

Probing diversity in the plankton: using patterns in Tintinnids (planktonic marine ciliates) to identify mechanisms

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Abstract

In diversity research, the use of survey data appears to have declined in favour of experimental or modeling approaches because direct relationships are difficult to demonstrate. Here we show that use of field data can yield information concerning the mechanisms governing diversity. First, we establish that tintinnids display a global latitudinal pattern of diversity similar to other pelagic organisms; species numbers appear to peak between 20° and 30° north or south. This common large scale spatial trend has been attributed to the gradient in water column structure across the global ocean. We then examine the generality of a relationship between planktonic diversity and water column structure by considering data from the Mediterranean Sea, in which water column structure changes seasonally. Among populations of foraminifera, tintinnids, and the dinoflagellates of the genus *Ceratium*, we compare data from trans-Mediterranean sampling conducted at different times and monthly changes in species richness at single sites. We find that water column structure alone appears to be a poor predictor of temporal changes in diversity. Lastly, we present an example of temporal changes in tintinnid diversity based on data from an oceanographic sampling station in the N. W. Mediterranean where resources, as chlorophyll, appear distinctly unrelated to changes in water column structure. We show that short-term temporal changes in diversity (week to week shifts) can be related to changes in chlorophyll concentration. We conclude that in tintinnids diversity can be directly linked to characteristics of food resources.

Introduction

Three major approaches are commonly employed in diversity research: experimentation, modeling, and survey, each of which possesses particular weaknesses. Here, after briefly reviewing the drawbacks of recent experimental and modeling efforts, we will illustrate the major problem involved in using survey data – that of distinguishing direct effects on diversity from co-varying or indirect factors. To show the utility of survey data we will begin by establishing the validity of using tintinnid ciliates as an example of a typical planktonic group. Then, we will use survey data to

explore factors co-varying with tintinnid diversity to determine if a plausible controlling mechanism influencing diversity can be identified.

The experimental approach has been employed most commonly to investigate the relationship between a single ecosystem function (production, nutrient regeneration, etc.) and diversity. Typically experimentation with planktonic communities has involved very simple petri dish or test tube communities of a few microbial species (e.g., Naeem & Li, 1998; Naeem et al., 2000) or even strains of the same species (e.g. Buckling et al., 2000; Kassen et al., 2000). Thus, conclusions have been drawn from short-term results with very rudimentary

communities. Extrapolation to the natural world has proven problematic especially as the little work which has been conducted by altering large, natural systems (such as whole lakes – e.g., Dodson et al., 2000), suggests that idiosyncratic, in other words unpredictable, results may be common. It is perhaps worth noting that with regard to marine benthic communities, experimentation with very simple communities has also shown ‘idiosyncratic’ effects of biodiversity on ecosystem function (Emmerson et al., 2001) or the existence of ‘synergistic interactions’ (Worm et al., 2002).

Modeling is an approach most often employed as a method to identify the factors governing diversity. The theoretical framework of modeling plankton communities can be traced back to Hutchinson’s “Paradox of the Plankton” (1961) in which three major mechanisms were proposed: (1) symbiosis or commensalism, (2) predation, and (3) non-equilibrium conditions. In recent years, theoretical studies have suggested the primacy of each of these mechanisms. Thus, species oscillations can explain diversity as non-equilibrium conditions are likely the rule (Huisman & Weissing, 1999) or specialization among predators or consumers is important (Hulot et al., 2000) as well as facilitation or commensalism (Loreau & Hector, 2001).

The survey approach-determining, and then attempting to explain, natural patterns of species abundance is the most time-honored as it dates back at least to Darwin (1859). The obvious drawback is that mechanisms governing biodiversity can only be inferred by co-variation and co-variation need not indicate causation. An excellent example of this has been reported with regard to planktonic foraminifera.

From the point of view of past and present species distributions, foraminifera are no doubt the best-studied marine planktonic group (Caron & Swanberg, 1990). Paleotemperatures can be estimated from oxygen isotopes in fossil tests (e.g., Wilf et al., 2003) and at least in fossil assemblages, the co-variation of diversity and annual average sea surface temperature permit the estimation of past climatic change (e.g., Williams & Johnson, 1975). Diversity appears fairly predictable from the type of environment (Ottens & Nederbragt, 1992). Among living foraminifera communities in the Atlantic, species

diversity was recently shown to be tightly correlated with annual sea-surface temperature, in a curvi-linear manner yielding maxima at 20–30° rather than a peak at the equator (Rutherford et al., 1999). The correlation was explained as due to the relation between annual sea surface temperature and both the depth and seasonality of the thermocline in the water column. Annual sea surface temperature appeared to be a proxy measure of the depth of the surface layer and therefore habitat volume for planktonic foraminifera somehow reflecting quantities of niches available for different species (Rutherford et al., 1999). However, the parameters which define or differentiate the niches are unknown.

Interestingly, molecular work has shown the existence of ‘cryptic species’ of foraminifera (de Vargas et al., 1999), that is morphologically very similar but genetically distinct populations. The genetically distinct populations appear to inhabit regions differing in productivity (de Vargas et al., 1999) or water column stability (de Vargas et al., 2002). Careful examination of the different ‘strains’ has also revealed apparently subtle morphological differences in, for example, shell porosity. However, once again what ecologically differentiates the populations is unknown.

