

Estuarine diversity of tintinnids (planktonic ciliates)

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In Chesapeake Bay, a large eutrophic and partially stratified estuary, we investigated diversity among tintinnids (Ciliophora, suborder Tintinninia) in September 1999. In contrast with the typical estuarine pattern, tintinnid diversity was high and increased with decreasing salinity from the mouth of the bay to the mid-bay region. Peak species numbers and diversity values [20–25 species, $H' (\ln) = 2.4–2.5$] were found in stations in the mesohaline (14–17‰) portion of the bay. Within the bay, diversity was not correlated with abundance or food levels, as measured by chlorophyll fluorescence, nor with predator (copepod) concentration. However, because high copepod concentrations corresponded to the less diverse southern bay populations, we examined the influence of copepods on tintinnid diversity in two field experiments using natural populations and a size-fractionation approach. Similar copepod predation rates on abundant tintinnid species (0.4–1 ml cleared copepod⁻¹ h⁻¹) were found in the experiments, but with distinct impacts on tintinnid diversity. In a slow-growing community of tintinnids, copepod predation decreased diversity relative to changes in communities without copepods, while in a community highly dominated by a rapidly growing tintinnid species, copepod predation increased diversity. Our results show that not all taxa found in estuaries are species poor, and in the highly dynamic plankton the relative influence of factors influencing diversity may change rapidly. Species richness in the Chesapeake Bay appears predictable from latitude.

INTRODUCTION

Estuaries, compared to offshore waters, are often characterized as habitats in which the biomass of aquatic organisms is high but their diversity is low. Standard reference works [e.g. (Kinne, 1971)] and textbooks on estuarine ecology [e.g. (Day *et al.*, 1989)] present inverse relationships between species abundance and salinity, typically for benthic invertebrates. Variability of the environment in terms of salinity is the usual explanation offered, although the pattern is also found in stable systems such as the Black Sea [e.g. (Deaton and Greenberg, 1986)]. Thus, for molluscs, low estuarine diversity has been linked to physiological difficulties of osmoregulation (Gainey and Greenberg, 1977). Phytoplankton commonly appear to follow a pattern of decreases in biomass coupled with increases in diversity from low-salinity waters of 5–8‰ towards the mouth of the estuary [e.g. (Muylaert and Sabbe, 1999)]. As with benthic molluscs, low estuarine diversity of phytoplankton, compared to that of coastal marine or oceanic waters, has been attributed to extreme dominance by a few forms able to

prosper in an osmotically adverse environment with otherwise favorable growth conditions [e.g. (Hulbert, 1963)]. Like phytoplankton, estuarine zooplankton communities have long been described as very abundant, but composed of few species [e.g. (Riley, 1967)]. Copepod assemblages then typically decrease in biomass and increase in diversity with salinity [e.g. (Mouny *et al.*, 1998)]. In contrast, benthic ciliates (protists) are diverse in brackish water sediments as well as in freshwater sediments (Fenchel *et al.*, 1997; Finlay *et al.*, 1998).

Studies of the aquatic flora and fauna of the Chesapeake are numerous [reviewed in Majumdar *et al.* (Majumdar *et al.*, 1987) and Malone *et al.* (Malone *et al.*, 1999)], and although none has focused on diversity among planktonic organisms, general observations suggest that a typical estuarine trend of diversity increasing with salinity is followed by phytoplankton (Sellner, 1987), mesozooplankton, especially copepods (Brownlee and Jacobs, 1987; Purcell *et al.*, 1999), as well as among macrofauna, specifically large benthic invertebrates (Newell and Ott, 1999) and fish (Wagner, 1999). Here we explore, in some detail, the diversity of tintinnid ciliates, a

component of the microzooplankton community in Chesapeake Bay.

Interestingly, very little data exist on diversity in microzooplankton, an important group in plankton communities as they are often the dominant consumers of phytoplankton and the preferred prey of copepods (Pierce and Turner, 1992). There would seem little reason, *a priori*, to hypothesize that diversity trends in microzooplankton might differ from phytoplankton or mesozooplankton. However, recent studies continue to underline the fact that even taxa that are closely associated ecologically need not display similar trends (Rohde, 1999), and taxa that are ecologically very different may share patterns (Fraser and Currie, 1996; Roy *et al.*, 1998, 2000; Rutherford *et al.*, 1999).

For example, latitudinal diversity trends of the parasites of teleost fishes apparently differ from that of their hosts (Rohde, 1999). In contrast, taxa that are quite different ecologically can share very similar diversity patterns. For example, annual sea surface temperature appears to be the best predictor of diversity in bivalves (Roy *et al.*, 2000), gastropods (Roy *et al.*, 1998), corals (Fraser and Currie, 1996) and planktonic Foraminifera (Rutherford *et al.*, 1999). For planktonic Foraminifera, the relationship between annual sea surface temperature and diversity is of sufficient strength that it has been used to reconstruct past climatic change [e.g. (Williams and Johnson, 1975)]. Because annual sea surface temperature can be related to the depth of the thermocline in the water column, it may represent a measure of habitat volume for planktonic Foraminifera, reflecting quantities of vertical niches available for different species (Rutherford *et al.*, 1999). However, for gastropods, bivalves and corals, the relationship of sea surface temperature to diversity appears much less direct, if not completely obscure (Fraser and Currie, 1996; Roy *et al.*, 1998, 2000). Thus, with regard to diversity, varieties of trends and mechanisms apparently co-occur.

Ciliates of the microzooplankton include tintinnid ciliates, a suborder of choreotrich ciliates 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. Although tintinnids are nearly always a minority component of the ciliate community, they are ideal for studies of species distributions and diversity. Unlike many groups of microbial organisms, species identifications, with some caveats, can be made using characteristics of lorica morphology. Thus, individuals, untreated other than preserved, may be identified by examination using a transmitted light microscope rather than requiring cytological staining, biochemical screening or RNA sequencing. Here we present data on the diversity of tintinnid ciliates in Chesapeake Bay in September 1999, based on samples collected along the main axis of the bay. In an earlier study (Dolan and Marrasé, 1995), tintinnid diversity was described as relatively low in the mid-bay region of the Chesapeake compared to oligotrophic Mediterranean waters. We hypothesized that tintinnid diversity would be highest in the more saline waters at the mouth of the bay, and that with distance from the bay mouth, diversity would decrease regularly as community biomass increased. We also examined the hypothesis that copepod predation affects tintinnid diversity (Cariou *et al.*, 1999). Field experiments were conducted to explore short-term temporal changes in natural populations of tintinnids with and without their predators, copepods.

METHOD

Sampling and experimental protocols

Sampling and experiments were conducted aboard the RV ‘Cape Henlopen’. To examine spatial trends, samples from nine stations along the main axis of the bay (Figure 1) were obtained on 20–21 September. Station locations,

Table I: Sampling station locations, physical characteristics and samples per station

Station	908	858	845	834	818	804	744	724	707
Date	Sept 20	Sept 21	Sept 21	Sept 21	Sept 21				
Latitude	39°08'N	38°58'N	38°45'N	38°34'N	38°18'N	38°04'N	37°44'N	37°24'N	37°07'N
Longitude	76°20'W	76°23'W	76°26'W	76°26'W	76°16'W	76°13'W	76°11'W	76°05'W	76°07'W
Station	7	17	22	21	16	21	22	14	11
depth (m)									
<i>n</i> depths	4	7	8	7	6	7	7	6	5
Surface ‰	9.16	14.20	16.06	16.42	17.65	18.34	19.62	22.61	20.84
Bottom ‰	13.04	19.26	21.17	19.97	19.70	21.94	23.88	23.89	26.64
Surface °C	21.74	22.29	22.54	22.70	22.81	22.62	22.78	22.91	23.32
Bottom °C	22.24	23.31	23.52	23.17	23.11	23.22	23.07	22.90	22.91

sampling times and data on salinity and temperature are given in Table I. At each station, four to seven depths throughout the water column were sampled using a Seabird CTD-Niskin bottle (20 l) rosette. The CTD probes provided data for water column profiles of salinity, temperature and relative chlorophyll fluorescence; samples were taken at approximately regular intervals as CTD fluorescence data showed little evidence of depth-related maxima or minima of chlorophyll. Data from a Turner Designs fluorometer reading fluorescence of water pumped from the hull pump at ~1.5 m depth were

also recorded. At each station, a 2 l volume of sample from each depth was concentrated to 20 ml by slowly and gently pouring the water through a 20- μ m-mesh Nitex screen fixed to the bottom of a 5-cm-diameter PVC tube. Concentrated water samples were fixed with Lugol's solution (2% final concentration).

Small-scale field experiments were conducted to examine the effects of predation by copepods on tintinnid diversity. In these short-term experiments (24 h), changes in tintinnid community composition were monitored in incubations of natural communities subjected to three levels of copepod predation: (i) no copepod predation, water filtered through 64- μ m-mesh screen to remove all copepods; (ii) *in situ* copepod predation, unaltered water with *in situ* copepod concentrations; (iii) elevated copepod predation, created by adding in the copepods caught on the 64 μ m mesh in treatment (i) to unaltered water with *in situ* copepod concentrations.

Field experiments were conducted on 22 September in the lower Rappahannock River (37°37.22'N, 76°24.09'W) and in the central main stem of the bay on 23 September (38°17.95'N, 76°17.09'W). For both experiments, the protocol began by filling a 20 l carboy with surface water using a bucket. Then, a trio of 2 l containers for unaltered water were filled. Next, 6 l of water were gently filtered through a submerged 64- μ m-mesh Nitex screen and both the filtrate and material caught on the screen were retained. Material caught on the screen was added to 6 l of unaltered water. The 6 l of 64- μ m-screened water were dispersed into three 2-l containers and, likewise, the 6 l of water to which had been added material caught on the 64 μ m screen were dispersed into three 2-l containers. Thus, for each level of copepod concentration (none, *in situ*, elevated) three containers were prepared. For each treatment, one of the three containers was sacrificed for a time zero sample following the depth-sample protocol given above. The remaining containers were placed in a flow-through seawater bath on deck. The translucent polyethylene containers were incubated for 24 h, and then all material in the bottle was concentrated to 20 ml and preserved as given for depth samples above.

