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Prey size selection, grazing and growth response of the small heterotrophic dinoflagellate *Gymnodinium* sp. and the ciliate *Balanion comatum*—a comparative study

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ABSTRACT: Prey selectivity, growth and feeding responses were studied in the ciliate *Balanion comatum* (17 µm) and the heterotrophic dinoflagellate *Gymnodinium* sp. (7 µm). Almost identical prey size spectra were found for the 2 organisms. Optimum prey size was 8 µm, while the lower and upper limits of prey capture were ~4 and 10 µm, respectively. Maximum growth and ingestion rates of *B. comatum* were slightly higher than those of *Gymnodinium* sp. Threshold prey concentration for growth of *B. comatum* and *Gymnodinium* sp. was 11 and 17 µg C l^{-1}, respectively. At 15°C, both organisms needed to ingest approx. 1 to 2% h^{-1} of their cell volume in order to sustain basic metabolic activity. Maximum specific clearance was 2 to 3 times higher for the ciliate compared to the dinoflagellate. *Gymnodinium* sp. survived for a longer time than *B. comatum* when deprived of prey organisms. *Gymnodinium* sp. cells were not ingested by *B. comatum*, although they were of a size which is optimal for *B. comatum*.

KEY WORDS: *Balanion comatum* · *Gymnodinium* sp. · Prey size spectra · Growth · Grazing · Swimming behavior

INTRODUCTION

Heterotrophic dinoflagellates and ciliates are quantitatively important parts of the marine planktonic food web (Smetacek 1981, Lessard 1991). Apart from mineralizing organic matter, they represent a link between primary production and metazooplankton (e.g. Beers & Stewart 1967). Most marine planktonic ciliates feed on prey which is about 10 times smaller than themselves (Heinbokel 1978, Jonsson 1986, Verity 1991). However, raptorial ciliates occur in the plankton (Montagnes et al. 1988, Nielsen & Kiørboe 1994). Heterotrophic dinoflagellates are raptorial feeders capable of feeding on prey items of their own size (Jacobson & Anderson 1986, Hansen 1992). Large dinoflagellates (>20 µm) have been found to feed on mainly chain-forming diatoms, dinoflagellates, other flagellates and ciliates (Jacobson & Anderson 1986, Gaines & Elbrächter 1987, Hansen 1991a, b, Jeong & Latz 1994), thus making large heterotrophic dinoflagellates potential competitors with copepods and cladocerans for microplankton prey (Lessard 1991, Hansen 1992). Only a few papers have been published on the trophic role of the small heterotrophic dinoflagellates (5 to 20 µm). These studies suggest that small heterotrophic dinoflagellates mainly feed on nanoflagellates, thereby potentially competing with planktonic ciliates for prey (Bjørnsen & Kuparinen 1991, Strom 1991). However, small dinoflagellates are within the size range of prey fed upon by their ciliate competitors. Thus, while small dinoflagellates may be competitors with ciliates for food, they are also potential prey for the ciliates.

The aim of the present study was to compare the functional biology of the small heterotrophic dinoflagellate *Gymnodinium* sp. [7 µm equivalent spherical diameter (ESD)] and the prostomatid ciliate *Balanion comatum* Wulff (17 µm ESD) in order to answer the fol-

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lowing questions: (1) Are these organisms competitors for nanoplankton prey? (2) Are there any differences in the functional and numerical responses of the 2 organisms when presented with the same prey? (3) Is the ciliate capable of feeding on the smaller dinoflagellate? (4) Can the observed differences be extrapolated to account for the different trophic roles of ciliates and small heterotrophic dinoflagellates in general?

MATERIALS AND METHODS

We isolated *Gymnodinium* sp. and *Balanion comatum* from water samples from the north of the Øresund, Denmark, in September 1995 at a temperature of 15°C, a salinity of 28 psu, and a depth of 10 m. Crude cultures were initially made by adding the cryptophyte *Rhodomonas salina* (Wislouch) Hill & Wetherbee to samples of natural sea water. After 1 to 3 wk, cells of *B. comatum* were transferred to a 65 ml tissue culture bottle (Nunclon®), isolated using a micropipette and fed *R. salina*. Cultures were not axenic.

A range of prey algae was used (Table 1). The algae used were all observed to swim with a constant speed of less than 100 µm s^{-1}. *Rhodomonas salina* and *Isochrysis galbana* was supplied from the culture collection of the Marine Biological Laboratory in Helsingør, University of Copenhagen. The other algae were obtained from The Scandinavian Culture Center for Algae and Protozoa, Dept of Algae and Fungi, Botanical Institute, University of Copenhagen, Denmark. Algae were grown in B-medium (Hansen 1989) based on Millipore filtered autoclaved sea water (salinity 30 to 32 psu) at a temperature of 15 ± 1°C. Algae were grown in aerated 250 ml Erlenmeyer glass flasks at an irradiance of 10 to 15 µE m^{-2} s^{-1} on a 16 h:8 h light:dark cycle. Stock cultures of *Gymnodinium* sp. and *Balanion comatum* were fed *R. salina*, and maintained in 270 ml transparent tissue bottles (Nunclon®) mounted on a plankton wheel (1 rpm). Otherwise the physical conditions were as stated above.

Cell volumes of algae (n = 20) and *Balanion comatum* (n = 20) were estimated from the linear dimensions of Lugol's fixed cells (final conc. 1%) using an inverted Olympus® microscope. Algae cells were assumed to be prolate ellipsoids. Due to the shape of the oral apparatus of *B. comatum*, the cell volume was estimated using the formula: $0.1875WL^2$, where W and L are the width and length of cells, respectively (Edler 1979).

Because of the irregular shape of *Gymnodinium* sp., the cell volume could not be estimated from linear dimensions. Instead, *Gymnodinium* sp. cells (n = 20 cells) fixed in Lugol's (final conc. 1%) were recorded using a video camera connected to a monitor and an Olympus® inverted microscope. Cell shapes of *Gymnodinium* sp. were drawn on a plastic transparency covering the monitor screen. The transparency was digitized using a MOP videoplan (Keytronic, Germany) and cell volumes were estimated by the algorithm of the MOP, which measures the maximum length and width of a 2-dimensional ellipsoid and subsequently rotates the object calculating the volume as a prolate ellipsoid. It is assumed that the shrinkage of predators and preys are of equal magnitude.

