

LIMNOLOGY AND OCEANOGRAPHY

November 2004

Volume 49

Number 6

Limnol. Oceanogr., 49(6), 2004, 1907–1914
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Attachment to suspended particles may improve foraging and reduce predation risk for tintinnid ciliates

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Abstract

We describe a new behavior of planktonic ciliates. The field-collected tintinnid *Eutintinnus inquilinus* attached with its lorica to a range of surfaces, including particulate aggregates. Most tintinnids remained attached with the aboral end of their lorica when well fed. On starvation, many tintinnids detached and resumed a free-swimming life. We hypothesize that the adhesive property of the lorica has evolved as an adaptation to attach to suspended aggregates or other seston particles. Attached *E. inquilinus* have a feeding rate that is 80% higher than free-swimming individuals because of the change in the fluid dynamics of the feeding current for attached *E. inquilinus*, which leads to steeper velocity gradients and higher flow rates close to the lorica. This mechanism will also operate for swimming suspension feeders attached to smaller particles that significantly increase the hydrodynamic drag. Selection for traits that enhance the velocity gradients in feeding currents of small plankton may be common and may partly shape behavioral patterns and functional morphology. When exposed to the calanoid copepod *Acartia clausi*, populations of *E. inquilinus* were less susceptible to predation than another *Eutintinnus* species of similar morphology but that were entirely free swimming.

The dynamics of colonization and biogenic degradation of aggregates in the water column (marine snow) have large consequences for the vertical material fluxes in the ocean and is believed to influence the global climate by acting as a sink for atmospheric carbon (e.g., Longhurst 1991). Particulate aggregates are considered to be hot spots of microbial processes (Caron et al. 1986; Grossart et al. 2003) and even of larger zooplankton (Kjørboe 2000). Several previous studies have described microbial communities associated with aggregates and showed that organisms may be enriched >100-fold compared with the ambient water (Silver et al. 1998; Simon et al. 2002). However, at present, little is known about behavioral or physiological mechanisms involved in the microbial colonization of and dispersal from aggregates.

Tintinnids (Choreotrichida) are ubiquitous planktonic ciliates with a characteristic test (the lorica) secreted around the cell body (e.g., Pierce and Turner 1993). Most species seem to be truly planktonic and free swimming, and previous references of tintinnids attached to substrates are rare. Blatterer and Foissner (1990) described an attached freshwater tintinnid, and there have been several reports of *Tintinnidium inquilinum* or *Tintinnus (Eutintinnus) inquilinus*, an attached marine tintinnid (Kofoid and Campbell 1929, 1939). There have also been several published observations of tintinnids found in samples that have diatoms attached to their loricae (Kofoid and Campbell 1929; Taylor 1982; Sassi et al. 1999). Often, this association involves tintinnids of the genus *Eutintinnus* and diatoms of the genus *Chaetoceros* (Taylor 1982). In particular, the tintinnid species *Eutintinnus apertus* has been observed with attached diatom chains of mainly *Chaetoceros* sp. (e.g., Kofoid and Campbell 1939; Cupp 1943; Hernandez-Becerril 1992).

In the present study, we describe the attachment of field-caught and laboratory reared *E. inquilinus* to solid surfaces, including aggregates. We propose the hypothesis that this tintinnid regularly colonizes aggregates in the water column and lives in a dynamic equilibrium of attached and free-swimming stages. In laboratory cultures, the dynamics of attachment and detachment in relation to the physiological status was investigated. We further examined two possible benefits to attached tintinnids compared with free-swimming individuals. On the basis of a hydrodynamic model, we test-

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Acknowledgments

We thank David Montagnes for very useful comments on the manuscript.

Financial support for the study was provided to P.R.J. by the Swedish Research Council through contract 621-2002-4770 and by the Hasselblad Foundation and to M.J. by the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning through contract 22.3/2003-0209.

