at 10 (13%) and 870 *G. polyedra* ml^{-1} (11%). Thus, negligible error was introduced into the calculation.

Carbon contents per cell were estimated from cell volume according to Strathmann (1967) for *Gonyaulax polyedra* (2.6×10^4 µm^3 in cell volume) and Beers et al. (1975) for *Protoperidinium* cf. *divergens* (1.2×10^5 µm^3).

Test of hypotheses. In Expts 3, 4, and 5, the concentration of *Protoperidinium* cf. *divergens* was fixed, while that of *Gonyaulax polyedra* varied in each experiment (Table 1). If ingestion and clearance rates of *Acartia tonsa* on *P.* cf. *divergens* at one *G. polyedra* concentration are significantly different from those at other *G. polyedra* concentrations in each experiment, $H_0 1$ can be rejected. Analysis of variance (ANOVA; Zar 1984) was used for the statistical test.

$H_0 2$ can be rejected, if there are values consistently below or above the line of unity (means no preference)

in the plot of the ratio of ingestion rates of *Acartia tonsa* on each prey (*Gonyaulax polyedra*:*Protoperidinium* cf. *divergens*) as a function of ratios of prey availability.

H_03 can be tested by examining the mortality rate of *Protoperidinium* cf. *divergens* due to *Acartia tonsa* predation (predation coefficient), g, as a function of *Gonyaulax polyedra* concentration. If g is not significantly greater than 0, then there will be no predation effect of *A. tonsa* on the population growth of *P.* cf. *divergens* and H_03 can be rejected.

Realized growth rates of *Protoperidinium* cf. *divergens*. To understand the population dynamics of *P.* cf. *divergens*, realized growth rates (= specific growth rate – mortality rate due to *Acartia tonsa* predation, $k - g$) of *P.* cf. *divergens* as a function of *Gonyaulax polyedra* concentration were calculated for densities of *A. tonsa* from 1 to 20 ind. l^{-1}. The data of Jeong & Latz (1994) on specific growth rates of *P.* cf. *divergens* as a function of *G. polyedra* concentration (k at the concentrations of 7 to 10 *P.* cf. *divergens* ml^{-1}, Expt 2 in their studies), and the data for mortality rate per *A. tonsa* at similar *G. polyedra* concentrations in this study were used for calculating the realized growth rates of *P.* cf. *divergens*. The Jeong & Latz (1994) data for the k values were used rather than those calculated from the present experiments because the short incubation time and relatively slow growth of *P.* cf. *divergens* in some control bottles led to only small changes in the *P.* cf. *divergens*; thus there was a great deal of uncertainty in the calculation of k. The k value of -0.001 h^{-1}, which was obtained at mean *G. polyedra* concentrations of 72 cells ml^{-1} by Jeong & Latz (1994), was used for k values at mean *G. polyedra* concentrations < 70 cells ml^{-1}. Generally *P.* cf. *divergens* can survive without added prey for at least 3 d, but its population decreases by cannibalism if incubation time is longer (Jeong unpubl.). Therefore, the use of the k value of -0.001 h^{-1} at mean *G. polyedra* concentrations < 70 cells ml^{-1} may be valid within 3 d.

The mortality rates (predation coefficients) at 20 *Acartia tonsa* l^{-1} were measured in this study, and used to calculate mortality rates at other *A. tonsa* densities. The resulting values of g are only approximate because mean prey concentrations can be different when *A. tonsa* density changes.

Swimming speeds of *Protoperidinium* cf. *divergens* and *Gonyaulax polyedra*. The swimming speeds of *P.* cf. *divergens* and *G. polyedra* as a function of *G. polyedra* concentration were measured using a video analyzing system. A total of 72 large *P.* cf. *divergens* were added to 3 ml multiwell chambers containing 2 ml filtered seawater and *G. polyedra* at concentrations of 12, 30, 60, 300, 1000, or 2000 *G. polyedra* ml^{-1}. After a 20 min acclimation period, swimming of *P.* cf. *divergens* and *G. polyedra* was

observed with a Zeiss Axiovert 135 inverted microscope at a magnification of 40 or 160×, and recorded with a Dage model 72S video camera onto VHS video tape. Observations were performed at 20°C. Only straight linear paths of fast-swimming cells were analyzed during single-frame playback to obtain both mean and maximum values. Average swimming speed was calculated based on the linear displacement in 1 s. Swimming speeds of 3 or 4 *P.* cf. *divergens* cells at each *G. polyedra* concentration, and of 10 *G. polyedra* were measured. The swimming speeds of *P.* cf. *divergens* cells with and without a pallium were measured separately.

