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Microzooplankton diversity: relationships of tintinnid ciliates with resources, competitors and predators from the Atlantic Coast of Morocco to the Eastern Mediterranean

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Abstract

We examined tintinnid (loricate ciliate microzooplankton) diversity using data from 11 stations between the Moroccan upwelling system and the oligotrophic Eastern Mediterranean. Taxonomic and morphological diversity of tintinnids was compared to phytoplankton distribution and size-structure, to the abundance of competitors in the form of oligotrich ciliates, and predators as copepods. Tintinnid taxonomic diversity was estimated as numbers of species and the Shannon Index, H'; morphological diversity was quantified by substituting size classes of lorica dimensions for species. Total chlorophyll was partitioned into micro-, nano- and pico-fractions using pigment data and a size-diversity was estimated by considering the 3 size classes as 3 species. Along a west-to-east gradient, average water column concentrations of most organism groups declined approximately an order of magnitude yielding tight correlations. However, tintinnid diversity, both taxonomic and morphological, increased from the Atlantic upwelling station into the western basin of the Mediterranean, and declined slightly towards the Eastern Mediterranean, paralleling shifts in the chlorophyll size-diversity estimate. Diversity varied with absolute or relative abundance of oligotrich or copepods, but different diversity metrics were significantly correlated only with phytoplankton size-diversity. We conclude that tintinnid diversity more closely reflects resource diversity than competitive interactions or predation.

Keywords: Species diversity; Plankton; Protists; Phytoplankton

1. Introduction

In recent years, significant advances have been made in explaining the "paradox of the plankton" (Hutchinson, 1961) with regard to phytoplankton. The distinct requirements and affinities for nutrients and light which have been known for some time to characterize different high-level taxa, such as a genera of diatoms or dinoflagellates

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(Margalef, 1978), are now known to characterize different strains of apparent single species such as *Prochlorococcus* (e.g., West and Scanlan, 1999). Thus, phytoplankton display a multitude of individual niche characteristics. Spatial or temporal heterogeneity in the water column (Flöder and Sommer, 1999) and the chaotic nature of multispecies competitions (Huisman and Weissing, 1999) appear sufficient to explain, if not predict, diversity. Interestingly, with regard to microzooplankton, our knowledge is rudimentary concerning niche characteristics while indirect relationships, quite strong statistically, have been established with diversity and environmental parameters.

The best known is the tight relationship between annual average sea surface temperature and species richness of planktonic foraminifera, on both regional (Williams and Johnson, 1975) and global scales (Rutherford et al., 1999). Annual sea surface temperature has been identified as a proxy measure of the depth of the surface layer, which probably reflects the number of niches available with depth within the surface layer (Rutherford et al., 1999). Similarly, the diversity of tintinnid ciliates in the surface layer (top 100 m) of the Mediterranean Sea was correlated to the depth of the chlorophyll maximum (Dolan, 2000).

The Mediterranean relationship was based on data from 2 cruises in late spring yielding a suite of stations between Spain and Cyprus. Both taxonomic measures, species-richness and H', as well as a rough measure of morphological diversity, standard deviations of lorica dimensions, increased with the depth of the chlorophyll maximum. However, the data set did not allow examination of other likely correlates or direct influences such as abundance of tintinnid consumers, copepods, or the community composition of the phytoplankton.

Here, we exploit a more complete data set and one covering a wider range of water column conditions, from 11 stations sampled in September 1999 and between the productive upwelling system of the Atlantic coast of Morocco and the oligotrophic Eastern Mediterranean Sea. We evaluated several possible direct influences on tintinnid diversity, in terms of both morphological and taxonomic diversity. Tintinnid diversity was examined relative to the distribution and composition of their food resource, phytoplankton, as well as the abundance of presumed predators, copepods, and presumed competitors, oligotrich ciliates.

There are distinct advantages to examining diversity trends among tintinnid ciliates compared to other groups of microzooplankters. While numerically a minority component they are nonetheless much more abundant than foraminifera or radiolarians (Thompson et al., 1999) and there is a wealth of data on their ecology (Dolan, 2000). Like foraminifera and radiolarians, species identifications can be made using characteristics of gross morphology, with some caveats (for a discussion see Cariou et al., 1999; Dolan, 2000; Dolan and Gallegos, 2001). Furthermore, tintinnids are a monophyletic group, constituting a single order even among competing ciliate classification schemes (e.g., Petz and Foissner, 1992; Lynn and Small, 1997), in contrast to other groups of planktonic ciliates, for example, "oligotrichs". Thus tintinnids are a group united ecologically as microzooplankters, morphologically as loricate ciliates, and phylogenetically as members of the order Tintinnida.

The underlying hypotheses of our study were firstly that tintinnid diversity was related to phytoplankton diversity, distribution or production. Although the mechanism is unclear, over large spatial scales diversity in the plankton appears inversely related to production (e.g., Huston, 1994). More directly, diversity among primary producers may generate consumer diversity (e.g., Lasserre, 1994). Alternatively, or in addition, resource (in this case phytoplankton) patchiness, for example in a turbulent environment, may inhibit single species dominance. We employed taxonomic pigment markers to estimate size-class diversity of phytoplankton. Chlorophyll distribution was examined in terms of the depth of the chlorophyll maximum and phytoplankton patchiness as discrete depth deviations from the average water column concentrations. Secondly, tintinnid diversity may be restricted because of the occupation of niches by oligotrich ciliates, which, like tintinnids, feed largely on nanoplankton-size

prey (Kivi and Setälä, 1995; Rassoulzadegan et al., 1988). We examined trends with regard to the absolute abundance of oligotrichs and ratios of oligotrich to tintinnid abundance. Lastly, correlations with copepod concentrations were examined as copepods, perhaps by feeding on the most abundant tintinnids (e.g., Dolan and Gallegos, 2001), or more intensely on medium-sized compared to large or small forms (Cariou et al., 1999), increase diversity by reducing dominance, akin to a "killing the winner" (Thingstad, 1998). These hypothetical relationships were examined in an attempt to determine factors directly related to microzooplankton diversity.

2. Methods

Between the 10th and 30th of September 1999 of the PROSOPE cruise, samples were obtained from 11 of the 12 stations located along a cruise track from the Moroccan Atlantic coast to the Eastern Mediterranean and back to the French Mediterranean coast (Fig. 1 and Table 1). Samples for ciliates and chlorophyll determinations were obtained with a CTD-Niskin bottle rosette using 121 Niskin bottles. Between the surface and 100 m depth 6–10 depths were sampled.

