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Morphology and Ecology in Tintinnid Ciliates of the Marine Plankton: Correlates of Lorica Dimensions

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Summary. Tintinnid ciliates, characterized by the possession of a lorica into which the ciliate cell can contract, are a common component of the marine microzooplankton. Lorica architecture and size range widely and classically distinguishes species. Here relationships between ecological parameters and lorica dimensions (lorica oral diameter (LOD), lorica length (LL) and lorica volume (LV) are examined using data from literature reports. The relationships between lorica dimensions and reproductive potential, using maximum reported growth rates of natural populations (n = 52 species) are assessed. Susceptibility to copepod predation and lorica dimensions are considered based on reports of clearance rates of *Acartia* species feeding on tintinnid ciliates (n = 7 species). Diet and lorica dimension is analyzed using data on mean maximum food size contained in field-caught cells (n = 20 species), and preferred food size based on prey size associated with maximal reported clearance rates (n = 15 species). Overall, LOD is closely related to most of the ecological parameters. Maximum growth rate is related to LOD with smaller LODs corresponding to higher growth rates, in contrast to LL and LV. Maximum prey size is positively related to both LOD and LL but more tightly with LOD. Preferred prey size is positively related to LOD and LV but more tightly related to LOD. Clearance rates of *Acartia* species feeding on tintinnids are significantly related only to LOD with small LODs corresponding to lower copepod feeding rates. Relationships excluding data on species of *Tintinnopsis*, the species-rich genus which generally dominates coastal communities, are also examined and show similar trends. In tintinnids, LOD, known to be a conservative and relatively reliable species characteristic, appears related to a wide range of ecological characteristics.

Key words: Ciliophora, allometry, niche, morphospecies, biodiversity, zooplankton

INTRODUCTION

Tintinnid ciliates are a ubiquitous component of the microzooplankton in marine systems. They feed

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primarily on nano-plankton sized phytoplankton. In the microzooplankton, tintinnids are generally a minor group compared to the other major groups commonly distinguished as "oligotrich ciliates" and "heterotrophic dinoflagellates" (e.g. Dolan *et al*. 1999). However, tintinnid feeding activity can at times dominate that of the microzooplankton (Karayami *et al*. 2005). Tintinnids in turn serve as prey for a variety of metazoan zooplankters such as copepods (Stoecker and Capuzzo 1990).

Tintinnid ciliates are characterized by the possession of a tubular or vase-shaped lorica harboring the ciliate cell. Based on molecular data, they represent a monophyletic group (Agatha and Strüder-Kypke 2007) and are then a coherent group based on morphology, phylogeny and ecology. The characteristics of the lorica have traditionally been employed to distinguish the over 1,000 described species. Among lorica characteristics used to distinguish species and form groups, the diameter of the oral end of the lorica, "lorica oral diameter" (LOD) appears to be the most reliable and conservative characteristic distinguishing species of otherwise similar lorica architecture (Balech 1959; Gold 1969; Gold and Morales 1975a, c, 1976a; Laval-Peuto and Brownlee 1986). Thus, diversity indexes of tintinnid communities have been correlated with indexes of 'morphological diversity' calculated using size-classes of oral diameters as proxies for species (Dolan *et al*. 2002, 2006).

Lorica morphology is not only a valuable taxonomic characteristic but has also been linked to ecological characteristics of tintinnids especially in terms of feeding activity. The maximal prey size ingested has been reported to be about 45% of the LOD and preferred prey size about 25% of LOD (Heinbokel 1978, Dolan *et al*. 2002). In terms of average community characteristics of tintinnids, seasonal shifts in average tintinnid community LOD have been reported in different coastal systems: the New York Bight (Gold and Morales 1975b), the Bay of Fundy (Middlebrook *et al*. 1978), Narragansett Bay (Verity 1987) and Jamaican coastal waters (Gilron *et al*. 1991). Such changes have been hypothesized as reflecting seasonal changes in size-spectrum of phytoplankton prey (Admiral and Venekamp 1986).

Tintinnid ciliates range widely in size, from about 20 μm in lorica length (LL) to several hundred μm. Notably, ciliate cell size has proven difficult to relate to the size of the lorica in any consistent fashion, occupying from 12–50% of the lorica (e.g. Gilron & Lynn 1989a). In addition, there is but a weak relationship between the oral diameter and total length of the lorica, based on data reported in the major monographic treatments of tintinnids (Fig. 1). Indeed, the distributions of the oral diameters (LODs), lengths (LLs), and volumes (LVs), while all non-normal (K-S normality test), appear distinct (Fig. 2). The distribution of LODs is less slightly less right-skewed (1.2) than the distribution of LLs (1.3). It should be noted that larger species, more conspicuous & easily found in net samples, may be over-represented in monographic data. However, the trends suggest that cell size, LL and LOD are not closely tied together but may vary independently in response to distinct selective forces and correlate with distinct ecological characteristics.

