Vol. 10: 277–288, 1983 | MARINE ECOLOGY – PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published January 20

Abundance, Species Composition and Feeding Impact of Tintinnid Micro-Zooplankton in Central Long Island Sound*

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ABSTRACT: Abundance and composition of tintinnid and phytoplankton species were followed in central Long Island Sound from August 1979 to October 1980. In all, 28 tintinnid species were observed; the greatest diversity occurred between September and April. Highest tintinnid concentrations occurred in summer, with concentrations of 10^3 or more individuals l^{-1} observed only when nanophytoplankton concentrations equalled or exceeded 1.3×10^5 cells l^{-1}. Although necessary, the occurrence of small food, alone, was not a sufficient condition for high tintinnid densities. Tintinnids in central Long Island Sound exhibited the same order of magnitude yearly community ingestion rates as did the copepods. The tintinnids were responsible for removing approximately 27 % of the annual primary production from this region. It is concluded that tintinnids are an integral part of the Long Island Sound plankton community, equal in importance to copepods.

INTRODUCTION

Considerable research has been carried out on the abundance and species composition of tintinnid protozoans in the world's oceans. Tintinnid abundance and composition have been recorded for the Okhotsk Sea (Hada, 1932) the Kuroshio water (Motoda and Marumo, 1963) and the Sea of Japan (Konovalova and Rogachenko, 1975). Sorokin (1977) reported concentrations in the Sea of Japan approaching 15,000 l^{-1}. For the Phillippine and Celebes Seas concentrations of 10 to 100 l^{-1} have been reported (Taniguchi, 1977). Studies have also been carried out in the East Sea of the USSR (Strelkov, 1955), the Black Sea (Morozovskaya, 1970), and the Red Sea (Kimor and Golandsky, 1977; Kimor and Golandsky-Baras, 1981). The Baltic area has been investigated by Hensen (1887), Gillbricht (1954) and Halme (1958), with Lohmann (1908) pointing out the apparent significance of certain micro-zooplankton in this area. Hedin (1976) reported concentrations of tintinnids for the Swedish west coast averaging 10 to 15 l^{-1}. Similar concentrations were found in the Arabian Sea (Zeitzschel, 1969). The North Atlantic Ocean (Zeitzschel, 1967) has also been studied with additional partial surveys carried out for the Northwest Atlantic Ocean (Fornshell, 1979) and North Sea (Lindley, 1975). Concentrations of tintinnids in the California current of about 50 l^{-1} were reported (Beers and Stewart, 1967), with 40 to 200 l^{-1} encountered in the eastern tropical Pacific Ocean (Beers and Stewart, 1971). Beers et al. (1980) carried out additional research in southern California nearshore waters. Tintinnid concentrations as high as 18,000 l^{-1} were reported for the southern California Bight (Heinbokel and Beers, 1979). Concentrations of 100 to 1,000 individuals l^{-1} were observed in the Peruvian coastal waters (Beers et al., 1971). Tintinnid densities in the eastern Mediterranean Sea reaching 30,000 l^{-1} were found by Vitiello (1964), demonstrating the extremely high concentrations these organisms can reach in the field.

Until recently, little information on tintinnid composition and abundance could be found for the coastal regions of the eastern United States. Gold and Morales (1975) presented a qualitative analysis of the tintinnids of the New York Bight over a yearly cycle. Hargraves (1981) reported data on abundance and species composition over several months for Narragansett Bay, Rhode Island. While the data for the areas discussed

*Contribution No. 330 of the Marine Sciences Research Center

0171-8630/83/0010/0277/$ 02.00

above are important, little information on temporal variation can be found.

Theoretical calculations, based on numerical abundance data and assumptions concerning feeding rates of eastern tropical Pacific micro-zooplankton, suggest that at times these organisms may consume as much as 70 % of the daily phytoplankton organic carbon production (Beers and Stewart, 1971). For Long Island Sound, Riley (1956) estimated that perhaps as much as 43 % of the net carbon fixed annually by photosynthesis may be removed by the micro-zooplankton and bacteria in the water column. Data of Capriulo and Carpenter (1980) for central Long Island Sound indicated that the micro-zooplankton (consisting predominantly of tintinnids) removed up to 41 % of the chlorophyll *a* standing crop per day and, at times, exhibited community ingestion rates equal to those of the copepod community. Heinbokel and Beers (1979), using data from Heinbokel (1978a, b), estimated that the tintinnids in the Southern California Bight were capable of ingesting approximately 4 % to 20 % of the daily primary production.

This paper is concerned with enhancement of the current understanding of tintinnid community structure in Long Island Sound. Abundance and species composition of tintinnids measured at a central Long Island Sound station from July 1979 through October 1980 are presented in relation to associated phytoplankton abundance and composition. These data, along with information on ingestion rates of field collected tintinnids feeding on natural food (Capriulo, 1982) and data on copepod abundance and feeding in Long Island Sound, are used to quantify and compare the grazing impact of these two important groups of herbivores.