Bioenergetics. Growth, ingestion and clearance rates were measured for *Balanion comatum* and *Gymnodinium* sp. fed *Rhodomonas salina* at prey concentration ranging from 200 to 7000 cells ml^{-1}. Experiments were carried out in 270 ml tissue culture bottles in triplicate as batch cultures under conditions described above. Prior to experiments, cultures of *Gymnodinium* sp. and *B. comatum* were preincubated at the experimental prey concentration for 24 h. Growth rate was measured as the increase in cell number and ingestion rate as the decrease in cells compared to controls without predators. Predator cells were added to the experimental bottles in concentrations which resulted in a decrease of the prey concentrations of 10 to 20% during the experiment. Samples were fixed in Lugol's (final conc. 1%) and at least 400 cells were counted using a 25 ml Utermöhl chamber or in a Sedgwick-Rafter chamber and an inverted Olympus® microscope.

Growth rate was calculated assuming exponential growth:

$$\mu(h^{-1}) = \frac{(\ln N_1 - \ln N_0)}{t}$$

where N_0 and N_1 are particle concentration at the beginning and end of the experiment, respectively, μ is the growth rate, and t is the duration of the experiment (h).

Table 1. Algae used and their corresponding size (as estimated spherical diameter, ESD)

Species	ESD (µm)	Algal class
Isochrysis galbana Parke	4.0	Prymnesiophyte
Chroomonas vectensis Carter	6.1	Cryptophyte
Plagioselmis prolonga Buchter	6.6	Cryptophyte
Rhodomonas salina (Wislouch) Hill & Wetherbee	7.8	Cryptophyte
Teleaulax amphioxeia (W. Conrad) Hill	8.5	Cryptophyte
Rhodomonas marina (Dangeard) Lemmermann	10.3	Cryptophyte

Ingestion rates of *Balanion comatum* and *Gymnodinium* sp. were calculated using an iterative model.

$$\frac{dx}{dt} = \mu_x x - Uy$$

$$\frac{dy}{dt} = \mu_y y$$

The model assumes that the concentrations of predators (y) and prey (x) increase exponentially, with the growth rate constants μ_y and μ_x, respectively. The mortality induced by the predator is Uy, and was calculated iteratively on a computer with steps of 0.01 h. U is the per capita prey uptake per unit time.

Clearance (F) is a function of the per capita prey uptake per unit time (U) and the average prey concentration (C):

$$F = \frac{U}{C}$$

C is calculated according to Frost (1972) to estimate the average cell concentration in an exponentially growing culture.

Growth yield (Y) was calculated according to the equation (Fenchel 1982a):

$$Y = \frac{\mu_y V_y}{U V_x}$$

where V_y and V_x are the cell volumes of *Balanion comatum* or *Gymnodinium* sp. and *Rhodomonas salina*, respectively.

Prey size selection. *Balanion comatum* and *Gymnodinium* sp. were fed algae ranging in size from 4 to 12 µm in order to study prey size preferences (Table 1). The algae were added at a constant biomass (cell number × cell volume) equivalent to 900 *Rhodomonas salina* cells ml^{-1} in the case of *Balanion comatum* and 1200 *R. salina* cells ml^{-1} in the case of *Gymnodinium* sp., a biomass which supports approximately 90% of the maximum growth rate for each of the 2 predators when fed *R. salina*. Otherwise the physical conditions were as described above.

Mixture experiment. This experiment was conducted to investigate the interaction between *Balanion comatum* and *Gymnodinium* sp. when they co-occur. Cultures of *Gymnodinium* sp. and *B. comatum* were mixed in a suspension of *Rhodomonas salina*. Controls were run in which *B. comatum* and *Gymnodinium* sp. were fed *R. salina* in separate cultures. All experiments were carried out in 750 ml tissue culture bottles in triplicate. At intervals of between 8 and 16 h, 50 ml was sampled from each bottle and replaced with fresh medium. The experiments were run until food was depleted.

Starvation experiment. Dense exponentially growing cultures of *Gymnodinium* sp. and *Balanion comatum* cells were diluted to a concentration of ~500 predators ml^{-1} in triplicate culture. After 6 h (*B. comatum*) and 12 h (*Gymnodinium* sp.), the first sample was taken. At this time no *Rhodomonas salina* cells were left in the cultures. The number of *B. comatum* and *Gymnodinium* sp. cells were counted and cell volume was estimated at the time points shown in Fig. 9.

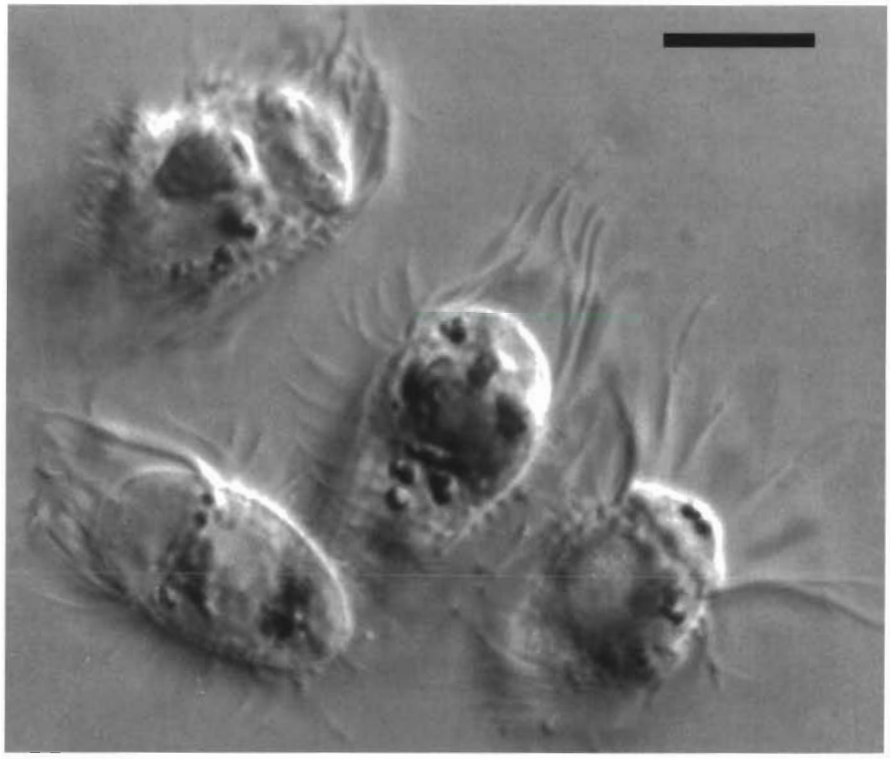
Locomotive pattern. The locomotive pattern of *Gymnodinium* sp. and *Balanion comatum* was studied by adding a cell suspension to a 2.7 ml multidish, which was subsequently covered with a cover slip. The multidish was placed under a Nikon® DIAPHOT microscope fitted with a video camera, and cells were recorded at a magnification of between ×80 and ×400. Cells were tracked for at least 1 s, yielding a minimum of 25 video frames per tracked cell. At least 40 cells of each predator were tracked. After recording, the video tape was played frame by frame and the cell positions were marked on plastic transparencies covering the screen. Subsequently, the transparencies were scanned into a computer data file and digitized using the program SigmaScan® (Jandel Scientific®, CA, USA).

