
A preliminary study of tintinnid diversity in the NW Mediterranean Sea

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Abstract. Tintinnid diversity in surface waters was investigated in the Bay of Villefranche in March, before the formation of the seasonal thermocline, and in May, following water column stratification. Tintinnid abundance was much greater in March (500 cells l⁻¹), corresponding to a bloom of *Sten-somella nivalis*, compared to May (30 cells l⁻¹). Nonetheless, high numbers of species were encountered on both dates: 32 in March and 39 in May, respectively. Diversity was higher ($H' = 2.5$) for the May date with low tintinnid concentrations. We examined taxonomic diversity and morphological diversity. Variance of lorica length was correlated with taxonomic diversity, in contrast to variance of lorica diameter, which was nearly invariant. We suggest that either species with similar lorica diameters exploit different prey items or competition for prey items is not the dominant factor in structuring tintinnid communities.

Introduction

Tintinnids are all members of the suborder Tintinnia and are planktonic ciliates, a group of organisms recognized as playing an important role in marine pelagic food webs. Characterized by the possession of a lorica, tintinnids have long been catalogued in net plankton collections (e.g. Jörgensen, 1924) and the literature on their taxonomy is large (e.g. Corliss, 1979). Likewise, there have been many studies which have quantified and underlined the significance of tintinnids as grazers of nanoplankton and picoplankton (e.g. Capriuolo *et al.*, 1991). While many reports exist which summarize abundances of common species and list species encountered (e.g. Rassoulzadegan, 1979), data allowing the calculation of common indices of diversity are rare. We were interested in estimating the magnitude of tintinnid diversity, its variability over short time scales, and the relationship between species diversity and morphological diversity.

Among benthic ciliates (a polyphyletic group), global and local diversity appear similar, meaning that most benthic species are cosmopolitan and always present, although possibly in difficult to detect concentrations (Finlay *et al.*, 1996; Fenchel *et al.*, 1997). However, this might not be the case for tintinnids, as many tintinnid genera are apparently not cosmopolitan (Pierce and Turner, 1993). Tintinnids may more closely resemble metazoan zooplankters in which global and local diversity are quite different. Metazoan zooplankton show distinct increases in diversity, over large geographical scales, e.g. with decreases in latitude (Angel, 1997), and locally with increases in water column structure (Longhurst, 1985). We hypothesized that tintinnid diversity in the Mediterranean should be high, as it is a relatively 'low-latitude' type of environment. We also hypothesized that diversity should increase with water column structure (i.e. with the establishment of vertical gradients of temperature and chlorophyll).

We were also interested in examining the relationship between species diversity and the diversity of tintinnid lorica morphologies. However, whether diversity should be reflected in varieties of lorica diameters or lengths is unclear. Lorica diameter is related to the maximum size of food particle that a tintinnid can ingest (Spittler, 1973; Heinbokel, 1978). Overall community averages of lorica diameter change seasonally and are thought to reflect changes in the size spectrum of food particles (Middlebrook *et al.*, 1987; Verity, 1987; Gilron *et al.*, 1991). If diversity is related closely to partitioning of food resources, variance in lorica diameter, indicating a variety of at least maximum sizes for food, should increase with diversity. Lorica length, or overall size, may have both costs and benefits. Lorica length has occasionally been related to susceptibility to copepod predation with large tintinnids hypothesized to be more subject to predation from copepods than smaller species (Ayukai, 1987). However, size can also confer an advantage in that bigger cells are thought to have lower minimum food requirements, in terms of bulk concentrations, relative to smaller ciliates, as larger ciliates can more easily exploit prey distributed in 'patches' (Rassoulzadegan, 1993).

We were interested in estimating the magnitude of tintinnid diversity, the influence of water column structure and the relationship of species diversity with morphological diversity. We sampled on two spring dates before and then during the formation of the seasonal thermocline in coastal waters of the NW Mediterranean. We also compare the diversity found at a single point in the western Mediterranean with data from previous studies which examined diversity over larger space and time scales in the Mediterranean Sea.