RESULTS

Feeding rates of *Acartia tonsa* on *Protoperidinium* cf. *divergens*

In Expts 1 and 2, *Protoperidinium* cf. *divergens* was the only prey. The ingestion rate (IR, prey eaten *Acartia tonsa*$^{-1}$ h^{-1}) of *A. tonsa* on *P.* cf. *divergens* increased linearly up to 14 prey eaten *A. tonsa*$^{-1}$ h^{-1} with increasing log-transformed mean prey concentration (MPC) over the range tested, 0.7 to 50 *Protoperidinium* ml^{-1} (Fig. 1A). The equation of the regression line of the pooled data from both experiments was IR = 0.886 + 3.074 × ln MPC (R^2 = 0.917). The maximum reported abundance of *Protoperidinium* in the coastal waters of southern California is 24 *Protoperidinium* ml^{-1} (Allen 1949). Interpolated ingestion rate at this prey concentration is 11 *Protoperidinium* eaten *Acartia*$^{-1}$ h^{-1}, or 106 ng C *Acartia*$^{-1}$ h^{-1}. Clearance rates of *A. tonsa* on *P.* cf. *divergens* were approximately constant at mean prey concentrations ≤7 *Protoperidinium* ml^{-1} (3 to 4 ml *Acartia*$^{-1}$ h^{-1}) (Fig. 1B), but decreased continuously to 0.6 ml *Acartia*$^{-1}$ h^{-1} at high prey concentrations.

Swimming speeds of *Protoperidinium* cf. *divergens* and *Gonyaulax polyedra*

The mean instantaneous swimming speed of *Protoperidinium* cf. *divergens*, 1.05 ± 0.15 mm s^{-1} (mean ± SD), was not significantly reduced by increasing *Gonyaulax polyedra* cell concentrations (ANOVA, p > 0.1) and was 2.5 times higher than that for *G. polyedra* (0.4 ± 0.07 mm s^{-1}). The maximum instantaneous swimming speeds of *P.* cf. *divergens* and *G. polyedra* were 1.26 and 0.51 mm s^{-1}, respectively. The mean instantaneous swimming speed of *P.* cf. *divergens* with a pallium (1.05 ± 0.24 mm s^{-1}) did not differ from that without a pallium. However, the swimming speed of
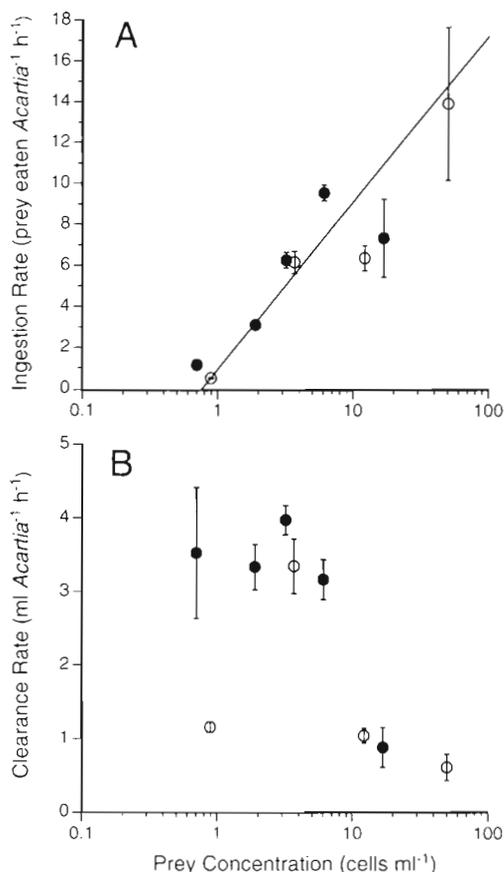
Fig. 1. *Acartia tonsa* feeding on *Protoperidinium* cf. *divergens* when it is the only prey. Symbols represent treatment means ± 1 SE. (A) Ingestion rate as a function of mean prey concentration. (O) Expt 1 (see Table 1); (●) Expt 2. Line represents the calculated linear regression. (B) Clearance rate as a function of mean prey concentration. Symbols as in (A)

P. cf. *divergens* could be lower during precapture motion (Jacobson & Anderson 1986) or for about 2 to 3 min after forming a pallium containing a *G. polyedra* cell (pers. obs.). The swimming speed of *G. polyedra* in this experiment was 1.8 times higher than the value for the same species measured by Kamykowski et al. (1992).