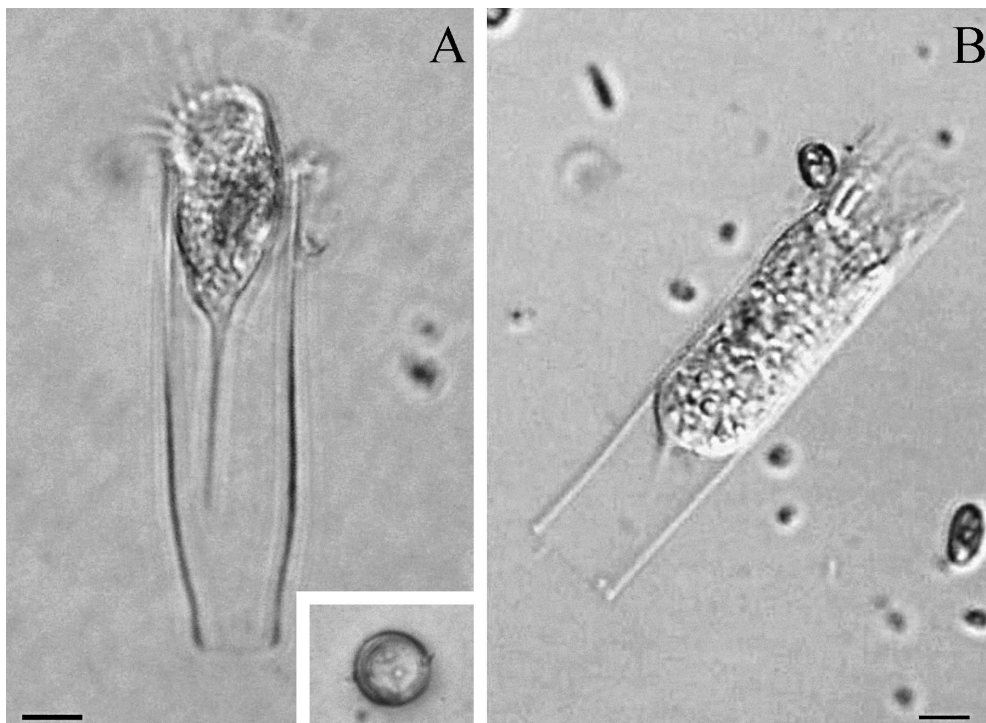


Fig. 1. Micrographs showing live tintinnid ciliates (A) *E. inquilinus* with the inset showing the aboral end attached to a surface, and (B) the entirely free-swimming *Eutintinnus* sp. Scale bars are 10 μm .

ed whether attached tintinnids feed more efficiently than free-swimming individuals. Attached tintinnids are also expected to be less susceptible to predation by some planktonic mesozooplankton, and we tested this hypothesis in incubation experiments with the copepod *Acartia clausi*. Finally, we discuss previous reports of tintinnid-diatom interactions in the light of the present findings on the attachment behavior of *E. inquilinus*.

Material and methods

Collection and culture—*E. inquilinus* (Müller 1776) and a probably undescribed *Eutintinnus* sp. (Fig. 1) were isolated outside Tjärnö Marine Biological Laboratory (TMBL) on the west coast of Sweden (58°38'N, 11°45'E). *E. inquilinus* was isolated from samples with a mixture of sediment and the water just above the sediment surface, and the *Eutintinnus* sp. was isolated from shallow water in a plankton net. Both ciliates were grown in 50-ml culture flasks (Nunc) in filtered, autoclaved seawater (pumped from 50 m depth outside TMBL; salinity = 30) with ethylene diaminetetraacetic acid (10 $\mu\text{mol L}^{-1}$) and additions of the suspended microalgae *Isochrysis galbana* Parke 1949 (Prymnesiophyceae) and *Rhodomonas baltica* Karsten 1898 (Cryptophyceae) (cultured in f/2 medium). The cultures were kept at 20°C under a natural light cycle (~18:6 h light:dark). Both *Eutintinnus* species were transferred to new bottles that contained culture medium and prey when the prey density became too low to support the growth of the ciliate (weekly to biweekly).

General behavior and ability to attach to natural substrates—Observations of the ciliates under the microscope revealed that *E. inquilinus*, in addition to swimming, attached the posterior end of the lorica to the culture flasks. The attachment process was examined under the microscope, and the ability of *E. inquilinus* to attach to different types of surfaces was tested. *E. inquilinus* was added to dishes of polystyrene plastic and to hydrophilic and hydrophobic (coated with dichlorodimethylsilane) glass dishes to test whether attachment differed on different surfaces.

We further explored attachment on natural substrates and tested whether the attachment was passive or active. Natural aggregates of decomposing material, mainly from filamentous red algae (e.g., *Ceramium* sp.), were collected outside TMBL and washed in culture medium before their addition to experimental bottles (50-ml, clear plastic; Nunc). Three treatments were replicated three times: live *E. inquilinus* + aggregates, live *E. inquilinus* without aggregates, and loricae from dead *E. inquilinus* + aggregates. Equal amounts of ciliates or empty loricae (150–200 ml^{-1}) were added to each bottle. In treatments with aggregates, three aggregates with a maximum linear dimension of ~1 cm were added to each bottle. All bottles were mounted on a plankton wheel (speed = 0.15 rpm) at 20°C under an 18:6 h light:dark regimen and left for 24 h. After the incubation period, the numbers of attached and swimming ciliates were counted by examining each bottle under an inverted microscope (10 replicate fields of 0.036 cm^2 , resulting in a total of 439 ciliates and empty loricae). The number of swimming ciliates was counted by changing the focus from one side of the bottle to the