For ciliate enumeration, 500 ml samples of whole water were preserved with Lugol's (2% final conc.) and stored refrigerated and in darkness except during transport and settling. The whole water samples were concentrated via settling and examined following the protocol detailed in Dolan and Marrasé (1995). Briefly, samples were preconcentrated in 500 ml graduated cylinders, and concentrates settled in standard sedimentation chambers. Concentrates equivalent to 333 ml of whole water were examined with an inverted microscope at 200×. Tintinnids were identified using lorica morphology and the species descriptions found in Campbell (1942), Jörgensen (1924) and Kofoid and Campbell (1929, 1939) and Marshall (1969).

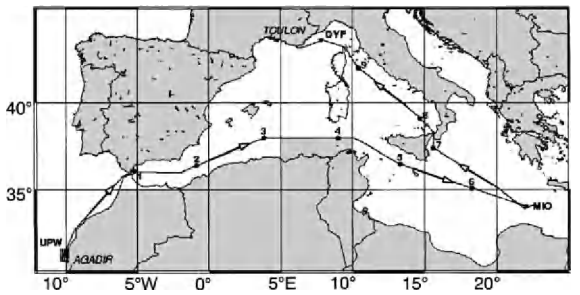

Fig. 1. Cruise track of the PROSOPE cruise in September 1999. Station locations given in Table 1.

Estimates of both taxonomic and morphological diversity were based on data pooled from all samples, equivalent to a total volume of about 2–3 l of water, from each station. While this procedure obscures depth-related shifts in community composition, found thus far to be insignificant (Cariou et al., 1999; Dolan, 2000; Dolan and Gallegos, 2001), it maximizes sample population size. We have found that examining volumes of 1–2 l allows reliable distinction between tintinnid populations from a variety environments (Dolan, 2000; Dolan and Gallegos, 2001). Metrics of taxonomic diversity were the Shannon index (ln-based, e.g., Magurran, 1988), and species richness or number of species.

Estimates of the morphological diversity of tintinnids were made with the formulae used for calculating the Shannon index H' employing size-classes of lorica oral diameters and lorica lengths in the place of species. Subjective judgement concerning the number of possible size classes was avoided by allowing the number of possible classes to equal the number of species found. Thus, for the population of each station, the total range found of lorica diameters or lengths was divided into a number of equal size classes with number of size classes set as equal to the number of species in the population found at that particular station. Morphological diversity was then potentially as great as taxonomic diversity but in practice, most size-classes were empty categories. Diversity of size-classes was employed rather than standard deviations of lorica dimensions to facilitate comparisons and avoid biases from the relationship between increases in standard deviations and means.

Ciliates other than tintinnids were placed in size-shape and, where possible, trophic categories. For

Table 1
Station locations, characteristics and sampling dates

Station	Latitude	Longitude	Date	°C at 0 m	sigma-*t*: 0 m → 100 m
UPW	30°59′N	10°03′W	10/09/99	27.4	26.2 → 26.8
1	36°05′N	05°12′W	14/09/99	28.5	25.6 → 27.8
2	36°24′N	00°51′W	15/09/99	28.7	24.9 → 28.3
3	37°59′N	03°50′E	16/09/99	28.5	24.5 → 28.2
4	37°59′N	08°32′E	17/09/99	28.4	25.4 → 28.5
5	36°28′N	13°19′E	18/09/99	28.4	25.8 → 28.8
6	35°04′N	18.18′E	19/09/99	28.0	25.4 → 29.0
7	37°24′N	15°37′E	26/09/99	29.0	25.6 → 29.0
9	41°54′N	10°26′E	28/09/99	24.5	26.1 → 28.6
DYF	43°24′N	07°49′E	30/09/99	29.3	26.7 → 28.9

example, the mixotrophic (Gustafson et al., 2000) ciliate *Mesodinium rubrum*, which was rare, was pooled with taxa of large morphologically distinct mixotrophic ciliates (*Tontonia*, *Laboea*). All remaining ciliates were considered heterotrophic. As the use of Lugol's fixative precluded identification of mixotrophic ciliates without distinctive gross morphologies (i.e., certain *Strombidium* species), the heterotrophic group likely contained some mixotrophs. 3 major size-categories were used (<25 μm, 25–40 μm, >40 μm) as the overwhelmingly commonest sizes found. The smallest oligotrichs were *Strobilidium* species of 15–20 μm in length; the next commonest forms were *Strombidium* species 30–45 μm in length. Larger oligotrichs were a heterogenous mixture of *Strombidium* and *Strombidinopsis*-like cells ranging from 50 to 100 μm in length. Here only pooled cell concentrations are reported as separate trophic or size groups showed very few distinct relationships.

For chlorophyll and other pigment determinations, 21 aliquots were filtered through GF/F filters, pigments extracted in methanol and samples processed by HPLC as detailed in Vidussi et al. (1996). Pigment data was translated into data on the taxonomic and size composition of the chlorophyll crop following the procedures detailed and justified in Vidussi et al. (2000, 2001). Briefly, 7 diagnostic pigments are used to estimate the portion of total chlorophyll attributable pico-, nano- and micro-sized phytoplankton. Zeaxanthin and chlorophyll *b* are used as markers of pico-sized (<2 μm) autotrophs. Nanoflagellates (2–20 μm) are diagnosed using 19′ hexanoyloxyfucoxanthin, 19′ butanolyoxyfucoxanthin, and alloxanthin. Diatoms and dinoflagellates, taken as micro-sized (>20 μm), are estimated using fucoxanthin and peridinin. The proportion of pico- or nano- or micro-attributed pigments, relative to the sum of all 7 accessory pigments is used to estimate the fraction of total chlorophyll as occurring in pico-, nano- or micro-sized phytoplankton taxa.

Trapezoidal integration was employed to calculate average concentrations of total chlorophyll *a* and chlorophyll in pico-, nano- and micro-size taxa. Based on average water column concentrations (0–100 m), an estimate of chlorophyll diversity, cell-size diversity, was made by calculating the Shannon index, H' (ln-based) considering pico-, nano- and micro-chlorophyll as 3 species. Two total chlorophyll *a* distributional parameters were also employed, the depth of the chlorophyll maximum and chlorophyll dispersion. Chlorophyll dispersion was calculated as the average discrete depth deviation, in terms of a percentage, from the overall water column average. Thus, a low value indicates homogenous chlorophyll concentrations and a high value represents patchy distribution. Calculation of phytoplankton parameters using data only from depths where ciliates were sampled or all depths sampled yielded very slight differences.

Primary production was estimated by the ^{14}C technique (e.g., Moutin et al., 1999). Single light-level, short-term incubations were employed. At each station, beginning at 12:00, samples from

10 m depth were incubated for 1 h on deck under 44% incident illumination, roughly equivalent to light conditions at 10 m depth.

