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Lethal effect of the dinoflagellate *Heterocapsa circularisquama* upon the tintinnid ciliate *Favella taraikaensis*

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ABSTRACT: We examined the effect of the toxic dinoflagellate *Heterocapsa circularisquama* in bloom concentrations on the mortality process of the tintinnid ciliate *Favella taraikaensis*. The number of viable *F. taraikaensis* decreased during the first 7 h of the incubation experiment and disappeared within 24 h at a *H. circularisquama* concentration of $\geq 6.4 \times 10^3$ cells ml^{-1}. Mortality of the ciliates occurred more rapidly with increasing concentrations of *H. circularisquama*. Morphological changes of *F. taraikaensis* cells, characterized by swollen and/or spherical forms, were observed after 4 and 7 h of incubation. Microscopic observations showed that *H. circularisquama* cells frequently adhered to the adoral membranelles of *F. taraikaensis*. The mean adhesion time of *H. circularisquama* cells to the adoral membranelles of *F. taraikaensis* was significantly longer than cells of the non-toxic dinoflagellate *Heterocapsa triquetra*. During the adhesion process, contact of *H. circularisquama* cells with the cytoplasm around the oral plug of *F. taraikaensis* was observed. Filtrate of *H. circularisquama* culture solution had no effect on the activity of *F. taraikaensis* cells. These results suggest that *H. circularisquama* causes physiological problems for *F. taraikaensis* through cell contact, with higher algal concentrations increasing the frequency of cell contact between *H. circularisquama* and *F. taraikaensis*, which may enhance the noxious effect of *H. circularisquama* on *F. taraikaensis*.

KEY WORDS: *Heterocapsa circularisquama* · Tintinnids · Ciliates · *Favella taraikaensis* · Growth inhibition · Cell contact

INTRODUCTION

Since first recorded in Uranouchi Bay in 1988, red tides of the dinoflagellate *Heterocapsa circularisquama* have caused mass mortality of pearl oysters and other bivalves, seriously damaging shellfish aquaculture and fisheries production in western Japan (Yamamoto & Tanaka 1990, Matsuyama et al. 1995). This dinoflagellate specifically kills bivalves, probably due to the production of toxins which repress bivalve feeding (Matsuyama et al. 1995, 1997, Nagai et al. 1996). Although its characteristics are not known in detail, the toxin is considered to be a protein-like substance localized on the cell surface (Matsuyama et al. 1997).

Zooplankton reject some red-tide flagellates as food sources. Uye & Takamatsu (1990) reported that calanoid copepods hardly feed on red-tide algae such as *Gymnodinium mikimotoi* or *Heterosigma akashiwo*. At least some tintinnid ciliates, an important component of microzooplankton, have a selective feeding ability (Stoecker et al. 1981) and can instantaneously reject *H. akashiwo* or *Rhodomonas* sp., which are poor food sources for tintinnids (Taniguchi & Takeda 1988). Growth inhibition of the tintinnid species *Favella ehrenbergii* by *Alexandrium tamarense* (Hansen 1989) and *Gyrodinium aureolum* (Hansen 1995) has been recognized in culture experiments. Negative responses to harmful flagellates by tintinnids or rotifers are probably caused by cell surface chemical compounds (Verity & Stoecker 1982, Egloff 1986) or toxic substances exuded from the algae (Hansen 1989, 1995).

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There has been only one study on the interactions between *Heterocapsa circularisquama* and zooplankton (Kamiyama 1997) which reported that the tintinnid *Favella taraikaensis* suffered mass mortality within a few days when the concentration of *H. circularisquama* exceeded ca 10^3 cells ml^{-1}, although the tintinnid ciliates *F. azorica* and *F. taraikaensis* actively fed on this alga at concentrations of less than 10^3 cells ml^{-1}. The mass mortality of *F. taraikaensis* indicates that *H. circularisquama* cells are specifically harmful to grazers under dense bloom conditions. Studies on the harmful effects of *H. circularisquama* are useful to elucidate the processes of bloom formation and decay in the coastal areas and to estimate the influence of a *H. circularisquama* bloom on the function of microbial food webs in coastal marine systems.