RESULTS

The ciliate was identified as *Balanion comatum* from observations made on protargol- and silver-stained specimens in the light microscope (Fig. 1) and with the use of a transmission electron microscope. The cell body is cup shaped, with a flattened oral end. While the cell volume depended on the food concentration (see Fig. 5), the oral disc was of constant size (9 µm). The oral disc is surrounded by oral dikinetids, with cilia measuring 8 µm in length, and an inner circle of tentacles (length 12 µm); there is 1 tentacle per dikinetid. The average dimension of cells growing at food saturation was approx. 20 × 15 µm.

Gymnodinium sp. (Fig. 2) is a spindle-shaped athecate dinoflagellate with an average length of 8 µm and a variable width depending on food concentration. The food vacuole is located in the anterior end of the cell. Prey organisms are captured by use of a tow filament and engulfed directly.

Ingestion rates of both *Balanion comatum* and *Gymnodinium* sp. increased with prey concentration until a maximum level was reached (Fig. 3). However, data obtained from the 2 organisms were fitted to different equations due to differences in their feeding biology. *Balanion comatum* ingested about 22 cells before it divided. Thus, the functional response can be considered as a Holling type II functional response. However, *Gymnodinium* sp. engulfed only about a single prey prior to cell division and ingestion rate is solely based on predator-prey encounter. The functional response of *Gymnodinium* sp. can therefore be considered as a Holling type I response.



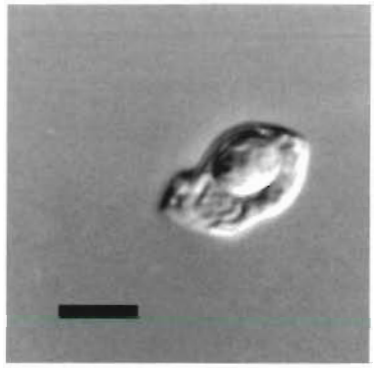


Fig. 2. *Gymnodinium* sp. Nomarski contrast interference microscopy. Cells are fixed under a hanging drop with 5% OsO_4. Scale bar = 5 µm

Fig. 1. *Balanion comatum*. Nomarski contrast interference microscopy. Cells are fixed under a hanging drop of 5% OsO_4. Scale bar = 10 µm

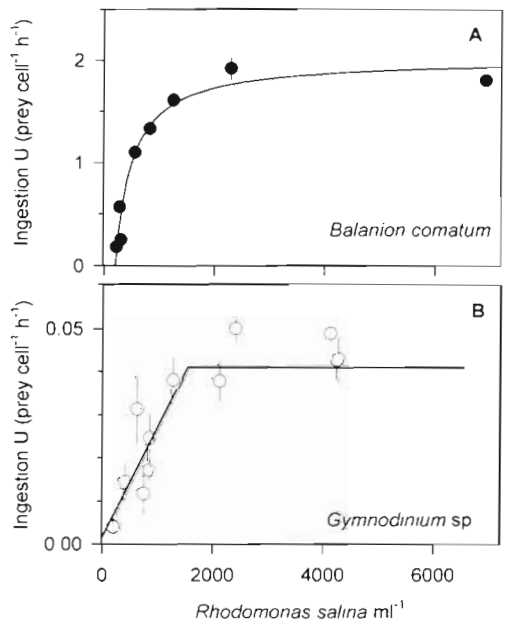


Fig. 3. Ingestion rate as a function of prey concentration. (A) *Balanion comatum*. The curve is fit to a Michaelis-Menten equation (Holling type II):

$$U(h^{-1}) = \frac{2.027(x-204)}{511+(x-204)}$$

(B) *Gymnodinium* sp. Curve represents a fit to a Holling type I functional response: $U(h^{-1}) = 0.00165 + (2.71 \times 10^{-3})x$ for $x < 1536$ *Rhodomonas salina* ml^{-1}, and $U(h^{-1}) = 0.043x$ for $x > 1536$ *R. salina* ml^{-1}. Data points represent treatment means ±1 SE

Balanion comatum had a maximum ingestion rate of ~2 *Rhodomonas salina* cells h^{-1} (Fig. 3), corresponding to a maximum specific ingestion rate (volume of prey ingested/predator volume) of ~15% h^{-1}. The maximum ingestion rate of *Gymnodinium* sp. was ~0.043 *R. salina* cells h^{-1} (Fig. 3), corresponding to a maximum specific ingestion rate of ~6% h^{-1}, which is 2 to 3 times lower than that of *B. comatum*.

The growth rate of *Balanion comatum* reached a maximum of 0.058 h^{-1} at a prey concentration of ~1000 *Rhodomonas salina* ml^{-1} (Fig. 4), while *Gymnodinium* sp. reached a maximum growth rate of 0.039 h^{-1} at a prey concentration of ~1300 *R. salina* ml^{-1} (Fig. 4).