Test of $H_0 1$ (effect of co-occurring prey)

In Expts 3, 4, and 5, the concentration of *Protoperidinium* cf. *divergens* was fixed in each experiment, while that of *Gonyaulax polyedra* varied. With increasing mean *G. polyedra* concentration (or total prey concentration), the ingestion rates of *A. tonsa* on *P.* cf. *divergens* decreased by 5.6 to 21.3 times (Fig. 2A), while ingestion on *G. polyedra* increased with a slight depression at the highest prey concentration (Fig. 2B). In Expt 3, the ingestion rates for each prey were clearly

depressed at the lowest mean *G. polyedra* concentration. With increasing mean *G. polyedra* concentration, the clearance rates of *A. tonsa* on *P.* cf. *divergens* decreased by 9.4 to 40.1 times (Fig. 3A), and clearance on *G. polyedra* also decreased with a depression at the lowest mean *G. polyedra* concentration in each experiment (Fig. 3B). Ingestion and clearance rates at one *G. polyedra* concentration were significantly different from those at other *G. polyedra* concentrations in each experiment (ANOVA: for ingestion rates, $p < 0.0025$ in Expts 4 and 5, and $p < 0.05$ in Expt 3; for clearance rates, $p < 0.001$ in all experiments). These results show that the presence of *G. polyedra* significantly affects the ingestion and clearance rates of *A. tonsa* on *P.* cf. *divergens*. Therefore, $H_0 1$ can be rejected.

The maximum ingestion rates of *Acartia tonsa* on *Gonyaulax polyedra* in Expts 3, 4, and 5 (85, 87, and 94 prey eaten $Acartia^{-1}$ h^{-1}, respectively) were observed at mean *G. polyedra* concentrations of 200 to
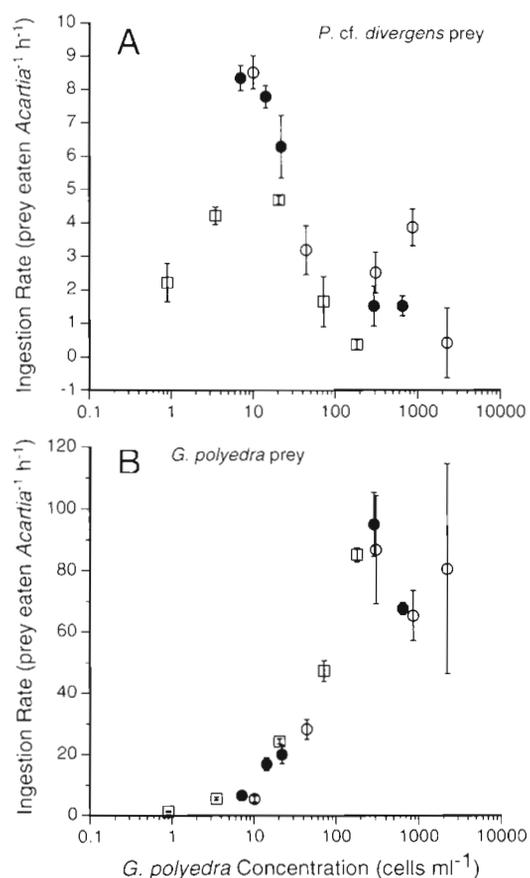