Here data are examined from a variety of scattered reports in an attempt to establish possible ecological correlates of lorica dimension, specifically that of oral diameter, length and volume, in tintinnid ciliates. Relationships are examined with maximum growth rates reported for species in natural populations. While tintinnids are subject to predation by a wide variety of organisms, most of the existing data concerns copepods for which ciliate microzooplankton are known to be important prey (Calbet and Saiz 2005). Data from studies of predation on tintinnid ciliates by copepods of the genus *Acartia* are reviewed. The relationship of maximum size of food ingested and preferred food size is re-examined as well.

The interest in examining possible ecological correlates of lorica dimensions is potentially of both theoretical and practical value. On the one hand, relationships
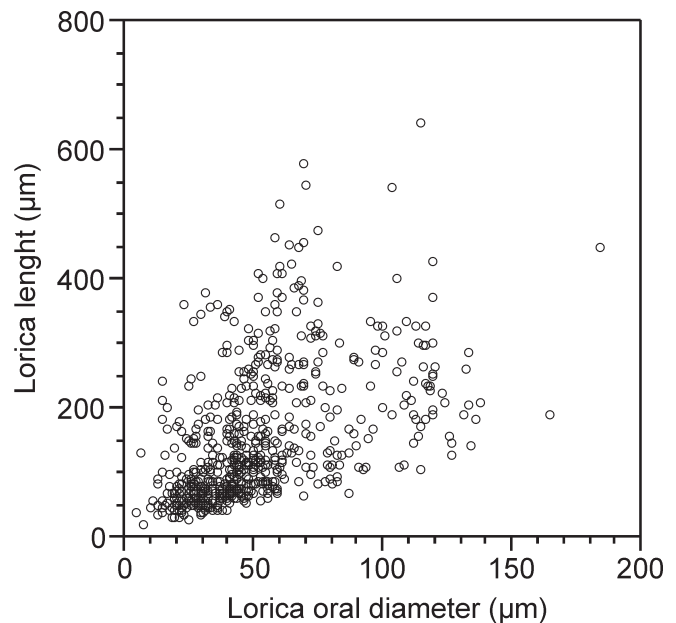
Fig. 1. Scatterplot of lorica oral diameter against lorica length for the 647 species of tintinnids for which average lorica dimensions are given in the monographs of Balech (1948), Campbell (1942), Hada (1938), Kofoid and Campbell (1929; 1939), and Marshall (1969). The two lorica dimensions are weakly related with an r² value of 0.244.
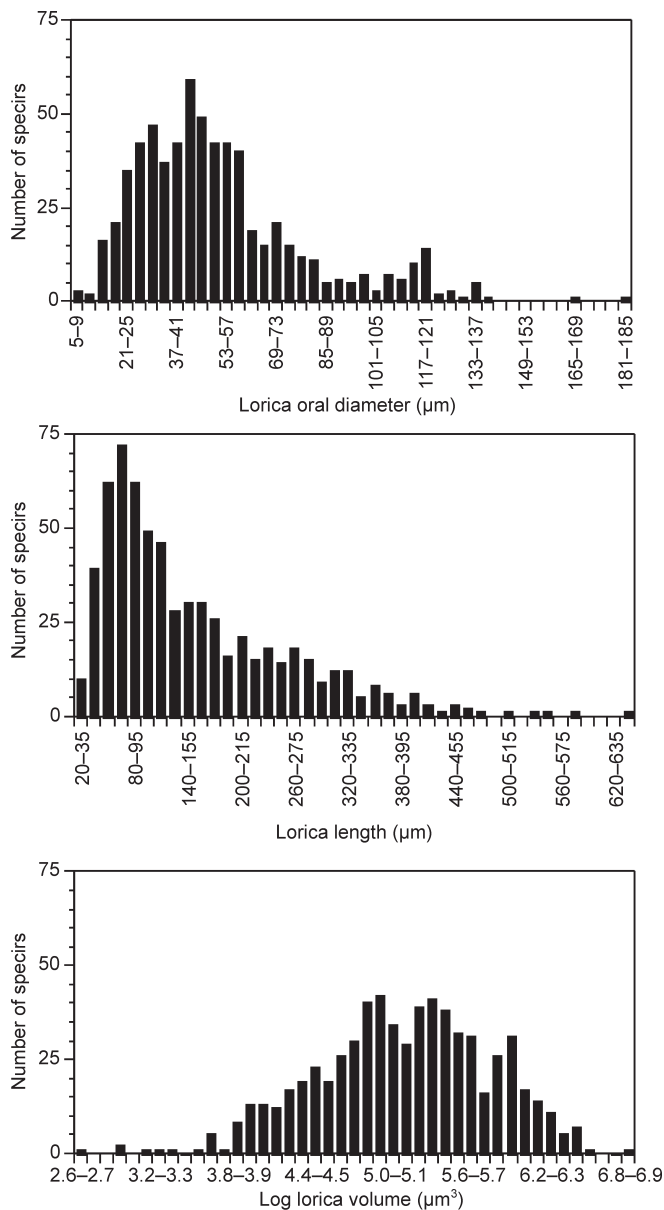
Fig. 2. Distributions of lorica dimensions among tintinnids based on the data shown and references given in Fig. 1. Note the distinct distributions of lorica oral diameters and lengths.