In copepods, among the mechanisms thought to maintain diversity, specialization in feeding may be much less important than the effects of predators (McGowan & Walker, 1980). In an environment characterized by a structured water column, i.e., with a well-defined thermocline, predation pressure may be stronger yielding greater diversity than environments with mixed water columns (McGowan & Walker, 1980, 1985; Longhurst, 1985). However, with regard to planktonic foraminifera, we are in a poor position to begin to identify what mechanism (food, predation, etc.) may be important in influencing diversity. We know relatively little about foraminiferan nutrition and growth (Caron et al., 1995) or trophic specialization (Swanberg & Caron, 1991) or their predators (Caron & Swanberg, 1990). In contrast to foraminifera, a fair amount is known about tintinnid ciliates.

Tintinnids are ciliates of the microzooplankton; they are characterized by the possession of a species-specific shell or lorica, shaped like a bowl or vase or tube, within which the ciliate cell can

withdraw (Fig. 1). While generally a small part of the ciliate community, they are much more abundant than foraminifera or radiolarians (Thompson et al., 1999) and there is a wealth of data on their ecology (see Dolan, 2000; Dolan et al., 2002).

As most planktonic ciliates, tintinnids are found largely in the surface layer of the sea where they feed on algae ranging in size from 2 to 20 microns. The generation times of tintinnids are similar to other planktonic ciliates and their algal prey (potentially a few hours). The dimensions of their lorica, specifically the diameter of the oral (or mouth) end, are related to their food. The oral diameter of the lorica is about four times the diameter of the prey ingested most efficiently (Dolan et al., 2002). Tintinnids are fed upon by a large variety of taxa. The stomach contents of

larval fish contain tintinnids almost as frequently as copepods (Turner, 1984). Different metazoan zooplankters are also known to feed on tintinnids ranging from copepods to gelatinous zooplankton (Stoecker & Capuzzo, 1990). However, given their numerical dominance among the zooplankton, copepods are generally thought to be the major predators of tintinnids. Interestingly, there appears to be no clear relationship between the size of a tintinnid's lorica and its susceptibility to predation by copepods (Stoecker & Capuzzo, 1990; Dolan & Gallegos, 2001), although most experimental work has been conducted with coastal species of copepods.

Like foraminifera and radiolarians, species identifications can be made using characteristics of gross morphology, with some caveats (for recent discussions see Cariou et al., 1999; Dolan, 2000; Dolan &

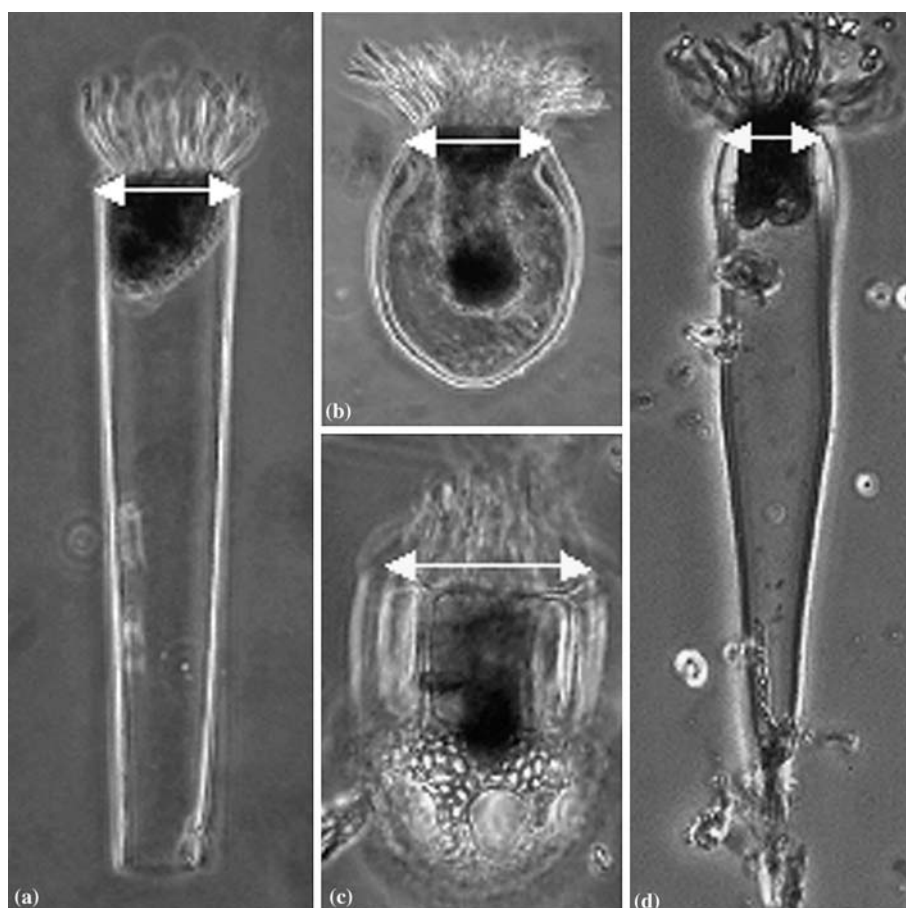


Figure 1. Photomicrographs of Tintinnids. Lugol's -preserved specimens collected from the Bay of Villefranche, N. W. Mediterranean Sea. Arrows indicate the oral opening, lorica oral diameter (LOD) of the lorica or shell into which the ciliate cell may withdraw. (a) *Eutintinnus fraknoi*, LOD = 40 μm . (b) *Proplectella fastigata*, LOD = 40 μm . (c) *Dictyocysta lepida*, LOD = 45 μm . (d) *Xystonellopsis brandti* LOD = 25 μm .