Due to differences in the functional biology of the ciliate and the dinoflagellate, the threshold prey concentration for growth (defined as the prey concentration at which $\mu = 0$) was determined differently. The threshold prey concentration for growth for *Balanion comatum* was determined by the formula:

$$\mu = \frac{\mu_{max}(x - x_0)}{K + (x + x_0)}$$

where μ_{max} is the maximum growth rate, x is the actual prey concentration, x_0 is the threshold prey concentration for growth and K is the prey concentration sustaining $0.5\,\mu_{max}$. Data was iteratively fitted to the model using Sigma plot® (Jandel Scientific). Threshold prey concentration for growth of *Gymnodinium* sp. was estimated as the intercept when $\mu = 0$. The threshold prey

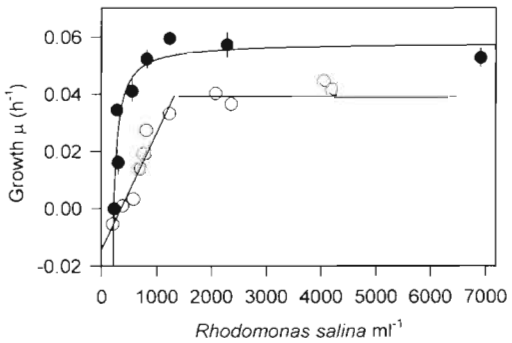


Fig. 4. Growth rate of *Balanion comatum* (●) and *Gymnodinium* sp. (○) as a function of prey concentration (x). See Table 2 and text for details. Data points represent treatment means ±1 SE

concentrations for growth of *B. comatum* and *Gymnodinium* sp. were approximately 227 ± 14 (±1 SE) and 382 ± 61 (±1 SE) *Rhodomonas salina* ml^{-1}, respectively. Results of these fits are shown in Table 2.

The cell volume of *Balanion comatum* increased from ~1100 μm^3 at low prey concentrations to ~2500 μm^3 at prey concentrations sustaining maximum growth rates (Fig. 5). The cell volume of *Gymnodinium* sp. increased from ~70 μm^3 at low prey concentrations to ~160 μm^3 at food saturation (Fig. 5).

Gymnodinium sp. and *Balanion comatum* had a yield of ~68 ± 10% (±1 SE) and 32 ± 8% (±1 SE), respectively, when cells were growing at maximum growth rates (Fig. 6). Yield decreased at prey concentrations less than ~600 and ~250 cells ml^{-1} for *Gymnodinium* sp. and *B. comatum*, respectively (Fig. 6). Maintenance requirements, defined as the specific ingestion rate at $\mu = 0$, were low (1 to 2% h^{-1}; Fig. 7) for both species.

The maximum specific clearance of *Balanion comatum* was ~2 times higher than that of *Gymnodinium* sp., 17 × 10^5 and 8.3 × 10^5 body volumes h^{-1}, respectively (Fig. 8). The maximum absolute clearance of *B. comatum* and *Gymnodinium* sp. was 2.8 and 0.053 μl h^{-1}, respectively (data not shown).

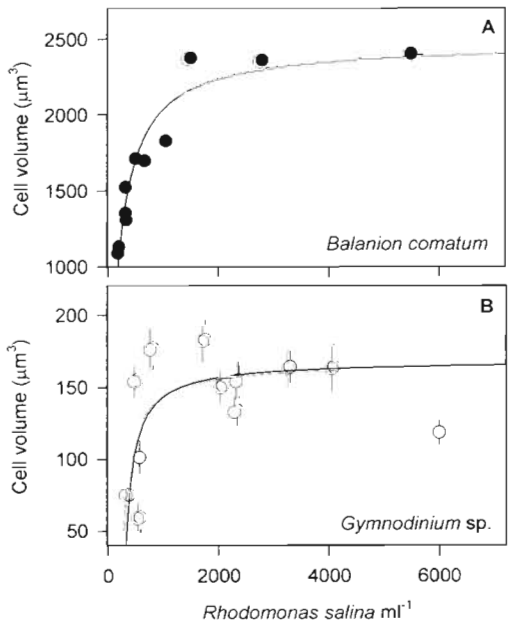


Fig. 5. Cell volume as a function of prey concentration (x). (A) *Balanion comatum*

$$V(\mu m^3) = \frac{2614(x + 58)}{338 + (x + 58)}$$

and (B) *Gymnodinium* sp.

$$V(\mu m^3) = \frac{168(x - 286)}{124 + (x - 286)}$$

for prey concentrations >400 *Rhodomonas salina* cells ml^{-1}. Data points represent treatment means ± 1 SE

When subjected to starvation, *Balanion comatum* immediately decreased in number and cell volume (Fig. 9). After 50 h, only 10% of the initial concentration of *B. comatum* was left, and cells had shrunk to ~400 μm^3 (9 μm ESD). After 60 h, no *B. comatum* cells were left in the culture. When subjected to starvation, *Gymnodinium* sp. produced swarmer cells (small fast-moving cells) which had a cell volume of about 60 to 70 μm^3. One third of cells immediately underwent 1 post feeding cell division and the average cell volume was reduced by 50% before cells died off. Most of the

Table 2. *Balanion comatum* and *Gymnodinium* sp. Values of maximum growth (μ_{max}) and ingestion (U_{max}) rates. Due to differences in feeding biology, data on *B. comatum* are fitted to a Holling type II response, while data on *Gymnodinium* sp. were fitted to a Holling type I response. x: actual prey concentration; K: prey concentration sustaining $0.5\mu_{max}$

Predator	Fit type	Equation	r^2	μ_{max}/U_{max} (h^{-1})	K (cells ml^{-1})
Growth					
Balanion comatum	Holling II	$\mu(h^{-1}) = 0.058(x - 227)/[315 + (x - 227)]$	0.89	0.058	315
Gymnodinium sp.	Holling I	$\mu(h^{-1}) = -0.0143 + 4.06 \times 10^{-5}x$ $x < 1318$	0.90	0.039	821
Ingestion					
Balanion comatum	Holling II	$U(h^{-1}) = 2.027(x - 204)/[511 + (x - 204)]$	0.96	2.027	511
Gymnodinium sp.	Holling I	$U(h^{-1}) = 0.00165 + 2.71 \times 10^{-5}x$ $x < 1536$	0.59	0.043	738

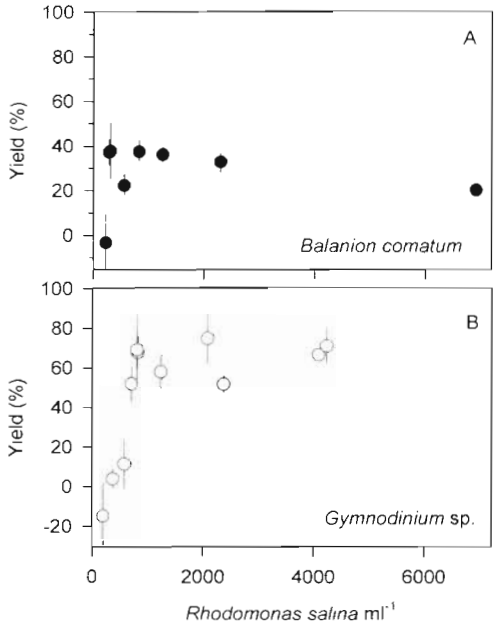


Fig. 6. Yield as a function of prey concentration for (A) *Balanion comatum* and (B) *Gymnodinium* sp. Data points represent treatment means ± 1 SE