next side. All aggregates were also examined, to assess the number of attached ciliates and empty loricae. Bottles were processed within 5 min, to reduce the possibility for ciliates to attach or detach during the counting process. For an additional estimate of numbers of free-swimming and attached ciliates, the number of ciliates was also counted in fixed samples. After counting the live ciliates, the ciliates were fixed with Lugol's acid solution (1% final concentration). A 1-ml subsample was immediately taken from each bottle, allowed to settle in a multiwell dish (Nunc), and the numbers of ciliates counted under an inverted microscope. Thereafter, the bottles were shaken vigorously to remove attached ciliates from surfaces and aggregates; then new subsamples were taken from each bottle, and the ciliates were counted in the same way. The number of attached ciliates was calculated by subtracting the first subsample taken before shaking the bottles from the second subsample taken after shaking the bottle.

Attached versus free swimming as a function of food depletion—In these experiments, we tested whether the attachment propensity of *E. inquilinus* changed when they were subjected to food depletion. Ten ciliates were added to each of 12 replicate dishes (Nunc multiwell) with 4 ml of suspension of the prey *I. galbana* (2×10^5 cells ml⁻¹). The numbers of free-swimming and attached ciliates were counted immediately after the ciliates were added and then monitored for 20 d. The number of attached ciliates on the plastic surface of each dish was counted in one field of view (0.57 cm²), and the number of free-swimming ciliates was counted by focusing from the bottom up to the surface (a total of 21,352 ciliates were counted). The relative swimming activity was calculated as the number of ciliates swimming in each well, compared with the total number of ciliates (swimming plus attached ciliates on the well walls). As a measure of nutritional status, the length of the ciliate cells was measured at the start of the experiment and at six successive times.

Feeding rate in attached and free-swimming ciliates—Feeding experiments were performed to test for a difference in the feeding rate between attached and free-swimming ciliates. *E. inquilinus* suspended with *I. galbana* were added to two 4-ml dishes (Nunc). A cover slip (2 × 2 cm) was added upright in the middle of each dish, to present a surface for the ciliates to attach to that could be removed after the experiment. The cover slips were observed under the microscope; when approximately equal amounts of ciliates were free swimming and attached to the cover slips (after ~10 min), spherical fluorescent plastic beads (6.4 μm diameter) were added to the dish (2,500 ml⁻¹). The ciliates were allowed to feed for 5 min, and then they were fixed with ice-cold glutaraldehyde (5% final concentration). Immediately after fixing the ciliates, the cover slips were removed and placed on top of a microscope slide, and ~100 μl containing suspended ciliates from each dish were added to other microscope slides and covered with a cover slip. Both the attached ciliates and the free-swimming ciliates were examined under the microscope in fluorescent light (400× magnification), and the number of fluorescent beads in the

ciliates was counted (at least 100 attached and 100 free-swimming ciliates from each dish).

Predation on attached and free swimming ciliates—To test whether predation by a copepod differed between attached and free-swimming ciliates, a feeding experiment was performed where *E. inquilinus*, that was known to attach to surfaces, and the free-swimming ciliate *Eutintinnus* sp. were subjected to the copepod predator *Acartia clausi*. The four treatments were: *E. inquilinus* with *A. clausi*, a control with only *E. inquilinus*, *Eutintinnus* sp. with *A. clausi*, and a control with only *Eutintinnus* sp., replicated four times for each treatment. The ciliates (1 ciliate ml⁻¹) in suspension with *I. galbana* were added to 250-ml clear plastic experimental bottles (Nunc), and the bottles were mounted on a plankton wheel (speed = 0.15 rpm) and left for 5 h, to allow ciliates to attach to surfaces. After the settlement period, four adult *A. clausi* females were added to each bottle in the predation treatments. The bottles were then incubated on the plankton wheel for 24 h. After 24 h, we made sure that all copepods were alive, and all bottles were examined under an inverted microscope, where the numbers of attached ciliates in 30 fields of view (0.036 cm²) were counted. After counting live ciliates, all bottles were fixed with Lugol's acid solution (1% final concentration). The bottles were shaken vigorously to remove attached ciliates, and 50-ml subsamples were allowed to settle in Utermöhl chambers (Utermöhl 1958) and counted under an inverted microscope (200× magnification). The clearance of ciliates shown by *A. clausi* was calculated according to the method of Frost (1972).