Here, we examined the inhibition effects of *Heterocapsa circularisquama* cells at high concentrations on the tintinnid ciliate *Favella taraikaensis* and observed the interactions between them in detail.

MATERIALS AND METHODS

Culture of tintinnids and prey phytoplankton. Strains of *Favella taraikaensis* were isolated from either supernatant seawater on incubated sediment collected from Hiroshima Bay or seawaters in Gokasho Bay and Hiroshima Bay. These ciliates were grown in 200 ml flasks with 150 ml of culture medium consisting of filtered and autoclaved seawater enriched with 0.1 ml l^{-1} of f/2 iron-EDTA trace metal solution (Stoecker et al. 1988). *Heterocapsa triquetra* only or a mixture of *H. triquetra* and *Gymnodinium* sp. at a total concentration in the order of magnitude of 10^3 cells ml^{-1} were supplied as food. Portions of the culture with food algae were transferred to new medium every 4 to 5 d to maintain the cultures.

Heterocapsa circularisquama (cell dimensions 18.1 × 12.4 µm) was isolated from Ago Bay in December 1992, and *Gymnodinium* sp. (cell dimensions 10.6 × 8.6 µm) and *Heterocapsa triquetra* (cell dimensions 23.0 × 17.1 µm) were isolated from Hiroshima Bay in June 1986 and in April 1991, respectively. These cultures were maintained in 50 ml culture flasks containing 25 ml of f/2 medium (Guillard & Ryther 1962).

Survival of *Favella taraikaensis* at high concentrations of *Heterocapsa circularisquama*. An experiment was conducted to study the effects on the survival of *Favella taraikaensis* at high concentrations of *Heterocapsa circularisquama* during short-term incubations. Five concentrations of *H. circularisquama* in the order of magnitude of 10^3 to 10^4 cells ml^{-1} were prepared as experimental treatments and a no food treatment was also made as a control. Two milliliters of each concentration were dispensed into 4 wells of multiple well plates (12 wells) and then 5 individuals of *F. taraikaensis* were inoculated into all wells. The plates were incubated at 20°C, 30 µmol photon m^{-1} s^{-1} with a 14h:10h light-dark photo cycle. Motile individuals which were able to swim in each well were counted at 4, 7, and 24 h of incubation with a stereomicroscope.

An identical experiment at a concentration of 2.86 × 10^4 cells ml^{-1} was repeated to observe in detail any morphological changes in *Favella taraikaensis*. Motile *F. taraikaensis* after 4 and 7 h of incubation were observed with an inverted epifluorescence microscope (Olympus IX70) attached to a VTR system (Ikegami time lapse video cassette recorder TVR-7480, Victor color video monitor TM-150S and Sony camera adapter CMA-D2). Using the film recorded before the incubation and after 4 h of incubation, the lateral cell area, representing the cell volume of *F. taraikaensis*, was measured using a high definition image processor (Nexus Inc. nexus 9000) to examine any morphological change of the *F. taraikaensis* cells.

***Heterocapsa circularisquama* uptake by *Favella taraikaensis* during short-term incubation.** This experiment was designed to examine whether or not mortality of *Favella taraikaensis* is due to the avoidance of feeding on *Heterocapsa circularisquama*. Part of the supernatant water was removed without agitation from a culture strain of *F. taraikaensis* when the density of *F. taraikaensis* reached >10 ind. ml^{-1}. Within this supernatant water, almost all the food algae were consumed and auto-fluorescence in the food vacuoles of *F. taraikaensis* due to food algae was hardly observed. Fifty milliliters of supernatant water was dispensed into each of three 100 ml flasks. Culture of *H. circularisquama* was added to each flask at final concentrations of 5.2×10^2, 5.2×10^3 and 1.35×10^4 cells ml^{-1}, and then incubation immediately started under conditions of 20°C and 30 µmol photon m^{-1} s^{-1}. Before the addition of the alga and at 10, 20, 30, 40, 50, 60 min of incubation, 2 ml of culture was taken off from each flask and transferred into a well of multiple well plates (24 wells) containing 0.2 ml of 20% buffered formaldehyde for fixation of the tintinnids. Auto-fluorescence particles inside food vacuoles of each *F. taraikaensis* were counted using an inverted epifluorescence microscope (DIAPHOT-TMD, Nikon). The average particle number of more than 20 individuals of *F. taraikaensis* at each time point was calculated for each treatment. The concentration of *Heterocapsa triquetra* cells carried over from the stock culture into the experimental medium was 12 cells ml^{-1}, and the mean number of auto-fluorescence particles in the food vacuoles was 0.3 cells $ind.^{-1}$ before the addition of *H. circularisquama*.