Copepod concentrations were estimated from 0 to 200 m vertical WP2 standard net tows (mesh size 200 μm). Net tow material was preserved with borax-buffered formaldehyde (4%) for subsequent taxonomic analysis using a stereomicroscope. Zooplankton samples were subsampled by the surface method: zooplankton were poured into a flat-bottomed receptacle of known surface area. After homogenization of the sample, three subsamples were picked out and each was decanted into a Dolfuss bowl. Specimens were sorted into different taxa and identified to species level for adult copepods, and genus level for copepodites. The number and relative abundance of the different taxa were calculated per cubic meter. Here only total concentrations of all post-naupliar forms are reported and considered. Detailed information on size and taxonomic composition will appear elsewhere. At Stations DYF and MIO, net tows were repeated at 24 or 48 h intervals and average values were employed.

Statistical relationships were examined using organism average water column concentrations, phytoplankton distribution parameters, and diversity metrics of tintinnids and phytoplankton employing the non-parametric Spearman rank correlation analysis.

3. Results

3.1. Phytoplankton characteristics

From the Atlantic upwelling site to the Eastern Mediterranean, primary production estimates (10 m depth) declined from about 200 to $<2\,\mu g\ C\,l^{-1}\,d^{-1}$ (Fig. 2). Average integrated (0–100 m) chlorophyll concentrations declined from 1.4 to $0.1\,\mu g\,l^{-1}$. Corresponding with these differences was an increase in the depth of the chlorophyll maximum layer from near surface at the upwelling site to about 100 m in the easternmost station. Chlorophyll dispersion, the average discrete depth deviation of chlorophyll from the water column average, showed an opposite trend with chlorophyll patchiness or dispersion higher in the east than the west. At the upwelling site, discrete depth concentrations deviated from the water column average of the station by 110% compared to 70–80% in the Eastern Mediterranean.

Phytoplankton community composition, based on diagnostic pigments, shifted predictably from a micro-sized dominated community of diatoms and dinoflagellates at the upwelling site to nearly equal proportions of nanoflagellates and autotrophic bacteria in the Eastern Mediterranean. In contrast to other phytoplankton parameters, chlorophyll cell-size diversity, estimated by treating the calculated micro-, nano- and pico-chlorophyll concentrations as different species, shifted irregularly from west-to-east. While minimal for the upwelling station, dominated by micro-sized taxa, maxima were estimated for the Western Mediterranean with estimated values showing declines towards the east.

3.2. Zooplankton distributions

For all the populations examined, concentrations differed by about an order of magnitude between west and east (Fig. 3). Tintinnid concentrations declined from about $100\,l^{-1}$ to around $20\,l^{-1}$; copepod abundance sampled over the top 200 m, ranged from approximately $0.6\,l^{-1}$ in the Western Mediterranean–$0.2\,l^{-1}$ at the eastern stations. Oligotrich concentrations of about $3000\,l^{-1}$ declined to about $500\,l^{-1}$ at the Eastern Mediterranean stations. Thus overall, concentrations of tintinnids, oligotrichs and copepods all declined from west-to-east, paralleling declines in primary production, chlorophyll concentrations, and chlorophyll dispersion and increases in the depth of the chlorophyll maximum layer. The distributional trends were reflected in positive correlations with chlorophyll concentrations and dispersion as well as negative correlations with the depth of the chlorophyll maximum layer (Table 2).

3.3. Tintinnid community characteristics

The upwelling assemblage was dominated by open water forms but included tintinnids generally found in coastal waters such as *Tintinnopsis*