may in part explain the large morphological variety displayed by the group as reflecting distinct ecological characteristics. On practical grounds, lorica dimensions, unlike species identifications, are amenable to automated or semi-automated analysis. If lorica dimensions can be related to ecological characteristics, it may be possible to relate the some of the ecological characteristics of a tintinnid assemblage based on simply on lorica dimensions without recourse to expert taxonomic

knowledge. Thus, analysis of tintinnid assemblages in terms of simple dimensions may provide information on not only species diversity but also on the ecological diversity of the assemblage.

MATERIALS AND METHODS

Relationships of lorica dimensions and maximum growth rates for 42 species were examined using data from studies of natural populations: Gilron and Lynn (1989b) a study in coastal Caribbean waters; Nagano and Uye (2002) an annual study in coastal waters of the Sea of Japan; Stoecker *et al*. (1983) in Perch Pond, NW Atlantic coast, and Verity (1986) a pluri-annual study in Narragensett Bay, NW Atlantic coast. All the rates were derived from experiments with incubations of natural populations of tintinnids in water which had been size-fractionated or filtered to remove metazoan predators. No attempt was made to correct or account for temperature as data were largely unavailable.

Lorica dimensions and susceptibility to copepod predation was examined based on data for 7 species of tintinnids. Copepod grazing, as maximal clearance rates, were extracted from reports on feeding in 3 species of *Acartia* which are all roughly comparable in size and represent most of the available data on copepod predation on tintinnids. Data on grazing by *Acartia tonsa* were taken from Gifford and Dagg (1988); Robertson (1983) and Stoecker and Egloff (1987). Clearance rates of *Acartia clausi* were extracted from Ayukai (1987) and for *Acartia hudsonica* from Turner & Anderson (1983).

Maximum prey size and lorica dimensions were examined using data on food vacuole contents of cells from natural populations of 20 species. Data reported in Heinbokel (1978) and Spitler (1973) on ingestion of starch particles were excluded as species-specific data were not reported. Data were extracted from Blackbourn (1974) and Kopylov and Tumantseva (1987) which reported average maximum sizes of prey found inside in food vacuoles of field-caught cells.

The relationships between preferred food size and lorica dimensions were examined using data on 15 species feeding on either a natural prey spectrum (Capriulo 1982, Rassoulzadegan 1978, Rassoulzadegan and Etienne 1981), a wide range of cultured phytoplankton of different sizes (Blackbourn 1974; Kamiyama and Arima 2001) or wheat starch particles (Kivi and Setälä 1995). Preferred food size was defined as the size corresponding with the maximum filtration rate reported for a given species.

Simple correlations were sought. Statistical relationships were examined using Statview (Abacus Concepts, Berkeley, CA, USA) to estimate correlation coefficients, slopes with associated error estimates and probabilities. Simple linear regression was employed to examine relationships of maximum growth rate, maximum food size, preferred food size and lorica oral diameter, lorica length, and log lorica volume. Copepod clearance rates, which varied over orders of magnitude, were log transformed. Wherever reported, author-supplied lorica dimensions and volumes were employed. Otherwise, average dimensions given in either Kofoid and Campbell (1929) or Marshall (1969) were used. Volumes were calculated using formulae for appropriate shapes. As species of the coastal genus *Tintinnopsis* appeared over-represented in the data, analysis were also performed excluding data on *Tintinnopsis* species.