Gallegos, 2001; Modigh & Castaldo, 2002). Tintinnids have the further advantage of representing a monophyletic group, even among competing ciliate classification schemes (e.g., Petz & Foissner, 1992; Lynn & Small, 1997). Recent molecular work (Snoeyenbos-West et al., 2002; Agatha et al., 2005) has largely confirmed the classical (based on morphology) taxonomic classification of tintinnids. Tintinnids are united ecologically as microzooplankters, morphologically as loricate ciliates, and phylogenetically as members of the order Tintinnida.

Before examining patterns of diversity in tintinnids, the first question one might ask is whether tintinnids are a typical or atypical group of plankters. That is, do tintinnids show a global pattern of diversity similar to other planktonic groups such as foraminifera and copepods and phytoplankton taxa or a 'microbial' pattern of "all species are everywhere" *sensu* Fenchel & Findlay (1997). Thus, this will be the first issue considered. Secondly, the relationship between water column structure and diversity among planktonic organisms will be considered. Temporal trends of diversity relative to water column structure in a system characterized by seasonal changes in water column stratification—the Mediterranean Sea, will be explored with regard to foraminifera, tintinnids and dinoflagellates of the genus *Ceratium*. Thirdly, changes in diversity will be examined at an oceanographic sampling station in the N. W. Mediterranean where resources, as chlorophyll, appear distinctly unrelated to changes in water column structure.

Methods

Global distribution of tintinnid species abundance

Literature reports furnishing species abundance for single points in time and space were used. When species abundance were given for more than one date, the date with maximum number of species was taken. Use of a single date from reports giving more than one measure was used to make such reports comparable to those of oceanographic campaigns, which formed the majority of the data points, giving a single estimate per location. No attempt was made to sort data by the sampling technique employed (i.e., plankton net tows or whole water collection). The oceanographic

campaign reports and research reports (Table 1) yielded a large number of data points ($n = 451$) with a near complete latitudinal coverage of 81°N to 75°S. The data base assembled represents a greatly expanded version of that previously presented (Dolan & Gallegos, 2001) which consisted of 168 data points.

Water column stratification and Mediterranean plankton

The link between water column structure and diversity was considered by examining reports of foraminifera community composition across the Mediterranean in the autumn when the Mediterranean is stratified and during winter mixis. Seasonal trends were considered by examining reports of species abundance at a single location over an annual cycle for tintinnids and dinoflagellates of the genus *Ceratium*. The relationship of tintinnid diversity with the size of the mixed layer, as indicated by the depth of the chlorophyll maximum layer, at the beginning and end of the stratified period was examined.

Data on foraminifera (species richness and \ln -based H' values) were based on a report of foraminifera community composition derived from sampling at 13 stations across the Mediterranean in autumn 1986 and 14 stations in winter 1988 (Pujol & Vergnaud Grazzini, 1995: Table 2). Data on species richness by month for tintinnids and a group of phytoplankters-dinoflagellates of the genus *Ceratium* was obtained from Rampi (1948: p. 53) based on material collected from 1938 to 1939 in the N. W. Mediterranean Sea near San Remo, Italy. The relationship between the depth of the chlorophyll maximum layer and tintinnid species richness or diversity (as H') at the beginning of the stratified period was examined using data from Dolan (2000: Fig. 1) based on samples obtained in June 1993 (Dolan & Marrasé, 1995) and May–June 1996 (Dolan et al., 1999). The relationship at the end of the stratified period was explored using data from Dolan et al., (2002: Figs. 2 and 3) based on sampling conducted in September 1999.

Temporal trends of tintinnid diversity

We examined tintinnid populations in the Bay of Villefranche in samples from a standard station

Table 1. Sources of data used to construct plots of latitude vs. species abundances

Study site	Latitude range	<i>N</i>	Reference
Barents Sea	72–70° N	6	Jensen & Hansen (2000)
Barents Sea	73–81° N	12	Boltovskoy et al. (1991)
Chesterfield Inlet Estuary	64–63° N	12	Rogers et al. (1981)
Skagerak (N Sea)	58° N	1	Hedin (1974)
Bedford Basin, NS	44° N	1	Paranjape (1987)
Bay of Fundy	45–42° N	3	Middlebrook et al. (1987)
Damariscotta estuary	44° N	1	Sanders (1987)
Akkeshi Bay, JP	43° N	1	Taguchi (1976)
Coastal Mediterranean	43° N	1	Cariou et al. (1999)
Narragansett Bay	42° N	1	Hargraves (1981)
Long Island Sound	41° N	1	Gold & Morales (1975)
Long Island Sound	41° N	1	Capriolo & Carpenter (1983)
Open Mediterranean	41–34° N	23	Dolan (2000)
Atlantic-Mediterranean	43–31° N	11	Dolan (2002)
Lagoa de Obidos, PT	40° N	1	Silva (1953)
Chesapeake Bay	39–37° N	9	Dolan & Gallegos (2001)
Atlantic	29–60° N	62	Garder (1946)
South Pacific Coastal	12° N	1	Gold & Morales (1977)
Sub & Tropical Pacific	34° N–25° S	62	Kofoed & Campbell (1939)
Atlantic & Pacific	64° N–39° S	160	Campbell (1942)
New Zealand Coastal	42–50° S	4	James & Hall (1995)
Bahia Blanca Estuary	38° S	2	Barria de Cao (1992)
SW Atlantic Open	34–60° S	18	Thompson et al. (1999)
SW Atlantic Shelf	40–56° S	16	Thompson et al. (2001)
S Atlantic	59–60° S	23	Wasik & Mikolajczk (1990)
Ross Sea	75° S	1	Monti & Fonda Umani (1995)

N value indicates the number of data points obtained. Note that out of a total of 451 points, the majority are from reports of oceanographic expeditions in which open water sites dominated (i.e., Kofoed & Campbell, 1939; Campbell, 1942; Garder, 1946).