Effects of exudate from *Heterocapsa circularisquama* on the survival of *Favella taraikaensis*. The effect

of dissolved substances released from *Heterocapsa circularisquama* on the survival of *Favella taraikaensis* was examined. Algal suspension (1.37×10^5 cells ml^{-1}) was centrifuged ($1600 \times g$, 10 min) and then the supernatant was filtered with a 0.22 µm pore-size filter (Millipore GV). The filtrate was used without dilution to prevent toxic substance from decomposing due to pH shift. The algal suspension and f/2 medium (control) were diluted 4 times with the culture medium for the ciliates. Final concentration in the treatment of algal suspension was 3.42×10^4 cells ml^{-1}. Two milliliters of each treatment were dispensed into 6 wells in multiple well plates (12 wells), and 5 individuals of *F. taraikaensis* were inoculated into each well. All treatments were incubated at 20°C and 30 µmol photon m^{-1} s^{-1} with a 14h:10h light-dark photo cycle. Motile individuals of *F. taraikaensis* were monitored over 4 d using a stereomicroscope.

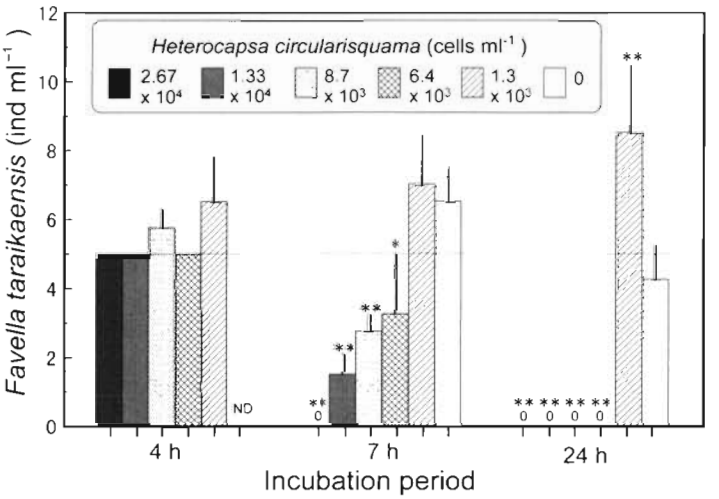

Fig. 1. *Favella taraikaensis*. Effect of the concentration of *Heterocapsa circularisquama* on survival. Vertical lines indicate standard deviation of the mean (n = 4). *p < 0.05, **p < 0.01, significantly different from values at the no food treatment

Observation of the interaction between *Heterocapsa circularisquama* and *Favella taraikaensis* cells. It is necessary to hold living ciliates in position to observe their behavior under the microscope. We used white vaseline for holding ciliates (Taniguchi & Takeda 1988). Several individuals of *Favella taraikaensis* were washed with algal-free medium and transferred to a hole slide glass coated with white vaseline, which had been filled with a few drops of a dense suspension of *Heterocapsa circularisquama* (cell concentration: $>10^5$ cells ml^{-1}). A cover slide was then placed over the vaseline ring. Some individuals of *F. taraikaensis* became stuck in the vaseline at times when this procedure was used. Although ciliates thus held could not move, their adoral membranelles continued to beat normally. The behavioral response of the membranelles of *F. taraikaensis* when exposed to *H. circularisquama* was observed and recorded using a VTR system attached to an inverted microscope as described above. We also observed the behavior of *F. taraikaensis* in response to *H. triquetra* in the same manner in order to compare it with the behavior observed in response to *H. circularisquama*.