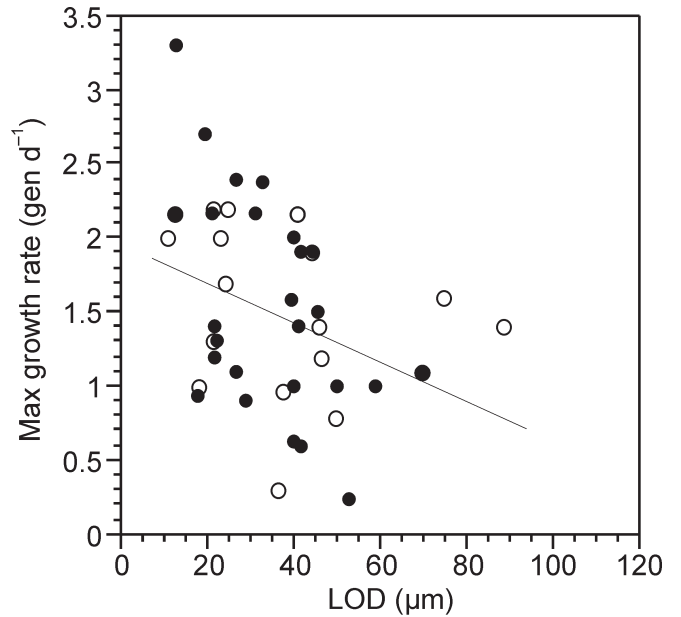*The complete data is available in a spread sheet as "Additional Material."*

RESULTS

Growth rate data of natural populations of the 42 species of tintinnids while dominated by species of the genus *Tintinnopsis* (23 species) included maximum observed rates of a wide range of species of the genera *Amphorellopsis*, *Codenellopsis*, *Eutintinnus*, *Favella*, *Helicostomella*, *Metacylis*, *Stenosemella*, and *Tintinnidium*. Results of the regression analysis are summarized in Table 1. Maximum observed growth rate is significantly related only to LOD. The regression equation, "maximum generations per day = 1.95 − (0.015 *LOD)," yields estimates of 1.65 vs. 1.2 generations d⁻¹ for tintinnids with LODs of 20 μm and 50 μm, respectively, a difference of about 40%. Examining data on species other than *Tintinnopsis*, which reduces the n from 42 to 19, no significant relationships were detected. A scatterplot of the data is shown in Fig. 3.
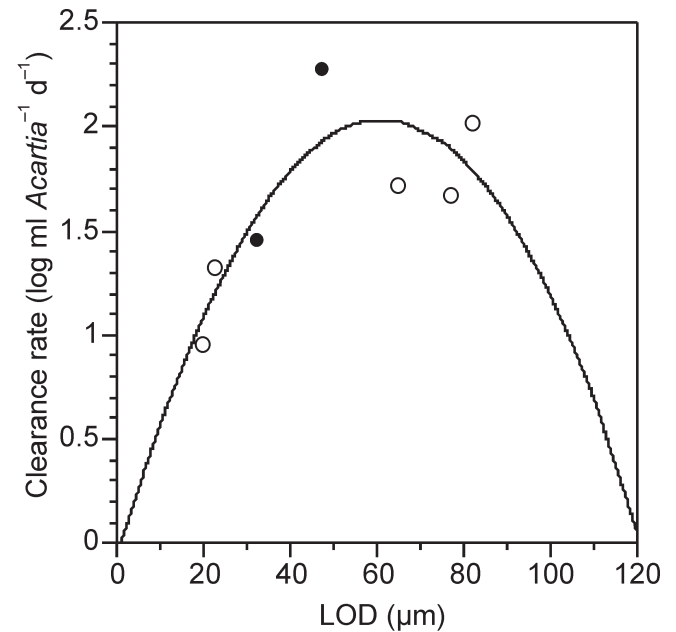
Clearance rate of *Acartia* spp. feeding on tintinnids included data on 7 species of *Tintinnopsis*, *Favella*, and *Eutintinnus*. Visual inspection of scatterplots suggested a curvilinear relationship reflecting an the expected 'hump-shaped' curve of feeding rate vs. prey size (Fig. 4). Results of a polynominal regression analysis are summarized in Table 2. Clearance rate is significantly related only to LOD, based on the probabilities of both x and x^2. Analyzing data on species other than *Tintinnopsis*, which reduces the n from 7 to 5, did not alter the relationships.

Fig. 3. Reproductive potential. Scatterplot of tintinnid lorica oral diameter and the maximum observed growth rate. Filled circles represent data from species *Tintinnopsis*. See discussion for details and Table 1 for statistics. Line represents the regresion relationship for the pooled data set.