Results

General morphology—*E. inquilinus* has a characteristic tapering lorica at the aboral end (Fig. 1A). The lorica oral diameter (LOD) was 21 ± 1.7 μm, the width of the aboral end was 13 ± 1.2 μm, and the length of the lorica was 97 ± 6.6 μm (mean ± SD, $n = 22$). The morphology of the lorica is similar to that of *E. apertus* (Kofoid and Campbell 1929). However, the LOD of our *E. inquilinus* (21 ± 1.7 μm) was significantly smaller than those in previous reports for *E. apertus*. Kofoid and Campbell (1939) listed the LOD of *E. apertus* as 36–39 μm, with a mean of 33 μm. Furthermore, *E. inquilinus* attached to surfaces by the aboral end of the lorica but did not appear to attach *Chaetoceros* cells or other particles to the oral end of the lorica, as has frequently been described for *E. apertus*. *E. inquilinus* is probably identical to the *T. inquilinum* revised in Kofoid and Campbell (1929). In addition to lorica measurements, *E. apertus* appears to be a tropical to subtropical, pelagic species, whereas *E. inquilinus* appears to be a temperate, neritic species. The other isolated tintinnid species, *Eutintinnus* sp. (most likely undescribed), was almost cylindrical, without the tapering aboral end. The size was smaller than that of *E. inquilinus*, with a LOD of 19 ± 2.2 μm, an aboral width of 17 ± 1.8 μm, and lorica length of 80 ± 6.9 μm (mean ± SD, $n = 22$). This species did not attach to surfaces and swam in slow, compared with *E. inquilinus*, helical paths.

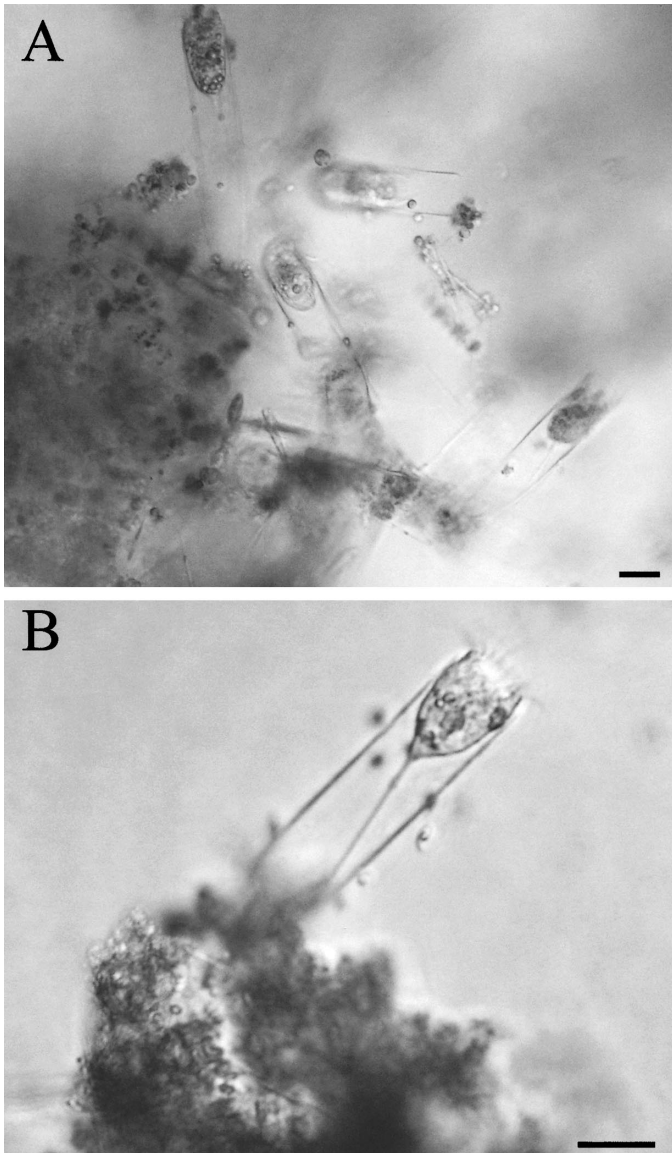


Fig. 2. Micrographs showing live *E. inquilinus*: (A) overview of an aggregate with several cells and (B) close-up of a feeding cell attached to an aggregate. Scale bars are 20 μm .