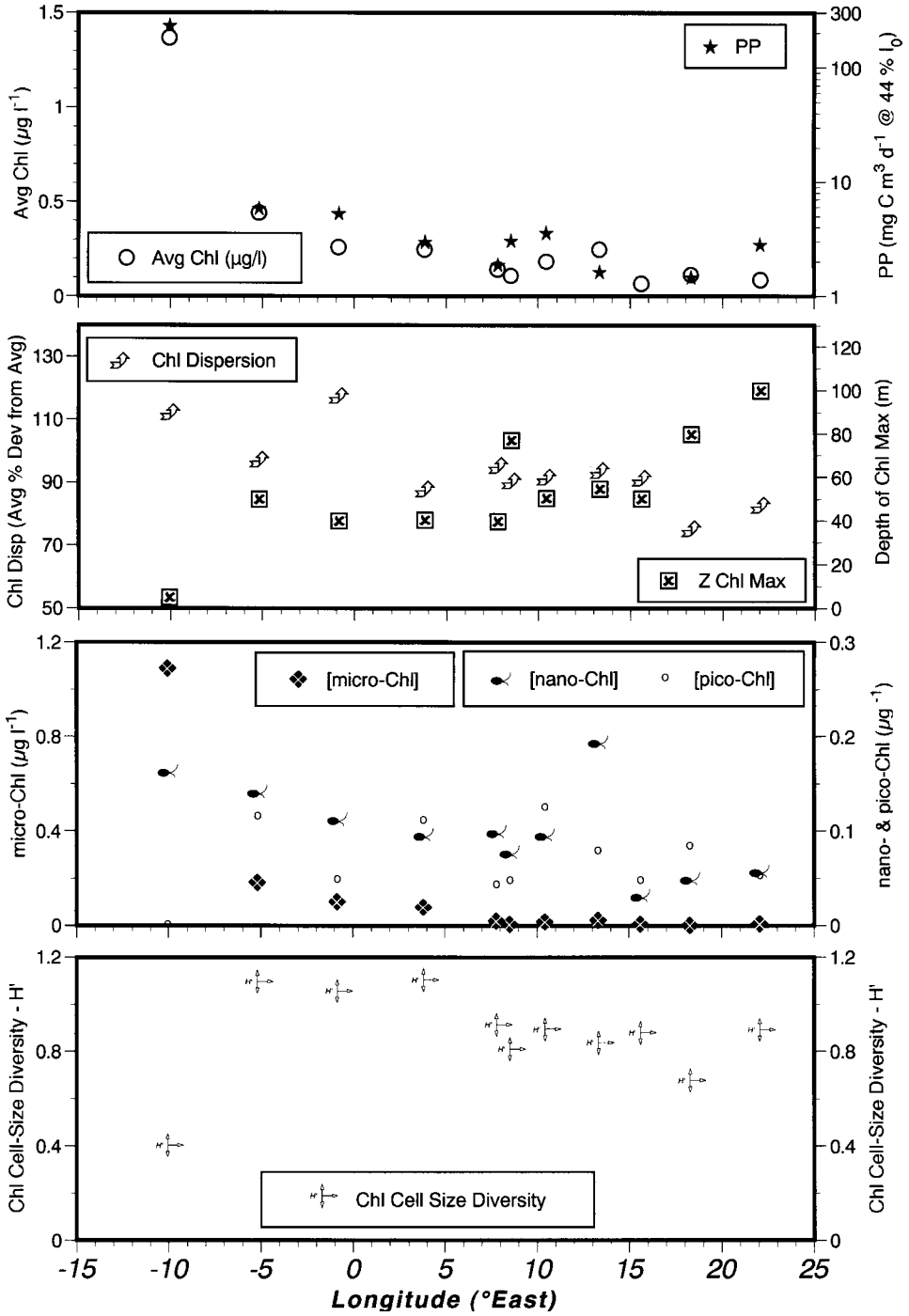

Fig. 2. Characteristics of the phytoplankton community sampled between the Atlantic coast of Morocco (plotted as −10° East) and Crete in the Eastern Mediterranean Sea: average chlorophyll *a* concentration over the top 100 m and surface layer (10 m) primary production, depth of the chlorophyll maximum layer and chlorophyll dispersion as average discrete depth difference from the water column average of chlorophyll concentration, calculated concentrations of chlorophyll in micro-, nano- and pico-sized taxa based on accessory pigment data, chlorophyll cell-size diversity estimated as ln-based H' Shannon index values calculated using micro-, nano- and pico-chlorophyll as 3 species.

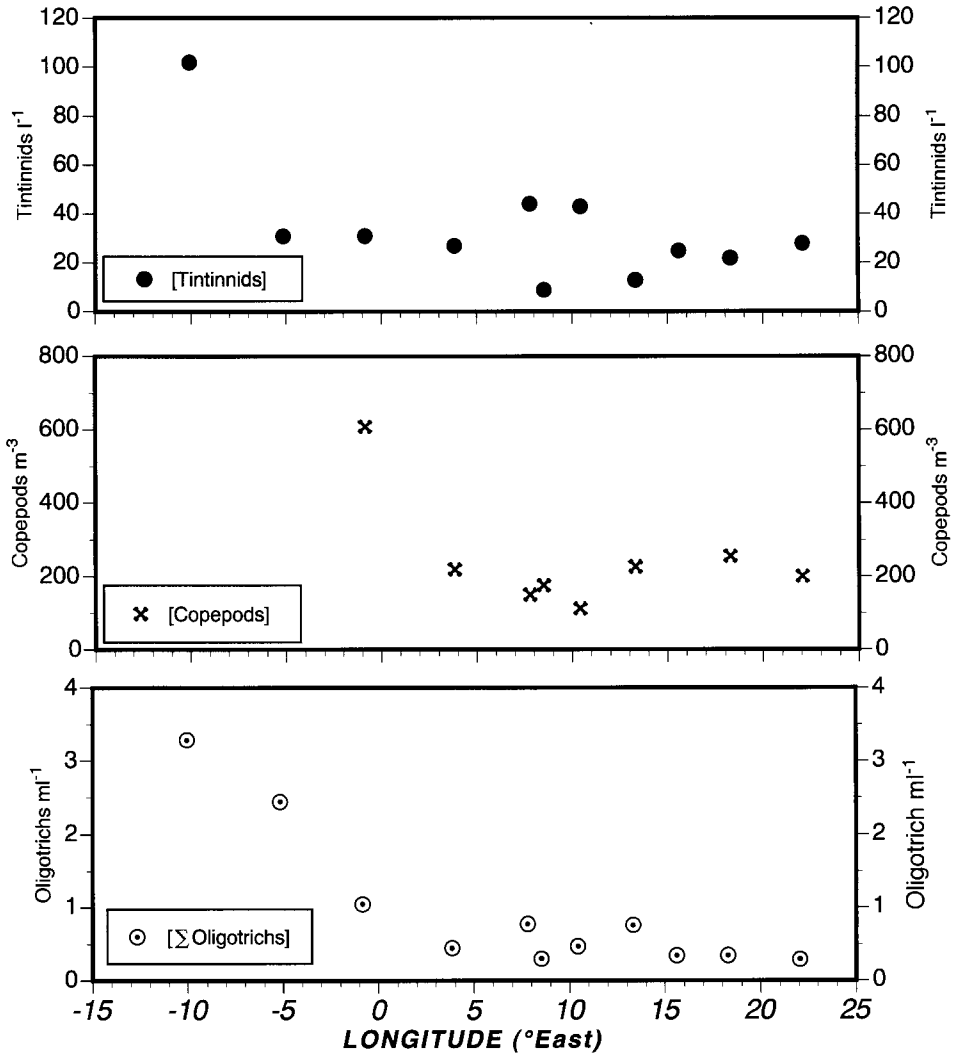

Fig. 3. Characteristics of the zooplankton community sampled between the Atlantic coast of Morocco (plotted as −10° East) and Crete in the Eastern Mediterranean Sea: average water column concentrations of tintinnid ciliates, oligotrich ciliates (0–100 m), and copepods (0–200 m). Tintinnid, oligotrich, and copepod concentrations declined from west-to-east as did chlorophyll *a*.

species. The dominant species (Fig. 4) were *Salpingella decurta* and *Metacylis mereschkowskii,* which together formed over 50% of the tintinnid community. Overall community averages for lorica dimensions were the highest of all the stations, due in part to the presence of the large species *Favella serrata*. Diversity was the lowest of all station estimates, with only 16 species found and an H' value estimate of 2.1 (Fig. 5). Corresponding with estimates of taxonomic diversity, the indices of morphological diversity, H' values for lorica diameters and length, were also low.

From the upwelling site into the Western Mediterranean, the dominant species remained *Salpingella* species. However, smaller species of the genus were common. The commonest species were *S. curta* representing 20% of tintinnid numbers, and *S. Faurie*, *S. minuta* and *S. decurtata,* each representing about 10% of the tintinnid population (Fig. 4). In addition to evenness, reflected by higher

Table 2
Spearman rank correlation relationships (Rho values) among average water column concentrations of zooplankton populations and phytoplankton parameters

	ΣChl	μChl	nChl	pChl	CMD	Disp	Prim prod
Tintinnids	0.518	0.618*	0.393	−0.055	−0.691*	591	0.539
Oligotrichs	0.891**	0.855**	0.834**	−0.082	−0.791**	0.873**	0.600
Copepods	0.405	0.286	0.125	0.024	0.095	−0.024	−0.163

Tintinnids and oligotrichs showed similar relationships with phytoplankton parameters. Average water column (approx. 0–100 m) integrated values of: total chlorophyll (ΣChl), chlorophyll attributable to micro-sized cells (μChl), nano-size cells (nChl), pico-size cells (pChl), oligotrichs and tintinnids. Copepod concentration estimates were based on material collected from 0 to 200 m. "CMD" denotes the depth of the maximum concentration of chlorophyll and "Disp" denotes chlorophyll dispersion, estimated for each station as the average deviation of discrete depth measures of chlorophyll from the overall water column average concentration of chlorophyll. Primary production (prim prod) incubations employed 44% incident surface illumination For all pairs, $n = 11$ except comparisons with copepods in which $n = 8$ and primary production with $n = 10$. Asterisks denote probability levels of 0.05, 0.01.