Fig. 4. Susceptability to predation. Scatterplot of tintinnid lorica oral diameter and the maximum observed clearance rate (log) of *Acartia* spp feeding on tintinnids. Filled circles represent data from species *Tintinnopsis*. See discussion for details and Table 2 for statistics. Line represents the regresion relationship for the pooled data set.

Table 1. Maximum growth rates and lorica dimensions. Results of linear regression analysis considering lorica dimensions in microns as the independent variable and maximum growth rate as generations per day as the dependant variable. Relationships denoted *all* include all data while those denoted *w/o Tps* excluded data on species of *Tintinnopsis*. The scatterplot is shown in Fig. 3.

	n	r^2	Slope ± se	p
LOD *all*	42	0.121	−0.015 ± 0.006	0.0237
LL *all*	42	0.002	−0.00003 ± 0.001	0.797
log LV *all*	42	0.044	−0.229 ± 0.168	0.1823
LOD *w/o Tps*	19	0.107	−0.008 ± 0.006	0.1721
LL *w/o Tsp*	19	0.0002	0.0008 ± 0.001	0.9524
log LV *w/o Tsp*	19	0.009	−0.063 ± 0.165	0.707

Table 2. Copepod grazing rates and lorica dimensions. Results of polynominal regression analysis considering lorica dimensions (µm), as the independent variable and maximum copepod clearance rate (log ml copepod^{-1} d^{-1}) as the dependant variable. Relationships denoted *all* include all data while those denoted *w/o Tps* excluded data on species of *Tintinnopsis*. The scatterplot is shown in Fig. 4.

	n	r^2	x ± se	p	x^2 ± se	p
LOD *all*	7	0.986	0.071 ± 007	0.0006	0.0.001 ± 0.0001	0.0049
LL *all*	7	0.937	0.17 ± 0.004	0.0085	0.00004 ± 0,00002	0.1072
log LV *all*	7	0.970	0.18 ± 0.23	0.47	0.027 ± 0.043	0.55
LOD *w/o Tps*	5	0.986	0.06 ± 0.01	0.0094	0.0004 ± 0.0001	0.0423
LL *w/o Tsp*	5	0.971	0.01 ± 0.003	0.0366	0.00002 ± 0.00002	0.3312
log LV *w/o Tsp*	5	0.991	0.05 ± 0.03	0.7327	0.045 ± 0.027	0.1903

Table 3. Maximum average prey size and lorica dimensions. Results of linear regression analysis considering lorica dimensions in microns as the independent variable and maximum observed prey size (equivalent spherical diameter, µm) as the dependant variable. Relationships denoted *all* include all data while those denoted *w/o Tps* excluded data on species of *Tintinnopsis*. The scatterplot is shown in Fig. 5.

|	n	r^2	Slope ± se	p
LOD *all*	20	0.763	0.32 ± 0.04	0.0001
LL *all*	20	0.363	0.06 ± 0.02	0.005
log LV *all*	20	0.719	12.4 ± 1.85	0.0001
LOD *w/o Tps*	15	0.702	0.32 ± 0.047	0.00001
LL *w/o Tsp*	15	0.332	0.06 ± 0.023	0.0246
log LV *w/o Tsp*	15	0.699	12.9 ± 2.35	0.001

Table 4. Preferred prey size and lorica dimensions. Results of linear regression analysis considering lorica dimensions in microns as the independent variable and preferred prey size, (equivalent spherical diameter, µm), that corresponding with the maximum reported clearance rate as the dependant variable. Relationships denoted *all* include all data while those denoted *w/o Tps* excluded data on species of *Tintinnopsis*. The scatterplot is shown in Fig. 6.

	n	r^2	Slope ±se	p
LOD *all*	15	0.399	0.18 ± 0.06	0.0116
LL *all*	15	0.096	0.02 ± 0.02	0.2603
log LV *all*	15	0.368	6.24 ± 6.42	0.0165
LOD *w/o Tps*	6	0.801	0.18 ± 0.05	0.0159
LL *w/o Tsp*	6	0.192	0.02 ± 0.02	0.3480
log LV *w/o Tsp*	6	0.951	8.34 ± 0.5	0.0009

Data on the maximum prey size found in wild individuals consisted of observations on 20 species of *Epiplocylis*, *Eutintinnus*, *Favella*, *Helicostomella*, *Proplectella*, *Rhabdonellopsis*, *Stenosemella*, *Tintinnidium* and *Tintinnopsis*. Maximum prey size was significantly related to LOD, LL, and log LV with the tightest fit associated with LOD and similar relationships with and without *Tintinnopsis* species (Table 3). The equation describing the relationship between LOD and maximum observed prey size, 'maximum prey size = (0.325 *LOD) + 0.22, gives an estimate of about 1/3 LOD.' A scatterplot of the data relating LOD to maximum prey size is shown in Fig. 5.