‘Point B’ (43°41’10” N, 7°19’00” E). Sampling was conducted, in principle, weekly. Discrete depth samples from 0, 10, 20, 30, 40, and 50 m were obtained using 5 l Niskin bottles. Temperature and salinity were measured using a Seabird CTD. Chlorophyll *a* samples were analyzed fluorometrically following acetone extraction. For tintinnids, a composite integrated water column sample of 4 l was concentrated using a 20 µm Nitex screen to 20 ml. This method yields tintinnid numbers as high as settling whole water samples (Pierce & Turner, 1994). The entire concentrate, in 3–10 ml aliquots, was settled in sedimentation chambers and examined with an inverted microscope at 200×. Based on previous studies, examining material from 4 l of water likely yielded species abundances of about 50% of those found through

examining large volumes (80 l) of water (Cariou et al., 1999). Tintinnids were identified using lorica morphology and the species descriptions found in Campbell (1942), Jörgensen (1924) and Kofoed and Campbell (1929, 1939). Here data from the 45 samples taken in 2002 (seven samples missing from equipment failure or bad weather) are presented.

Results

Global distribution of tintinnid species abundance

Plotting species richness, averaged over increments of 5° latitude or individual points estimates (Fig. 2), gave the commonly found relationship between latitude and species abundance. In both

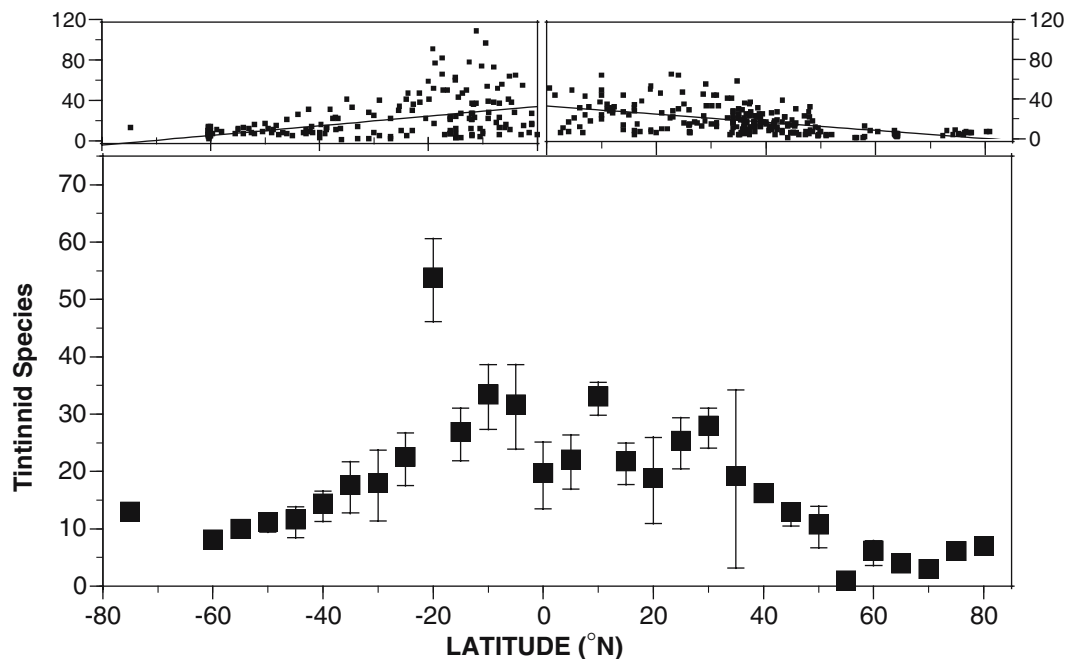


Figure 2. Latitudinal distribution of tintinnid species abundance based on reports given in Table 1. Top panels show individual data points. Bottom panel shows species abundances averaged within bands of 5° of latitude, error bars indicate SE of the averages. Linear regression equation for the southern latitude estimates (individual data points) is $r = 0.45$, $x = 0.48 \times \text{latitude} + 0.37$. Linear regression equation for the northern latitude estimates (individual data points) is $r = 0.53$, $x = 0.41 \times \text{latitude} + 0.33$.

the southern and northern hemispheres, species richness increases from the poles to lower latitudes with a peak around 20–30° followed by a slight decline toward the equator. Quite similar equations describe the relationships between latitude and species richness for the northern and southern hemispheres (Fig. 2).

Water column stratification and Mediterranean plankton

Water column dynamics are well characterized for the Mediterranean Sea (e.g., Bethoux, 1989). The seasonal stratification of the water column begins in the spring and ends with mixis in autumn; the cool Mediterranean deep water is formed at the surface in winter. Superimposed on the seasonal changes in water column structure throughout the Mediterranean is a general west to east gradient of declining nutrient and chlorophyll concentrations as well as primary production. During the stratified period, there is also a marked gradient of increasing mixed layer depth from west to the east (e.g.,

Dolan et al., 1999). Thus, oligotrophy increases and when the surface mixed layer is present, from late spring to early autumn, the surface layer is larger and less productive going from the west to the east.

Comparing mixed and stratified conditions, for the foraminifera species richness appears higher in the stratified period comparing estimates across the Mediterranean for February and September (Fig. 3). However, the differences are neither large nor consistent and diversity appears about the same in the autumn compared to the winter. Thus, on a seasonal time scale, changes in water column structure do not appear to be directly related to changes in the diversity of planktonic foraminifera.