Sample processing

Material from discrete depth samples was processed in two different ways. Individual aliquots of concentrated sample, equivalent to 100 ml of water, were examined for all the depth samples from Stations 858 and 707 to check for depth-related differences in diversity in two contrasting stations. Individual discrete depth samples, equivalent to 200 ml, were examined for surface and bottom samples for each of the nine stations to compare surface to bottom water communities. Given a lack of marked depth-related

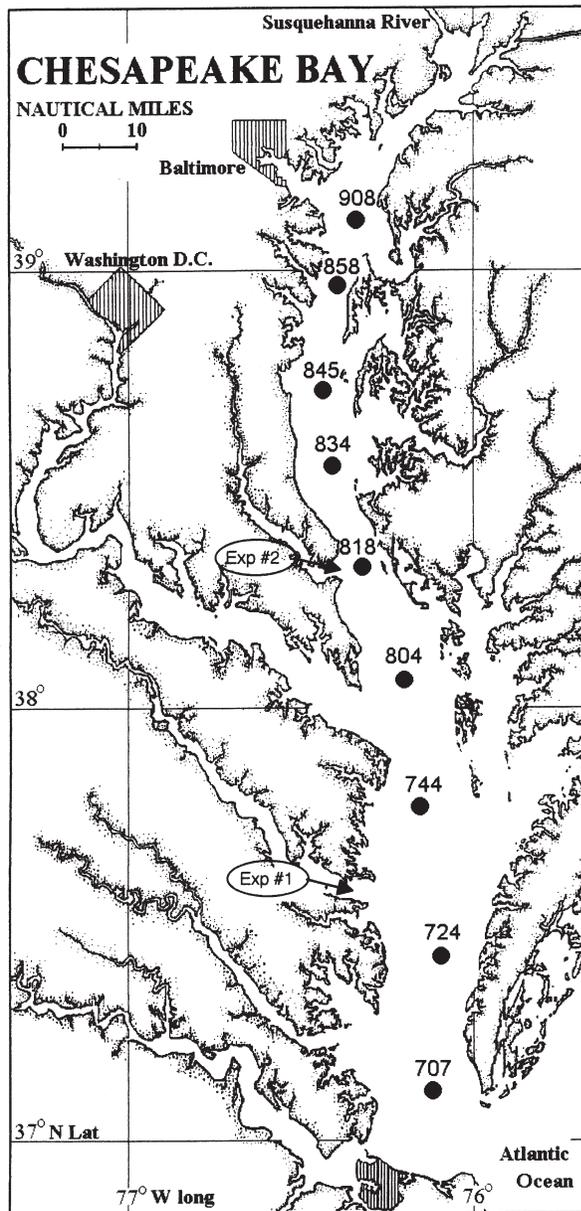


Fig. 1. Locations of stations sampled in September 1999. Arrows show sampling locations for the first and second experiments (Exp #1 and Exp #2) exploring the effect of copepod predation on tintinnid diversity.

shifts, a single integrated water sample was prepared for each of the nine stations. For each station, trapezoidal integration was used to calculate milliliter volumes needed from each discrete depth sample to yield a single integrated water column sample equivalent to 4 l of unconcentrated water. For each station, the integrated water column sample was used to establish species–area (in the form of species–volume) and K-dominance curves, estimates of the number of species and Shannon index (H' ; ln based), as well as averages and standard deviations of tintinnid lorica dimensions.

Each individual 1 or 2 ml of concentrated sample (representing material from 100 or 200 ml of water) was pipetted into the base plate of a Zeiss sedimentation chamber, a second milliliter of distilled water added to fill the chamber if needed, and the chamber sealed and allowed to settle. Subsequently, the entire surface of the chamber was examined using an inverted microscope at $\times 160$ total magnification. Tintinnid identifications were made based on lorica morphology and following Kofoid and Campbell (Kofoid and Campbell, 1929, 1939), and Marshall (Marshall, 1969). Some species of tintinnids can display different lorica morphologies [e.g. (Gold and Morales, 1976; Davis, 1981; Laval-Peuto, 1983; Wasik and Mikolajczyk, 1994)]. However, only a few of the 32 species encountered in this study appeared variable and may or may not represent single species (*Tintinnopsis nana*, *Tintinnopsis rapa-parva*, *Tintinnopsis subacuta*, *Favella panamensis*). We adopted a conservative approach, pooling apparent varieties. Empty loricas were not enumerated.

Species–volume relationships were constructed by sequentially examining 1 ml aliquots, each representing material from 100 ml of water. For each station, 15 aliquots of 1 ml were examined. The cumulative volume of 1500 ml was used for all the stations as species numbers appeared to plateau for the first stations examined, the extreme stations 908 and 707, at ~ 1500 ml. The cumulative number of species encountered was plotted against cumulative volume examined. Data from the entire 1500 ml were used to generate estimates of number of species, values of the Shannon index, average concentration and K-dominance plots for each station. For the latter, species are ranked from 1 to x , with species 1 representing the largest percentage of total individuals, species 2 the second largest, etc., plotted against cumulative dominance (= cumulative percentage of total individuals), number of species, values of the Shannon index and average concentration. Data from the first aliquots for each station were used to generate estimates of community averages and standard deviations of lorica dimensions (lorica oral diameter and lorica length) based on 100–150 organisms. Additional material was examined for most stations to provide estimates of copepod abundances (all

post-naupliar stages pooled) based on raw counts of at least 30 individuals. Station 908, the least saline station, was an exception as copepods were present only in concentrations of $\leq 1 \text{ l}^{-1}$.

Samples from copepod grazing experiments were processed in a manner similar to those for the discrete depth samples. All material from each of the 2 l sample containers (t_0 samples and t_{24} samples) was concentrated to 20 ml using 20- μm -mesh Nitex screening. Single to several 1 ml aliquots were examined from each container to provide raw counts ≥ 100 of the most abundant tintinnid species. All of the remaining material from the incubated samples was examined to determine exact copepod concentrations in the experimental containers.

Data analysis

A total of $>10\,000$ specimens were enumerated. Simple correlations were employed to examine relationships between diversity, both species abundance and the Shannon index, and station parameters of tintinnid concentration, chlorophyll fluorescence, copepod concentration and morphological variability. Morphological variability was quantified in the form of standard deviations of community averages of lorica oral diameters and lengths.

For the copepod grazing experiments, a standard set of equations [i.e. (Frost, 1972)] was used to provide estimates of tintinnid community growth rates, and copepod clearance rates for the two or three most abundant tintinnid species in each experiment. The set of equations uses changes in concentration in the absence of grazers to calculate prey growth rates, and the differences between these rates and rates in the presence of grazers are used to estimate grazer clearance rates. Copepod predation effects on tintinnid diversity were examined by plotting the change in diversity (H') over the 24 h incubation period as a function of copepod concentration.

RESULTS

Vertical trends

The salinity structure of the bay in the central channel, based on water column profiles from the nine stations sampled, is given in Figure 2. From north to south, salinity at the surface varied from 9 to 21‰ and bottom water salinity increased from 13 to 27‰. Average water column salinity increased regularly from north to south and all the stations showed a vertical salinity gradient of 4–6‰. However, based on vertical profiles from two contrasting stations, 858 and 707, the vertical salinity structure was not reflected in any clear depth-related trends in either tintinnid concentrations or diversity (Figure 3).

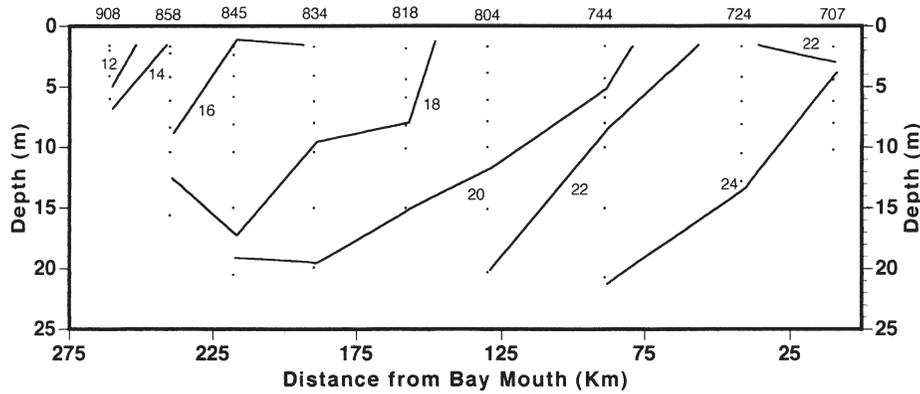


Fig. 2. Salinity structure along the mainstem of Chesapeake Bay, 20–21 September 1999. Lines denote isohalines and points the locations of Niskin bottle samples. Exact and map locations of the station numbers given along the top axis appear in Table I and Figure 1.

In both surface and bottom samples, the highest numbers of species were found in samples from the mid-bay stations (845, 834, 818). At most stations, surface samples contained more species than bottom samples (Figure 4), with those found in bottom samples a subset of those found in the surface samples. Species abundances in neither surface samples nor bottom samples were related to salinity (Table II). As depth-related trends appeared much weaker than north–south trends, subsequent analysis focused on depth-integrated samples.

Species–volume and K-dominance relationships

Construction of species–area or, in the case of plankton, species–volume curves revealed marked differences as well as similarities among the stations sampled. Clear differences were apparent between the mid-bay stations

and those at the northern or southern ends of the bay (Figure 5). The fewest species (~10) were found at the extreme northern station (908) and the extreme southern stations (724, 707). Considerably higher numbers of tintinnid species (15–25) were found in the intermediate stations (from Station 858 to Station 744). While species numbers varied, the shapes of the curves were roughly the same among the stations. For all nine stations, increases in numbers of species encountered decreased sharply at 600–700 ml and a clear plateau was reached for most stations before 1500 ml were examined. There was a relationship between the total species found in a sample volume equal to 1500 ml and the average number of species found in sample aliquots equivalent to 100 ml. Total species encountered was about seven more than the average found in 100 ml (Figure 6). This indicates that, at all stations, there were about seven species

Table II: Correlation matrix showing relationships between species abundances, salinity and station depths in surface, bottom and water column integrated samples for the nine Chesapeake Bay stations

	Bot # spp	Surf ‰	Bot ‰	Total m	WC # spp
Surf # spp	0.805**	-0.510	-0.364	0.581	0.869**
Bot # spp		-0.512	0.507	0.139	0.635
Surf ‰			0.929***	0.085	0.376
Bot ‰				0.252	-0.155
Total m					0.775**

Species abundances in surface, bottom and integrated water samples are abbreviated as Surf # spp, Bott # spp, and WC # spp, respectively. Surface and bottom salinity are abbreviated as Surf ‰ and Bot ‰, and station depth as Total m. For all comparisons, n = 9; significance levels are shown as **0.01 and ***0.001.