Method

We examined tintinnid populations in the Bay of Villefranche in samples from a standard station 'Point B' (43°41'10"N, 7°19'00"E). On 18 March and 6 May 1998, triplicate water samples were obtained from 0, 10, 20, 30, 40 and 50 m using 5 l Niskin bottles. Temperature and salinity were measured using a Seabird CTD. Chlorophyll *a* samples were measured fluorometrically following acetone extraction. For tintinnids, each replicate 5 l sample was concentrated to 60 ml using a 20 mm Nitex screen. This method yields tintinnid numbers as high as settling whole-water samples (Pierce and Turner, 1994). The entire concentrate, in 10 ml aliquots, was settled in sedimentation chambers and examined with an inverted microscope at $\times 200$. Thus, for each date, material from 75 l was examined. Tintinnids were identified using lorica morphology and the species descriptions found in Balech (1959), Campbell (1942), Jørgensen (1924) and Kofoed and Campbell (1929, 1939). Lorica dimensions of 10–20 individuals for each species were measured with an ocular micrometer.

The Shannon and Simpson diversity indices for each 5 l sample were calculated. Here, we report only Shannon values as Simpson index figures showed the same trends. Sampling error, more specifically the undersampling of rare species, was evaluated by using jack-knife estimates for the cumulative species as a function of the volume of water examined. Diversity indices and jack-knife calculations were made using the 'Biodiversity Professional' [beta release; McAleece, N.,

Lambshead, P.J.D., Patterson, G.L.J. and Gage, J.D., 1997; distributed by the Natural History Museum, London, through the NHM web site ([HTTP://www.NHM.AC.UK/ZOOLOGY/BDPRO](http://www.nhm.ac.uk/zooology/bdpro))]. Data on lorica diameters and lengths from the triplicate samples were pooled to calculate a variance estimate (SD) of the average lorica dimensions.

Results

The early spring sampling showed a homogeneous water column in terms of temperature ($\sim 14^{\circ}\text{C}$) and salinity (38 p.p.t.). Chlorophyll concentrations ranged from ~ 0.2 to $0.6 \mu\text{g l}^{-1}$ with a maximum at ~ 30 m depth. The tintinnid community was dominated by *Stensomella nivalis*. Total abundance was high, averaging ~ 500 cells l^{-1} , and roughly paralleled chlorophyll. The community average lorica diameter was nearly constant with depth and variance of lorica diameter was unrelated to diversity. Abundance of tintinnids was inversely related to diversity with the highest values of indices corresponding to 0 and 50 m depth samples which contained few *S.nivalis*. Despite the near total dominance of the tintinnid community by *S.nivalis*, reflected in H' values of near zero at 30 m (Figure 1), a large number of species (32) was encountered (Table I).

Data from the late spring sampling showed the establishment of a temperature gradient ranging from 14 to 16°C between 50 and 0 m depth. Chlorophyll concentrations were similar to those of March with, however, higher concentrations at near-surface depths. Tintinnid concentrations were much lower than in March, averaging ~ 40 cells l^{-1} , and diversity was markedly higher with H' values between 2.5 and 3. A more even distribution among species was evident (Figure 2). Diversity was unrelated to tintinnid abundance. As in March, community lorica averages did not vary significantly with depth nor was variance related to diversity.

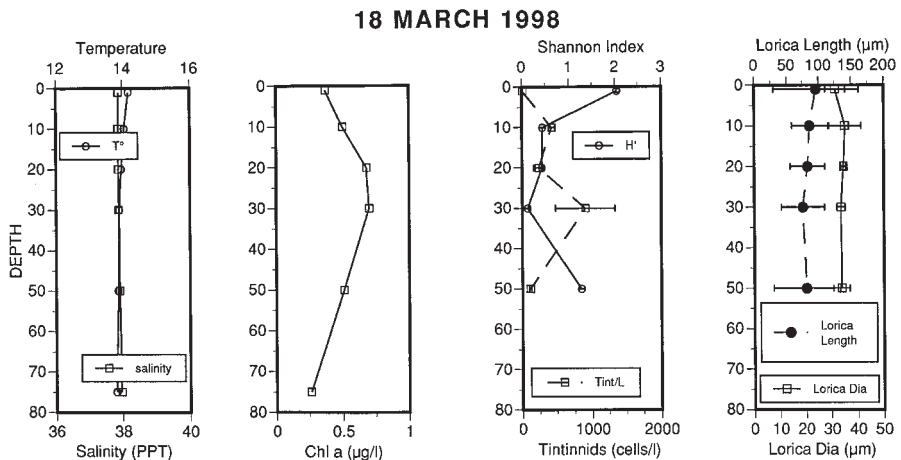


Fig. 1. Data from the 18 March sampling. Vertical profiles of temperature, salinity, chlorophyll *a* concentration, tintinnid abundance, diversity and variance (SD) of average community lorica dimensions.