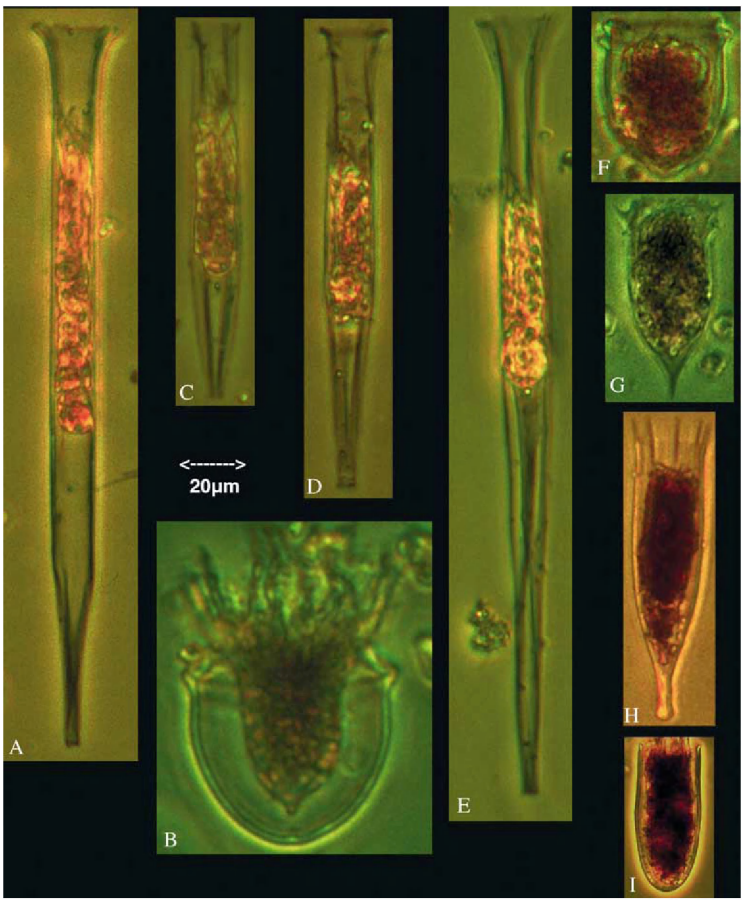

Fig. 4. Examples of dominant (50% of cell numbers) tintinnid species. The upwelling station community was composed mainly of *Salpingella decurtata* (A) and *Metacylis mereschkowskii* (B). Peak diversity was recorded for Station 2 among the 4 commonest species *S. curta* (D) represented 20% of cell numbers and *S. decurtata*, *S. minuta* (C), and *S. faurei* (E) each represented about 10% of the tintinnid community. The DYF community station was composed mainly of the species *S. decurtata* (19%) with *Acanthostemella conicoides* (G) and *A. lata* (F) forming 17% and 12% of cell numbers. In the far eastern station, MIO, the community was dominated by *Dadayiella ganymedes* (H), *Undella clevei* (I), and *S. faurie* (E).

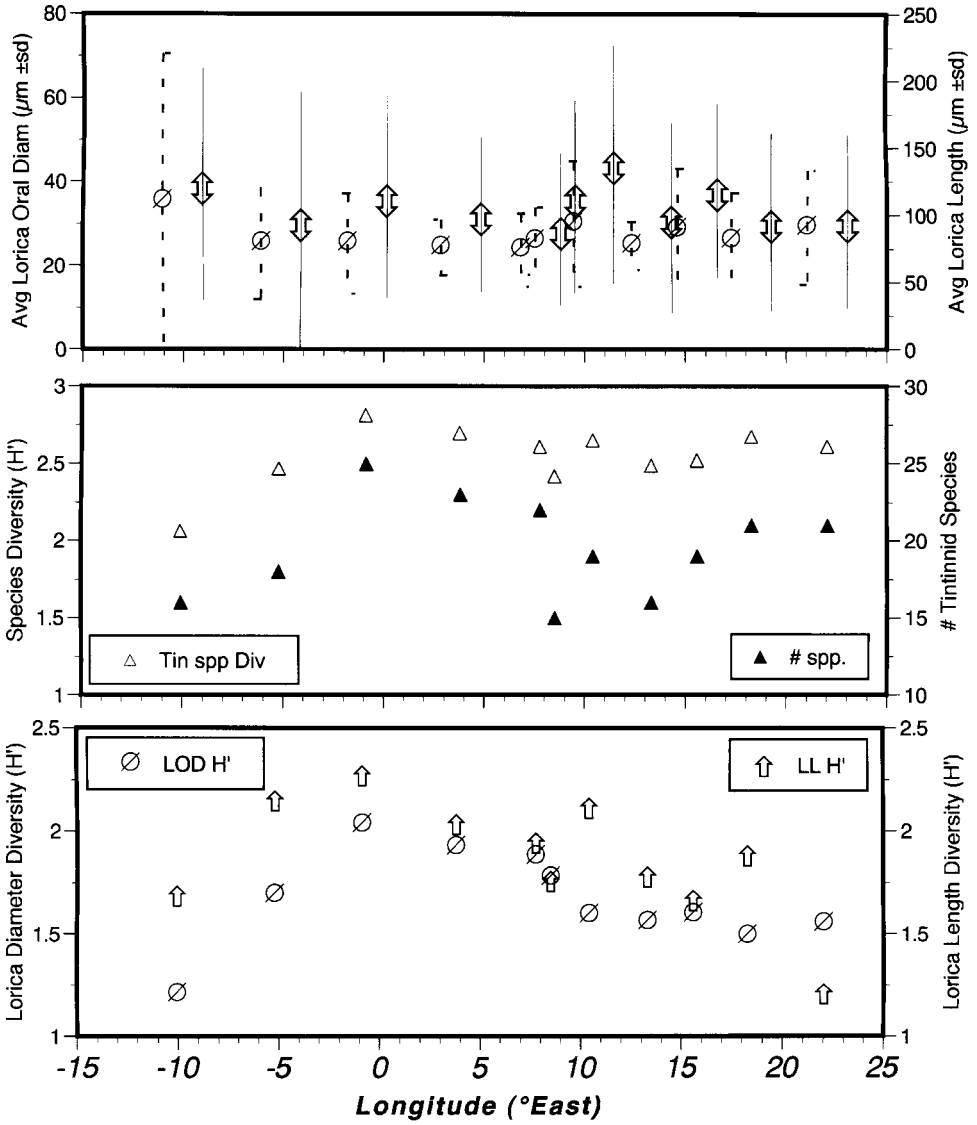

Fig. 5. Characteristics of the tintinnid community sampled between the Atlantic coast of Morocco (plotted as −10° East) and Crete in the Eastern Mediterranean Sea: tintinnid community averages of lorica oral diameter and lorica length, (±SD), taxonomic diversity as species richness, Shannon index values (ln-based) and morphological diversity as H' values.