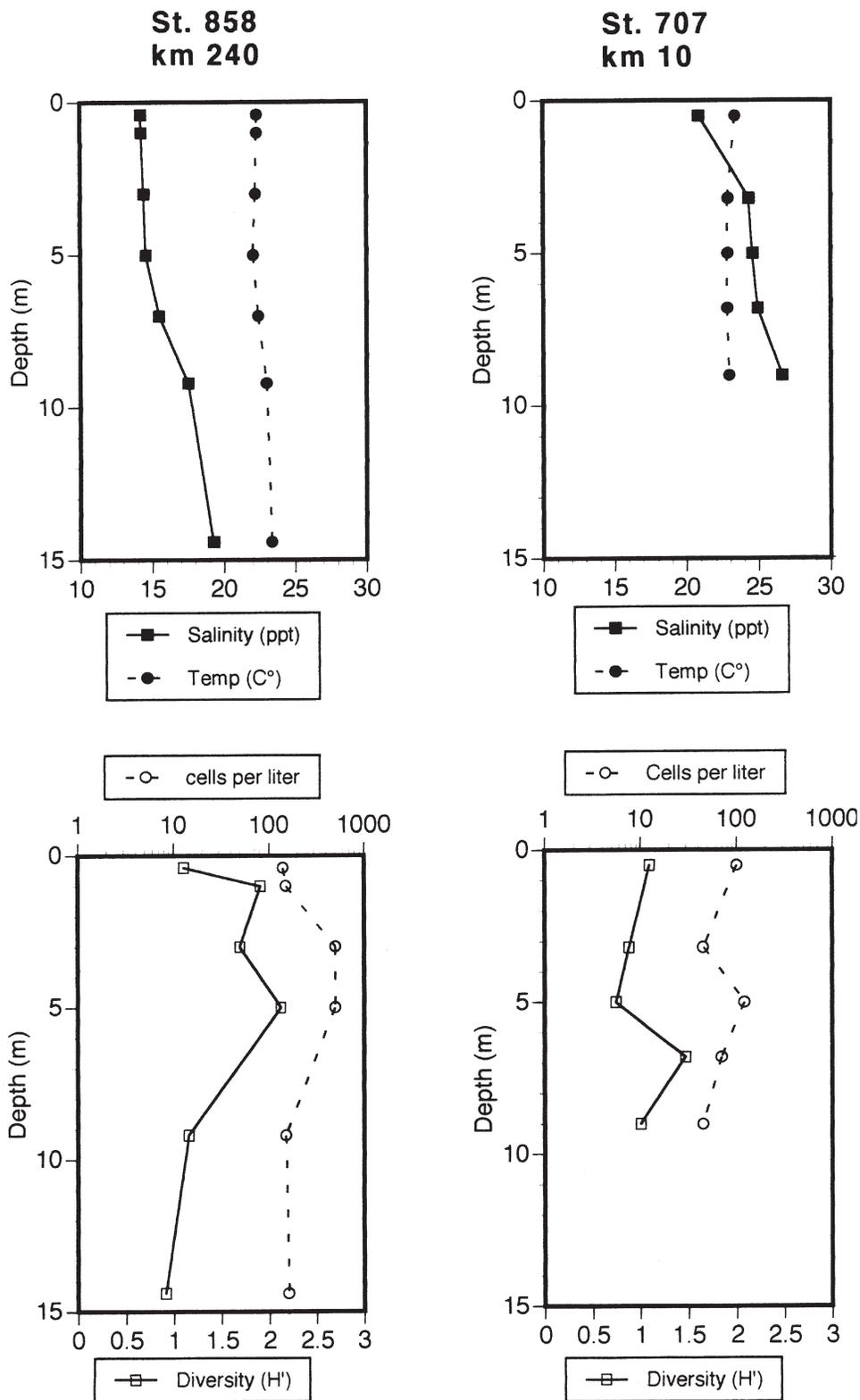


Fig. 3. Vertical profiles of salinity, temperature, tintinnid abundance and diversity for a northern and a southern bay station. Note that while tintinnid abundance (cells ml⁻¹) and diversity, the Shannon index H' , roughly parallel one another, neither shifts regularly with depth, nor appears related to depth discontinuities in salinity or temperature.

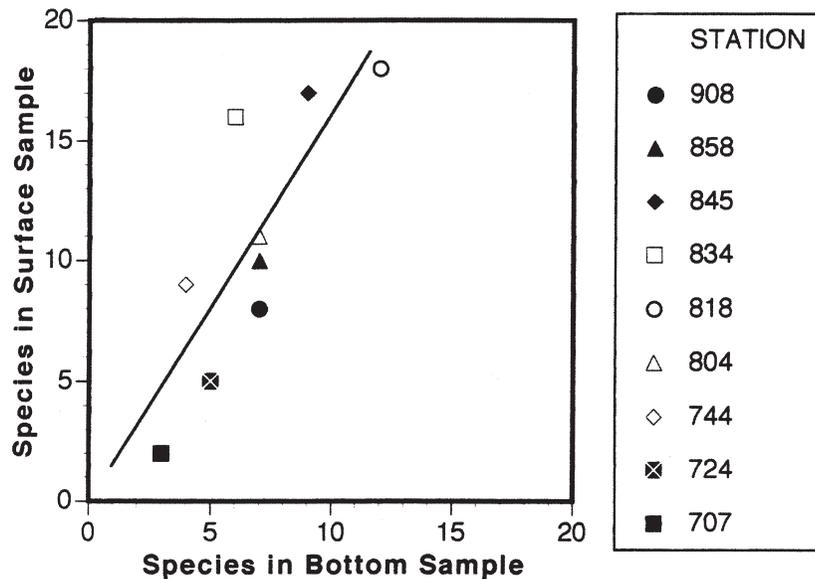


Fig. 4. Scatterplot of tintinnid species abundances in bottom and surface samples for the nine Chesapeake Bay stations. Species abundances are those recorded from examinations of material equivalent to 200 ml of water. Overall, species abundances in surface and bottom samples were significantly correlated ($P < 0.05$). Note that surface samples usually contained more species than bottom samples and peak species abundances were found in the mid-bay stations (see Figure 1 for station locations and Figure 2 for bottom sample depths).

present in 'trace concentrations' of $<5-10$ individuals l^{-1} .

The identity of the trace, as well as the dominant, species differed considerably from station to station (Table III). The distinct differences between stations in the composition of the tintinnid community are also illustrated by the distributional patterns of widely distributed species. Shifts from occupying a dominant position to being found in trace concentrations were common, and absolute abundance was positively related to relative importance in the tintinnid community (Figure 7). Overall, the tintinnid community was highly variable both in terms of total abundances as well as species composition.

K-dominance curves showed trends similar to those with regard to species richness (Figure 8). Stations at both the northern and southern ends of the bay appeared highly dominated by a few forms, with $>50\%$ of the tintinnid community composed of one or two species. Stations 858 and 845 showed the most 'even' or 'equitable' species distributions; nonetheless, only three or four species represented $\sim 50\%$ of the tintinnids.

Spatial relationships of diversity

Spatial trends of species per station, and values of the Shannon index, roughly paralleled one another (Figure 9). As reflected in the species-volume and K-dominance curves, diversity was highest in the middle stations of the bay and minimal at the northern and southern stations.

Peak values of diversity measures were recorded for Stations 858 and 845 (20–25 species, $H' = 2.4-2.5$). The peaks in the H' values, while reflecting larger numbers of species, were due mostly to increases in evenness, with the majority of tintinnid numbers accounted for by three to five rather than one or two species (Figure 8). Diversity, estimated as species per station or H' , was not linearly related to tintinnid concentrations, chlorophyll fluorescence or copepod concentrations. However, peak concentrations of copepods (17–35 copepods l^{-1}) were found in the southern bay stations, and corresponded to minima in tintinnid concentrations and diversity metrics. Shifts in community averages of lorica lengths and oral diameters were slight in comparison with the variability of other parameters. Few parameters were significantly related (Table IV). Tintinnid taxonomic diversity was weakly related to morphological variability, as the standard deviations of average lorica length were correlated with H' ($r = 0.72$, $P = 0.03$, $n = 9$), but not with numbers of species. Copepod concentrations were correlated with the standard deviations of lorica oral diameter ($r = 0.67$, $P = 0.04$, $n = 9$).

Copepod predation experiments

In the first experiment, the tintinnid community remained nearly unchanged in the containers without copepods, showing little net change in concentrations or values of the Shannon H' index (Figure 10). Initial concentrations of total tintinnids averaged ranged from 0.5 to 1 tintinnid

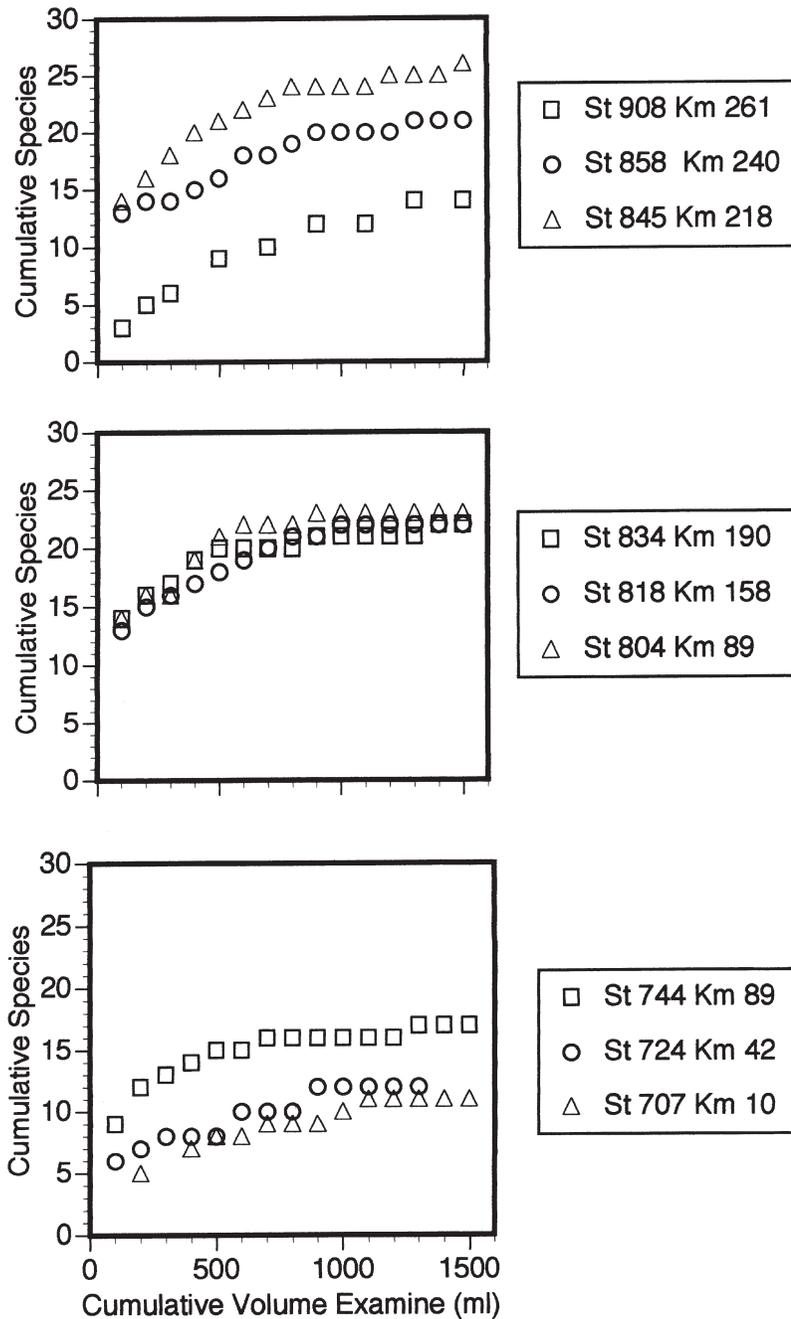


Fig. 5. Plots of numbers of species encountered as a function of volume examined of integrated water column samples for the Chesapeake Bay stations. Fifteen aliquots of sample, equivalent to 100 ml of original water volume, were examined for each station. Maximum numbers of species were found in material from the mid-bay stations 858, 845, 834 and 804. Note that numbers of species increase regularly until material from 500–1000 ml of water is examined, and then plateau, for most of the stations.