RESULTS

Fig. 1 shows the growth/survival response of *Favella taraikaensis* at various concentrations of *Heterocapsa circularisquama* over 24 h. The density of *F. taraikaensis* significantly decreased after 7 h of incubation with $\geq 6.4 \times 10^3$ cells ml^{-1} of *H. circularisquama*. The decrease occurred more rapidly with increasing concentrations of *H. circularisquama*. After 24 h, *F. taraikaensis* had mostly died at concentrations of $\geq 6.4 \times 10^3$ cells ml^{-1} but increased at the concentration of 1.3×10^3 cells ml^{-1}. A decrease under the no food treatment was not observed.

After 4 or 7 h of incubation, morphological changes in *Favella taraikaensis* were observed at a high concentration of *Heterocapsa circularisquama* (2.86×10^4 cells ml^{-1}); some of the tintinnid cells swelled (Fig. 2B, C), or became spherical in shape after shedding their loricae (Fig. 2D). Abnormal mobility, i.e. backwards swimming behavior (Hansen 1989), was also observed. All the tintinnids finally lysed after being immobilized. The mean apparent lateral cell area of *F. taraikaensis* (n = 10) was 3462 ± 804 μm^{-2} at the beginning of incubation but had significantly increased after 4 h of incubation (5960 ± 1317 μm^{-2}, $p < 0.001$). Increasing cell volume of *F. taraikaensis* evidently was not due to feeding because only a few auto-fluorescent particles were observed in the food vacuoles of swollen tintinnids.

Microscopic observation with the VTR system showed the characteristic interaction between *Favella taraikaensis* and *Heterocapsa circularisquama*. *H. circularisquama* cells frequently adhered to the AZM (adoral zone of membranelles) of *F. taraikaensis* (Fig. 3A). Apparently, this behavior was not part of the feeding process of *F. taraikaensis* because tintinnids finally rejected the adhered cells. The mean adhesion time of a *H. circularisquama* cell to the AZM was 63 ± 66 s (n = 20), significantly longer than that of the non-toxic *Heterocapsa triquetra* (0.4 ± 1.1 s, $p < 0.001$). Direct contact of *H. circularisquama* cells with the cell surface around the oral plug of *F. taraikaensis* was observed during the adhesion process (Fig. 3B).