H' values, species richness was markedly higher as well. Increases in the estimates of morphological diversity accompanied the increases in estimates of taxonomic diversity. Peak values of all the diversity estimates occurred in the Western Mediterranean.

From the western to the Eastern Mediterranean changes in the species pool were noted. However, *Salpingella* species remained common but the identity of the dominant species and genus differed in each eastern station. At stations 5, 6, and MIO the commonest species were, respectively, *Craterella tortulata*, *Acanthostomella conicoides* and *Dadayiella ganymedes* (Fig. 4). The tintinnid community of the Tyrheninean Sea (Station 9), dominated by *Salpingella decurtata* and *S. faurie*, resembled that of the western basin stations.

Overall, 73 species, representing a surprising variety of lorica architectures (Fig. 6) were encountered in examining about 1000 individuals found in material from a total of roughly 221 of water. The general pattern was that species richness and H' estimates of taxonomic and morphological diversity all declined from the peak values recorded for the Western Mediterranean. Although the different measures of taxonomic and morphological diversity showed similar spatial trends, among the different measures, only species richness and species H' were correlated with one another (Table 2) suggesting that species diversity and morphological diversity were independent parameters (Table 3).

3.4. Relationships with Tintinnid diversity

Tintinnid diversity as species richness, diversity of lorica diameters and diversity of lorica lengths was significantly correlated only with phytoplankton cell-size diversity (Table 4 and Fig. 7). Other phytoplankton parameters (primary production, chlorophyll concentration, depth of the maximum layer, dispersion) produced non-significant, and inconsistent (both positive and negative) relationships with measures of the taxonomic and morphological diversity of tintinnids. Likewise, oligotrich abundance, both absolute and relative to tintinnid concentrations was neither significantly nor consistently related to tintinnid diversity estimates. Interestingly, although copepod concentrations were not related significantly to any tintinnid diversity metrics, all the correlations were positive. Complete reanalysis of the data excluding the upwelling station, as a possible outlier, gave largely identical results.

4. Discussion

Both phytoplankton and metazoan zooplankton diversity appear inversely related to primary production in the world ocean (e.g., Huston, 1994). The pattern has been explained in terms of the relationship between water column structure and primary production. High diversity is associated with stable water column structure of marked chemical and physical gradients, providing a structured environment but with low input of nutrients for phytoplankton production (Angel, 1993). However, within a structured water column, the identity of the main mechanism maintaining metazoan zooplankton diversity, be it resource partitioning, predation or "contemporaneous disequilibrium", remains obscure (McGowan and Walker, 1979; Longhurst, 1985).

The mechanisms maintaining microzooplankton diversity are no less obscure. The thickness of the surface mixed layer has been related to species richness of foraminifera in the world ocean (Rutherford et al., 1999). North–south trends in tintinnid diversity found in the southern Atlantic have been attributed to water column stratification (Thompson et al., 1999) and the depth of the chlorophyll maximum correlated with tintinnid diversity in the Mediterranean Sea (Dolan, 2000). These are all indirect relationships, that is, without a direct link to the maintenance of diversity. Here we made an attempt to identify a dominant mechanism acting within the water column.

The magnitude of taxonomic and morphological diversity we encountered in late summer was very similar to that found before based on early summer sampling (Dolan, 2000). The species found were largely the same and average station values of H' and numbers of species (averages of

Fig. 6. Examples of tintinnid lorica architecture among species found in the Mediterranean Sea. There was a common lorica structure to dominant species. Species with a honeycomb lorica structure, whether large such as *Xystonella treforti* (A), *Xystonellopsis paradoxa* (B) and *Climacocylis sipho* (E), or small like *Poroecous curta* (F) or *Climacocylis scalaroides* (D) were overall very rare. Likewise, species characterized by loricas with windows such as *Dictyocysta elegans* (H) or with a coarse structure such as *Codonellopsis orthoceras* (C) or *Codonella nationalis* (J) while common did not dominate the tintinnid community. The overwhelming majority of the tintinnid community was composed of species with nearly transparent hyaline lorica such as seen in the dominant species shown in Fig. 4 and in *Craterella tortulata* (I), *Paraundella aculeata* (K), *Dadayiella pachytoecus* (M) *Amphorellopsis tetragona* or an unidentified *Salpingella* species with a prismatic lorica (N).

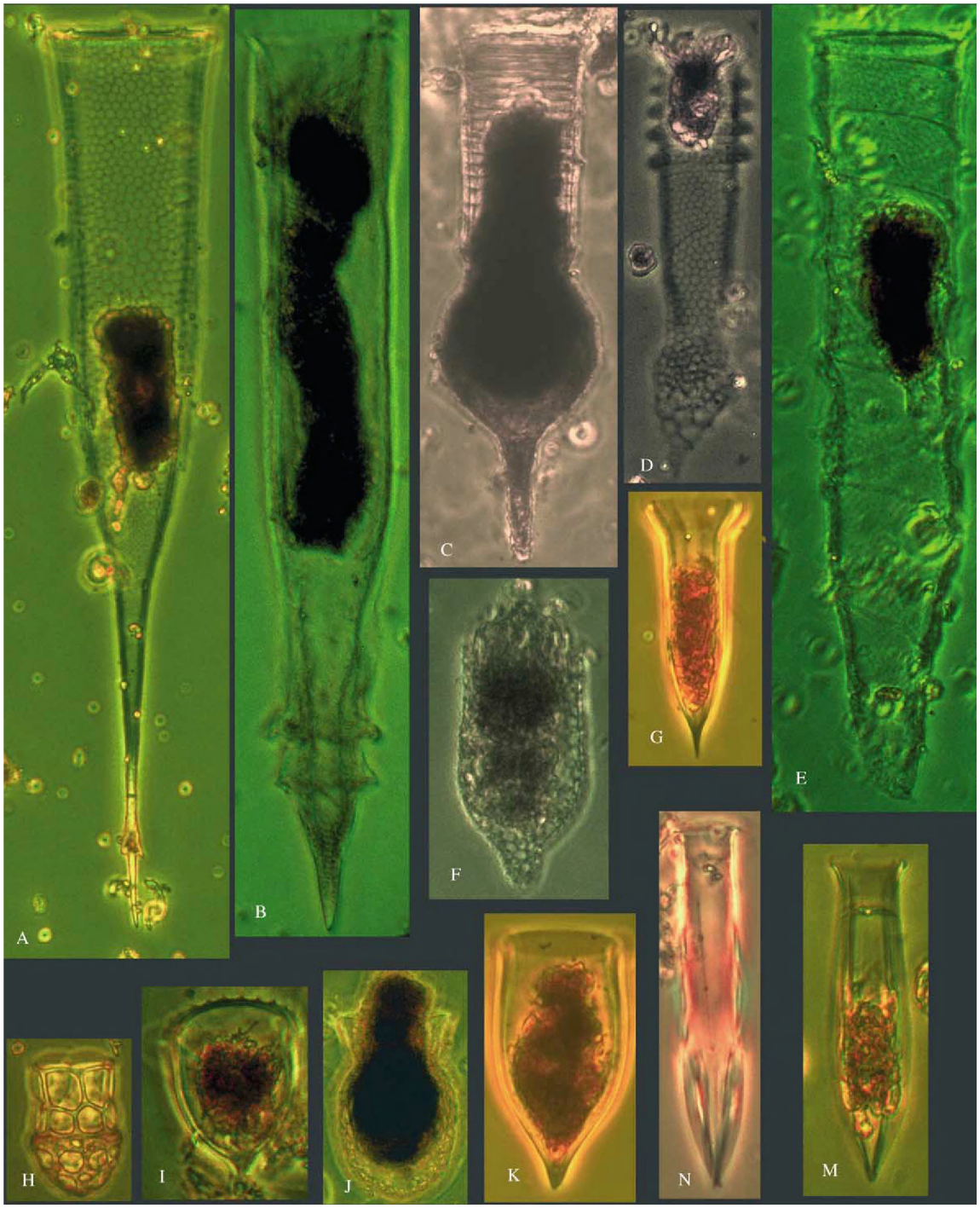
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Table 3
Spearman rank correlation relationships (Rho values) among metrics of taxonomic and morphological diversity of tintinnids