ml⁻¹. Three tintinnid species were sufficiently abundant to allow estimates of copepod predation rates, based on changes in concentrations in the containers with copepods compared to containers without copepods. Rates averaged ~0.5 ml cleared of tintinnids copepod⁻¹ h⁻¹, with

larger species (*T. subacuta*, *Tintinnidium* sp.) appearing to suffer lower predation rates than a smaller species (*Eutintinnus pectinus*). Changes in tintinnid community diversity were negatively related to the concentrations of copepods in the container (Figure 10). The shifts in *H'*

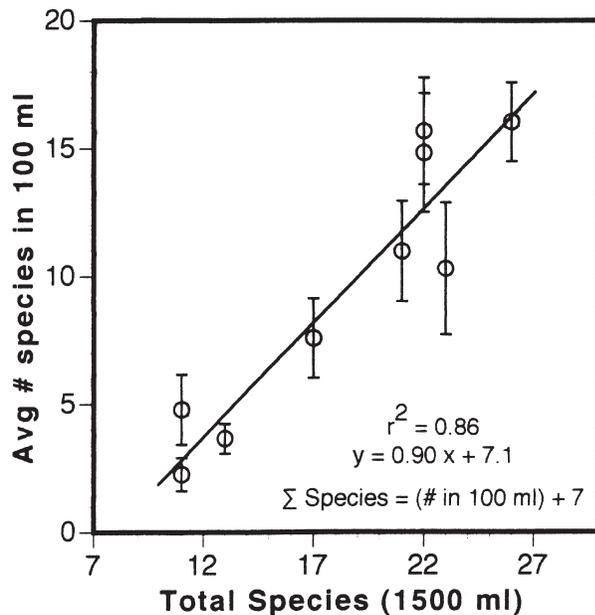


Fig. 6. Plot of the average number of species found in the 100 ml aliquots versus the number of species found in the total of 1500 ml of integrated water sample. Each point represents the average of 15 aliquots and the error bar the SD. Regression yielded an average relationship for all the stations of total species about equal to seven more than the number found in 100 ml.

values largely reflected a marked increase in the dominance of a few large species such as *Favella panamensis* in containers with copepods.

In the second experiment, total tintinnid concentrations were similar to those in the first experiment, but the species composition differed. The tintinnid community was dominated (~75% of cell numbers) by a large ($45 \times 120 \mu\text{m}$ lorica) *Tintinnidium* species which grew rapidly in the containers without copepods (generation time = 16 h). Dominance by this species increased in the absence of copepods from ~75 to ~92%. Estimates of copepod clearance rates on the *Tintinnidium* species were nearly identical to the average rate estimated in the first experiment (Figure 10). Copepod grazing was associated with net increases in H' values as dominance of the tintinnid community by the *Tintinnidium* species was reduced in containers with copepods. The net increases in diversity were roughly proportional to the concentration of copepods in the containers.

DISCUSSION

The abundances of tintinnids recorded, for the nine stations, averaged $\sim 600 \text{ cells l}^{-1}$ over the water column (Figure 9) and were not unusual for Chesapeake Bay in September (Dolan, 1991; Coats and Revelante, 1999), nor in comparison to other coastal systems such as the New

York Bight (Capriulo and Carpenter, 1983) or Narragansett Bay (Hargraves, 1981; Verity, 1987). The tintinnid species found in Chesapeake Bay in September (Table III) were mainly within genera classified as neritic (*Favella*, *Helicostomella*, *Metacylis* and *Tintinnopsis*), or cosmopolitan (such as *Eutintinnus*) (Pierce and Turner, 1993). There were no obvious trends in the types of species found (lorica material types, genera, etc.) in northern landward versus southern seaward stations.

There was also little evidence of vertical differences in species compositions. However, as Chesapeake Bay is hydrologically dominated by marine input and moderately stratified, such a finding is perhaps not surprising. The bay is a textbook example of a moderately stratified coastal plain estuary with a two-layer circulation pattern (Pritchard, 1967; Boicourt *et al.*, 1999). In Chesapeake Bay, the bottom layer travels landward at average current speeds about twice that of the seaward-bound surface waters (Goodrich and Bloomberg, 1991). The pycnocline region, as the border between water masses moving rapidly in opposite directions, is an area of some turbulent mixing rather than a sharp barrier between surface and bottom waters. A common characteristic of the tintinnid communities found was that surface samples contained a few more species than those found in the corresponding bottom sample (Figure 4). It should be noted that vertical differences do occur in the Chesapeake, depending on the season. For example, in summer, when bottom waters are anoxic in the mid-bay, tintinnids are absent in deep samples (Dolan and Coats, 1991).

Other characteristics, common to all the stations, were (i) an apparent plateau in the number of species found as the 'volume equivalent' approached material from 1.5 l of water (Figure 5) and (ii) the presence of several species in 'trace' concentrations (Figure 6; Table III). The 'trace species' were generally different from station to station, with some species appearing as a dominant in one station and a trace in another (Figure 7). Consistently, two to five species accounted for >80% of tintinnids (Figure 8) and a much larger number of species (10–15) were present in either low or trace concentrations. It should be noted that a concentration of 5 cells l^{-1} , here considered a 'trace concentration', would represent a large fraction of typical open-water communities totaling $\sim 20 \text{ cells l}^{-1}$ [e.g. (Dolan, 2000)]. The possibility that even more species could have been detected had material from larger volumes (e.g. >10 l) been examined cannot be excluded. Thus, at every station, enough species were present to form a diverse community. However, despite similar potentials, there were distinct differences in diversity among the different parts of Chesapeake Bay.

The mesohaline, mid-bay stations (858, 845, 834 and

Table III: Tintinnid species encountered at each Chesapeake Bay station

Species	Station								
	908	858	845	834	818	804	744	724	707
Tintinnopsis									
<i>acuminata</i>	t	t	x	x	x	t	x	2	
<i>amphorella</i>					t	t			
<i>baltica</i>			t		t	t	x		
<i>compressa</i>			t						
<i>dadayi</i>	t	x	x	x	x	t	t	x	1
<i>fimbriata</i>		t	t	t		t	t		
<i>levigata</i>	t	x	x	t	x	t	t		t
<i>minuta</i>	t	x	x	1	1	x		t	t
<i>nana</i>		x	x	x	2	1	t		t
<i>parva</i>		t	x	x	x	2	x	x	t
<i>radix</i>		t	x	x	x	t			
<i>subacuta</i>	1	x	x	x	x	x	x	t	
<i>tocantinensis</i>	x	x	x	x	x	x	x	1	2
<i>turbo</i>	x		t	t	t				
sp. 30 × 60		t	t	t					t
sp. 40 × 120			t						
Eutintinnus	2	2	1	2	x	x	t	t	
<i>pectinus</i>									
sm 15 × 75	t				x	t	t	t	t
lg 36 × 155					t		x	t	t
<i>foldy</i>		x	t	x		t	t		
Metacylis jørgensenii	x	t	x	x	x	x	2	t	t
sp 2-908	t								
sp 2-818			t		x				
sp 3		x	x	x		t			
Tintinnidium									
sp sm	x	1	2	x	x	x	t		t
sp lg		x	x	x	x	t			
sp #3				t					
Dadayiella ganymedes									
<i>Favella panamensis</i>		t	t	t	x	t	1	t	t
Helicostomella subulata									
		t	x	x	x	t	t		
'Eutintinnidium'									
new genus?		t	t	t	t	t			
Proplectella parva									
						t			
Stations	908	858	845	834	818	804	744	724	707

Presence is shown by 'x', dominance as the first or second most abundant species is denoted by '1' or '2', respectively; presence only in trace concentrations (<10 l⁻¹) is shown as 't'.

818; see Figure 1) showed higher diversity and concentrations of tintinnids compared to either the oligohaline northern station or the southern polyhaline stations. The differences were substantial; the mid-bay stations

contained about twice the number of species, and higher values of *H'*, than either oligohaline or polyhaline stations (Figure 9). It is unclear exactly why mesohaline stations showed higher diversity. The species

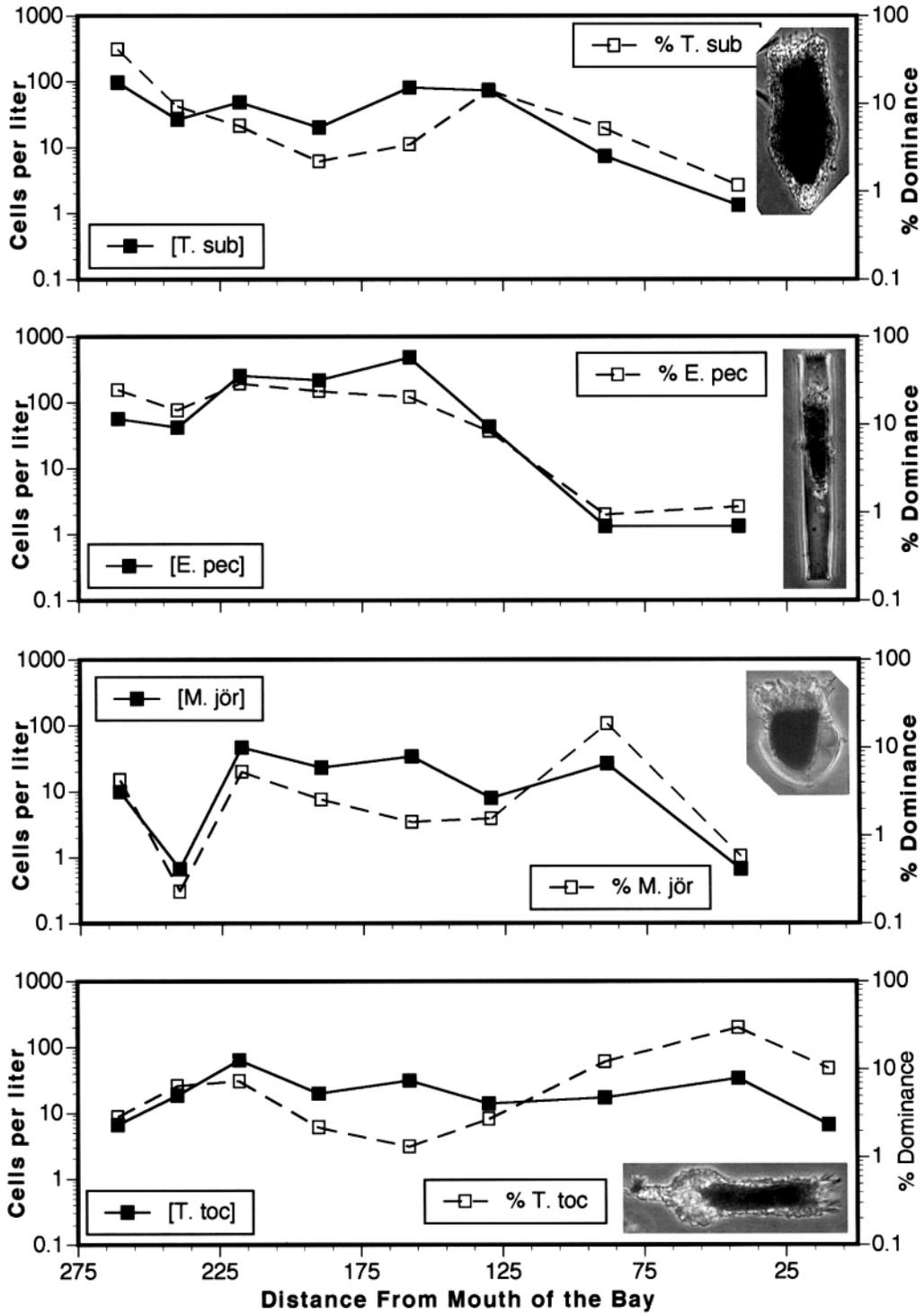


Fig. 7. Changes in concentrations and relative importance as a percentage of total tintinnid numbers, percentage dominance plotted for four widely distributed species from the north to the southern mouth of the bay. Inset photographs are of roughly similar scale, showing the distinct lorica morphologies of *T. subacuta* (*T. sub*), *E. pectinus* (*E. pec*), *Metacylis jörgensii* (*M. jör*) and *Tintinnopsis tocatinensis* (*T. toc*). Note that, in general, shifts in concentration parallel shifts in dominance. Data are from the total population examined in 1500 ml of integrated water column sample for each station.