Fig. 2. Ingestion rates of *Acartia tonsa* on mixed diets of *Gonyaulax polyedra* and *Protoperidinium* cf. *divergens*, the latter at 3 to 10 cells ml^{-1} Symbols represent treatment means ± 1 SE. (A) *P.* cf. *divergens* prey. (□) Expt 3 (see Table 1); (●) Expt 4; (O) Expt 5. (B) *G. polyedra* prey. Symbols as in (A)
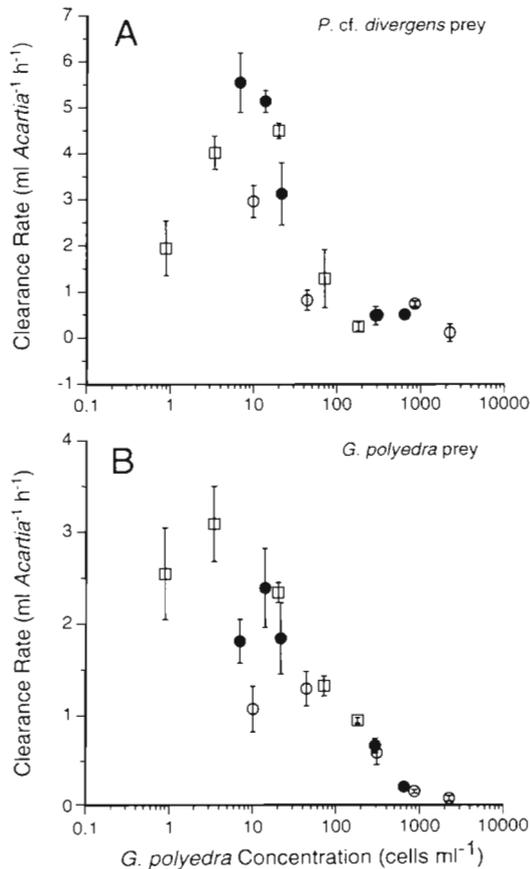
Fig. 3. Clearance rates of *Acartia tonsa* on mixed diets of *Gonyaulax polyedra* and *Protoperidinium* cf. *divergens*. Symbols represent treatment means ± 1 SE. (A) *P.* cf. *divergens* prey. (□) Expt 3 (see Table 1); (●) Expt 4; (○) Expt 5. (B) *G. polyedra* prey. Symbols as in (A)

310 cells ml^{-1}, while those on *Protoperidinium* cf. *divergens* (4.7, 8.5, and 8.3 prey eaten *Acartia*$^{-1}$ h^{-1}, respectively) were observed at mean *G. polyedra* concentrations of 7 to 20 cells ml^{-1}. Ingestion rates of *A. tonsa* on *P.* cf. *divergens* decreased to 0.3 prey eaten *Acartia*$^{-1}$ h^{-1} at a mean *G. polyedra* concentration of 2200 cells ml^{-1}. Based on Kiørboe et al. (1985) and Støttrup & Jensen (1990), the estimated maximum daily ration for *A. tonsa* feeding on combined prey was approximately 250 % of its own body carbon.

Test of H$_0$2 (preference for either prey)

The ratio of ingestion rates of *Acartia tonsa* on each prey as a function of ratios of prey availability indicated no evidence of a strong preference of *A. tonsa* for *Protoperidinium* cf. *divergens* over *Gonyaulax polyedra* (Fig. 4A). The ratio of prey availability is the mean *G. polyedra* concentration divided by the mean

P. cf. *divergens* concentration. The line of unity means no preference (Murdoch 1969). The ratio of clearance rates of *A. tonsa* on each prey as a function of ratio of prey availability showed no strong trend in selectivity (Fig. 4B). However, H$_0$2 can be partially rejected because there were values consistently below the line of unity at low ratios of prey availability (*G. polyedra*:*P.* cf. *divergens* <5.2) or low total prey concentration (ca 6 to 26 cells ml^{-1} or 29 to 91 ng C ml^{-1}). One exception occurred at the lowest prey concentration (21 ng C ml^{-1}) which is close to the feeding threshold for *A. tonsa* (7 to 18 ng C ml^{-1}) (Reeve & Walter 1977). *A. tonsa* gained similar amounts of carbon from each prey at *G. polyedra*:*P.* cf. *divergens*
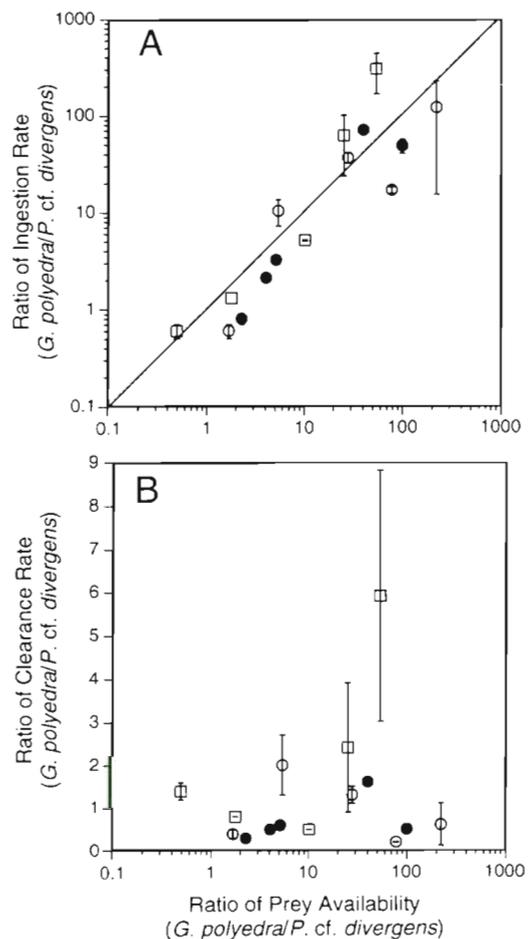