	Taxonomic		Morphometric	
	H'	No. of species	LOD H'	LL H'
H'	—	0.875*	0.445	0.464
No. of species	—	—	0.484	0.416
LOD H'	—	—	—	0.591
LL H'	—	—	—	—

Although measures of taxonomic diversity vs. morphological diversity largely co-vary positively, they are not tightly related. For each station, estimates of taxonomic and morphological diversity were based on a pooled sample consisting of all individuals encountered in all samples from the station. Taxonomic metrics were the Shannon index, ln-based (H') and numbers of species. Morphological metrics were Shannon indexes of the diversity of lorica oral diameters (LOD-H') and lorica lengths (LL-H') was calculated by substituting size-classes for species (see methods for details). For all pairs, $n = 11$.
*Denote the single significant relationship ($p = 0.01$).

Table 4
Spearman rank correlation relationships (Rho values) between parameters of planktonic populations and metrics of the taxonomic and morphological diversity of tintinnids

	Taxonomic		Morphometric	
	No. of species	H'	LOD H'	LL H'
(Chl *a*)	0.002	−0.118	0.100	0.582
Chl Max Z	−0.216	0.027	−0.373	−0.382
Chl Dispers	−0.061	−0.245	0.255	0.436
Chl Size H'	0.611*	0.455	0.755*	0.664*
(Oligotrichs)	−0.002	−0.191	0.082	0.545
(Oligo)/(Tin)	−0.298	−0.355	0.309	0.427
(Copepod)	0.399	0.452	0.024	0.119

Chlorophyll size-diversity appears to be the most closely related parameter to measures of both taxonomic and morphological diversity of tintinnids. For each station, estimates of taxonomic and morphological diversity were based on a pooled sample consisting of all individuals encountered in all samples from the station. Taxonomic metrics were the Shannon index, ln-based (H') and numbers of species. Morphological metrics were Shannon indexes of the diversity of lorica oral diameters (LOD-H') and lorica lengths (LL-H') was calculated by substituting size-classes for species (see methods for details). For the planktonic populations, average water column (approx. 0–100 m) integrated values were used: total chlorophyll (Chl *a*), total oligotrichs (Oligotrichs). Copepod concentration estimates were based on material collected from 0–200 m. Chlorophyll dispersion (Chl Dispers) estimated as the average discrete depth deviation (%) from the water column average, and a phytoplankton size diversity parameter (Size H') reflecting the relative contributions of micro-, nano- and pico-size cells. For all pairs, $n = 11$ except comparisons with copepods in which $n = 8$.
*Denote the probability level of 0.05.

about 2.5 and 20 tintinnid species, respectively) found before resemble closely the data presented here (Fig. 5). Morphological diversity, in the form of standard deviations of lorica lengths accompanied increases in H' values with the depth of the chlorophyll maximum. Predation pressure was hypothesized as possibly explaining the trends, but data permitting evaluation of possible predation pressure or resource diversity were not available (Dolan, 2000).

Exploiting a more complete data set, we searched for simple correlations between parameters corresponding with a direct diversity-maintaining or promoting mechanism. We recognized that only strong relationships would be detectable as data were from a small number of stations but covering large gradients. Our data analysis leads to the conclusion that phytoplankton diversity, in terms of cell sizes, is more closely related to tintinnid diversity, both morphological

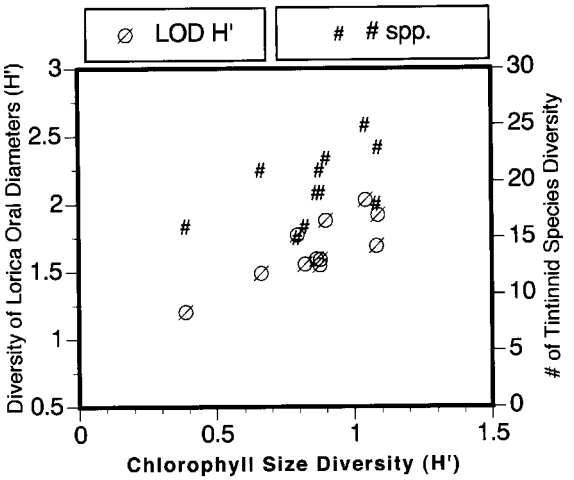

Fig. 7. Scatterplot of phytoplankton size diversity represented by Shannon index values for communities composed of 3 "species", micro-, nano- and pico-chlorophyll against tintinnid species diversity and diversity of tintinnid lorica diameters. Both relationships are significant (Table 4) and species richness is not directly related to lorica oral diameter (Table 3).

and taxonomic, than the abundance of competitors or predators or the distribution of chlorophyll in the water column. Clearly, we do not exclude the influence of resource distribution, competition or predation but merely found that resource diversity appears more important or is more easily detected.