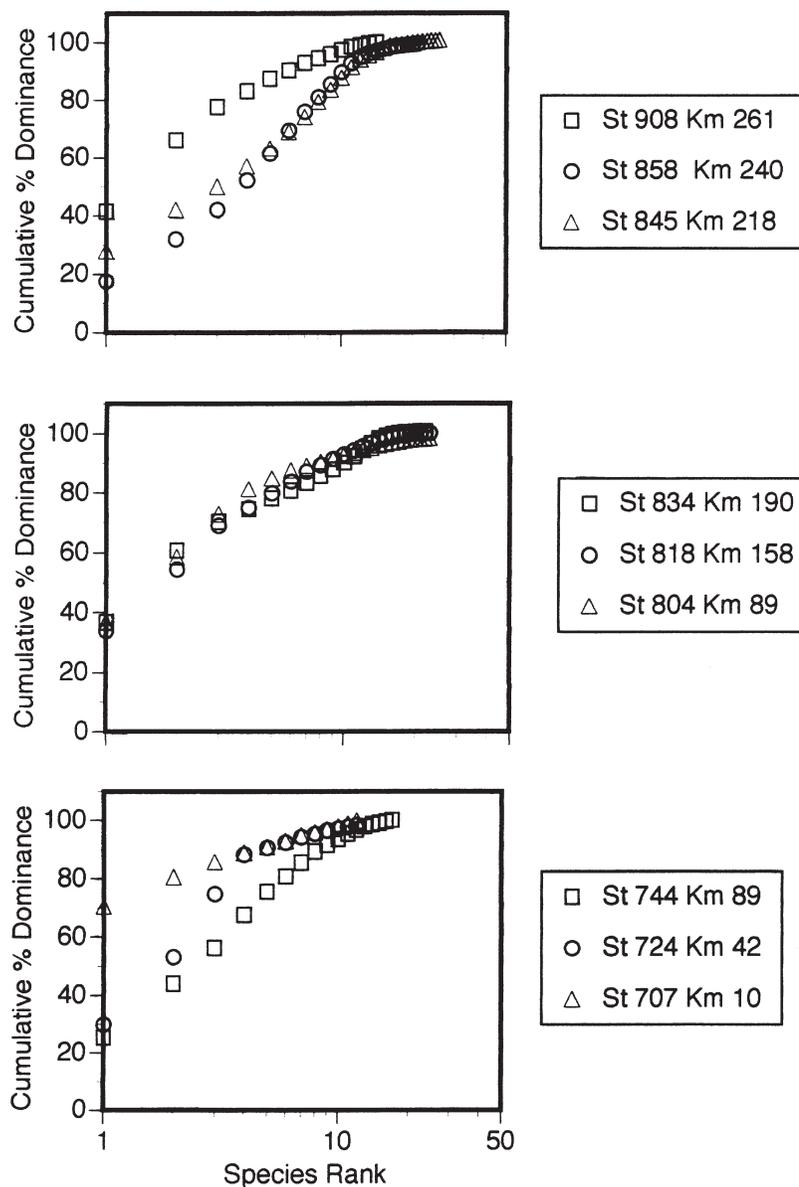


Fig. 8. Plots of species rank versus cumulative dominance or ‘K-dominance’ curves. Species are ranked from 1 to x , with species 1 representing the largest percentage of total individuals, species 2 the second largest, etc., plotted against cumulative dominance (= cumulative percentage of total individuals). Data are from the total population examined in 1500 ml of integrated water column sample for each station.

distributions (Table III) showed little evidence of distinct south bay and north bay communities with the mesohaline mid-bay as simply a zone of overlap. However, the mesohaline Chesapeake differs from both the oligohaline northern bay and the polyhaline southern bay in a number of physical and biological characteristics.

A positive relationship was found between station depth and tintinnid diversity (Table II), and in physical terms the mid-bay contains the deepest area of the mainstem of the bay. The ancient Susquehanna river bed is found at

~30 m depth between Stations 858 and 834. The increased depth of the mesohaline section is associated with higher bottom current speeds (Goodrich and Bloomberg, 1991). Algal stocks and primary production are maximal in this region and associated with high nutrient inputs (Harding *et al.*, 1999). Seasonal bottom water anoxia occurs in the mesohaline Chesapeake Bay and has received a good deal of attention (Taft *et al.*, 1980; Officer *et al.*, 1984; Seliger *et al.*, 1985; Smith *et al.*, 1992). By early summer, bottom water arriving from the south is low in

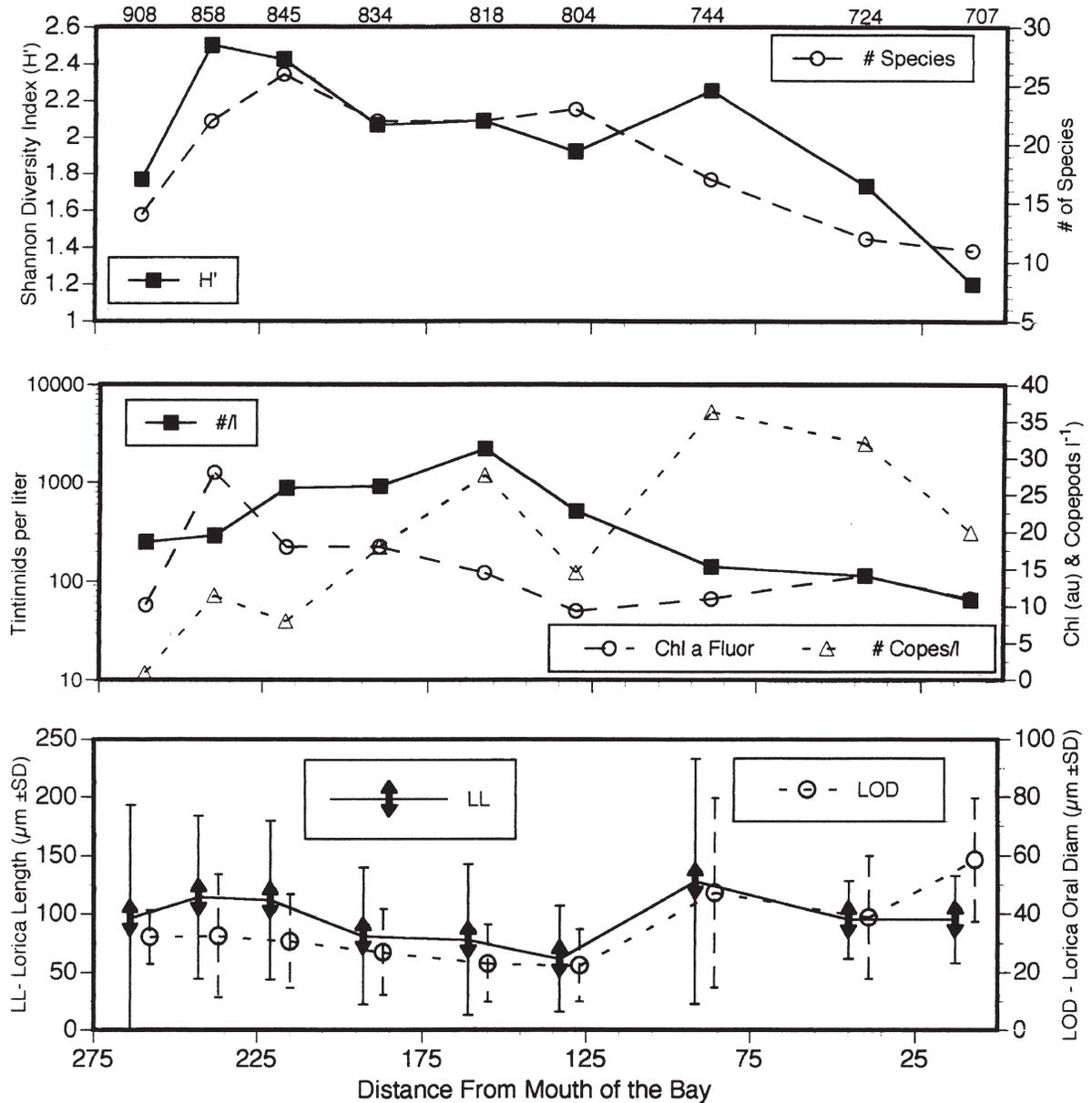


Fig. 9. Spatial shifts in various parameters from the northern bay station to the southern mouth of Chesapeake Bay. The top panel shows north to south trends in the diversity of the tintinnid community in terms of the H' index and species abundance, based on material representing 1500 ml of integrated water column sample. The middle panel shows shifts in tintinnid and copepod concentrations, based on material representing 1500 and 1500–6000 ml, respectively, of integrated water column sample. Chlorophyll fluorescence, in arbitrary units (au), represents surface layer chlorophyll from water pumped through the vessel hull pump. The bottom panel shows spatial trends in tintinnid community averages of lorica dimensions with error bars showing SD.

oxygen (from down-bay oxygen use in the bottom layer) and, *in situ*, with rising water temperatures, the remaining oxygen is consumed, mainly fueled by organic matter produced in surface waters in previous seasons or in the southern bay. Commonly from June through August, waters below the pycnocline are anoxic and hydrogen sulfide is detectable in the deepest waters. Deep bottom waters are only occasionally re-oxygenated due to wind mixing from summer storms (Malone *et al.*, 1986).