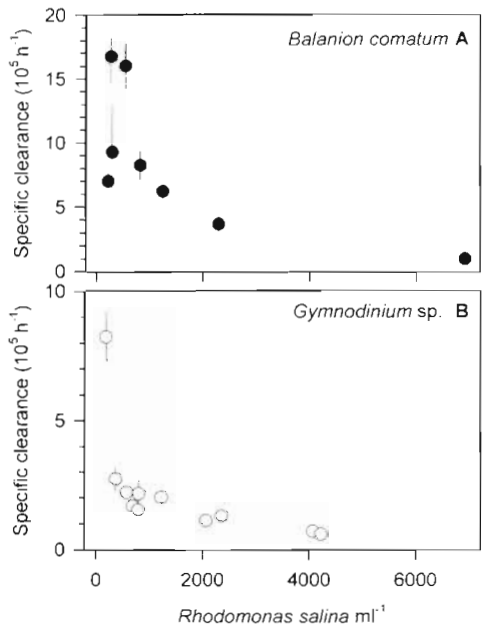


Fig. 8. Specific clearance (body volumes h^{-1}) as a function of prey concentration for (A) *Balanion comatum* and (B) *Gymnodinium* sp. Data points represent treatment means ± 1 SE

Gymnodinium sp. cells (80%) were left after 150 h (Fig. 9). Formation of resting cysts was not observed in any of the investigated species.

The prey size spectrum for *Gymnodinium* sp. is almost identical to that of *Balanion comatum* (Fig. 10). The optimum prey size was 8 µm (ESD). The lower limit of prey capture was 4 µm ESD and the upper limit close to 10 µm ESD. Generally there is a good agreement between the prey size spectrum based on growth rate and the one based on ingestion rates. However, in

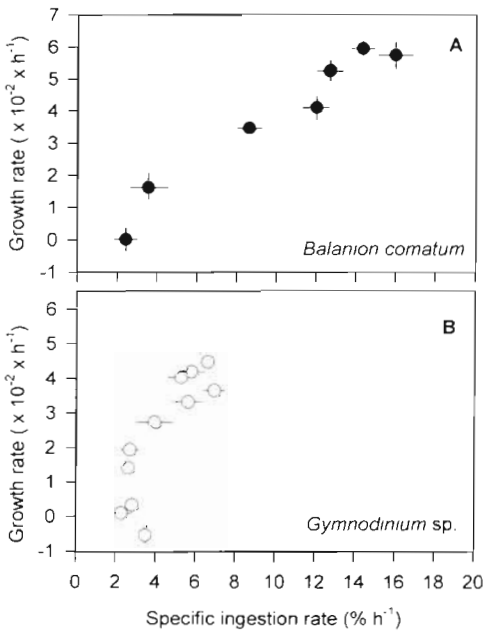


Fig. 7. Growth rate (μ) as a function of specific ingestion rate (U) for (A) *Balanion comatum* and (B) *Gymnodinium* sp.

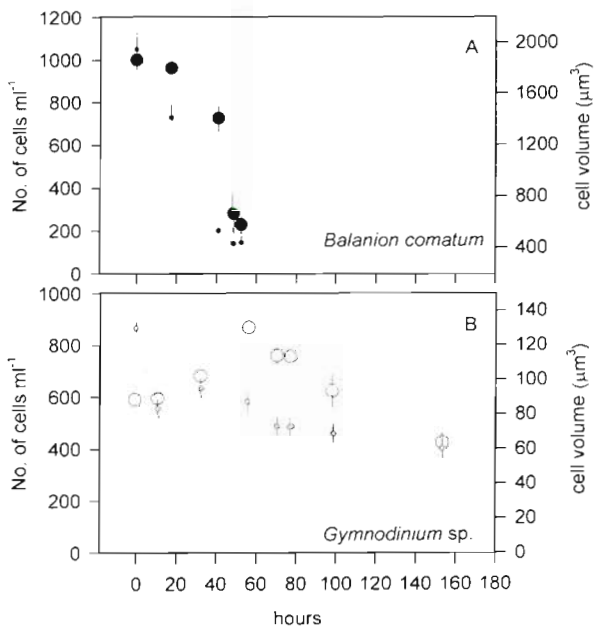


Fig. 9. Starvation. (A) *Balanion comatum*. The number of predator cells (●) and the volume of the starving predator (···•···). (B) *Gymnodinium* sp. The number of predator cells (○) and the volume of the starving predator (···○···). Data points represent treatment means ± 1 SE

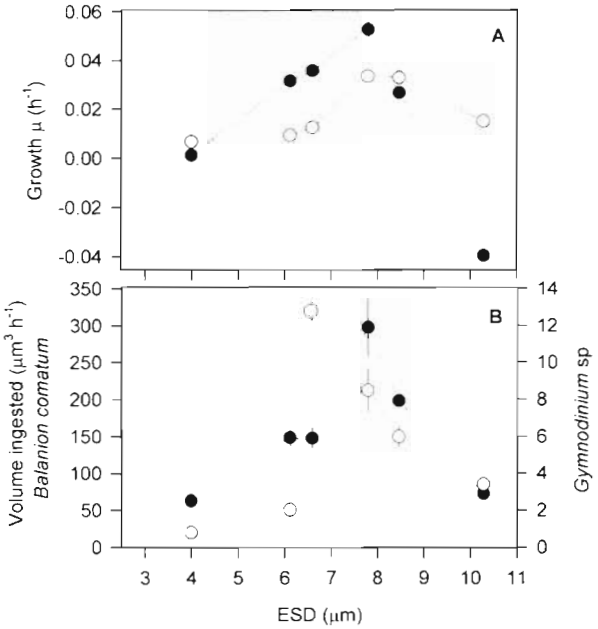


Fig. 10. Prey size spectra. (A) Growth rate (μ) (h^{-1}) as a function of prey size (ESD) and (B) ingestion rate as a function of prey size (μm^3 $cell^{-1}$ h^{-1}) for *Balanion comatum* (●) and *Gymnodinium* sp. (○). Data points represent treatment means ± 1 SE