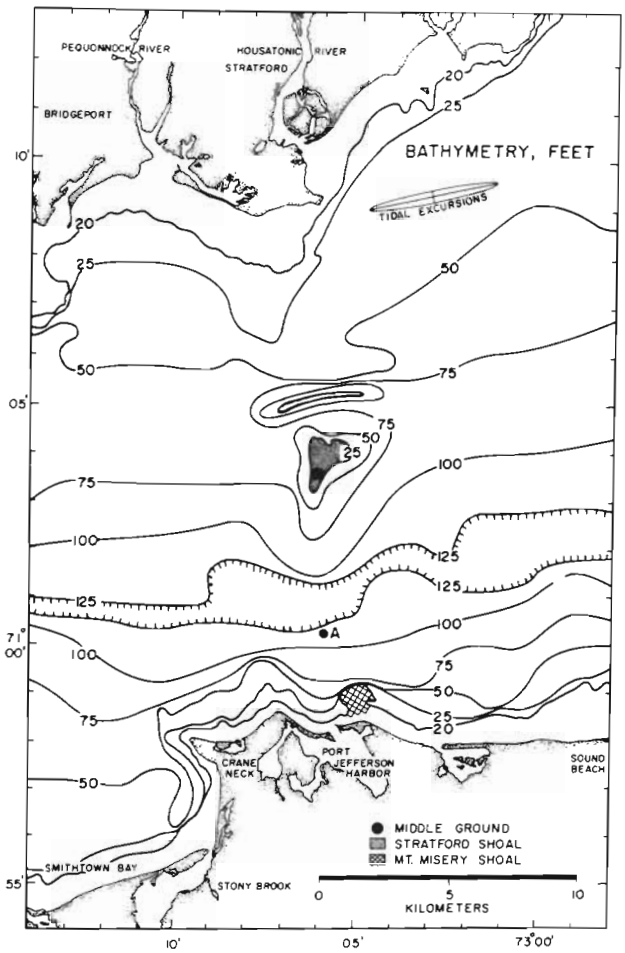

Fig. 1. Study area (Station A), located 3.6 km outside of Port Jefferson Harbor (water 31 m deep) in central Long Island Sound

MATERIALS AND METHODS

This study was conducted as part of a larger endeavor which included the measurement of ingestion rates of field-collected tintinnids feeding on natural food (Capriulo, 1982) and a comparison of the feeding activities of field-collected tintinnids and copepods fed identical natural food (Capriulo and Ninivaggi, 1982). All sampling was carried out at a station in Long Island Sound (Station A, Fig. 1) in water 31 m deep. Water samples were collected from 1 and 5 m depths in 10 l Niskin bottles and from the surface in plastic buckets. The temperature of all samples was recorded.

Particle-size/biomass distributions were determined by means of a Particle Data Inc.® automated electronic counting system consisting of a high resolution 128 channel analyzer interfaced with a PDP8 computer. Calibrated 190 and 380 µm orifice tubes were utilized and the resulting data sets blended. Some of the limitations imposed by the use of particle counters are discussed in Capriulo (1982) and Capriulo and Ninivaggi (1982).

Subsamples of the counted material were fixed with Lugol's solution and later analyzed microscopically to determine both phytoplankton and micro-zooplankton composition. For the phytoplankton, 15 ml of 100 ml subsamples were centrifuged for several hours, concentrating the cells in a final volume of 1 ml. The 1 ml concentrate was introduced into a Sedgwick-Rafter cell and random strips were analyzed, at 500× magnification, to determine species composition and abundance. Counting error was estimated according to the method of Lund et al. (1958). For the micro-zooplankton, 2.5 l of sample were fixed, placed in graduated cylinders and allowed to settle for several days. The supernatant was removed by aspiration until a final volume of 100 ml was achieved. Of this concentrated sample 25 to 50 ml were centrifuged at 100×

Table 1. Species abundance and composition of tintinnids at Station A in Long Island Sound from August 1979 through October 1980. Total ciliate abundance is presented at bottom (ind. l^{-1}) ± the approximate 95 % confidence intervals. Numbers in columns are percentages of total tintinnid numbers. Relative abundance from low (+) to high (+ + +) is also presented for organisms which could not be enumerated accurately