Now consider temporal changes at a single site. Based on monthly sampling at a coastal station, species richness of two trophically distinct populations, tintinnids and *Ceratium* of the phytoplankton, show similarities (Fig. 4). For both groups, species richness was highest during the unstratified winter period and lowest during the summer corresponding with the stratified period.

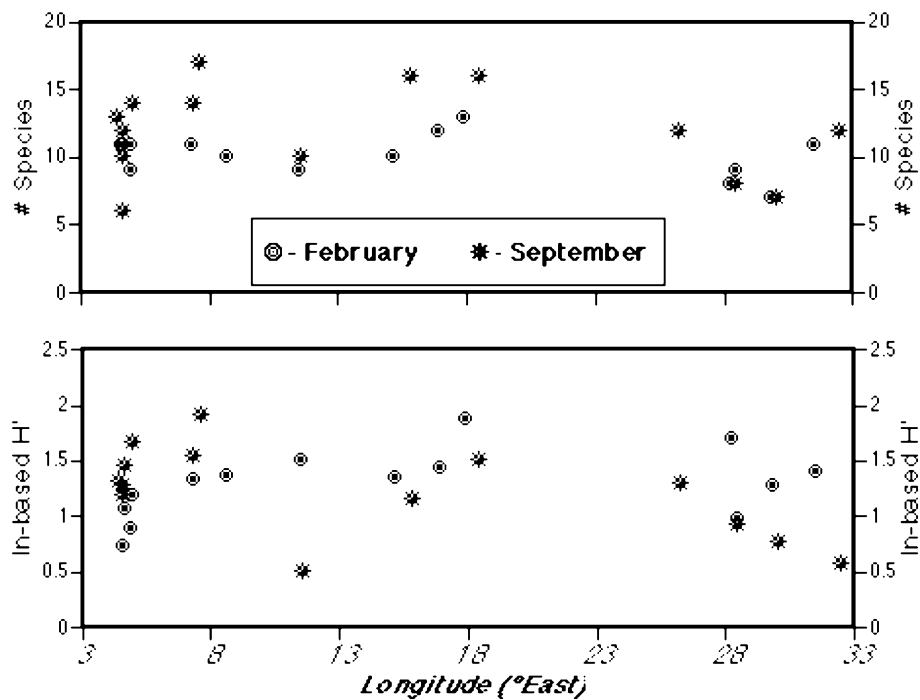


Figure 3. Estimates of the diversity of foraminifera across the Mediterranean Sea in February when the water column is mixed and September when the water column is stratified based on data presented by Pujol & Vergnaud Granzini (1995). Note that species richness was generally higher in the September compared to February samples. However, this was not true of H' values.

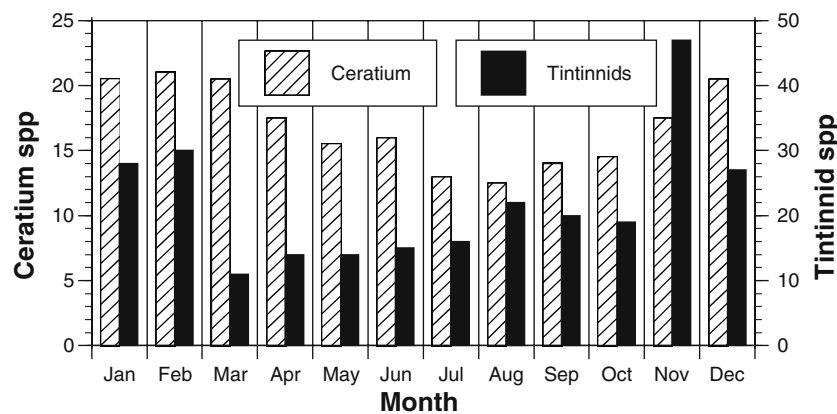


Figure 4. Species richness data by month for the phytoplankton genus *Ceratium* and tintinnids for waters off San Remo, N. W. Mediterranean Sea, based on a report by Rampi (1948). Note that species richness appears lowest during the summer and highest in the winter for the two trophically distinct groups of organisms.

Based on the admittedly weak evidence of monthly sampling, diversity as species richness (in two distinct groups) appears lowest in the structured, relatively stable water column of the summer.

A separate, and the last question with regard to the effect of structure of the water column, is that

of comparing the characteristics of water columns structured to different degrees and at different times. A comparison of species richness and diversity (H') as a function of the depth of the chlorophyll maximum layer at the beginning and end of the stratified period shows very different

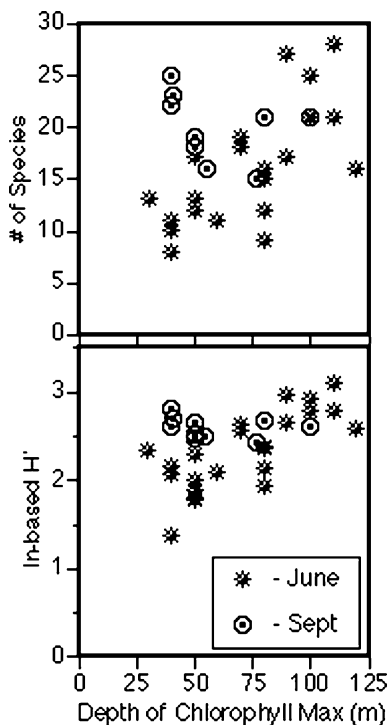


Figure 5. The relationship between species richness (top panel) or diversity as H' (bottom panel) and the depth of the chlorophyll maximum layer in June, early in the season of the stratified water column, and in September, near the end of water column stratification in the Mediterranean Sea. Data are from a variety of sites across the Mediterranean Sea taken from Dolan (2000) and Dolan et al., (2002).

trends (Fig. 5). Samples obtained in June from a transect across the Mediterranean show a positive relationship between the depth of the chlorophyll maximum layer and tintinnid diversity. In contrast, samples from a September transect do not show any particular relationship of species richness or H' with the depth of the chlorophyll maximum layer. However, tintinnid diversity (both taxonomic and morphological) was related to the size structure of the phytoplankton community. Diversity of resources, roughly considered as size-classes of chlorophyll, was correlated with both morphological and species diversity of tintinnids (Dolan et al., 2002).