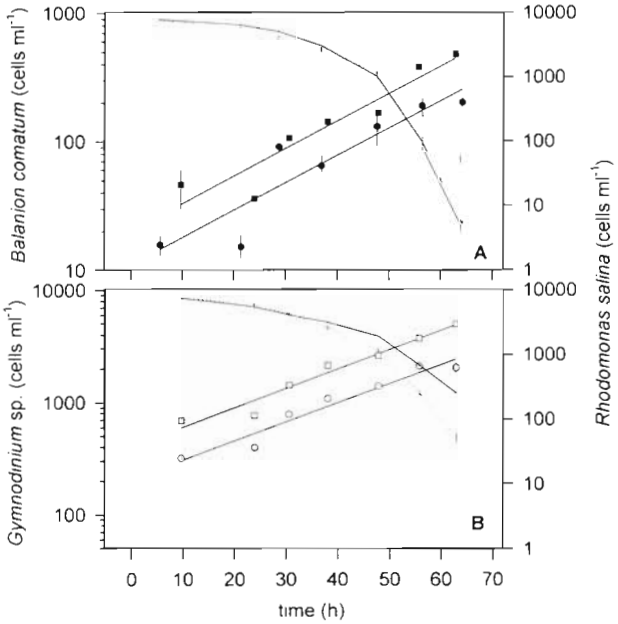


Fig. 11 Mixture experiments. (A) Cell concentration of *Balanion comatum* in mixed cultures with *Gymnodinium* sp. and *Rhodomonas salina* (●) and in the control experiment where *Balanion comatum* only co-occurs with *R. salina* (■). (B) Cell concentration of *Gymnodinium* sp. in mixed cultures with *Balanion comatum* and *Rhodomonas salina* (○) and in the control experiment where it only co-occurs with *R. salina* (□). In both plots, dotted and solid curves refer to cell concentration of *R. salina* in the mixed culture and in the control, respectively. Data points refer to cell concentration ± 1 SE

one case (*Gymnodinium* sp. fed *Plagioselmis prolonga*) a very high ingestion rate was not reflected in the growth rate, indicating a low growth efficiency.

The average growth rates of *Gymnodinium* sp. and *Balanion comatum* obtained when they were grown together on *Rhodomonas salina* did not differ significantly from growth rates obtained in cultures where they were grown alone on *R. salina* (*t*-test: *Gymnodinium* sp., $p = 0.8106$, $t = 0.246$; *B. comatum*, $p = 0.7451$, $t = 0.334$), indicating that *B. comatum* is unable to feed on *Gymnodinium* sp. and vice versa (Fig. 11, Table 3).

Gymnodinium sp. cells either drifted passively or swam in an almost straight path with an average speed of 195 ± 10 μm s^{-1} (± 1 SE) corresponding to 25 body lengths s^{-1}. Drifting was never observed in starved *Gymnodinium* sp. cells. Upon making contact with other objects, *Gymnodinium* sp. cells tumbled and subsequently performed a burst with a maximum speed of 6600 μm s^{-1}. Thereafter, swimming speed decreased asymptotically to 195 μm s^{-1} or to passive drifting. The distance traveled during a burst was up to 400 μm. *Balanion comatum* swam in helices at an average speed of 375 ± 22 μm s^{-1} (± 1 SE) corresponding to 19 body lengths s^{-1}. Bursts were observed with a maximum speed of 1100 μm s^{-1}. The burst was stopped drastically and the cell almost stopped swimming for some time (0.5 to 1 s) after which the cell resumed its original swimming speed. The distance traveled during bursts was often up to 1000 μm.

Table 3. *Balanion comatum* and *Gymnodinium* sp. Growth rate (h^{-1}) in the mixture experiment. No significant differences in growth rates were observed between control and mixture experiments (for test used see text). n: number of replicates

Species	Experiment	Growth rate (h)	r^2	n
Gymnodinium sp.	Control	0.039	0.96	7
Gymnodinium sp.	Mixture experiment	0.039	0.93	7
Balanion comatum	Control	0.051	0.88	7
Balanion comatum	Mixture experiment	0.053	0.80	7

DISCUSSION

Prey selection

Gymnodinium sp. (7 μm) and *Balanion comatum* (17 μm) both feed on autotrophic nanoflagellates 4 to 10 μm in diameter and may be considered as competitors for similar-sized food. However, to what degree can this ob-

servation be used to generalise on the competition between small dinoflagellates and ciliates?

Gymnodinium sp. ingests single cells by direct engulfment, which is a common feeding mechanism among heterotrophic dinoflagellates (Gaines & Elbrächter 1987, Hansen 1991b). We found that *Gymnodinium* sp. had an optimum prey size corresponding approximately to its own size, which in specific terms is similar to that obtained for *Gyrodinium spirale*, which also feeds using this feeding mechanism (Hansen 1992). Other feeding mechanisms found among heterotrophic dinoflagellates include pallium feeding and feeding tubes. These feeding mechanisms also allow the dinoflagellate to ingest relatively large prey. In summary, predator:prey size ratios found among the dinoflagellates range between 0.4:1 and 7:1 (see Table 4). Hence, *Gymnodinium* sp. does not differ from the large majority of dinoflagellates described so far. Note, however, that *Noctiluca scintillans* is an exception by being capable of ingestion of a much broader range of prey due its ability to glue prey items into large packages (see Gaines & Elbrächter 1987, Buskey 1995).

Some studies have suggested that heterotrophic dinoflagellates ingest particles of the size of bacteria (Lessard & Swift 1985, Strom 1991). The study of Lessard & Swift (1985) demonstrated uptake of thymidine-labelled bacteria in heterotrophic dinoflagellates, but their investigation did take into account the following: (1) Thymidine may have accumulated in the food chain. Thus, bacteria may have been fed upon by heterotrophic nanoflagellates and ciliates, which subsequently were fed upon by the heterotrophic dinoflagellates. (2) Bacteria may be parts of aggregates of a much larger size, making them available for heterotrophic dinoflagellates. Strom (1991) documented feeding of a *Gymnodinium* sp. (12 µm) on the cyanobacteria *Synechococcus* sp. (1.2 × 2.4 µm) when presented in mixture with the prymnesiophyte *Isochrysis galbana* (4.5 µm). However, *Synechococcus* sp. is a rather large autotrophic bacteria with a volume which is 20 to 30 times that of marine heterotrophic bacteria in natural environments (Lee & Fuhrmann 1987, Simon & Azam 1989).