Behavior and ability to attach to surfaces—Field samples of settled detrital aggregates and mineral grains collected in shallow water showed extensive attachment of the tintinnid *E. inquilinus* (Fig. 2). Laboratory-reared *E. inquilinus* attached within minutes to all tested surfaces—artificially made aggregates (from phytodetritus), polystyrene plastic, and hydrophilic and hydrophobic glass surfaces. Most tintinnids attached to surfaces by their aboral end (Fig. 2B), although some individuals made contact with other parts of the lorica. Attachment typically occurred shortly after contacting a surface with the membranelles at the anterior end. On contact, a series of ciliary reversals turned the ciliate, with the aboral end facing toward the surface, which often lead to attachment to the surface. From microscopic inspection, the aboral end of the lorica appeared to come in direct contact with the surface without any trace of adhesive, bac-

teria, or fibrillar bodies (Fig. 1A). Attached *E. inquilinus* continued to create water currents with the membranelle zone, and the capture and ingestion of autotrophic microflagellates was frequently observed. The attachment of *E. inquilinus* was reversible, and many tintinnids were seen to detach from a surface. Detachment was apparently preceded by some change in the feeding flow field, making the initially erect tintinnid swing around an attachment point of the lorica. Within 1 min, the adhesive bond broke, and the tintinnid swam off the surface.

When live *E. inquilinus* and empty loricae were exposed with and without natural aggregates, the percentage (mean \pm SE) of recovered loricae of dead *E. inquilinus* was much lower ($3.3 \pm 0.27\%$), compared with the percentage of live ciliates ($37 \pm 7.3\%$) (analysis of variance [ANOVA], $F_{2,5} = 14.8$, $p = 0.009$). The low recovery rate indicated that empty loricae rapidly attached to available surfaces, maybe because of the movement of the plankton wheel. Inspection revealed that many of the empty loricae attached to each other and to aggregate surfaces. For live ciliates, no difference in the percentage of swimming ciliates was detected between treatments with and without aggregates (Tukeys honestly significantly different, $p > 0.05$).

Attached versus free-swimming ciliates as a function of food depletion—In a growing population, most *E. inquilinus* were initially attached (Fig. 3). Attached *E. inquilinus* were seen in different stages of cell division, and the maximum growth rate observed of the mainly attached population was estimated as $0.86 \pm 0.01 \text{ d}^{-1}$ (mean \pm SE). Coinciding with a reduction in cell size, which indicates food depletion and the onset of starvation, the proportion of free-swimming *E. inquilinus* increased (Fig. 4A). Eventually, after several days of low food concentrations, the proportion of attached ciliates again increased. The rate of initial growth shows that there is an increase in the number of attached tintinnids, with little addition of swimming individuals (Fig. 3), which suggests that released daughter cells quickly attached to the container walls.

Feeding rate in attached and free-swimming ciliates—The short-term feeding rate of *E. inquilinus* was tested simultaneously for attached and free-swimming individuals. The clearance of fluorescent microbeads was $2.1\text{--}5.1 \mu\text{l}^{-1} \text{ h}^{-1}$ and was, on average, 83% higher for attached tintinnids (Table 1). No significant difference was detected between the two experiments (two-factor nested ANOVA, $F_{1,2} = 1.8$, $p = 0.2$). The difference in feeding rate was highly significant (one-factor ANOVA on pooled data from both experiments, $F_{1,525} = 19.9$, $p < 0.0001$).

Predation on attached and free-swimming ciliates—The tintinnid *E. inquilinus*, with a large proportion of the population attached, suffered less predation than the free-swimming *Eutintinnus* sp. when it was exposed to the copepod *A. clausi*. The copepod cleared *Eutintinnus* sp. ~ 3 times more efficiently than *E. inquilinus* (Table 2), and this effect was statistically significant (one-factor ANOVA, $F_{1,6} = 13.7$, $p = 0.01$).