Temporal trends of tintinnid diversity

Water column stratification at "Point B" at the entrance to the Bay of Villefranche (N.W. Medi-

terranean Sea) changes predictably with the season. An iso-thermic, well-mixed water column is typical of the winter months. Thermal stratification begins in mid-spring and a strongly stratified water column with a surface layer of about 10 m depth is typically present from June through September. Water column stratification breaks down in October and water temperatures are near iso-thermic by early winter. Interestingly, chlorophyll concentrations remain relatively low year-round ($0.2 \mu\text{g l}^{-1}$) with unpredictable peaks occasionally appearing (e.g., Dolan et al., 1995; Mostajir et al., 1995; Bustillo-Guzman et al., 1995). Thus, at Point B water column structure varies independently of algal stock, in other terms, food resources for zooplankton.

Data gathered in 2002 (Fig. 6) clearly shows the independence of water column structure, in the form of the difference in density between 0 and 75 m, from chlorophyll concentration. Casual inspection of the graphs showing temporal changes in chlorophyll, stratification, tintinnid diversity and concentration reveals that water column stratification is unrelated to tintinnid concentrations and diversity. Chlorophyll trends however parallel those of tintinnid concentration, and species abundance appears more closely related to tintinnid than chlorophyll concentration.

Simple regression analysis confirms a significant relationship ($r = 0.53$) between chlorophyll and tintinnid concentration (Fig. 7). Species abundance and total concentration of tintinnids co-vary positively but are not significantly ($r = 0.23$) related (Fig. 7). Given that (1) chlorophyll determines tintinnid concentration and (2) species abundance varies with tintinnid concentrations, changes in chlorophyll should, through changing tintinnid concentrations, influence diversity. This can be examined by plotting weekly changes in chlorophyll against weekly changes in tintinnid diversity and this indeed shows that the two parameters are tightly related ($r = 0.74$). Thus, as a mechanism explaining temporal changes in diversity, chlorophyll or resources appears a likely mechanism, especially compared to water column structure. While we can not exclude other mechanisms, such as predation, the close relationship with changes in chlorophyll suggests a direct link.

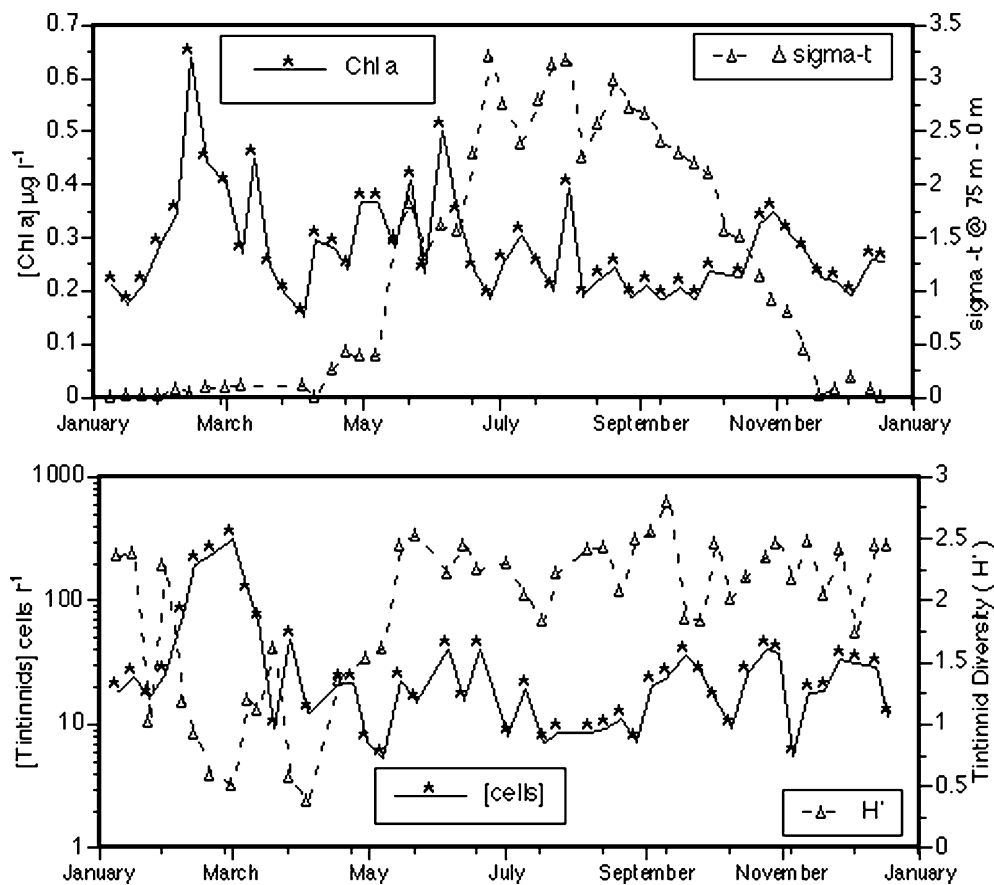


Figure 6. Temporal changes of water column characteristics and the tintinnid community at Point B, Bay of Villefranche in 2002, based on weekly sampling. Top panel shows changes in water column stratification and average chlorophyll concentration. Bottom panel shows species diversity and tintinnid concentrations.