While the mesohaline portion of the Chesapeake is a site of intense biological activity, and supported the most dense as well as diverse populations of tintinnids, among the nine bay stations, there was no clear relationship between concentrations of tintinnids and diversity (Table IV). Likewise, there was no simple relationship between diversity and predator abundance or chlorophyll concentration (Table IV). In this regard, it should be noted that, in general, even tintinnid abundances are

Table IV: Correlation matrix showing relationships between tintinnid community characteristics and copepod concentrations from integrated water samples and surface layer chlorophyll fluorescence for the nine Chesapeake Bay stations

	H'	LOD sd	LL sd	[tins]	Chl fluor	[copes]
# spp	0.766*	-0.227	0.430	0.596	0.4540	-0.190
H'		0.149	0.715*	0.301	0.6400	-0.006
LOD sd			0.608	-0.431	0.090	0.669*
LL sd				0.159	0.241	0.370
[tins]					0.107	0.103
Chl fluor						-0.185

spp, species abundance; LOD sd, standard deviation of tintinnid community lorica oral diameter; LL sd, standard deviation of tintinnid community lorica length; [tins], average water column concentration of tintinnids; [copes], average water column concentration of copepods (all post-naupliar forms pooled); Chl fluor, surface layer chlorophyll fluorescence from the ship's hull pump. For all comparisons, $n = 9$; significant relationships are indicated by an asterisk (0.05 level).

rarely correlated with any environmental parameters other than weak relationships with temperature [e.g. (Hargraves, 1981; Capriulo and Carpenter, 1983; Sanders, 1987; Verity, 1987; Graziano, 1989)]. This is no doubt because abundances can shift rapidly in response to environmental changes, but with variable time lags. The small-scale copepod experiments showed that diversity can shift rapidly and unpredictably with a given factor such as predation. Therefore, lack of any clear correlates with diversity when dealing with medium time and space scales (days and kilometers) may be expected.

For example, the field experiments clearly demonstrated that predation can have opposite effects on diversity (Figure 10). In the two experiments, similar concentrations of copepods feeding at similar rates had distinctly different effects on tintinnid diversity. In the first experiment, copepods feeding on a slowly growing, relatively diverse community nearly eliminated two species in the experimental bottles, and copepod concentration was associated with declines in diversity. In the second experiment, the tintinnid community was overwhelmingly dominated by a rapidly growing species and copepod predation reduced the dominance of the dominant species, increasing diversity relative to tintinnids incubated without copepods. As with predation, one can easily imagine different effects of shifts in food availability depending on whether or not a change in food concentration would favor or disfavor the dominance of a single tintinnid species.

While the lack of strong vertical trends in tintinnid diversity may have been predictable, and the mesohaline peak in diversity perhaps understandably obscure, the overall magnitude of tintinnid diversity in the Chesapeake, as a eutrophic estuary, appears surprisingly high.

It is likely that the September sampling fell during the period of peak diversity as the greatest number of phytoplankton species occurs in autumn (Mulford, 1972). However, species richness and values of H' for the Chesapeake are similar to those found for the different areas of the Mediterranean Sea (Figure 11), which were based on examining material from similar volumes of water, 1.5 and 2 l, for stations of the Chesapeake and Mediterranean, respectively. Thus, tintinnid diversity in the Chesapeake appears to differ little from an oligotrophic sea. Unfortunately, little comparative data on H' values of different tintinnid communities exist. However, a number of reports concerning systems not far geographically from the Chesapeake furnish numbers of species for single points in time and space, allowing comparison to species found per station in the Chesapeake in September.

Reports dealing with two other well-known US Atlantic coast systems, Narragansett Bay (Hargraves, 1981; Verity, 1987) and the New York Bight (Gold and Morales, 1975; Capriulo and Carpenter, 1983), give maximal species richness roughly similar to those found in individual stations of Chesapeake Bay. Maximal species numbers of 18 and 11–26 species, respectively, occur in late summer and early fall in Narragansett Bay and the New York Bight. The correspondence of species richness, at least in order of magnitude, among Chesapeake Bay, New York Bight, Narragansett Bay and the Mediterranean Sea, which differ greatly in a number of characteristics (e.g. chlorophyll concentration, salinity, depth, etc.), was unexpected. However, these systems are found at about the same latitude, suggesting that some factor associated with latitude may act as a dominant factor determining species richness. This possibility was examined

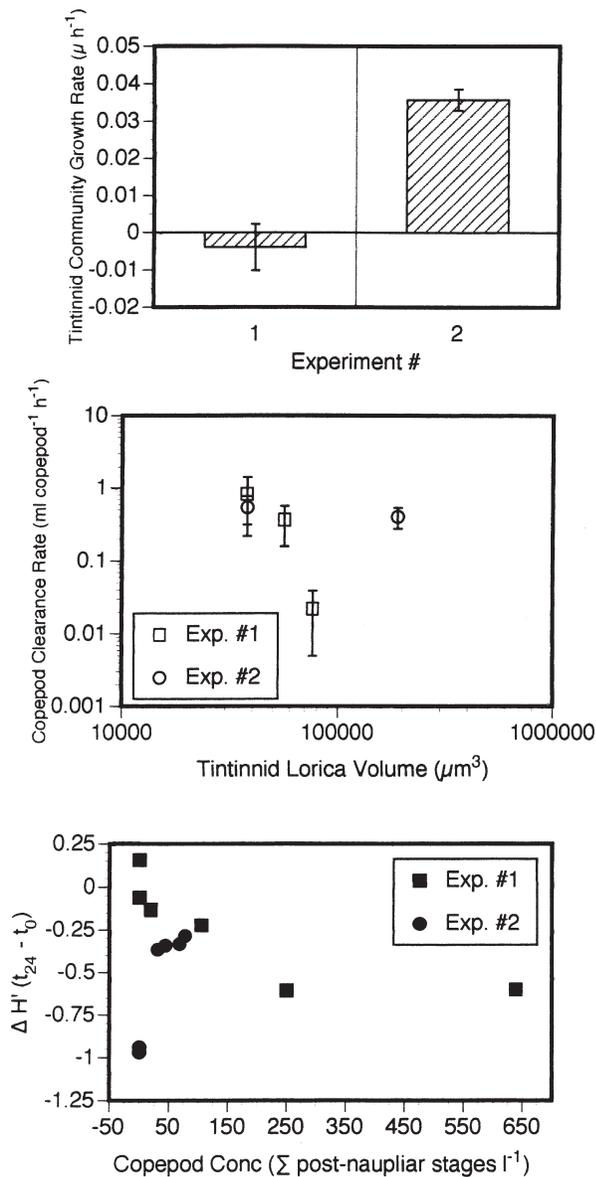


Fig. 10. Results of experiments using natural populations to investigate short-term shifts in tintinnid diversity associated with copepod predation. The top panel shows average tintinnid community growth rates without copepods (64- μm -screened water) in the two experiments; error bars show the range of values recorded. The middle panel shows copepod clearance rates plotted as a function of tintinnid lorica volume, estimated in the two experiments; clearance rate estimates are based on changes in abundances of individual tintinnid species in incubations with and without copepods. Clearance of tintinnid species shown is, from smallest to largest, *E. pectinus*, a small *Tintinnidium* sp., *T. subacuta* and a large *Tintinnidium* sp. The bottom panel shows net changes in the diversity of the tintinnid communities after 24 h of incubation as a function of copepod concentration, with each point representing an individual incubation. Note that in the first experiment diversity decreases with copepod concentration, while in the second experiment the presence of copepods appears to lessen declines in diversity among tintinnids without copepods.

by plotting species abundance against latitude, using data from a large number of locations (Table V).

To permit comparison with data from a September sampling in Chesapeake Bay, only reports furnishing species abundances for single points in time and space, as opposed to annual, seasonal, or multi-station or multi-date lists, were used, but regardless of sampling technique employed (i.e. plankton net tows or whole water collection). When species abundances were given for more than one date, the date with maximal species numbers was taken. No attempt was made to conduct a complete literature search; easily accessible reports were examined until a reasonable number of data points were accumulated (>150) with a near complete latitudinal coverage (81°N–75°S).

Plotting species richness, averaged over increments of 5° latitude or individual points estimates (Figure 12), showed a close relationship between latitude and species abundance. The data imply that rather than environmental type, some factor that shifts with latitude commonly determines species abundances of tintinnids. A large variety of parameters vary with latitudinal gradients in various ways. Relationships range from the simple, direct, linear relationship between latitude and solar energy input to indirect curvilinear relationships, such as with annual sea surface temperature, and coincidental relationships such as between latitude and world ocean area (global area minus land area). Latitudinal diversity gradients are, of course, very well known among terrestrial taxa as well. The identification of factors underlying latitudinal diversity gradients has long been, and remains, a very active area of research [e.g. (Gaston, 2000)].

Here, no attempt will be made to speculate as to the underlying cause(s) of a latitudinal diversity gradient [reviewed recently in Gaston (Gaston, 2000)] among tintinnid ciliates, but rather simply to demonstrate its apparent existence. This is of significance as such a diversity gradient is hypothesized not to exist among benthic ciliates. Benthic ciliate taxa are thought to show a pattern in which global and local diversity are equal; all species are considered cosmopolitan and present in all locales, albeit in difficult to detect concentrations (Fenchel *et al.*, 1997; Finlay *et al.*, 1998, 1999). While many tintinnid species appear cosmopolitan, Figure 12 shows that global and local diversity seem very different. It may be argued that if all species are always present, but most in very low concentrations, then more species are found in low-latitude environments because larger volumes of water are sampled due to low organismal concentrations. However, among the reports listed in Table IV, there was no relationship between volumes of water sampled (when given) and numbers of species reported. For example, for a coastal NW Mediterranean station, Cariou *et al.* (Cariou

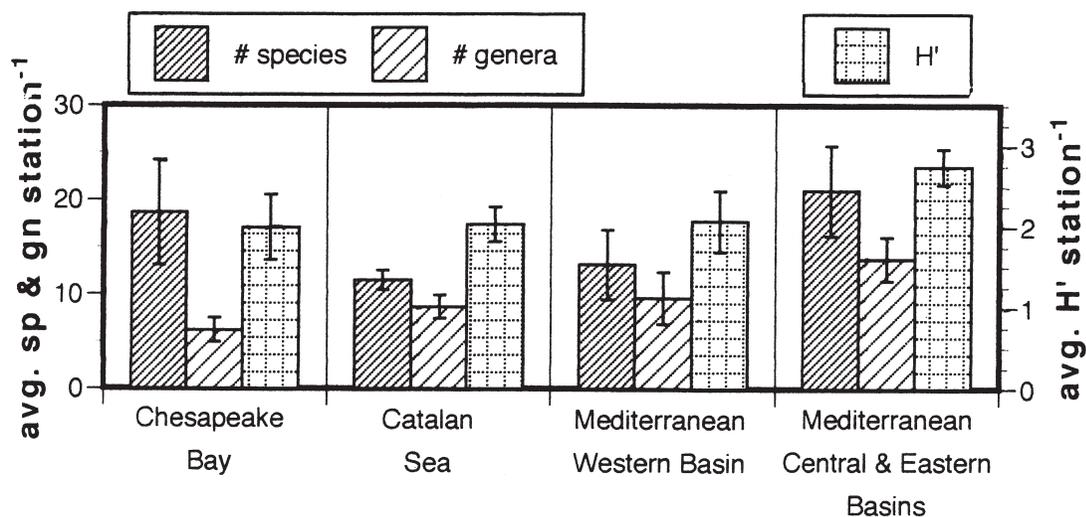


Fig. 11. Comparison of tintinnid community diversity in Chesapeake Bay and three areas of the Mediterranean Sea [from Dolan (Dolan, 2000)], all based on examinations of material representing 1500–2000 ml of water gathered throughout the water column. Average values, with error bars showing SD, for Chesapeake Bay ($n = 9$), the Catalan Sea between the coast of Spain and the Balearic Islands ($n = 6$), the western basin of the Mediterranean ($n = 6$), and the central and eastern basins of the Mediterranean ($n = 11$).

et al., 1999) examined material from 75 l and found 32–39 species compared to 25 species for Station 845 in the mesohaline Chesapeake in material from 1.5 l, or the 29 species found at an eastern Mediterranean station in material from 2 l of water (Dolan, 2000). Hence, it is difficult to ascribe latitudinal differences to artifacts of sampling effort or sample volume.