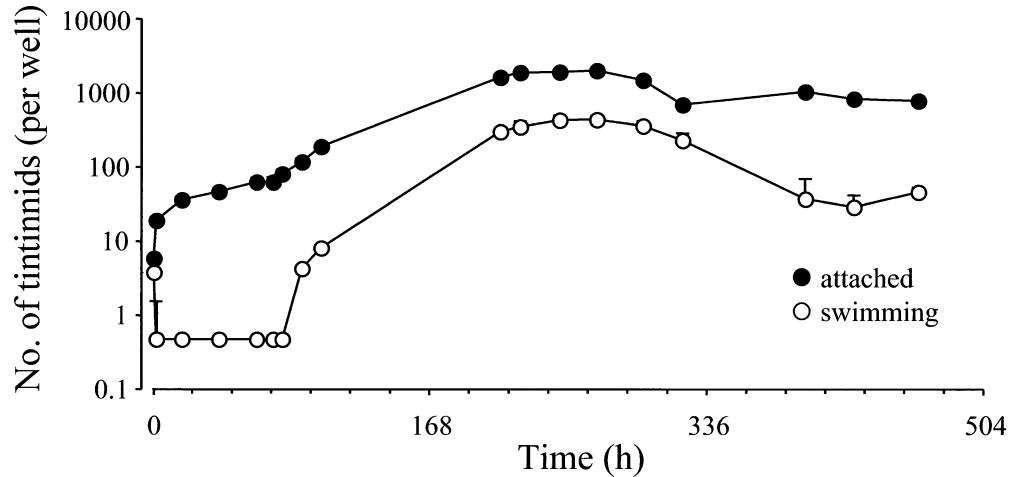


Fig. 3. Development of *E. inquilinus* populations in batch cultures showing the concentrations of attached and swimming individuals (mean \pm SE, $n = 12$).

Discussion

Tintinnids are regarded as almost entirely planktonic. Tintinnid cysts (Kamiyama 1996) and empty loricae (Dale 1989) occur in benthic habitats, but, to our knowledge, there are few reports of live tintinnids from benthic samples or attached to surfaces (Kent 1882; Kofoid and Campbell 1929; Blatterer and Foissner 1990). Kofoid and Campbell (1929) mentioned that *T. inquilinum* (which is possibly synonymous

with *E. inquilinus*) attaches to algae, although no further details are given. Several authors have reported the tintinnid *E. apertus* in planktonic samples that are attached to diatom chains (Cupp 1943; Taylor 1982 and references cited therein; Sassi et al. 1999). The genus *Chaetoceros* seems to dominate in records of diatoms attached to tintinnids (e.g., Taylor 1982), but other attached diatom genera are also known. Previous descriptions have usually depicted a small chain of diatom cells attached to the outer wall of the lorica. The

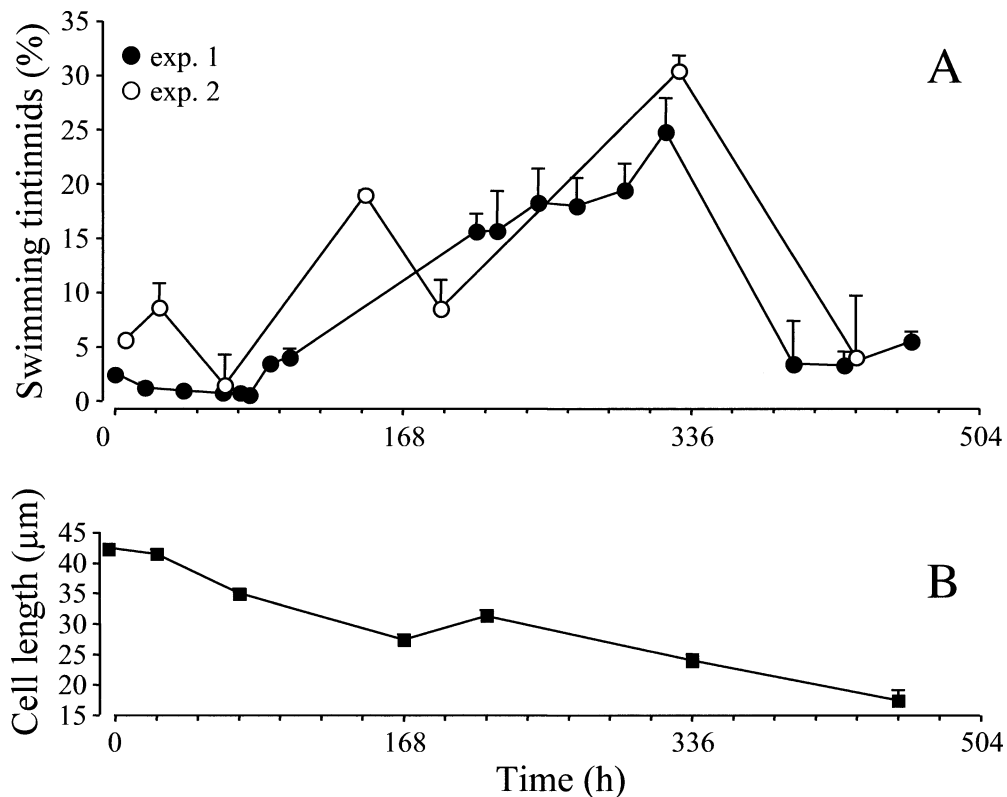


Fig. 4. (A) The percentage of swimming *E. inquilinus* in batch cultures (mean \pm SE, $n = 12$) for two separate experiments. (B) The change in cell length with time in experiment 2 (mean \pm SE, $n = 30$).