Fig. 4. Prey selection of *Acartia tonsa* on mixed diets of *Gonyaulax polyedra* and *Protoperidinium* cf. *divergens*. Symbols represent treatment means ± 1 SE. The ratio of prey availability is the mean *G. polyedra* concentration divided by the mean *P.* cf. *divergens* concentration. (A) Ingestion rate on *G. polyedra*, relative to ingestion rate on *P.* cf. *divergens*, compared to relative availability of *G. polyedra*. (□) Expt 3 (see Table 1); (●) Expt 4; (○) Expt 5. (B) Clearance rate on *G. polyedra*, relative to clearance rate on *P.* cf. *divergens*, compared to relative availability of *G. polyedra*. Symbols as in (A)

carbon biomass ratio of 1.78 in Expt 4. *P.* cf. *divergens* was 68% of the copepod's ration by volume when similar volumes of each prey (*G. polyedra*: 3.7×10^5 μm^3 ml^{-1}; *P.* cf. *divergens*: 4.2×10^5 μm^3 ml^{-1}) were offered in Expt 4. There was no evidence of a consistent preference by *A. tonsa* at high prey availability ratios or high total prey concentration (ca >52 cells ml^{-1}).

The maximum clearance rates of *Acartia tonsa* on *Protoperidinium* cf. *divergens* in each experiment (4.5, 5.5, and 2.9 ml *Acartia*$^{-1}$ h^{-1}) were higher than those for *Gonyaulax polyedra* (3.1, 2.4, and 1.3 ml *Acartia*$^{-1}$ h^{-1}, respectively).

Test of $H_0 3$ (predation effect on growth)
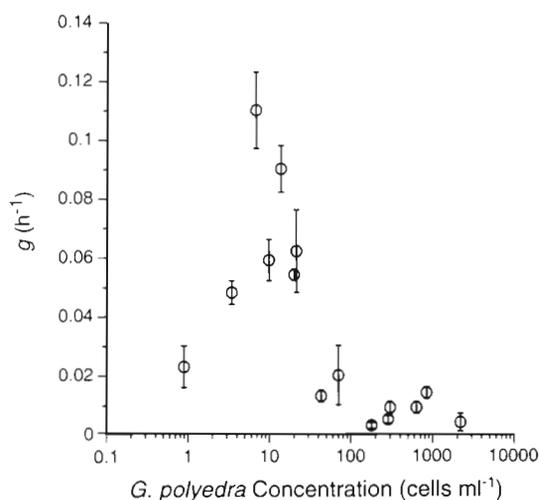
$H_0 3$ can be tested by examining the mortality rate of *Protoperidinium* cf. *divergens* due to *Acartia tonsa* predation (predation coefficient *g*), as a function of *Gonyaulax polyedra* concentration. If *g* is not significantly greater than 0, then there will be no predation effect of *A. tonsa* on the population growth of *P.* cf. *divergens*. The mortality rates decreased with increasing *G. polyedra* concentration except at very low *G. polyedra* concentrations (Fig. 5). The rates were significantly greater than 0 ($p < 0.05$, 1-tailed t-test; Zar 1984) at all *G. polyedra* concentrations, except at *G. polyedra* concentrations of 72 ($0.05 < p < 0.1$) and 2200 ($p > 0.1$) cells ml^{-1}. Therefore, $H_0 3$ can be rejected at *G. polyedra* concentrations ≤ 870 cells ml^{-1}, but not at 2200 cells ml^{-1}.

Realized growth rates of *Protoperidinium* cf. *divergens*

Realized growth rates of *Protoperidinium* cf. *divergens* increased with increasing *Gonyaulax polyedra* concentration except at very low *G. polyedra* concentrations (Fig. 6). With 20 *Acartia tonsa* l^{-1}, at *G. polyedra* concentrations of 300 to 870 cells ml^{-1}, there was almost no net population growth of *P.* cf. *divergens*. The realized growth rates at 2200 *G. polyedra* ml^{-1} were not affected by *A. tonsa* density. The observed density of *A. tonsa* during the red tides dominated by *G. polyedra* in the coastal waters of southern California is about 7 *Acartia* l^{-1} (Morey-Gaines 1980). At *A. tonsa* densities ≤ 12 *Acartia* l^{-1} and *G. polyedra* concentrations < 70 cells ml^{-1}, the realized growth rates were negative and strongly affected by *A. tonsa* density, while at *G. polyedra* concentrations > 100 cells ml^{-1}, realized growth rates were positive and relatively weakly affected.