The relationships of preferred food size, defined as that corresponding with the highest clearance rate, drew on data for 15 species of the genera *Helicostomella*, *Favella*, *Stenosemella* and *Tintinnopsis*. Significant relationshi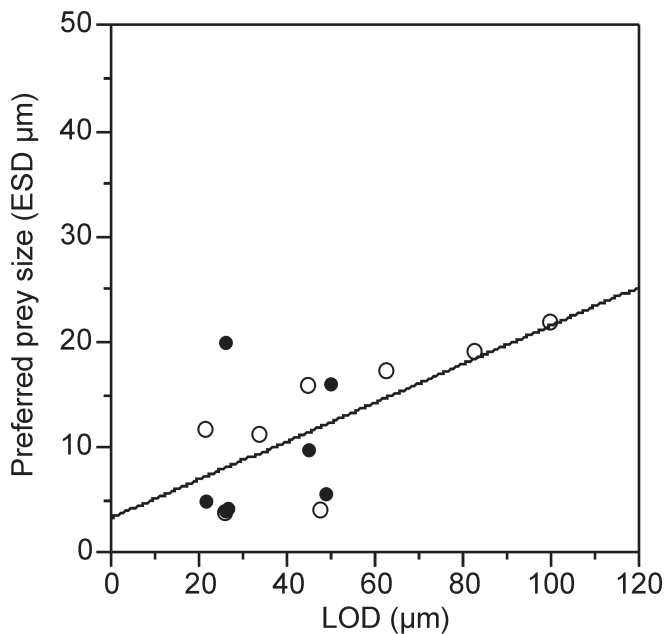ps of preferred food size and LOD and log LV were found but not LL with the tightest relationship being with LOD. Similar relationships were evident considering data without *Tintinnopsis* spp., except that the tightest correlation was found with log LV (Table 4). A scatterplot of the data relating LOD to preferred prey size is shown in Fig. 6. The equation relating preferred prey size to LOD, 'preferred prey size = (0.18 * LOD) + 3.3, gives an estimate of preferred prey size equal to about 20% of LOD.

DISCUSSION

Lorica morphology in tintinnid ciliates has historically been used to distinguish species (e.g. Claparède and Lachmann (1858–1860) and remains today the basis of tintinnid classification schemes (e.g. Lynn 2008).
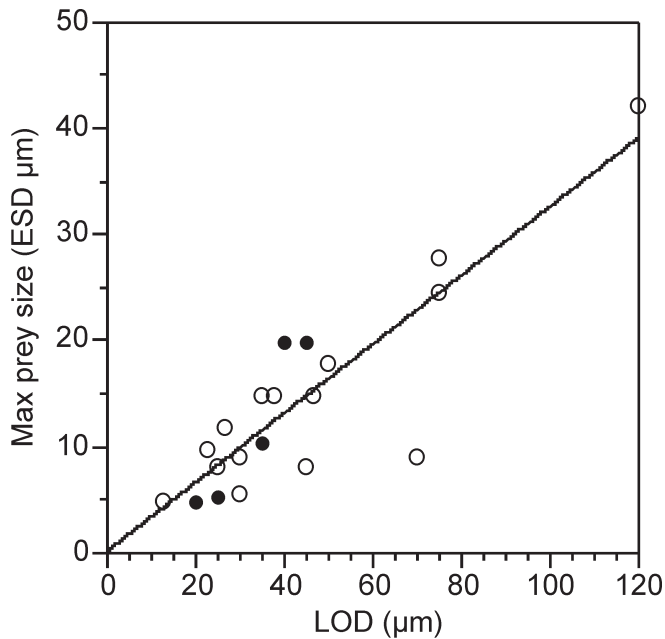
Fig. 5. Maximum prey size. Scatterplot of tintinnid lorica oral diameter and the average maximum prey size observed in tintinnids. Filled circles represent data from species *Tintinnopsis*. See discussion for details and Table 3 for statistics. Line represents the regresion relationship for the pooled data set.


Fig. 6. Preferred prey size. Scatterplot of tintinnid lorica oral diameter and the prey size corresponding with maximum filtration rate in tintinnids. Filled circles represent data from species *Tintinnopsis*. See discussion for details and Table 4 for statistics. Line represents the regression relationship for the pooled data set.