Discussion

Global distribution of tintinnid species abundance

The pattern we found for tintinnid ciliates (species richness increases from the poles to lower latitudes with a peak around 20°–30° followed by a slight decline toward the equator) has been described for a very large variety of marine pelagic taxa ranging from tuna to foraminifera (Angel, 1993; Rutherford et al., 1999; Worm et al., 2003). Latitudinal diversity gradients are, of course, very well known among terrestrial taxa as well. Identification of factors underlying latitudinal diversity gradients has long been, and remains, a very active area of research (e.g., Gaston, 2000). The apparently common peaks of species richness at about 25° N or 25° S, for

example recently described for tintinnids through the Indian Ocean (Modigh et al., 2003), are intriguing. However, here we are not concerned with determining the underlying cause(s) of a latitudinal diversity gradient among tintinnid ciliates but rather simply demonstrating its existence.

The existence of a latitudinal gradient of species richness in tintinnids is of some significance because in other groups of ciliates, specifically benthic ciliates, global and local species richness are thought to be equal; that is all species are cosmopolitan and present in all locales, albeit in perhaps very difficult to detect concentrations (Fenchel et al., 1997; Finlay et al., 1998, 1999; Finlay, 2002). This conclusion has been drawn from the results of intensive examination and treatment (incubation of material to provoke excystment of

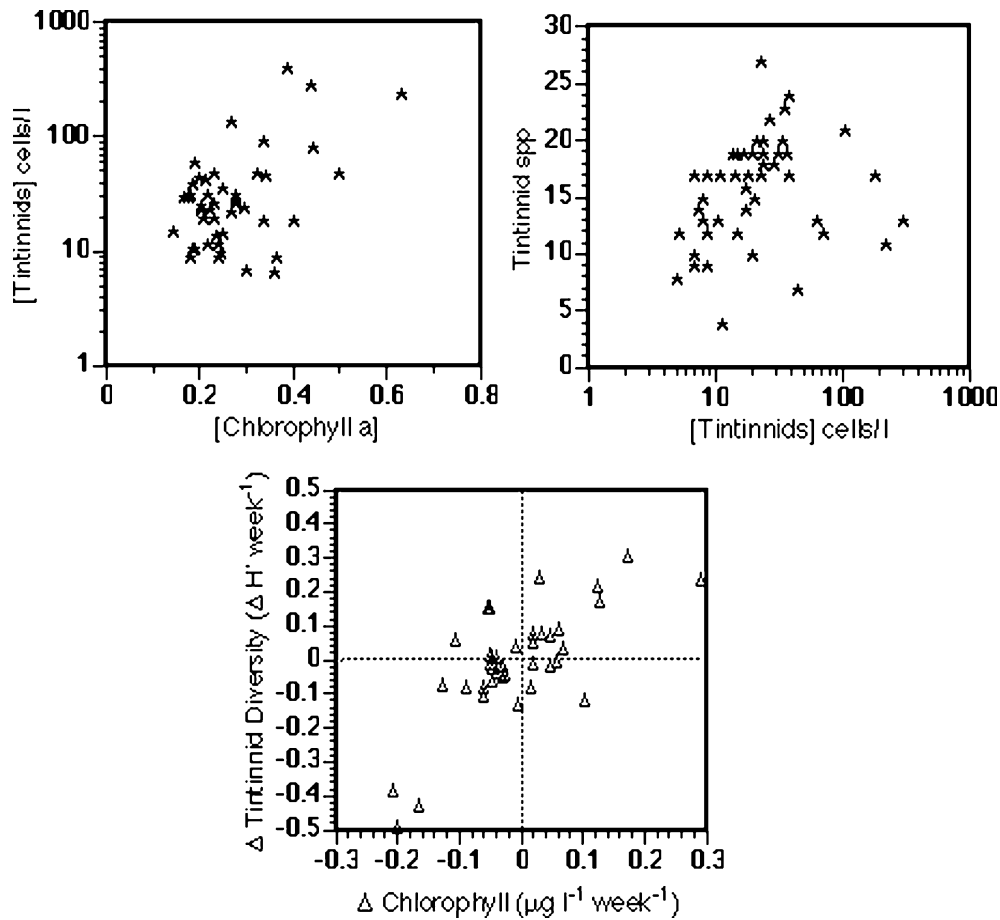


Figure 7. Scatter plots of the relationships between chlorophyll and tintinnid concentrations, tintinnid concentrations and species abundance, weekly changes in chlorophyll and tintinnid diversity as ln-based H' Shannon values. Chlorophyll and tintinnid concentrations are significantly related ($r = 0.53$, $n = 45$); but tintinnid species richness is not related to tintinnid concentration. Weekly changes in chlorophyll are significantly related to weekly shifts in tintinnid diversity values ($r = 0.74$, $n = 40$).

cysts, etc.) of samples yielding large and similar assemblages, regardless of sample origin. Thus, a latitudinal gradient in the species richness of benthic ciliates should not exist.