DISCUSSION

The results of these experiments reject $H_0 1$ (that the presence of co-occurring red-tide dinoflagellate prey does not significantly affect the ingestion and clearance rates of copepods on *Protoperidinium*), but do not completely reject $H_0 2$ (that copepods do not distinguish between the heterotrophic dinoflagellate *Protoperidinium* and co-occurring red-tide dinoflagellate prey) or $H_0 3$ (that copepod predation does not affect
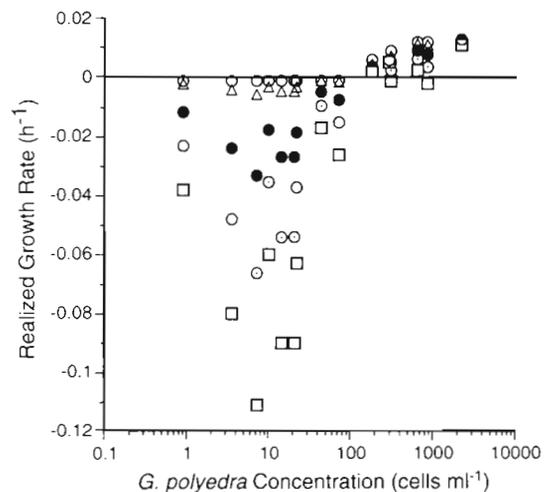
Fig. 5. Mortality rate of *Protoperidinium* cf. *divergens* due to *Acartia tonsa* predation (predation coefficient *g*), as a function of *Gonyaulax polyedra* concentration. Plotted points have been collated from Expts 3, 4, and 5. Symbols represent treatment means ± 1 SE

Fig. 6. Realized growth rate (= specific growth rate – mortality rate due to *Acartia tonsa* predation) of *Protoperidinium* cf. *divergens* population as a function of *Gonyaulax polyedra* and *A. tonsa* densities. *A. tonsa* densities were 1 (△), 6 (●), 12 (○), and 20 (□) ind. l^{-1}. Specific growth rates of *P.* cf. *divergens* (○) as a function of *G. polyedra* concentration are from Jeong & Latz (1994)

the population growth of *Protoperidinium* during either simulated red-tide or non-red-tide periods).

The importance of *Protoperidinium* as prey for *Acartia* seems to depend on the concentrations of co-occurring red-tide dinoflagellate prey. Ingestion and clearance rates of *A. tonsa* on *P.* cf. *divergens* were significantly affected by the presence of *Gonyaulax polyedra*. When *P.* cf. *divergens* concentration was fixed, ingestion rates of *A. tonsa* on *P.* cf. *divergens* decreased continuously with increasing mean *G. polyedra* concentrations, while the rates for *G. polyedra* increased with a slight depression at the highest prey concentration.

In general, there is no evidence of a strong preference of *Acartia tonsa* for *Protoperidinium* cf. *divergens* over *Gonyaulax polyedra*. However, there were values consistently below the 1:1 line (suggesting a weak preference) at low ratios of prey availability (*G. polyedra*:*P.* cf. *divergens*) or low total prey concentration. However, *A. tonsa* seemed to feed without strong prey selection at total prey concentrations > 52 cells ml^{-1}, or total carbon biomass > 179 ng C ml^{-1}.

Jonsson & Tiselius (1990) argue that *Acartia tonsa* exhibits 2 different feeding behaviors in mixtures of planktonic ciliates and a microflagellate *Cryptomonas balticum*. At low to moderately high food concentrations (≤ 230 ng C ml^{-1}), *Acartia* exhibits raptorial feeding behavior in which it sinks passively in search of large prey which are remotely detected and individually captured, while at high algal food concentrations it switches to suspension-feeding behavior. *A. tonsa* may distinguish the fast-swimming *Protoperidinium* cf. *divergens* from slow-swimming *Gonyaulax polyedra* with raptorial feeding behavior at low prey concentrations, but not at high prey concentrations, when mechanical or chemical signals of fast-swimming *P.* cf. *divergens* may be disturbed by large numbers of *G. polyedra*. During *A. tonsa* suspension feeding, there may be no feeding preference because the sizes of