Tintinnid diversity in Chesapeake Bay demonstrates that estuaries are not species-poor habitats for all taxa. An apparent latitudinal gradient of diversity exists among tintinnids, in contrast with that hypothesized for benthic ciliates. Considering then a single group of ciliates—tintinnids—a different pattern relative to other co-occurring planktonic taxa such as copepods or

Table V: Sources of data shown in Figure 12 relating species abundances to latitude

Study site	Latitude range	n	Reference
Barents Sea	73–81°N	12	Bolotovskoy <i>et al.</i> , 1991
Chesterfield Inlet Estuary	64–63°N	12	Rogers <i>et al.</i> , 1981
Skagerak (North Sea)	58°N	1	Hedin, 1974
Bay of Fundy	45–42°N	3	Middlebrook <i>et al.</i> , 1987
Damariscotta estuary	44°N	1	Sanders, 1987
Coastal Mediterranean	43°N	1	Cariou <i>et al.</i> , 1999
Narragansett Bay	42°N	1	Hargraves, 1981
Long Island Sound	41°N	1	Gold and Morales, 1975
Long Island Sound	41°N	1	Capriuolo and Carpenter, 1983
Open Mediterranean	41–34°N	23	Dolan, 2000
South Pacific Coastal	12°N	1	Gold and Morales, 1977
Sub and Tropical Pacific	34°N–25°S	62	Kofoid and Campbell, 1939
New Zealand Coastal	42–50°S	4	James and Hall, 1995
Bahia Blanca Estuary	38°S	2	Barria de Cao, 1992
SW Atlantic	34–60°S	18	Thompson <i>et al.</i> , 1999
S Atlantic	59–60°S	23	Wasik and Mikolajczk, 1990
Ross Sea	75°S	1	Monti and Fonda Umani, 1995

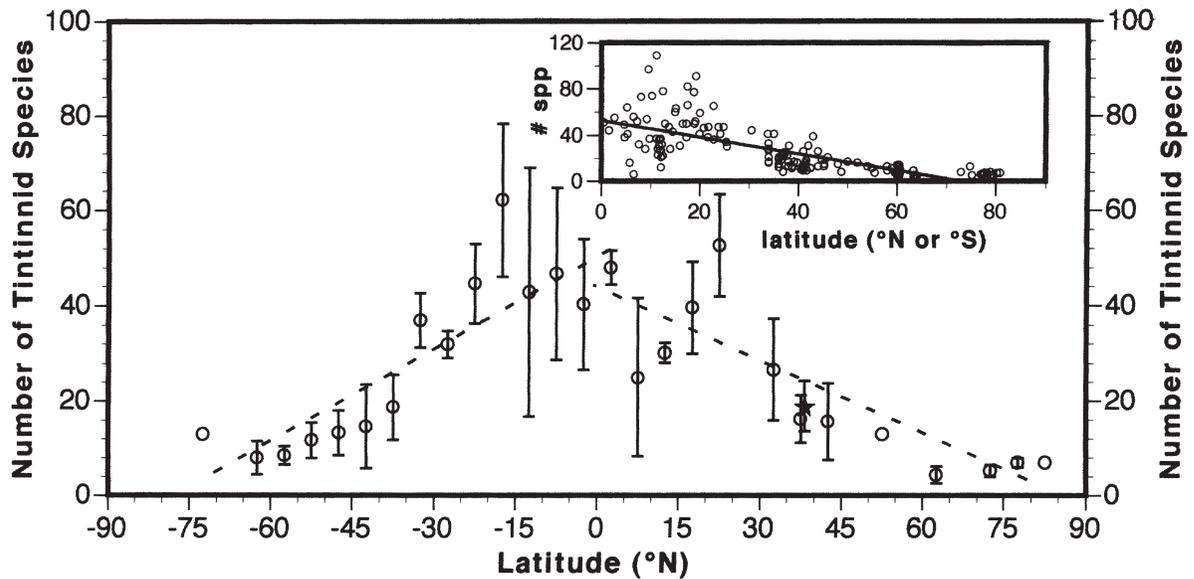


Fig. 12. Latitudinal trends in tintinnid species abundance, based on the report given in Table V. Species abundances were averaged within sets of 5° of latitude and were plotted against the mid-points of the 5° bands. Error bars show the standard deviations of the 5° band estimates. Regression relationships are: for the southern latitude estimates ($n = 13$), $r^2 = 0.75$, $x = 0.703 \times \text{lat} + 0.531$; for the northern latitudes ($n = 13$), $r^2 = 0.70$, $x = -0.50 \times \text{lat} + 0.452$. The inset graph shows individual data points ($n = 168$, $r^2 = 0.55$, $x = 0.801 \times \text{lat} + 0.550$).

phytoplankton can be found, as well as differences compared to other ciliates, those inhabiting the benthos. Our knowledge concerning the positive associations of diversity with basic ecosystem characteristics such as stability and efficiency of nutrient cycling is relatively solid [e.g. (McCann, 2000; Tilman, 2000)]. However, our understanding of the mechanisms influencing marine pelagic biodiversity appears considerably less solid, if not vague (Smetacek, 1996).

ACKNOWLEDGEMENTS

We gratefully acknowledge the captain and crew of the RV 'Henlopen' for ship operations. Financial support for this study was provided by the Smithsonian Institution Office of Fellowships and Grants, the Centre Nationale de la Recherche Scientifique, Université Paris VI, the US National Science Foundation through grant OCE-970365, and the US Environmental Protection Agency through grant R826943. The comments of Wayne Coats on a previous version of this manuscript led to significant improvements.

REFERENCES

Barria de Cao, M. S. (1992) Abundance and species composition of Tintinnina (Ciliophora) in Bahía Blanca Estuary, Argentina. *Estuarine Coastal Shelf Sci.*, **34**, 295–303.

- Boicourt, W. C., Kuzmic, M. and Hopkins, T. S. (1999) The inland sea: circulation of the Chesapeake Bay and the Northern Adriatic. In Malone, T. C., Malej, A., Harding, L. W., Jr, Smolaka, N. and Turner, R. (eds), *Ecosystems at the Land–Sea Margin: Drainage Basin to Coastal Sea*. American Geophysical Union, Washington, DC, pp. 81–130.
- Bolotovskoy, D., Vivequin, S. M. and Swanberg, N. R. (1991) Vertical distribution of tintinnids and associated microplankton in the upper layer of the Barents Sea. *Sarsia*, **76**, 141–151.
- Brownlee, D. C. and Jacobs, F. (1987) Mesozooplankton and microzooplankton in the Chesapeake Bay. In Majumdar, S. K., Hall, L. W., Jr and Austin, H. M. (eds), *Contaminant Problems and Management of Living Chesapeake Bay Resources*. Pennsylvania Academy of Science, Philadelphia, PA, pp. 217–269.
- Capriulo, G. M. and Carpenter, E. J. (1983) Abundance, species composition and feeding impact of tintinnid micro-zooplankton in central Long Island Sound. *Mar. Ecol. Prog. Ser.*, **10**, 277–288.
- Cariou, J.-B., Dolan, J. R. and Dallot, S. (1999) A preliminary study of tintinnid diversity in the NW Mediterranean Sea. *J. Plankton Res.*, **21**, 1065–1075.
- Coats, D. W. and Revelante, N. (1999) Distributions and trophic implications of microzooplankton. In Malone, T. C., Malej, A., Harding, L. W., Jr, Smolaka, N. and Turner, R. (eds), *Ecosystems at the Land–Sea Margin: Drainage Basin to Coastal Sea*. American Geophysical Union, Washington, DC, pp. 207–240.
- Davis, C. C. (1981) Variations of lorica shape in the genus *Pytochocylis* (Protozoa: Tintinnia) in relation to species identification. *J. Plankton Res.*, **3**, 433–443.
- Day, J. W., Jr, Hall, C. A. S., Kemp, W. M. and Yanez-Arancibia, A. (1989) *Estuarine Ecology*. John Wiley & Sons, New York.
- Deaton, L. E. and Greenberg, M. J. (1986) There is no horochalanicum. *Estuaries*, **9**, 20–30.