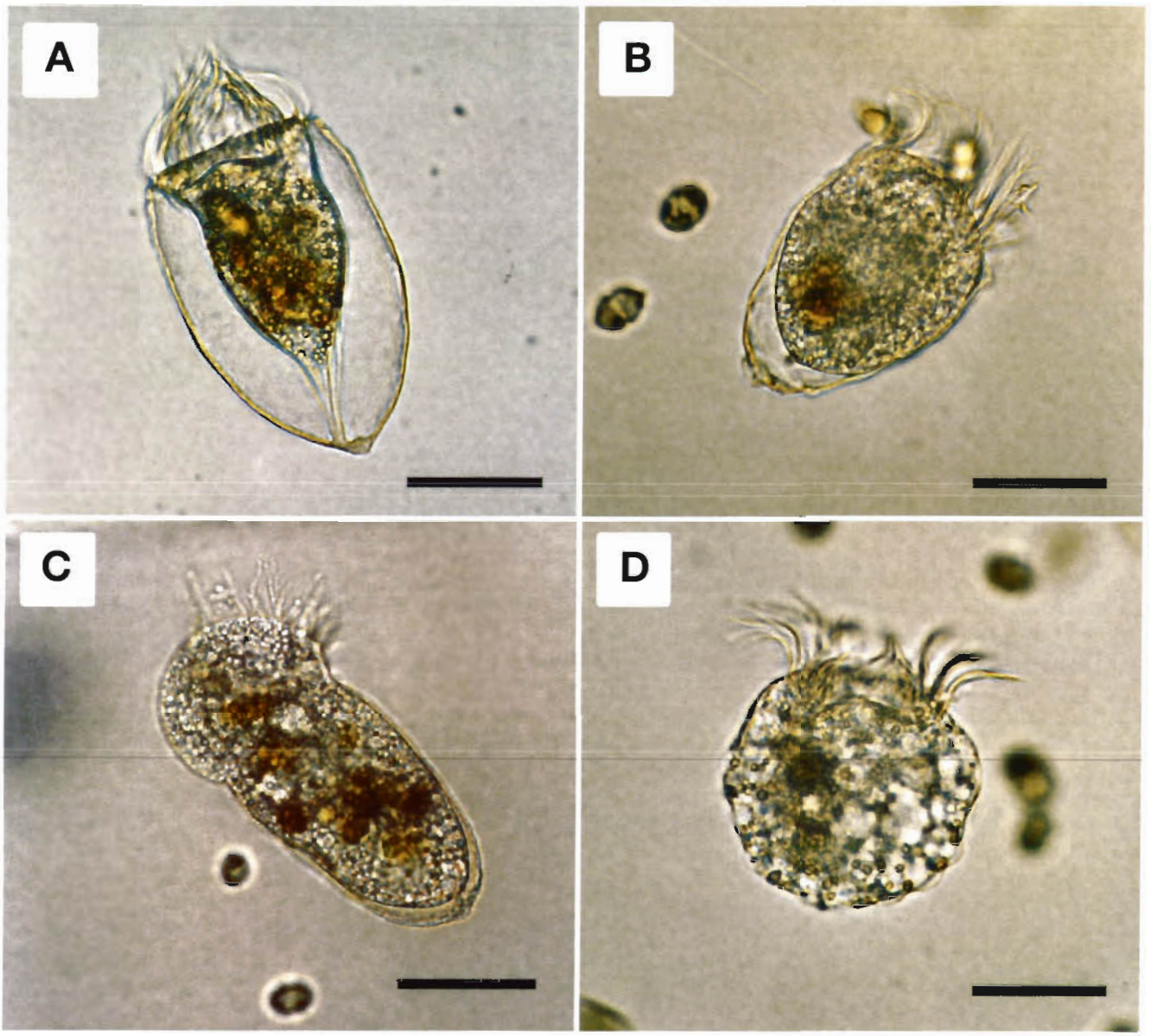

Fig. 2. *Favella taraikaensis*. Morphological changes caused by *Heterocapsa circularisquama*. (A) A normal individual (before the experiment); (B, C) swollen individuals (after 4 and 7 h of incubation, respectively); (D) a swollen naked individual (after 4 h of incubation). Scale bars = 50 µm

Fig. 4 represents the number of *Heterocapsa circularisquama* cells ingested by *Favella taraikaensis* as a function of the incubation period. The cell number of *H. circularisquama* cells ingested by *F. taraikaensis* generally increased for the first 60 min. Ingestion at a concentration of 5.2×10^3 and 1.35×10^4 cells ml^{-1} was significantly higher than that at a concentration of 5.2×10^2 cells ml^{-1} after 10, 20, 40, 60 min of incubation, but ingestion at the other times was not significantly different among the 3 different treatments ($p \geq 0.05$). These results indicate that during short-term incubations (≤60 min) *F. taraikaensis* can feed on *H. circularisquama* even at levels as high as 1.35×10^4 and 5.2×10^3 cells ml^{-1} and mortality of *F. taraikaensis* was not caused by starvation due to the rejection of *H. circularisquama*.

Fig. 5 shows the effect of the exudate from *Heterocapsa circularisquama* on the survival of *Favella taraikaensis*. Motile *F. taraikaensis* disappeared after 7 h of incubation in the dense suspension of *H. circularisquama*, although the number of motile individuals between the other treatments was not significantly different at this time point. Mortalities in the addition of the exudate treatment and the control treatment simi-