Nonetheless, the lorica-based classification of tintinnids has been challenged on multiple grounds. For example, recent re-descriptions have convincingly argued that single species have been given several different names based on relatively slight differences in lorica shape and size (e.g. Agatha 2010a, Agatha and Riedel-Lorjé 2006, Agatha and Tsai 2008). Indeed, very variable lorica architecture has been documented in supposed single species (e.g. Boltovskoy *et al.* 1990, Laval-Peuto 1981). Furthermore, molecular studies suggest that some genera, such as *Tintinnopsis* may be polyphyletic (Snoeybos-West *et al.* 2002). However, while lorica morphology may be a less than certain taxonomic characteristic, (e.g. Alder 1999) it does appear to correlate with some basic ecological parameters.

Lorica oral diameter shows a significant, albeit relatively weak, relationship with maximum observed growth rate, in contrast to the volume or length of the lorica which appear unrelated to maximum observed growth rate (Table 1). Among ciliates and other protists, it is well known that maximum reproductive rate declines with cell size (e.g. Fenchel 1974). Hence, an explanation for the relationship of LOD and growth rate is that oral diameter is much more closely linked to ciliate cell size than lorica length or volume. Data extracted from Gilron & Lynn (1989a) which examined ciliate cell volume in 17 tintinnid species supports this hypothesis (Fig. 7).

The scatter apparent in the data of maximum reported growth rate may be genuine or in part reflect uncorrected temperature effects as data was unavailable for the majority of growth rate estimates. Furthermore, it should be stressed that the data consist of maximum observed growth rate in field experiments which may be a poor proxy for actual reproductive potential. Given these error sources, the finding of a weak but significant relationship between LOD and maximum observed growth suggests that there is a relationship between LOD and maximum growth rate.

The data set used to probe the relationship between lorica dimension and susceptibility to predation was small, consisting of data on only 7 tintinnid species subjected to predation by 3 different species of the calanoid copepod *Acartia*. None the less, a highly significant relationship was found suggesting that small LOD species are subject to lower predation rates, based on the maximum filtration rates reported (Table 2; Fig. 4). Lorica volume and length appeared unrelated to copepod predation rates. The mechanism behind an appar-
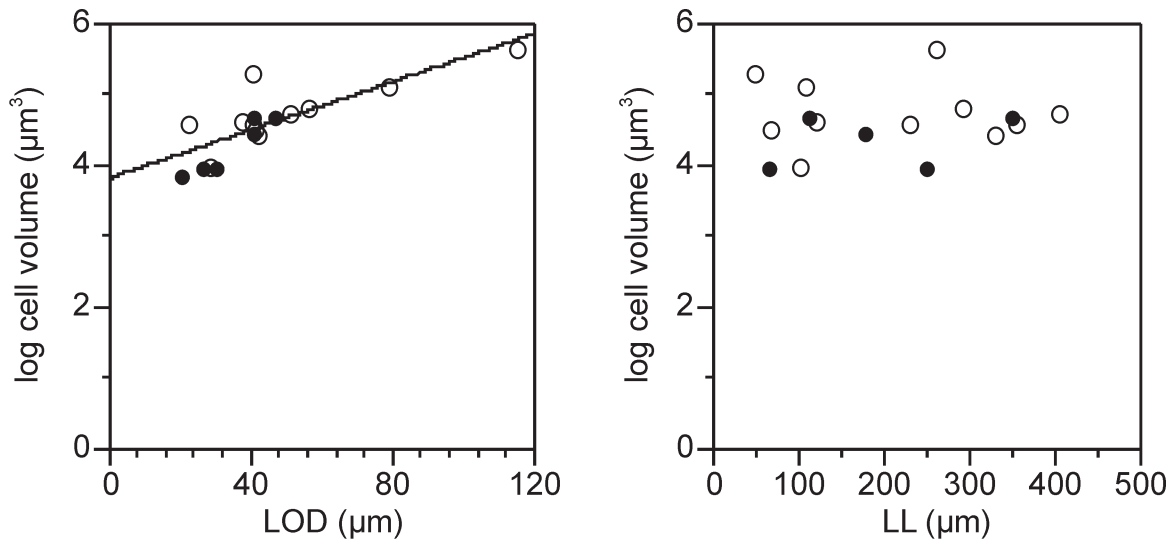
Fig. 7. Tintinnid cell volume and lorica dimensions. Scatterplots of lorica oral diameter and lorica length against cell volumes in 17 species based on data extracted from Gilron and Lynn (1989a). Filled circles represent data from species *Tintinnopsis*. Lorica oral diameter is significantly related to cell volume ($r^2 = 0.602$) in contrast to lorica length. Line represents the regresion relationship for the pooled data set.

ent preference for LOD rather than length or volume is obscure. Possibly LOD is reflected in swimming speed, yielding increases in predator detection or encounter rates. Alternatively, *Acartia* capture success may depend more on prey width than length. Given that *Acartia* species are characteristic of estuarine and coastal waters, the extension of the relationship to open water systems dominated by other copepod genera, seems plausible but remains uncertain.