Table I. Tintinnid species found on 18 March. Lengths and diameters refer to lorica dimensions in micrometers

Species	No. of specimens	Length	Diameter
<i>Acanthostomella conicoides</i>	13	35.4	20
<i>Acanthostomella obtusa</i>	16	28	16
<i>Amphorella minor</i>	76	96.6	40.4
<i>Amphorella quadrilineata</i>	4	155	56
<i>Amphorella</i> sp. a	2	34	11
<i>Amphorellopsis acuta</i>	1	66	31
<i>Codonella aspera</i>	25	94.3	54.5
<i>Codonella galea</i>	8	107	68.8
<i>Codonellopsis lata</i>	1	34.5	21
<i>Codonellopsis orthoceras</i>	2	250	66
<i>Codonellopsis pusilla</i>	63	38	16.5
<i>Codonellopsis schabi</i>	86	108.5	41.4
<i>Craterella armilla</i>	8	31	31
<i>Craterella oxyura</i>	3	31.2	19.5
<i>Cyttarocylis eucecryphalus</i>	1	127	117
<i>Dictyocysta lepida</i>	3	71.4	43.5
<i>Dictyocysta speciosa</i>	2	72.5	48
<i>Dadayiella ganymedes</i>	36	94	25.8
<i>Eutintinnus fraknoui</i>	2	340	54.5
<i>Eutintinnus inflatus</i>	1	94	25
<i>Eutintinnus tubulosus</i>	11	141.5	31.8
<i>Proplectella claparedei</i>	24	76.5	39.8
<i>Protorhabdonella curta</i>	3	42	31
<i>Salpingella attenuata</i>	1	290.7	35
<i>Salpingella laminata</i>	272	65.5	11.5
<i>Steenstrupiella steenstrupii</i>	7	130	41
<i>Stensomella nivalis</i>	24 165	47.8	20
<i>Stensomella ventricosa</i>	467	93.3	45
<i>Tintinnopsis beroidea</i>	6	82.4	34.8
<i>Tintinnopsis levigata</i>	22	73.2	35.9
<i>Tintinnopsis radix</i>	1	357	46

The community average of lorica diameter was very similar to the March date, although a larger number of species (39) was found (Table II).

The importance of *S.nivalis* in the March samples was clear in comparing K-dominance curves of the March and May communities (Figure 3). The March community of tintinnids was ~95% composed of individuals of *S.nivalis*. In the May samples, the most common species, *Acanthostomella conicoides*, represented ~20% of total individuals. Plotting the jack-knife estimations of numbers of species as a function of volumes of water examined showed a good agreement between estimated numbers of species and actual values (Figure 4). For both sampling dates, undersampling of rare species may have represented an underestimation of total numbers of species by 5–10.

Variance of lorica length was much greater than lorica diameter in both the March and May communities (Figures 1 and 2). Variances in lorica length were positively correlated with taxonomic diversity, in contrast to variance in lorica diameter (Figure 5).

6 MAY 1998

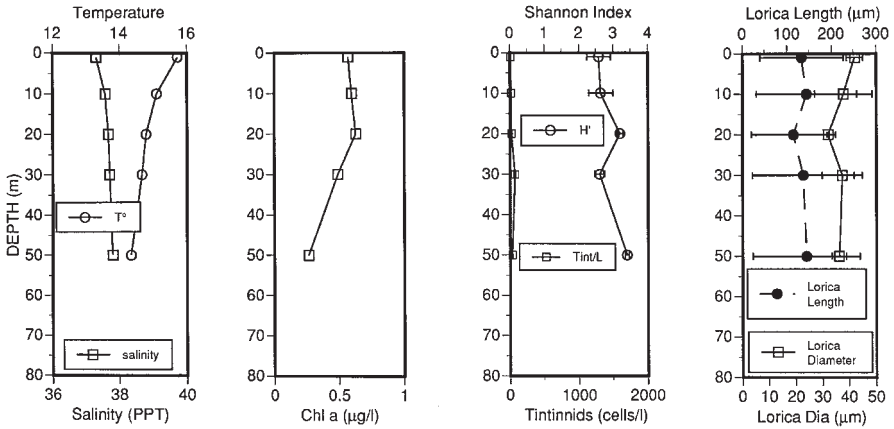


Fig. 2. Data from the 6 May sampling. Vertical profiles of temperature, salinity, chlorophyll *a* concentration, tintinnid abundance, diversity and variance (SD) of average community lorica dimensions.