- Dolan, J. R. (1991) Guilds of ciliate microzooplankton in the Chesapeake Bay. *Estuarine Coastal Shelf Sci.*, **33**, 137–152.
- Dolan, J. R. (2000) Tintinnid ciliate diversity in the Mediterranean Sea: longitudinal patterns related to water column structure in late spring–early summer. *Aquat. Microb. Ecol.*, **22**, 20–30.
- Dolan, J. R. and Coats, D. W. (1991) Changes in fine-scale vertical distribution of ciliate microzooplankton related to anoxia in Chesapeake Bay waters. *Mar. Microb. Food Webs*, **5**, 81–94.
- Dolan, J. R. and Marrasé, C. (1995) Planktonic ciliate distribution relative to a deep chlorophyll maximum: Catalan Sea, N.W. Mediterranean, June 1993. *Deep-Sea Res. I*, **42**, 1965–1987.
- Fenchel, T., Esteban, G. F. and Finlay, B. J. (1997) Local vs global diversity of microorganisms: cryptic diversity of ciliated protozoa. *Oikos*, **80**, 220–225.
- Finlay, B. J., Esteban, G. F. and Fenchel, T. (1998) Protozoan diversity: converging estimates of the global number of free-living ciliate species. *Protist*, **149**, 29–37.
- Finlay, B. J., Esteban, G. F., Olmo, J. L. and Tyler, P. A. (1999) Global distribution of free-living microbial species. *Ecography*, **22**, 138–144.
- Fraser, R. H. and Currie, D. J. (1996) The species richness–energy hypothesis in a system where historical factors are thought to prevail: coral reefs. *Am. Nat.*, **148**, 138–159.
- Frost, B. W. (1972) Effects of size and concentration of food particles on the feeding behaviour of the marine planktonic copepod *Calanus pacificus*. *Limnol. Oceanogr.*, **17**, 805–817.
- Gainey, L. F. and Greenberg, M. J. (1977) Physiological basis of the species abundance–salinity relationship in molluscs: a speculation. *Mar. Biol.*, **40**, 41–49.
- Gaston, K. J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.
- Gold, K. and Morales, E. A. (1975) Seasonal changes in lorica sizes and the species of Tintinnida in the New York Bight. *J. Protozool.*, **22**, 520–528.
- Gold, K. and Morales, E. A. (1976) Studies on the sizes, shapes and development of the lorica in agglutinated Tintinnida. *Biol. Bull.*, **150**, 377–392.
- Gold, K. and Morales, E. A. (1977) Studies on the Tintinnida of Enewetak Atoll. *J. Protozool.*, **24**, 580–587.
- Goodrich, D. M. and Blumberg, A. F. (1991) The fortnightly mean circulation of Chesapeake Bay. *Estuarine Coastal Shelf Sci.*, **32**, 451–462.
- Graziano, C. (1989) On the ecology of Tintinnids (Ciliophora: Oligotrichida) in the North Irish Sea. *Estuarine Coastal Shelf Sci.*, **29**, 233–245.
- Harding, L. W., Jr, Degobbi, D. and Precali, R. (1999) Production and fate of phytoplankton: annual cycles and interannual variability. In Malone, T. C., Malej, A., Harding, L. W., Jr, Smolaka, N. and Turner, R. (eds), *Ecosystems at the Land–Sea Margin: Drainage Basin to Coastal Sea*. American Geophysical Union, Washington, DC, pp. 131–172.
- Hargraves, P. E. (1981) Seasonal variations of tintinnids (Ciliophora: Oligotrichida) in Narragansett Bay, Rhode Island. *J. Plankton Res.*, **3**, 81–91.
- Hedin, H. (1974) Tintinnids on the Swedish west coast. *Zoon*, **2**, 123–133.
- Hulbert, E. M. (1963) The diversity of phytoplankton populations in oceanic, coastal, and estuarine regions. *J. Mar. Res.*, **21**, 81–93.
- James, M. R. and Hall, J. A. (1995) Planktonic ciliated protozoa: their distribution and relationship to environmental variables in a marine coastal ecosystem. *J. Plankton Res.*, **17**, 659–683.
- Kinne, O. (1971) Salinity: animals: invertebrates. In Kinne, O. (ed.), *Marine Ecology: A Comprehensive, Integrated Treatise on Life in Oceans and Coastal Waters*. Wiley-Interscience, New York, pp. 821–824.
- Kofoed, C. A. and Campbell, A. S. (1929) A conspectus of the marine and fresh-water Ciliata belonging to the suborder Tintinninea, with descriptions of new species principally from the Agassiz expedition to the eastern tropical Pacific 1904–1905. *Univ. Calif. Pub. Zool.*, **34**, 1–403.
- Kofoed, C. A. and Campbell, A. S. (1939) The Tintinninea of the eastern tropical Pacific. *Bull. Mus. Comp. Zool. Harvard Coll.*, **84**, 1–473.
- Laval-Peuto, M. (1983) Sexual reproduction in *Favella ehrenbergii* (Ciliophora, Tintinnia): taxonomic implications. *Protistologica*, **19**, 503–512.
- Majumdar, S. K., Hall, L. W., Jr and Austin, H. M. (1987) *Contaminant Problems and Management of Living Chesapeake Bay Resources*. Pennsylvania Academy of Science, Philadelphia, PA.
- Malone, T. C., Kemp, W. M., Ducklow, H. W., Boynton, W. R., Tuttle, J. H. and Jonas, R. B. (1986) Lateral variation in the production and fate of phytoplankton in a partially stratified estuary. *Mar. Ecol. Prog. Ser.*, **32**, 149–160.
- Malone, T. C., Malej, A., Harding, L. W., Jr, Smolaka, N. and Turner, R. (eds) (1999) *Ecosystems at the Land–Sea Margin: Drainage Basin to Coastal Sea*. American Geophysical Union, Washington, DC.
- Marshall, S. M. (1969) *Protozoa, order Tintinnia*. Cons. Int. Explor. Mer, Fiches d'Identification de Zooplancton, fiches 117–127.
- McCann, K. S. (2000) The diversity–stability debate. *Nature*, **405**, 228–233.
- Middlebrook, K., Emerson, C. W., Roff, J. C. and Lynn, D. H. (1987) Distribution and abundance of tintinnids in the Quoddy region of the Bay of Fundy. *Can. J. Zool.*, **65**, 594–601.
- Monti, M. and Fonda Umami, S. (1995) Tintinnids in Terra Nova Bay–Ross Sea during two austral summers (1987/88 and 1989/90). *Acta Protozool.*, **34**, 193–201.
- Mouny, P., Dauvin, J. C., Bessineton, C. and Elkaim, B. (1998) Biological components from the Seine estuary: first results. *Hydrobiologia*, **373/374**, 333–347.
- Mulford, R. A. (1972) An annual plankton cycle on the Chesapeake Bay in the vicinity of Calvert Cliffs, Maryland, June 1969–May 1970. *Proc. Acad. Nat. Sci. Philadelphia*, **124**, 17–40.
- Muylaert, K. and Sabbe, K. (1999) Spring phytoplankton assemblages in and around the maximum turbidity zone of the estuaries of the Elbe (Germany), the Schelde (Belgium/the Netherlands) and the Gironde (France). *J. Mar. Syst.*, **22**, 133–149.
- Newell, R. I. E. and Ott, J. A. (1999) Macrobenthic communities and eutrophication. In Malone, T. C., Malej, A., Harding, L. W., Jr, Smolaka, N. and Turner, R. (eds), *Ecosystems at the Land–Sea Margin: Drainage Basin to Coastal Sea*. American Geophysical Union, Washington, DC, pp. 265–294.
- Officer, C. B., Biggs, R. B., Taft, J. L., Cronin, L. E., Tyler, M. A. and Boynton, W. R. (1984) Chesapeake Bay anoxia: origin, development, and significance. *Science*, **223**, 22–27.
- Pierce, R. W. and Turner, J. T. (1992) Ecology of planktonic ciliates in marine food webs. *Rev. Aquat. Sci.*, **6**, 139–181.
- Pierce, R. W. and Turner, J. T. (1993) Global biogeography of marine tintinnids. *Mar. Ecol. Prog. Ser.*, **94**, 11–26.
- Pritchard, D. W. (1967) Observations of circulation in coastal plain estuaries. In Lauff, G. H. (ed.), *Estuaries*. American Association for the Advancement of Science, Washington, DC, pp. 37–50.

- Purcell, J. E., Malej, A. and Benovic, A. (1999) Potential links of jellyfish to eutrophication and fisheries. In Malone, T. C., Malej, A., Harding, L. W., Jr, Smolaka, N. and Turner, R. (eds), *Ecosystems at the Land–Sea Margin: Drainage Basin to Coastal Sea*. American Geophysical Union, Washington, DC, pp. 241–264.
- Riley, G. A. (1967) The plankton of estuaries. In Lauff, G. H. (ed.), *Estuaries*. American Association for the Advancement of Science, Washington, DC, pp. 316–326.
- Rogers, G. F., Roff, J. C. and Lynn, D. H. (1981) Tintinnids of Chesterfield Inlet, Northwest Territories. *Can. J. Zool.*, **59**, 2360–2364.
- Rohde, K. (1999) Latitudinal gradients in species diversity and Rapoport's rule revisited: a review of recent work and what can parasites teach us about the cases of the gradients? *Ecography*, **22**, 593–613.
- Roy, K., Jablonski, D., Valentine, J. W. and Rosenberg, G. (1998) Marine latitudinal diversity gradients: tests of causal hypotheses. *Proc. Natl Acad. Sci. USA*, **95**, 3699–3702.
- Roy, K., Jablonski, D. and Valentine, J. W. (2000) Dissecting latitudinal diversity gradients: functional groups and clades of marine bivalves. *Proc. R. Soc. London Ser. B*, **267**, 293–299.
- Rutherford, S., D'Hondt, S. and Prell, W. (1999) Environmental controls on the geographic distribution of zooplankton diversity. *Nature*, **400**, 749–752.
- Sanders, R. W. (1987) Tintinnids and other microzooplankton—seasonal distributions and relationships to resources and hydrography in a Maine estuary. *J. Plankton Res.*, **9**, 65–77.
- Seliger, H. H., Boggs, J. A. and Biggley, W. H. (1985) Catastrophic anoxia in the Chesapeake Bay. *Science*, **228**, 70–73.
- Sellner, K. (1987) Phytoplankton in Chesapeake Bay: role in carbon, oxygen and nutrient dynamics. In Majumdar, S. K., Hall, L. W., Jr and Austin, H. M. (eds), *Contaminant Problems and Management of Living Chesapeake Bay Resources*. Pennsylvania Academy of Science, Philadelphia, PA, pp. 134–157.
- Smetacek, V. (1996) Biodiversity and production in the water mass. In Hempel, G. (ed.), *The Ocean and the Poles*. Gustav Verlag, Jena, Germany, pp. 207–216.
- Smith, D. E., Leffler, M. and Mackierman, G. (1992) *Oxygen Dynamics in the Chesapeake Bay*. Maryland Sea Grant, College Park, MD.
- Taft, J. L., Hartwig, E. O. and Loftus, R. (1980) Seasonal oxygen depletion in Chesapeake Bay. *Estuaries*, **3**, 242–247.
- Thompson, G. A., Alde, V. A., Boltovskoy, D. and Brandini, F. (1999) Abundance and biogeography of tintinnids (Ciliophora) and associated microzooplankton in the Southwestern Atlantic Ocean. *J. Plankton Res.*, **21**, 1265–1298.
- Tilman, D. (2000) Causes, consequences and ethics of biodiversity. *Nature*, **405**, 208–211.
- Verity, P. G. (1987) Abundance, community composition, size distribution, and production rates of tintinnids in Narragansett Bay, Rhode Island. *Estuarine Coastal Shelf Sci.*, **24**, 671–690.
- Wagner, C. M. (1999) Expression of the estuarine species in littoral fish of the lower Chesapeake Bay tributaries. *Estuaries*, **22**, 304–312.
- Wasik, A. and Mikolajczyk, E. (1990) Tintinnids near pack-ice between South Shetland and the South Orkney Islands (26 Dec. 1988–18 Jan. 1989). *Acta Protozool.*, **29**, 229–244.
- Wasik, A. and Mikolajczyk, E. (1994) Annual cycle of tintinnids in Admiralty Bay with an emphasis on seasonal variability in *Cymatocylis affinis/convallaria* lorica morphology. *J. Plankton Res.*, **16**, 1–8.
- Williams, D. F. and Johnson, W. C., II (1975) Diversity of recent planktonic Foraminifera in the southern Indian Ocean and late Pleistocene paleotemperatures. *Quatern. Res.*, **5**, 237–250.

Received on November 29, 2000; accepted on April 17, 2001