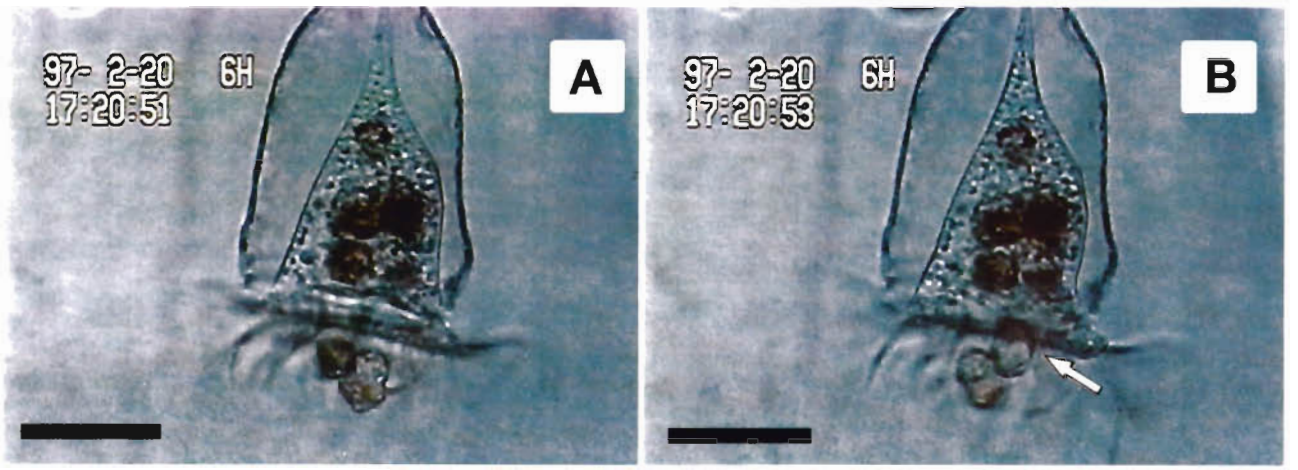

Fig. 3. Interaction between *Favella taraikaensis* and *Heterocapsa circularisquama*. (A) Adhesion of 2 cells of *H. circularisquama* to the adoral membranelles of *F. taraikaensis*; (B) contact of the *H. circularisquama* cell with the cell surface around the oral plug of *F. taraikaensis* during the adhesion process (arrow). Scale bars = 40 µm

larly occurred after 48 to 72 h of incubation and were therefore assumed to be due to starvation. These results indicate that the *H. circularisquama* exudate does not enhance the mortality of *F. taraikaensis*.

DISCUSSION

A high concentration of phytoplankton causes a decrease of tintinnid growth at times even if the alga is not toxic (Verity 1985, Kamiyama 1997). However, it is evident that the retardation of growth rates is different from mortality. In the present study, *Favella taraikaensis* died more rapidly at the high concentrations of *Heterocapsa circularisquama* than under no food conditions (Fig. 1), indicating that the decrease of *F. taraikaensis* was probably due to a toxic interaction with *H. circularisquama*. The reaction of *F. taraikaensis* to *H. circularisquama* is very characteristic. Hansen (1989) reported that toxic substances exuded from *Alexandrium tamarense* inhibited swimming behavior and the growth of *Favella ehrenbergii*. However, in the present study, the filtrate from a dense suspension of *H. circularisquama* did not influence the survival of *F. taraikaensis* (Fig. 5). Similarly, the alga-free medium of *H. akashiwo* (as *Olithodiscus luteus*), rejected as food by various zooplankton, did not influence the ingestion or growth of tintinnids and rotifers (Verity & Stoecker

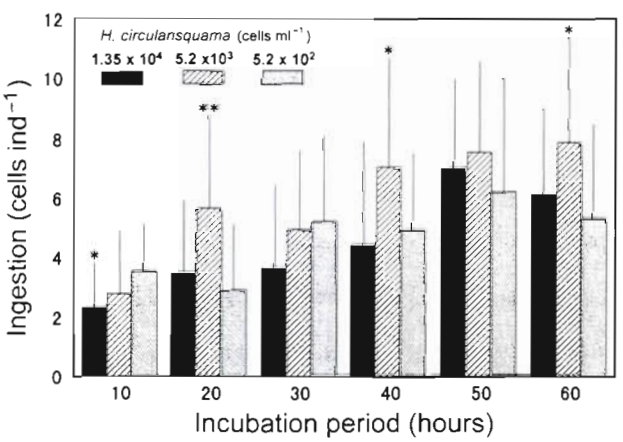

Fig. 4. *Favella taraikaensis*. Cell uptake as a function of incubation period and concentration of *Heterocapsa circularisquama*. Vertical lines indicate standard deviation of the mean (n = 20 to 24). $^{*}p < 0.05$, $^{**}p < 0.01$, significantly different from the values at the algal concentration of 5.2×10^2 cells ml^{-1}