The mechanism behind ubiquitous distribution of species is ubiquitous dispersal which effectively prevents endemism (Finlay & Esteban, 2004). Evidence at present can be found to support both global dispersal as well as endemism among marine microbes. For protists, there is evidence of wide dispersal as well as genetic isolation. For example, some taxa of foraminifera appear to experience genetic exchange between arctic and antarctic populations (Darling et al., 2000). In other species (defined morphologically), the quite similar morphologies mask genetic divergence be-

tween arctic and antarctic populations (Darling et al., 2004). With regard to prokaryotes, the pattern of 'all species are everywhere' should presumably exist yet there is ample evidence of the existence of endemism among some taxa of free-living prokaryotes (Hedlund & Staley, 2004). One may conclude then, that while many microbes are everywhere not all are.

With regard to tintinnids, while many species are cosmopolitan, Figure 2 shows that global and local diversity do seem very different. Furthermore, tintinnids show a pattern of latitudinal diversity common among pelagic marine taxa. Confirmation of latitudinal changes in species richness of tintinnid communities was recently reported in a study of tintinnids between 29° South

and 60° South in the southwestern Atlantic in which latitude was found to be associated with about 50% of the variability in diversity (Thompson, 2004). Nonetheless, it must be admitted that an apparent latitudinal gradient of species abundance does not disprove a cosmopolitan distribution of all species. A gradient in species abundance may simply reflect a gradient in the abundance of more or less distinct niches permitting the development and co-existence of more species.

What defines these niches is unknown. For example, it has been claimed that zooplankton diversity is not related to phytoplankton diversity but rather to phytoplankton biomass (Irigoien et al., 2004). However, these conclusions have been challenged (Dolan, 2005). Thus, even the relationship between zooplankton and phytoplankton diversity is unclear.

Water column stratification and Mediterranean plankton

In the Atlantic, the depth of the mixed layer has been proposed as a correlate of foraminiferan species richness (Rutherford et al., 1999). Our examination of water column structure as an influence (direct or indirect) on diversity in Mediterranean plankton failed to provide evidence of a major rôle. Firstly, for Mediterranean populations of foraminifera, there appears to be little difference between species richness in February when the water column is mixed compared to September with a well-defined surface layer (Fig. 3). Secondly, historical reports based on monthly sampling for dinoflagellates (*Ceratium*) and tintinnids actually suggest the opposite. In coastal waters of the N. W. Mediterranean, species richness appears highest during late autumn and winter when the water column is subject to the most turbulent mixing (Fig. 4). Thirdly, data from transects across the Mediterranean Sea in June compared to September, showed distinct trends in tintinnid diversity despite similarities in water column structure (Fig. 5). Perhaps then, not unexpectedly, planktonic diversity does not show a simple relationship with water column structure.

Temporal trends of tintinnid diversity

The overall lack of a relationship between stratification of the water column and diversity was also

seen in the temporal series from the Rade de Villefranche. At 'Point B' stratification follows regular seasonal trends while algal stock varies irregularly (Fig. 6). We found that diversity in tintinnids was loosely related to tintinnid abundance which was, in turn, loosely related to algal stock, measured as chlorophyll concentration. These relationships suggested that changes in chlorophyll (food resources) may be related to changes in diversity in tintinnids. Indeed, we found that the weekly changes in chlorophyll concentration were tightly correlated with shifts in tintinnid diversity (Fig. 7). Thus, as a mechanism controlling temporal changes in diversity, chlorophyll or resources appears a likely mechanism, especially compared to water column structure. While we can not exclude other mechanisms, such as predation, the close relationship with changes in chlorophyll suggests a direct link.

We should point out that the Rade de Villefranche may be an unusually dynamic system. For each season, the assemblage is generally dominated by 1–3 species representing about 50% of the population and the identity of the seasonally dominant species has apparently varied comparing reports based on samples taken in the 1950s (Balech, 1959) and the 1970s (Rassoulzadegan, 1979). This is in contrast to the Bay of Naples in which species assemblages appear consistent since the 1930s despite considerable changes in nutrient input into the bay (Modigh & Castalado, 2002). Thus, one might conclude that the Bay of Villefranche is an unusually dynamic system. However, the cycle of seasonal abundance in the bay (distinct peaks in late winter and late autumn separated by a summer minimum) appears common to the Western Mediterranean as it has been found in the Bay of Algiers (Vitello, 1964) and the Gulf of Marseille (Travers, 1973). Large interannual (1952–1959) differences in the identity of the dominant tintinnid species have been found for waters off Blanes, Spain (Margalef, 1957, Margalef & Morales, 1960). Thus, the relationships described for the Bay of Villefranche may be common. These relationships suggest that diversity appears more easily related to shifts in resources than the physical structure of the environment.

Diversity issues have taken center stage in many areas of biology. Fundamental points of view such as 'diversity is a characteristic of ecosystem func-

tion' vs. 'diversity governs ecosystem function' are currently subjects of debate (Naeem, 2002). With regard to marine systems, a few years ago it was remarked that our understanding of marine pelagic biodiversity appears vague (Smetacek, 1996). This is probably due in part to the fact that different mechanisms proposed as important in maintaining diversity in pelagic populations are often closely related. Thus, a structured water column coincides with diverse and stable communities of phytoplankton, herbivorous copepods and predacious copepods (McGowan & Walker, 1980, 1985; Venrick, 1990, 1999).

Here we have attempted to sort out possible mechanisms using field survey data established on different spatial and temporal scales. Tintinnid ciliates appear to be a reasonable model of marine pelagic organisms as their latitudinal diversity gradient pattern is similar to those found in a large variety of taxa. Considering a variety of data from the Mediterranean Sea, the seasonal appearance of a structured water column does not appear to be positively related to planktonic diversity. We showed that temporal changes in tintinnid diversity appeared unrelated to water column structure but could be linked to changes in resources. Thus, overall, resources appear to directly influence diversity.

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