P. cf. *divergens* and *G. polyedra* are large enough to support complete prey retention (Nival & Nival 1976).

Lack of a strong preference of *Acartia tonsa* for *Protoperidinium* cf. *divergens* over *Gonyaulax polyedra* results in low mortality rates of *P.* cf. *divergens* due to *A. tonsa* predation at high *G. polyedra* concentrations. In particular, the mortality rates at a *G. polyedra* concentration of 2200 cells ml^{-1}, even with 20 *A. tonsa* l^{-1}, were not significantly different from zero. The concentration of *G. polyedra* during red tides off southern California has often exceeded 2000 cells ml^{-1} (e.g. Holmes et al. 1967). A dense layer of *G. polyedra* may provide a 'refuge' for *P.* cf. *divergens*, which can grow relatively rapidly at high *G. polyedra* concentrations (Jeong & Latz 1994). This may be an explanation for the high abundance of *Protoperidinium* during local red tides off southern California. However, at low *G. polyedra* concentrations, 3 factors may enable *A. tonsa* to limit the population growth of *P.* cf. *divergens*: (1) the weak preference of *A. tonsa* for *P.* cf. *divergens* over *G. polyedra*, (2) the high mortality rates of *P.* cf. *divergens* due to *A. tonsa* predation, and (3) no or relatively low population growth of *P.* cf. *divergens*.

Potential of *Protoperidinium* as prey for *Acartia tonsa*

The ingestion and clearance rates of *Acartia tonsa* on *Protoperidinium* cf. *divergens* are similar to those on naked and tintinnid ciliates of similar volumes (Table 2). The maximum clearance rate of *A. tonsa* on *P.* cf. *divergens* in this study, 5.5 ml *Acartia*$^{-1}$ h^{-1}, is comparable to those on ciliates of similar volumes (Robertson 1983, Stoecker & Egloff 1987, Jonsson & Tiselius 1990, Stoecker & Capuzzo 1990), and higher than those on large autotrophic dinoflagellates *Gonyaulax polyedra* and *Gymnodinium sanguineum* (Berggreen et al. 1988).

Table 2. Comparison of ingestion and clearance rates of *Acartia tonsa* on the heterotrophic dinoflagellate *Protoperidinium* cf. *divergens* and ciliates of similar volumes at similar prey concentrations. Ingestion and clearance rates corrected to 19°C using $Q_{10} = 2$. AD: autotrophic dinoflagellate; HD: heterotrophic dinoflagellate; NC: naked ciliate; T: tintinnid ciliate. na: not available

Prey	Prey volume (10^5 μm^3)	Prey density (ind. ml^{-1})	Ingestion (prey *Acartia*$^{-1}$ h^{-1})	Clearance (ml *Acartia*$^{-1}$ h^{-1})	Mixed with other prey	Source
Protoperidinium cf. *divergens* (HD)	1.2	2.0	3.3	3.3	No	This study
		2.1	4.7	4.5	*Gonyaulax polyedra* (AD)	
Tintinnopsis tubulosa (T)	1.4	2.0	3.6	2.4–7.2	No	Robertson (1983)
Strobilidium sp. (NC)	0.7–1.1^a	1.7	3.0	1.8	*Favella* sp. (T)	Stoecker & Egloff (1987)
Strobilidium spiralis (NC)	1.5	0.8	na	3.1	No	Jonsson & Tiselius (1990)

^{a} Calculated from ESD (50 to 60 μm)

Prey density, size, motility, and quality have been suggested as important factors affecting the feeding rates of copepods when the prey is suitable (Price et al. 1983, Wiadnyana & Rassoulzadegan 1989, Jonsson & Tiselius 1990, Stoecker & Capuzzo 1990, Gifford & Dagg 1991). The swimming speed of *Protoperidinium* cf. *divergens* was similar to ciliates of similar volumes, such as *Laboea strobila* (Jonsson & Tiselius 1990). There are a few data on the biochemical composition of *Protoperidinium*. However, the similarity of ingestion and clearance rates of *Acartia* on *Protoperidinium* and ciliates of similar volumes at similar conditions suggests that quality of *Protoperidinium* as food for *Acartia* is not very different from ciliates. It would be very interesting to test selective feeding of *Acartia* on *Protoperidinium* and co-occurring tintinnids or other ciliates.