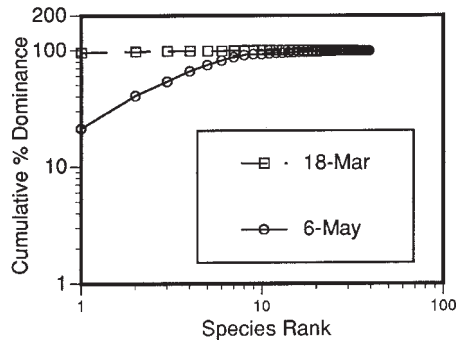


Fig. 3. K-dominance curves of the March and May tintinnid communities. The March community was overwhelmingly dominated by *S.nivalis*. In May, the most abundant species was *A.conicoides*, accounting for ~20% of the total number of individuals.

Discussion

Our data could be critiqued on the grounds that basing tintinnid species identification on lorica morphology can be hazardous. Although less than ideal, lorica morphology is generally used as tintinnid infraciliature, the basis of alpha-level ciliate taxonomy (Corliss, 1979), has been described for very few species (Choi *et al.*, 1992; Petz and Foissner, 1993). While some tintinnid species are apparently capable of expressing different lorica morphologies (Gold and Morales, 1976; Davis, 1981; Laval-Peuto, 1983; Wasik and Mikolajczyk, 1994), studies of field populations have rarely shown co-existence of different lorica morphotypes of the same species.

Table II. Tintinnid species found on 6 May. Lengths and diameters refer to lorica dimensions in micrometers

Species	No. of specimens	Length	Diameter
<i>Acanthostomella conicoides</i>	462	35.4	20
<i>Acanthostomella minutissima</i>	3	34	31
<i>Amphorella laackmanni</i>	2	66	20
<i>Amphorella minor</i>	260	93.4	37.3
<i>Amphorella quadrilineata</i>	1	155	55
<i>Canthariella prymidata</i>	1	53	28
<i>Climacocyclus scalaroides</i>	6	194.5	35
<i>Codonella aspera</i>	6	94.3	54.5
<i>Codonella galea</i>	5	107	68.8
<i>Codonellopsis pusilla</i>	6	42	17.5
<i>Codonellopsis schabi</i>	6	108.5	41.4
<i>Craterella armilla</i>	3	31	31
<i>Craterella oxyura</i>	10	31.2	19.5
<i>Craterella torulata</i>	1	31.5	20.5
<i>Cyttarocyclus eucecryphalus</i>	1	127	115
<i>Dadayiella curta</i>	1	169	26
<i>Dadayiella cuspis</i>	1	80	26
<i>Dadayiella ganymedes</i>	151	93.7	27.9
<i>Dictyocysta mitra</i>	2	73	44
<i>Dictyocysta speciosa</i>	6	72.5	48
<i>Eutintinnus apertus</i>	18	70	38
<i>Eutintinnus fraknoi</i>	20	380	59
<i>Eutintinnus medius</i>	2	255	50
<i>Eutintinnus tenuis</i>	1	270	46
<i>Eutintinnus tubulosus</i>	32	158	31.8
<i>Favella serrata</i>	1	316	100
<i>Proplectella claparedei</i>	9	76.5	39.8
<i>Protorhabdonella curta</i>	195	44.7	25.9
<i>Salpingella attenuata</i>	6	358	36.3
<i>Salpingella gracilis</i>	6	375.5	38
<i>Salpingella laminata</i>	79	127.3	11.5
<i>Steenstrupiella steenstrupii</i>	285	132	37.1
<i>Stensomella nivalis</i>	432	47.8	20
<i>Stensomella ventricosa</i>	20	93.3	44.9
<i>Tintinnopsis beroidea</i>	1	82.4	34.8
<i>Tintinnopsis campanula</i>	11	178.5	117
<i>Tintinnopsis levigata</i>	2	73.2	35.9
<i>Tintinnopsis lobiancoi</i>	1	400	137.7
<i>Tintinnopsis radix</i>	127	360	47.8

We found a large number of tintinnid species on both sampling dates. We believe that this results from the considerable effort invested in examining material screened from large volumes of water using a fine-mesh (20 μm) screen. Our sampling error can be gauged by comparing jack-knife estimations of species expected versus actual numbers (Magurran, 1988) and indicates that few 'rare' species were missed in the volumes of water sampled (Figure 6).