The characterization of the phytoplankton community based on accessory pigments, while inferior to direct microscopic observation, has certain advantages. Relative to microscopic examinations, pigment analysis is rapid and inexpensive. It has been used to distinguish communities of different oceanic regimes (Claustre, 1994; Vidussi et al., 2000), quantify particular taxa, such as those associated with DMSP (Belviso et al., 2001) as well as define the size structure of phytoplankton communities (Vidussi et al., 2001).

Although diversity in the phytoplankton community may appear as a very obvious mechanism generating diversity among grazers (e.g., Lasserre, 1994), to our knowledge, it has never been shown. Although a simple relation between the diversity of food and consumers is appealing, selective feeding is required for consumer diversity to reflect food diversity. Morphological diversity trends paralleled phytoplankton size-diversity trends (Figs. 2 and 5). This finding implies that tintinnid morphology should be related to prey size. For tintinnids, prey size has been commonly related to lorica dimensions, in particular oral diameters, but the relationship has not been well quantified.

For individual species, a general rule of maximum prey size of about half the oral diameter was formulated by Heinbokel (1978). Observations on the community level consist of data showing seasonal changes in overall community averages of oral diameters shifting with phytoplankton composition (Middlebrook et al., 1987; Verity, 1987). Nonetheless, individual species generally appear to ingest a wide spectrum of prey sizes; for example, a large variety of Mediterranean tintinnids examined in a field study contained the autotrophic picoplankter *Synechococcus* (Bernard and Rassoulzadegan, 1993). Given our results suggesting a strong relationship between morphological diversity of tintinnids and phytoplankton size diversity, we wished to determine if a more precise relationship could be drawn between tintinnid lorica diameters and prey ingested.

We examined results of tintinnid feeding studies in which a wide spectrum of prey were offered in the form of individual prey species or results of studies examining feeding on a natural spectrum of possible food items. Data we recorded were prey size (equivalent spherical diameter) for which filtration rate was maximal and the reported lorica oral diameter. Absolute values of clearance rates were not used as rates vary directly with prey concentration which differed considerably among studies. Comparing different species, we found a robust relationship showing the size of the prey most efficiently filtered to be about 25% of oral diameter (Fig. 8). Thus, it appears reasonable to characterize the lorica diameter of a tintinnid species as a correlate of its preferred prey size. A further complexity can be added in the form of selective feeding among prey of the same or similar size. Studies have argued both for and against the phenomena in a single species, *Favella ehrenbergii* (Stoecker et al., 1981; Hansen, 1995).

Selective feeding among algae of similar size may explain the co-occurrence of species with

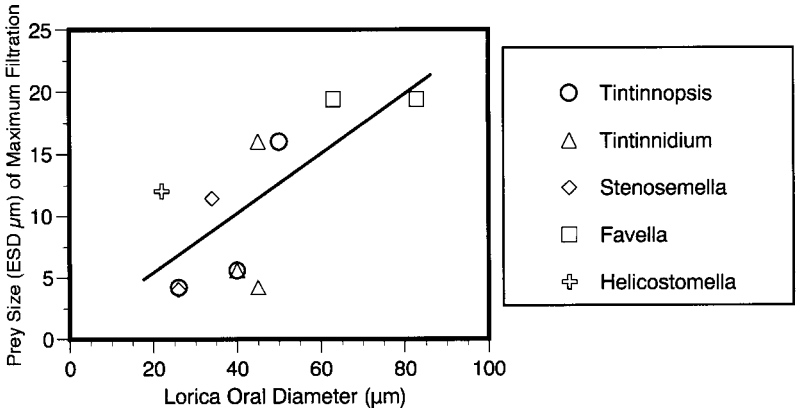

Fig. 8. The relationship between tintinnid lorica oral diameter and prey size yielding maximum filtration rate pooling reports on species in 5 tintinnid genera. Data from Capriulo (1982), Kamiyama and Arima (2001), Kivi and Setälä (1995), Rassoulzadegan (1978), Rassoulzadegan and Etienne (1981).

similar lorica diameters, if resource partitioning is the unique mechanism maintaining diversity. For example, in the most diverse tintinnid community encountered, Station 2, the 4 species forming 50% of the community have very similar sized lorica diameters ranging from about 15 to 20 μm (Fig. 4). The four species would, according to the lorica diameter relationship, prey most efficiently on food within the narrow range of 3.8–5 μm diameter.

Nonetheless, we believe the dominant mechanism explaining tintinnid taxonomic diversity in our data set is resource partitioning. Our data show a relationship between phytoplankton size distribution and tintinnid lorica size distribution also reflected in taxonomic diversity. We can reject the possibility that food diversity could be the result rather than a cause of a diverse tintinnid community. For tintinnids, with typical clearance rates of about $10\,\mu l\,h^{-1}$ tintinnid^{-1} (see Kivi and Setälä, 1995) very high population abundances ($>1000\,l^{-1}$) would be required for their feeding to significantly influence phytoplankton community composition. However, we cannot extend this argument to the entire community of grazers.

For example, from our estimates of oligotrich ciliate and copepod abundances and rough estimates of probable filtration rates, the combined activity of these grazers could directly influence phytoplankton community composition. Estimates of oligotrich filtration rates average about $2\,\mu l\,h^{-1}$ (Kivi and Setälä, 1995). Estimates of filtration rates of open water copepods vary considerably with prey size, type and abundance (Caparroy et al., 1998). However, from Mauchline's review (1998), a mean value of $5–10\,ml\,h^{-1}$ copepod^{-1} appears reasonable for mid-sized Mediterranean copepods (i.e., *Centropages*). With average oligotrich concentrations of about $1000\,l^{-1}$, and copepod concentrations of $0.3\,l^{-1}$ combined, they likely clear about 15% of the surface layer per day. Considering that the algal community appears, on average, to reproduce only every 3–4 days throughout most of the Mediterranean in the summer (Dolan et al., 1999), and adding in the grazing activity of heterotrophic flagellates and metazoan grazers other than copepods, it is likely that nearly all phytoplankton production is consumed by grazers, except at the upwelling station.

Thus, the community composition of the phytoplankton, which we identify as a major mechanism influencing tintinnid diversity, is itself likely influenced by the aggregate community of grazers, an influence super-imposed on resource competition within the phytoplankton. It appears that while proximal influences on diversity for an individual group may be unidentifiable, the ultimate explanation likely lies in the chaotic nature (Huisman and Weissing, 1999) of an ecosystem in which a multitude of rapidly

reproducing taxa, in each trophic level, compete for a number of resources within a physically instable system. A major question that remains is one of quantification—why a peak of 25 (and not more or less) species of Foraminifera in the Atlantic (Rutherford et al., 1999) or tintinnids in the Mediterranean (Fig. 5)?

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