An important observation is that the presently investigated *Gymnodinium* sp. has a lower prey size limit of about 4 µm, suggesting that small dinoflagellates (<10 µm) do not feed on single cells of heterotrophic bacteria, unlike most other groups of nanoflagellates <10 µm (Fenchel 1982a, Eccleston-Parry & Leadbeater 1994). In conclusion, no experiments have so far documented, beyond reasonable doubt, that heterotrophic dinoflagellates are able feed on prey in the size range of naturally occurring heterotrophic bacteria in marine environments.

A prey size spectrum has not previously been established for prostomatid ciliates. However, the freshwater species *Balanion planctonicum* (15 µm) preyed upon a 10 µm flagellate (Müller 1991, Sommaruga & Psenner 1993), while a marine *Balanion* sp. (34 µm) grew best on the 17 µm dinoflagellate *Heterocapsa triqueta* (Stoecker et al. 1986). We found that the 17 µm *Balanion comatum* grew best on *Rhodomonas salina* of 8 µm, indicating a general predator:prey ratio of 2:1 for species belonging to the genus *Balanion*. This is in contrast to aloricate oligotrich ciliates, which have an optimum predator:prey size ratio of about 8:1 (Jonsson 1986, 1987), but similar to loricate oligotrichs (tintinnids), which are able to ingest prey of a size which corresponds to a predator:prey size ratio of approx. 2.5:1 (Heinbokel 1978). Thus, it appears that small (<20 µm) heterotrophic dinoflagellates compete with small (<20 µm) prostomatids and loricate and aloricate oligotrichs (40 to 60 µm) for prey in the 4 to 10 µm size range.

It is surprising that *Balanion comatum* apparently cannot catch *Gymnodinium* sp. cells, even though *Gymnodinium* sp. is of an optimal prey size for *B. comatum*. We believe that the reason for this is that *Gymnodinium* sp. performs a fast escape response when making contact with objects, while the algae used in the experiment do not, thereby making it impossible for the ciliate to catch the dinoflagellate. While data on swimming behavior in heterotrophic dinoflagellates are available in the literature (Jacobson & Anderson 1986, Strom & Buskey 1993), this is, to our knowledge, the first time burst swimming has been reported in dinoflagellates. We have observed burst swimming in other small gymnodinoid dinoflagellates (unpubl. obs.), indicating that this may not be an unique trait for this species.

Bioenergetics

The growth rate of the ciliate *Balanion comatum* was higher than that of the dinoflagellate *Gymnodinium* sp. at prey concentrations which supported balanced growth (Figs. 3 & 4), indicating that the ciliate may potentially out-compete the dinoflagellate in natural environments. The maximum growth rate of *Gymnodinium* sp. is close to the expected value which can be calculated from published relationships between growth rate and size (Hansen 1992, Sherr & Sherr 1994). The maximum growth rate of *B. comatum* is almost identical to the growth rate obtained for the freshwater *B. planctonicum* at a similar temperature (Müller 1991). The maximum growth rate of *B. comatum* is relatively low when compared to the expected maximum growth rate calculated from relationships between maximum growth rate and size of ciliates

(Fenchel & Finlay 1983, Montagnes 1996 and references therein). However, the maximum growth rate of *B. comatum* is comparable to or even higher that that of other planktonic (and larger) ciliates feeding on nanoplankton (Table 4).

Gymnodinium sp. and *Balanion comatum* have almost similar threshold prey concentrations for growth, 18 and 11 µg C l^{-1}, respectively (Table 4, Fig. 4). Values of threshold prey concentrations for growth taken from the literature are shown in Table 4. The threshold prey concentrations for growth of *Gymnodinium* sp. and *B. comatum* are both at the lower end of reported values within the 2 groups. Considerable variation is found in the estimates of the threshold prey concentrations for growth among both ciliates and heterotrophic dinoflagellates. However, data for ciliates and heterotrophic dinoflagellates fall within the same range. Consequently, no relationship between predator size and threshold prey concentration is found in either of the groups (Table 4). The high variability may reflect different 'strategies' within the groups, but may equally be explained by the difficulty in obtaining reliable results. In fact, some of the obtained threshold values are extremely high (200 to 300 µg C l^{-1}). Laboratory data may overestimate the threshold prey concentration if (1) the prey is of a suboptimal size or quality (see Table 4), (2) the prey is not evenly distributed during incubation or (3) prey concentration is being depleted during incubation. In fact, often only the initial prey concentration is measured. Thus, at present it is impossible to tell if there are significant differences in threshold prey concentration for growth between ciliates and dinoflagellates.

So far most laboratory experiments have been carried out under steady state conditions. However, steady state conditions are rarely found in nature, because pelagic environments are indeed heterogeneous in time and space (Andersen & Sørensen 1986, Owen 1989, Franks 1995). Also, selective predation by metazooplankton may affect populations of ciliates and small dinoflagellates differently.

Adaptations to a heterogeneous environment

Protists that live in heterogeneous environments have evolved adaptations to cope with fluctuations in food availability, a phenomenon often referred to as a feast and famine existence. Such adaptations can involve complex life cycles (resting cysts and swarmer formation) and the ability to regulate metabolism when food conditions change.

Formation of resting cysts is widespread among ciliates and heterotrophic dinoflagellates (e.g. Goodman 1987, Fenchel 1990). Resting cysts have not been reported among species in the genera *Balanion* and

Table 4. Maximum growth rates and threshold prey concentration taken from the literature for growth of heterotrophic dinoflagellates and planktonic ciliates. Literature values were converted to carbon assuming 0.12 pg C μm^{-3} (Strathmann 1967). A conversion factor from volume to carbon of 0.2 pg C μm^{-3} was used to convert number of *Rhodomonas salina* to carbon in the present experiment (data not shown). Data on growth rates are adjusted to 15°C using Q_{10} = 2.8. nd = not determined