The maximum abundance so far reported for *Protoperidinium* in coastal waters off southern California, 24.0 *Protoperidinium* ml^{-1} (Allen 1949), is slightly higher than that of tintinnids, 18.6 tintinnids ml^{-1} (Heinbokel & Beers 1979). During non-bloom periods, the abundance of *Protoperidinium*, about 0.1 to 2.0 *Protoperidinium* ml^{-1} (Allen 1949), is much higher than that of tintinnids (Heinbokel & Beers 1979). Therefore, *Protoperidinium* is likely to be more important than tintinnids as prey for copepods in coastal waters off southern California.

In the open ocean the abundance of *Protoperidinium* is ≤ 0.6 *Protoperidinium* ml^{-1}, but usually < 0.1 *Protoperidinium* ml^{-1} (Gifford & Dagg 1991, Lapota et al. 1992). Still, *Protoperidinium* could be an important prey item for oceanic copepods because it is sometimes relatively abundant (Lessard 1984, Gifford & Dagg 1991). Gifford & Dagg (1991) showed that heterotrophic dinoflagellates including *Protoperidinium* were important food items for *Neocalanus plumchrus*, and the ingestion rate of *N. plumchrus* on heterotrophic dinoflagellates was comparable to that on ciliates in the subarctic north Pacific Ocean. However, in open Gulf of St. Lawrence, Ohman & Runge (1994) found that the ingestion rate of *Calanus finmarchicus* on aloricate ciliates was approximately twice that on dinoflagellates including *Protoperidinium*.

Comparison of *Acartia* feeding on 2 grazing heterotrophic protists and their co-occurring dinoflagellate prey

Protoperidinium and the large tintinnid ciliate *Favella* are abundant during red tides or blooms dominated by dinoflagellates (Allen 1949, Prakash 1963, Stoecker et al. 1983, 1984, Jeong unpubl.), and may

have a considerable grazing impact on dinoflagellate populations (Stoecker et al. 1983, Jeong & Latz 1994). Although they may both feed on the same dinoflagellate prey in the field (Prakash 1963), in the laboratory, *Protoperidinium* cf. *divergens* achieved its highest growth rate feeding on the larger dinoflagellate *Gonyaulax polyedra* (36 µm in equivalent spherical diameter) (Jeong & Latz 1994), while *Favella* had its highest growth rate feeding on the smaller dinoflagellate *Heterocapsa triquetra* (18 µm) (Stoecker et al. 1981, 1983).

Acartia tonsa did not show a strong preference for *Protoperidinium* cf. *divergens* over *Gonyaulax polyedra*, as it did for *Favella* over *Heterocapsa triquetra*. Ingestion and clearance rates of *A. tonsa* on *P.* cf. *divergens* were clearly affected by the presence of *G. polyedra*, while those on *Favella* only sometimes by the presence of *H. triquetra* (Stoecker & Sanders 1985).

The preference of *Acartia* for *Favella* and lack of preference for *Protoperidinium* over co-occurring dinoflagellates may be accounted for by differences in the mechanical or chemical signals of the 4 prey species. The mechanical stimulus may be related to volume of prey, swimming speed, and intensity of ciliary or flagellar movement. The *P.* cf. *divergens* to *Gonyaulax polyedra* volume ratio is much smaller than that of *Favella* to *Heterocapsa triquetra*. There are no data on the swimming speed of *H. triquetra*; however, since it has a similar shape and volume to *Scrippsiella trochoidea*, their swimming speeds are assumed to be similar (0.15 mm s^{-1}; Kamykowski et al. 1992). The ratio of the swimming speed of *P.* cf. *divergens* to that of *G. polyedra* is 2.5, less than the ratios of 4.8 to 6.6 estimated for *Favella* (Buskey & Stoecker 1989) to *H. triquetra*. The signal generated by the movement of cilia is likely to be different from that of flagella (Holwill 1974). Therefore, the differences in the mechanical stimuli generated by the movements of *Favella* and *H. triquetra* may be greater than those of *P.* cf. *divergens* and *G. polyedra*, providing a mechanism for *Acartia* to differentiate *Favella* from *H. triquetra* more easily than *P.* cf. *divergens* from *G. polyedra*.

Based on the data of Jeong & Latz (1994), *Protoperidinium* is likely to be more similar in size and motility to co-occurring dinoflagellate prey than many of its microzooplanktonic competitors. Co-occurring dinoflagellate prey for *Protoperidinium* could also be critical alternative prey for *Acartia*, and their presence may significantly reduce predation by the copepods on *Protoperidinium*. Therefore, compared to other competing microzooplankton grazers, *Protoperidinium* may have the advantage of reduced predation pressure from *Acartia* when it co-occurs with its dinoflagellate prey.

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