Table 1. Clearance (mean \pm SE, expressed as $\mu\text{l h}^{-1}$) of fluorescent bead suspension (6.4 μm) by attached and swimming *Eutintinnus inquilinus*. Results are shown for two separate experiments and their weighted mean.

Cilates	Experiment 1 (n)	Experiment 2 (n)	Weighted mean
Attached	5.1 \pm 0.56(102)	4.0 \pm 0.43(161)	4.4 \pm 0.34(263)
Swimming	2.1 \pm 0.45(103)	2.6 \pm 0.34(161)	2.4 \pm 0.27(264)

tintinnid species *E. pinguis* and *E. lusus-undae* have also been recorded with attached diatoms (Kofoid and Campbell 1939). No convincing hypotheses about the adaptive significance of tintinnid-diatom associations have been proposed. However, the association between *E. apertus* and the diatoms *Chaetoceros tetrastichon* and *Chaetoceros dadayi* suggests some adaptive significance, because these diatoms appear to closely fit the loricae of *E. apertus*. Hernandez-Becerril (1992) also reported these diatoms as being rare in the plankton. For other tintinnids, the association may be completely nonadaptive and may only represent the accidental adhesion of diatoms (and possibly other debris) to the sticky lorica. Our findings for *E. inquilinus*, however, suggest that adhesion to other particles or surfaces may be a common phenomenon. Adhesion to a diverse set of tested surfaces, including particulate aggregates, was rapid and at times involved almost the entire population (Figs. 2, 3). We propose that the adhesive lorica of *E. inquilinus*, and possibly of some other *Eutintinnus* species, may be an adaptation for attachment to suspended particles or aggregates in the water column. There is also a possibility that benthic surfaces—for example, sessile plants and animals may also act as a substrate for *E. inquilinus*.

The present experimental results for *E. inquilinus* suggest that adhesion to and detachment from surfaces—for example, aggregates or other seston, is reversible and is an active response to physiological state. The lower proportion of attached live tintinnids compared with empty loricae indicates that detachment is under active control. This is also supported by the observed swinging motion of the ciliate body preceding detachment. The swinging motion may be caused by a change of the orientation of the propulsive membranelles resulting in a rotational torque as described by Fenchel and Jonsson (1988). The largest fraction of attached individuals was observed for well-fed tintinnids (Fig. 4B). On starvation, many individuals detached and remained free swimming for some days. A similar behavioral response to starvation has been reported for other protists, where high feeding rates are correlated to a sedentary or attached phase and the onset of starvation induces a free-swimming dispersal phase (Fenchel and Jonsson 1988; Jonsson and Johansson 1997; Fenchel and Blackburn 1999). A likely explanation is that this behavioral shift is an adaptation to increase survival where food resources are patchy in space (Fenchel 1989).

We have found no published observations of tintinnids attached to aggregates. Silver et al. (1998) found natural aggregates enriched with planktonic oligotrich ciliates, which

Table 2. Clearance rate (mean \pm SE) by the copepod *Acartia clausi* feeding on *Eutintinnus inquilinus* (attached and free-swimming) and *Eutintinnus* sp. (free-swimming).

Prey species	Behavior	Clearance rate (ml copepod ⁻¹ d ⁻¹) (n)
<i>Eutintinnus inquilinus</i>	Attached/free-swimming	18 \pm 8.7 (4)
<i>Eutintinnus</i> sp.	Free-swimming	56 \pm 5.7 (4)

are closely related to tintinnids. From laboratory studies, the freshwater oligotrich ciliate *Strobilidium gyrans* is known to reversibly attach to surfaces with its adhesive aboral end (Grim and Halcrow 1979). The only study, to our knowledge, showing a reversible association between a planktonic protist and aggregates in the field is that of Tiselius and Kjørboe (1998), where the large heterotrophic dinoflagellate *Noctiluca scintillans* was found to dynamically colonize and detach from diatom aggregates.