Species	Predator ESD (µm)	Max. growth rate, μ (h^{-1})	Threshold (µg C l^{-1})	Prey species	ESD (µm)	Source
Dinoflagellates						
Gymnodinium sp	7	0.043	18	*Rhodomonas salina*	8	This study
Gymnodinium sp.	12	0.043	10	*Isochrysis galbana/Synechococcus* sp.	4.5/1.5	Strom (1991)
Gyrodinium spirale	27	0.027	246	*Heterocapsa triquetra*	16	Hansen (1992)
Oblea rotunda	23	0.017	20	*Ditylum brightwellii*	23	Strom & Buskey (1993)
Oblea rotunda	23	0.010	50	*Dunaliella tertiolecta*	6.5	Strom & Buskey (1993)
Protoperidinium crassipes	73	0.008	247	*Gonyaulax polyedra*	37	Jeong et al. (1994)
Protoperidinium cf. *divergens*	61	0.013	262	*Gonyaulax polyedra*	37	Jeong et al. (1994)
Protoperidinium huberi	48	0.017	10	*Ditylum brightwellii*	23	Buskey et al. (1994)
Ciliates						
Eutintinnus pectinis	31	0.054	14	*Isochrysis galbana/Monochrysis luthen*	nd	Heinbokel (1978)
Favella azorica	nd	0.054	17	*Heterocapsa triquetra*	16	Kamiyama (1997)
Favella ehrenbergii	57	0.034	6	*Heterocapsa triquetra*	16	Hansen (1995)
Favella taraikaensis	nd	0.048	10	*Heterocapsa triquetra*	16	Kamiyama (1997)
Tintinnopsis acuminata	24	0.043	15	*Isochrysis galbana*	5	Verity (1985)
Tintinnopsis vasculum	51	0.050	15	*Dicrateria inornate*	nd	Verity (1985)
Lohmaniella spiralis	31	0.037	8	*Pyramimonas* sp.	6	Jonsson (1986)
Strobilidium neptuni	60	0.059	325	*Chroomonas salina*	8	Montagnes (1996)
Strobilidium veniliae	56	0.026	75	*Isochrysis galbana:Chroomonas salina* (1:1)	5.5:8	Montagnes (1996)
Strombidinopsis cheshiri	63	0.037	6	*Thalassiosira pseudonana*	4	Montagnes et al. (1996)
Strombidium reticulatum	42	0.049	8	*Pyramimonas* sp.	6	Jonsson (1986)
Strombidium siculum	38	0.023	16	*Thalassiosira pseudonana*	4	Montagnes (1996)
Balanion comatum	17	0.058	11	*Rhodomonas salina*	8	This study

Gymnodinium and none of our isolates formed resting cysts. However, we cannot totally exclude cyst production in these genera, because cyst formation can be clone specific and even selected against within a few generations (Fenchel 1989).

Production of swarmers was only observed in *Gymnodinium* sp. in the present study. Reports on the existence of swarmer cells is very rare in heterotrophic dinoflagellates. To our knowledge only the naked heterotrophic dinoflagellates *Polykrikos kofoidii* (Morey-Gaines & Ruse 1980) and *Gymnodinium fungiforme* (Spero & Moreé 1981) have been described to include swarmers in their life cycles. Production of swarmers is unknown in planktonic ciliates, but is common in benthic ciliates (e.g. Fenchel 1990).

The ability to slow down metabolism to a minimum is known among protists (e.g. Fenchel 1982b, 1989, 1990). Some ciliates can survive for a period corresponding to 40 times their own minimum generation time (Fenchel 1990). However, the few planktonic ciliates studied so far are not able survive for very long when starved, only approx. 2 to 3 minimum generation times (Fenchel 1989, Montagnes 1996). In this respect, *Balanion comatum* is no exception; it is able to starve for ~4 times the minimum generation time. Reports on the ability of heterotrophic dinoflagellates to reduce metabolism when starved are sparse. The heterotrophic dinoflagellate *Gyrodinium spirale* can prolong survival by reducing its metabolism (Hansen 1992). However, the question of how long they are able to survive was not addressed. Jeong & Latz (1994) found that the large planktonic heterotrophic dinoflagellate *Protoperidinium divergens* survived for at least 9 times its minimum generation time, while Strom (1991) reported on a *Gymnodinium* sp. which was able to starve more than 30 times its minimum generation time. Our *Gymnodinium* sp. was able to starve for more than 10 times its own minimum generation time. Thus, although the information on the ability of planktonic ciliates and heterotrophic dinoflagellates to prolong survival is limited, the data suggest that heterotrophic dinoflagellates may be able to cope better with starvation than planktonic ciliates.

What are the benefits of prolonging survival for the dinoflagellate? Generally, prolonged survival will give the the organism more time to encounter patches in time or space. A compilation of swimming speed data on ciliates and dinoflagellates presented in Buskey et al. (1993) and Hansen et al. (in press) suggest that ciliates generally swim 2 times faster than dinoflagellates, although the variation is large. The maximum distance travelled for an organism is a function of swimming speed, time and tumbling frequency. In the case of *Gymnodinium* sp., a cell subjected to starvation is able to travel about 100 m assuming a speed on 195 µm s^{-1}, a non-tumbling swimming pattern, and a survival time of 150 h. However, due to the production of swarmers during starvation, the 'genome' of the cell almost doubles the potential distance travelled (200 m). In the case of *Balanion comatum*, the maximum distance travelled is about 75 m assuming a speed of 376 µm s^{-1} and a survival time of 55 h. Thus, *Gymnodinium* sp. has potentially a competitive advantage compared to *B. comatum* when food is patchy in time and space.

Metazooplankton grazing on ciliates and small dinoflagellates

Grazing by metazooplankton on ciliates has been reported to range from insignificant to important (Stoecker & Sanders 1985, Wiadnyana & Rassoulzadegan 1989, Fessenden & Cowles 1994, Nielsen & Kiørboe 1994). Field and laboratory experiments have shown that the greatest grazing impact on the ciliate stock by copepods is when phytoplankton concentrations are low and dominated by small phytoflagellates (e.g. Jonsson & Tiselius 1990, Nielsen & Kiørboe 1994, Atkinson 1996). However, the swimming behavior of the ciliates also plays a role. Some ciliates, like *Strobilidium* spp. and *Myrionecta rubra*, are able to escape by burst swimming (3000 to 7000 µm s^{-1}) when attacked by metazoan predators (Jonsson & Tiselius 1990, Gilbert 1994). Data on metazooplankton grazing on small heterotrophic dinoflagellates are lacking. However, laboratory experiments on prey size selection by copepods suggest that particles the same size as *Gymnodinium* sp. are retained with an efficiency which is less than 10% of that obtained on particles the same size as *Balanion comatum* (Frost 1972, Nival & Nival 1976, Berggreen et al. 1988). In conclusion, the grazing impact on ciliates by metazooplankton might under some conditions be much higher than that on small heterotrophic dinoflagellates.

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