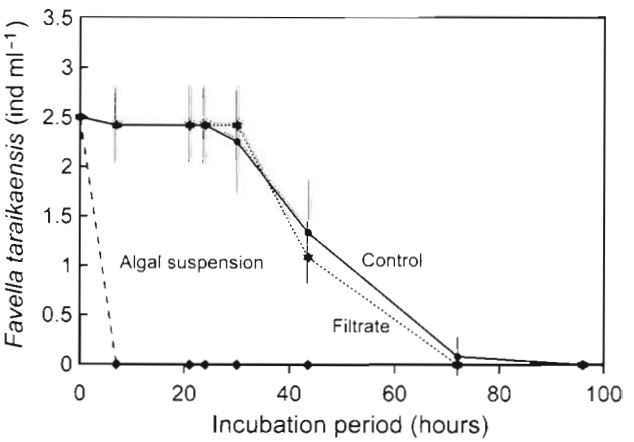

Fig. 5. *Favella taraikaensis*. Survival response to the suspension (◆) and filtrate (✱) of *Heterocapsa circularisquama*. Algal concentration: 3.42×10^4 cells ml^{-1} for suspension and 1.37×10^5 cells ml^{-1} for filtrate. Control (●) is the result in fresh medium. Vertical lines (solid line: control; dotted line: filtrate) indicate standard deviation of the mean (n = 6)

1982, Egloff 1986). However, *F. taraikaensis* usually avoids capturing *H. akashiwo* cells and rapidly ejects the cells from the peristomial cavity, if it accidentally captures them (Taniguchi & Takeda 1988). This is evidently different from the phenomenon that *F. taraikaensis* could feed on *H. circularisquama* for a short period, irrespective of the concentrations.

There are 3 possibilities that may explain the toxic mechanism: toxicity derives from the intracellular components, the extracellular products or the cell surface. The most probable site of toxicity is considered to be on the cell surface of *Heterocapsa circularisquama* because of the following points. *Favella taraikaensis* could actively ingest *H. circularisquama* cells (Fig. 4 present study, Kamiyama 1997) and grew under low concentrations of this alga (Fig. 1), indicating that intracellular substances of the alga have no effect on the mortality of *F. taraikaensis*. The toxic substance may be largely insoluble with little of it dissolving into the surrounding seawater because the culture filtrate of *H. circularisquama* did not suppress the survival of *F. taraikaensis*, although there is a possibility that the toxic effect may be reduced once the substance is exuded from the cell due to decomposition. A characteristic attachment behavior of *H. circularisquama* to *F. taraikaensis* was observed, suggesting that a chemical substance existing on the cell surface of *H. circularisquama* is a probable cause of the mortality of *F. taraikaensis* due to cell contact.

The adhesion of *Heterocapsa circularisquama* to the AZM of *Favella taraikaensis* may be an important process in the mechanism of *F. taraikaensis* mortality. The attachment of *H. circularisquama* is probably irritating to *F. taraikaensis*. It appeared likely that abnormal behavior such as backwards swimming occurred in an attempt to brush off *H. circularisquama* cells. *F. taraikaensis* can usually feed on preferred food algae within 1 s (Taniguchi & Takeda 1988). In the present study, the attachment of *Heterocapsa triquetra* cells to the AZM of *F taraikaensis* occurred only momentarily. Long-term adhesion of *H. circularisquama* to the membranelles implies that *H. circularisquama* cells have a specific ability to attach to the AZM. Using a scanning electron microscope, adhesive substances were observed on the cell surface of *H. circularisquama* (Y. Matsuyama pers. comm.). Alternatively, there is a possibility that *F. taraikaensis* produces extracellular adhesive substances such as mucus when *H. circularisquama* cells make contact with the AZM of *F. taraikaensis*. However, if this phenomena were important, it would occur irrespective of the algal concentrations and suppress tintinnid feeding at low concentrations of *H. circularisquama*, which is inconsistent with the results of this study, i.e. that *F. taraikaensis* can actively feed on *H. circularisquama* and grow at low concentrations of this alga.