We found differences between the two sampling dates, corresponding to differences in water column conditions. The relatively 'unstructured' water column on 18 March harbored a more abundant but less diverse tintinnid community compared to the 6 May sampling (Figures 1 and 2). However, the differences

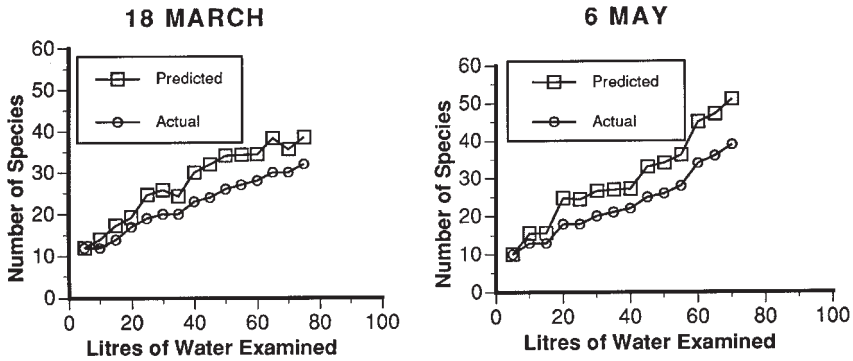


Fig. 4. Jack-knife estimations of species expected in a given volume of water (number of samples) compared to actual data. Note that, for both dates, the jack-knife estimates indicate that few rare species were undersampled.

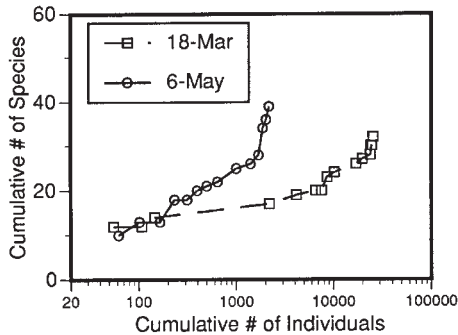


Fig. 5. Cumulative numbers of species versus individuals examined, for the March and May samplings.

between the two dates were largely the result of the presence of an abundant population of one species on 18 March: *S.nivalis*. It is noteworthy that the bloom of *S.nivalis* did not appear to exclude other species, i.e. there were still large numbers of species present, and *S.nivalis* bloomed against a background of a sparse yet diverse tintinnid community. Comparison of the two dates, excluding all data on *S.nivalis*, yielded similar values of total community abundance as well as diversity indices (data not shown). While recognizing the inherent limits of only two sampling dates, it appears that both structured and unstructured water columns can harbor diverse tintinnid communities.

On both dates, diversity appeared unrelated to trophic specialization, at least as indicated by varieties in lorica diameter. Overall, these observations lead to the suggestion that either species with similar lorica diameters exploit different prey items or competition for prey items is not the dominant factor in structuring tintinnid communities. Taxonomic diversity was related to variance in lorica length (Figure 5) and one possible force promoting such morphological diversity

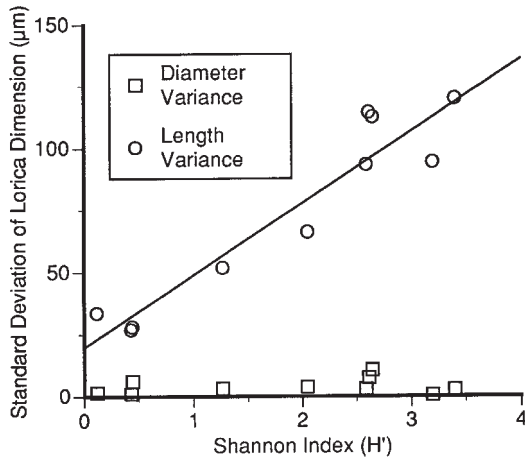


Fig. 6. Plots of Shannon index values of taxonomic diversity against measures of morphological diversity, population variances (SD) of tintinnid community lorica diameter and lorica length. Average values of the discrete depth replicates for both the March and May samplings ($n = 10$).

may be predation pressure. While data are sparse (reviewed in Stoecker and Capuzzo, 1990), there is some evidence suggesting that predation on tintinnids by copepods is influenced by the size of the tintinnid. However, the relationship may not be simple. Most studies have dealt with copepod species of the genus *Acartia* in which maximum reported predation rates do not appear to vary in a linear manner as a function of tintinnid lorica volume; species with very large loricas may be less subject to copepod predation (Figure 7). It is worthwhile recalling that size also involves trade-offs in terms of cellular energetics, with larger size associated with a capability to exploit lower minimum food concentrations (Rassoulzadegan, 1993), but associated with lower maximum growth rate (Pérez *et al.*, 1997). These relationships are obscured further in tintinnids as lorica volume is apparently a poor predictor of cell plasma volume (Gilron and Lynn, 1989).