The relationship found between average maximum prey size and LOD, LL and log LV echo previous findings of the relationship between LOD and maximum food size ingested established by Spittler (1973), Blackbourn (1974) and Heinbokel (1978). The data analyzed here are different in that they represent only prey found inside field-caught individuals as opposed to including data on the ingestion of starch particles. This likely explains the finding of maximum prey size of about 1/3 LOD as opposed to the figure of 45% of LOD commonly cited in reviews (e.g. Capriuolo 1990). While the strongest relationship was found with LOD (Fig. 5), significant relationships were also apparent with LL and log LV (Table 3). It should be noted that the relationships are based on the averages of maximum observed natural prey items. It is not uncommon to find individuals having ingested extraordinarily large prey items, e.g. *Favella* having ingested *Tintinnopsis cylindrica* (Gavrilova and Dolan 2007).

Preferred prey size, estimated as the prey size corresponding with the maximum clearance rate, was significantly related to both LOD and log LV (Table 4). The tightest relationship was with LOD, equating preferred food size to about 20% of LOD (Fig. 6). This is similar to relationship previously reported by Dolan *et al.* (2002) of 25% based on slightly a smaller data set. While it appears reasonable to characterize the lorica diameter or volume of a tintinnid species as a correlate of its preferred prey size, it should be recalled that selective feeding in ciliates among identical-size sized prey is well documented (e.g. Christaki *et al.* 1998, Sanders 1988). Among tintinnids, studies have argued both for and against the phenomena in a single species, *Favella ehrenbergii* (Stoecker *et al.* 1981, Hansen 1995). The relationships documented here most likely reflect a mechanical effect such as increased swimming speeds associated with larger LOD and log LV permitting increased encounter rates with generally rarer large prey items or simply spacing of oral membranelles increasing with LOD and log LV.

Relationships were examined without data from *Tintinnopsis* spp to see if relationships extended beyond the single over-represented genus. The major trends were unchanged with the exclusion of data on *Tintinnopsis* species. While this suggests that the relationships described may then be extrapolated to tintinnids in general, it should be noted nearly all of the data

concerned tintinnids from coastal environments. This admitted, open water tintinnid communities often contain many of the same species as those found in near shore environments (with the notable exception of *Tintinnopsis* spp.). Therefore, there is little *a priori* reason to expect that the simple relationships derived from data on coastal tintinnids would not extend to open water tintinnids.

A question which remains is the adaptive value or ecological correlate of lorica length. For example, the value of quite long loricas for relatively small cell sizes found in many open water forms (e.g. *Salpingella, Climacocylis*). These large loricas likely represent a considerable metabolic cost not only in terms of fabrication but also in terms of cell motility. Comparing sedimentation rates of empty hyaline loricas, Suzuki and Taniguchi (1995) found a positive relationship between lorica size and sinking rate. It is tempting to speculate that long loricas into which the cell may contract far from lorica opening, may be provide refuge against other protistan predators, for example heterotrophic dinoflagellates. Defense against physical contact with protistan predators may also explain the existence of a variety distinct forms of lorica closing apparatuses known in tintinnids (Agatha 2010b).

The analysis presented here, showing that distinct LODs correspond with distinct ecological correlates in part explains the large morphological variety displayed by the group as reflecting adaptation to distinct ecological niches. Characterization of tintinnid assemblages simply in terms of LODs can then provide information on the ecological diversity of the assemblage. Furthermore, such information may be obtainable using automated or semi-automated image analysis systems.

CONCLUSION

In tintinnid ciliates, characterized by the possession of a lorica, diverse ecological characteristics appear to be relatable to dimensions of the lorica and most tightly with lorica oral diameter (LOD). Maximum observed growth rates of wild populations is inversely related to oral diameter as is ciliate cell size. Predation rates of species of the copepod *Acartia* feeding on tintinnids increases with LOD. The maximum size of natural prey ingested and preferred prey size both scale with LOD. Characterization of tintinnid communities simply in terms of LODs can provide information on the ecological characteristics of the species assemblage.

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Supporting information

A complete data set is available as additional material accompanying this paper at the journal website.