The attachment of *Heterocapsa circularisquama* to the AZM may not be a key factor in causing the mortality of *Favella taraikaensis* because this behavior would have taken place during the feeding process when *F. taraikaensis* could actively feed on *H. circularisquama*. The toxicity of *H. circularisquama* cannot affect *F. taraikaensis* from the lateral and aboral direction because of the protection provided by the lorica. The main cause of mortality of *F. taraikaensis* is probably direct cell contact with the cytoplasm around the peristomial cavity or oral plug, as observed in this study.

Uchida et al. (1995) reported that *Heterocapsa circularisquama* kills another dinoflagellate, *Gyrodinium instriatum*, by cell contact. Further, the mortality of pearl oysters due to *H. circularisquama* was considered to be caused by direct contact of *H. circularisquama* with the body of oysters (Nagai et al. 1996, Matsuyama et al. 1997). In this study, mass mortality of *Favella taraikaensis* under higher concentrations of *H. circularisquama* was probably caused by an increased incidence of cell contact. It is unknown at present whether the lethal effects of *H. circularisquama* on such organisms are caused by the same toxic substance. Further studies are necessary to identify the toxic substance, which is probably contained in the cell surface components.

As for the interaction between *Heterocapsa circularisquama* and other protists, the lethal effect of *H. circularisquama* may depend on the protection mechanisms of the protists; *H. circularisquama* can more easily influence naked organisms as compared to loricated organisms such as tintinnids. Considerable mortality of *Favella taraikaensis* at high concentrations of *H. circularisquama* (less than 7 h) took longer than that of the naked flagellate *Gyrodinium instriatum* (less than 15 min; Uchida et al. 1995).

The many swollen or naked *Favella taraikaensis* became immobile and their feeding inactive, suggesting that physiological problems inside *F. taraikaensis* cells occurred. Toxic substances from *Alexandrium tamarense* and *Gyrodinium aureolum* make tintinnid ciliates swell and finally lyse (Hansen 1989, 1995), consistent with the response of *F. taraikaensis* to *Heterocapsa circularisquama*.

Based on the results from the present study and on previous findings (Kamiyama 1997), cells ingested by *Favella taraikaensis* probably do not cause the physiological problem observed in the tintinnid. Specifically, toxic substances of *Heterocapsa circularisquama* do not have an effect on *F. taraikaensis* in its food vacuoles. Lack of toxic effects in the food vacuoles implies that the toxicity effect is unstable against a pH shift or digestive intracellular enzymes in the food vacuole (Capriulo 1990). Toxicity of *H. circularisquama* for

bivalves is due to a protein-like substance involving the outer cell components and its activity is easily stopped by chemical treatment with trypsin and sodium dodecylsulfate (Matsuyama et al. 1997).

In conclusion, the harmful effects of *Heterocapsa circularisquama* on *Favella taraikaensis* are assumed to be due to the following mechanism. *Favella taraikaensis* can effectively ingest *H. circularisquama* cells under pre-bloom concentrations. In this situation toxic substances do not have harmful effects on *F. taraikaensis*, because cell contact between the 2 organisms rarely occurs. With increasing concentrations of *H. circularisquama*, the chances of adhesion to the AZM of *F. taraikaensis* increase, and *F. taraikaensis* are unable to brush away *H. circularisquama* cells from their AZM. When the concentration of *H. circularisquama* reaches $\geq$6400 cells ml^{-1}, cell contact between cell surfaces of *H. circularisquama* and *F. taraikaensis* causes *F. taraikaensis* to swell, become immobilized and finally lyse. Such a mortality process in ciliates due to direct contact with a dinoflagellate has not previously been reported. Understanding the harmful effects of *H. circularisquama* on their grazers is essential not only to analyze the mechanism of bloom formation and decay in nature but also to estimate the effects of this dinoflagellate on the function of microbial food webs as one major component of pelagic matter fluxes in coastal marine systems. For these purposes, further information on the interaction between *H. circularisquama* and zooplankton should be accumulated.

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