We found ~40 species in a single location on a single date in the western Mediterranean by examining ~3000 individuals. It may be of interest to determine whether using this effort over larger time and space scales would reveal more species. One method of approaching this question is through consideration of data from studies on larger temporal and spatial scales, plotting numbers of individuals versus numbers of species (Gray, 1997). Sample data from a study of the Catalan Sea and a transect across the Mediterranean are plotted in Figure 8 for comparison with our single date and place data from the 6 May sampling. The Catalan Sea samples were gathered from six stations along a 100-nautical-mile transect over a period of 5 days in June (see Dolan and Marrasé, 1995). The Mediterranean transect data were based on samples from 18 stations gathered over a 4 week period in May and June along a cruise track of ~1600 nautical miles (see Dolan *et al.*, 1999). Both studies employed sedimentation of whole-water

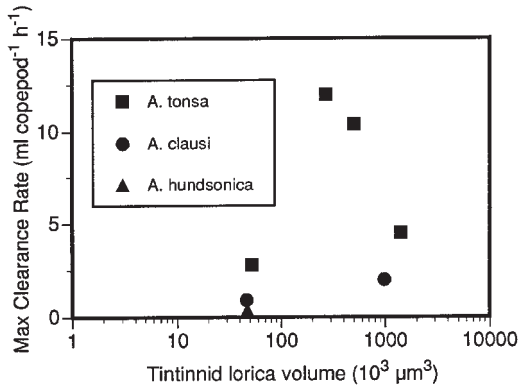


Fig. 7. Results from various laboratory studies of copepods of the genus *Acartia* offered tintinnid ciliates as prey; maximum reported clearance rates as a function of tintinnid lorica volume [data from Stoecker and Capuzzo (1991), Table 4]. Note that copepod clearance rates do not show a simple linear relationship with tintinnid lorica volume, both small and large forms appear to be cleared less efficiently than intermediate-sized tintinnids. The common Mediterranean species of *Acartia* is *A. clausi*.

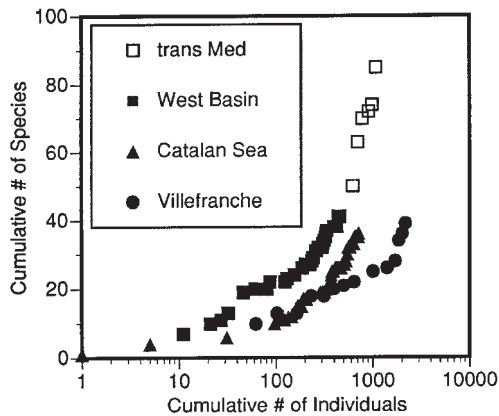


Fig. 8. Area–species curves for the May sampling at Point B compared to curves from a study of the Catalan Sea (data from Dolan and Marassé, 1995), and transects across the western basin of the Mediterranean (West Basin), and across the western, central and eastern basins (trans Med) of the Mediterranean (data from Dolan *et al.*, 1999).

samples, comparable to samples concentrated with a fine-mesh ($20 \mu\text{m}$) net (Pierce and Turner, 1994).

Interestingly, the data suggest that employing low to intermediate levels of effort (examining <500 individuals) can reveal similar numbers of species in samples gathered from locations separated by tens of kilometers and a few days, compared to a single site on a single date. In contrast, when the spatial scale and temporal scale of sampling are increased to hundreds of kilometers and weeks, even low levels of effort appear to yield more species and, employing high levels

of effort (examination of $\times 10^3$ individuals), the number of species encountered increases markedly with the temporal and spatial scales of sampling. Thus, in tintinnids, it appears that local and global diversity are different, resembling more the patterns found in planktonic metazoans (e.g. Angel, 1997) rather than those in benthic ciliates (Finlay *et al.*, 1996).

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