How could the evolution of an ability to attach to particles and aggregates, benefit *E. inquilinus*? Generally, aggregates are believed to offer higher local concentrations of nanosized protists, which are potential prey for *E. inquilinus* (Simon et al. 2002). It has further been suggested that attached suspension feeders have an advantage based on hydrodynamics (Emlet and Strathmann 1985; Fenchel and Ockelmann 2002; Christensen-Dalsgaard and Fenchel 2003). The argument is that, for an attached suspension feeder, all the force applied can be used to create a strong velocity gradient in the feeding current with a high local flow rate close to the cell body. In contrast, the propulsive thrust generated by a free-swimming plankter is almost balanced by the forward swimming motion and results in close to parallel flow lines with a lower mean flow rate close to the cell body. The hydrodynamic drag of the cell body will, however, create some velocity gradients out from the propulsive center. The difference in flow rate between an attached and a free-swimming plankter thus depends on the drag of the plankter and the radius of the functional filter (Christensen-Dalsgaard and Fenchel 2003). Tiselius and Jonsson (1990) derived a simplistic model for low Reynolds number showing that an attached suspension feeder is expected to generate a flow rate that is 50% higher per force unit than that of a free-swimming plankter. In accordance with this prediction, Fenchel and Ockelmann (2002) found a 50–100% increase in the flow rate around mollusk larvae when they were functionally tethered compared with nontethered. A similar study for heterotrophic flagellates showed that attached flagellates produced up to 70% higher flow rates than free-swimming individuals (Christensen-Dalsgaard and Fenchel 2003). To our knowledge, however, the present study is the first to directly show a higher feeding rate for attached individuals compared to free swimming (Table 1). The mean benefit of 83% is statistically higher (one-sample *t*-test, $t = 2.15$, $df = 263$, $p = 0.03$) than predicted by Tiselius and Jonsson (1990) and indicates that their model assumptions are too simplistic.

Our study finally suggests that attachment to surfaces makes *E. inquilinus* less susceptible to predation by calanoid

copepods compared with a similar congeneric, free-swimming tintinnid. Alternative explanations for the threefold reduction in the predation rate (Table 2) include morphological differences or differences in swimming behavior (Broglia et al. 2001). The free-swimming *Eutintinnus* sp. was somewhat smaller and showed a slightly slower swimming speed, factors that should both act to reduce rather than increase the encounter rate with a planktonic copepod, thus further inflating the difference in susceptibility to predation. We used an unrealistic experimental system in which the container walls functioned as available surface for tintinnid attachment. The reduction in predation on *E. inquilinus* with a large fraction of attached individuals is difficult to extrapolate to field conditions. Copepods may avoid feeding close to the extensive and solid boundaries found in the experimental containers to a larger extent than the boundaries of natural aggregates. We can only speculate that calanoid copepods also feed less efficiently on aggregate surfaces. Some calanoid copepods are known to feed directly on aggregates, and other predators may increase the risk of predation for attached ciliates—for example, some poecilostomatoid copepods (Kiørboe 2000) and pallium-feeding dinoflagellates (Jacobson and Andersson 1986). The effect of attachment on predation risk is thus dynamically dependent on the types of predators present.

Our hypothesis that *E. inquilinus* reversibly attach to aggregates is speculative and awaits support from direct observations on natural aggregates. However, even if this and other *Eutintinnus* species only attach to short-chain diatoms, as has been suggested from previous work, the arguments regarding a feeding advantage may remain valid. Single chains of attached diatoms will act as a drift anchor, adding drag to the tintinnid body and increasing the flow through the ciliary filter. From published illustrations of *E. apertus* with attached *C. dadayi* (Taylor 1982), we calculated that the exposed surface, and thus drag, could be increased by a factor of three. This drift-anchor effect has been demonstrated for both mollusk larvae (Fenchel and Ockelmann 2002) and heterotrophic flagellates (Christensen-Dalsgaard and Fenchel 2003). In fact, the lorica itself will increase both gravitational tethering (Emler and Strathmann 1985) and hydrodynamic drag, which should increase the flow rate through the ciliary filter. This may explain some of the ornamentation found on the loricae of some species such as *Xystonellopsis*, *Dictyocysta*, *Stelidiella*, and *Rhabdonella*. It may also explain why the oral end flares in some species, including *Eutintinnus* and *Salpingella*, increasing their drag.

In conclusion, we hypothesize that some tintinnid species of the genus *Eutintinnus* may at times attach to suspended particles and aggregates. The selective advantage includes higher food availability close to aggregates, a higher feeding rate for attached tintinnids caused by a more efficient flow field, and possibly a refuge from some planktonic predators. Our results highlight the possible significance of adaptations that enhance the velocity gradients in feeding currents of small plankton. This may further contribute to an improved understanding of the evolution of behavioral patterns and functional morphology.

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Received: 8 March 2004

Accepted: 11 July 2004

Amended: 31 May 2004