Date and total tintinnid abundance	Aug 9 **1979** 7.61 × 10^3 ±15%	Aug 22 2.80 × 10^2 ±40%	Sep 5 2.91 × 10^2 ±49%	Sep 24 1.85 × 10^3 ±20%	Oct 4 7.70 × 10^2 ±31%	Oct 31 5.89 × 10^2 ±40%	Nov 7 4.29 × 10^2 ±40%	Nov 28 1.11 × 10^3 ±27%	Dec 12 4.00 × 10^2 ±49%	Jan 8 **1980** 9.09 × 10^2 ±38%	Jan 22 1.60 × 10^3 ±29%	Feb 11 7.41 × 10^2 ±46%	Mar 20 9.77 × 10^2 ±34%	Apr 15 3.67 × 10^2 ±45%	May 9 2.68 × 10^2 ±50%	Jun 3 4.47 × 10^2 ±50%	Jun 25 7.94 × 10^2 ±36%	Jul 24 5.50 × 10^3 ±18%	Aug 7 1.26 × 10^4 ±20%	Sep 24 8.09 × 10^2 ±40%	Oct 7 1.80 × 10^3 ±25%	Oct 17 1.01 × 10^3 ±30%
Tintinnid species																						
Favella ehrenbergii																	<20 l^{-1}	<20 l^{-1}				
Helicostomella subulata	0.4																					
Metacylis annulifera															6.7	5.9						
Stenosemella nivalis																				3.4		
Stenosemella oliva				3.4	2.5	7.1	3.6	3.6	10.5	15.6	21.7	22.7	3.4	30.4			2.7		0.9	6.9	3.7	7.0
Stenosemella steini				1.1					31.6	15.6	2.2			4.3								2.3
Titinnidium fluviatile	+		+ +	+	+ +								+									
Tintinnopsis acuminata		3.5		9.1	22.5	7.1	25.0	21.8	5.3	6.2	15.2	18.2	10.3	8.7	20.0		13.5	0.5	1.3	20.7	17.1	7.0
Tintinnopsis baltica		7.1						1.8		12.5			6.9			5.9	5.4	0.5				16.3
Tintinnopsis beroidea			26.3			7.1	7.1	23.6	21.1	28.1	15.2	18.2	13.8	13.0	6.7		10.8	0.5	1.5		3.7	
Tintinnopsis incurvata				1.1																		
Tintinnopsis karajacensis						3.6																
Tintinnopsis minuta	98.9	28.6	73.7	75.0	60.0	46.4	39.3	32.7	10.5		6.5	4.5	13.8	4.3	20.0	82.4	48.6	97.4	95.7	34.5	64.6	51.2
Tintinnopsis nana				6.8	10.0	3.6	3.6		5.3			9.1	3.4			5.9				6.9	4.9	7.0
Tintinnopsis nucula				1.1																3.4		
Tintinnopsis parva	0.4	57.1			2.5	17.9	10.7	3.6		12.5	13.0	9.1	13.8	8.7	13.3			0.5	0.4	3.4	2.4	4.7
Tintinnopsis rapa						3.6		1.8	10.5		2.2	4.5		8.7							1.2	
Tintinnopsis tubulosa		3.5					3.6	7.3		6.2	4.3	9.1							<20 l^{-1}	3.4		
Tintinnopsis tubulosoides				2.3						3.1					6.7					3.4		
Tintinnopsis urnula																				3.4		2.3
Tintinnopsis vasculum													20.7	17.4	6.7							
Tintinnopsis ventricosoides					2.5	7.1		3.6	5.3		10.9	4.5			13.3		2.7	0.5	0.2	10.3	1.2	2.3
Unidentified tintinnid	0.4						3.6				8.7		13.8	4.3								
Unidentified hyaline tintinnid															6.7		16.2				1.2	
Non-tintinnid ciliates (ind. l^{-1})																						
Unidentified naked ciliates		50	229				92	20						32	6442	1474	472					
Strombilidium sp.																3158	21					
Unidentified rotifers																	+ + +					
Total ciliate abundance	7.61 × 10^3 ±15%	3.30 × 10^2 ±36%	5.20 × 10^2 ±36%	1.85 × 10^3 ±20%	7.70 × 10^2 ±31%	5.89 × 10^2 ±40%	5.21 × 10^2 ±36%	1.13 × 10^3 ±27%	4.00 × 10^2 ±49%	9.09 × 10^2 ±38%	1.60 × 10^3 ±29%	7.41 × 10^2 ±46%	9.77 × 10^2 ±34%	3.99 × 10^2 ±45%	6.71 × 10^3 ±30%	5.08 × 10^3 ±20%	1.29 × 10^3 ±27%	5.50 × 10^3 ±18%	12.56 × 10^4 ±20%	8.09 × 10^2 ±40%	1.80 × 10^3 ±25%	1.01 × 10^3 ±30%

gravity for about 2 h. Again the supernatant was drawn off until 1 ml remained. The concentrate was then introduced into a Sedgwick-Rafter cell and analyzed as outlined above for the phytoplankton.

RESULTS

Tintinnid Species Abundance and Composition

Total tintinnid abundance in the upper 1 m of water at Station A, in central Long Island Sound, varied from 268 to 12600 l^{-1} throughout the year, with 24 species in all having been encountered (Table 1, Fig. 2). The highest concentrations (5500 to 12600 individuals l^{-1}, for both years of this study occurred during July and August during the temperature maximum (Fig. 2). Tintinnid composition on these occasions was completely dominated (96 % to 99 %) by the small tintinnid *Tintinnopsis minuta* (13 μm wide and ≃ 18 μm long). Ciliates other than tintinnids occasionally were predominant with highest concentrations (= 6000 l^{-1}) observed in May and June just prior to the surge in abundance of *T. minuta* in July (Fig. 2, Table 1). In addition, rotifers, which did not preserve well and therefore could not be quantified, were found to be the dominant small grazers at times.

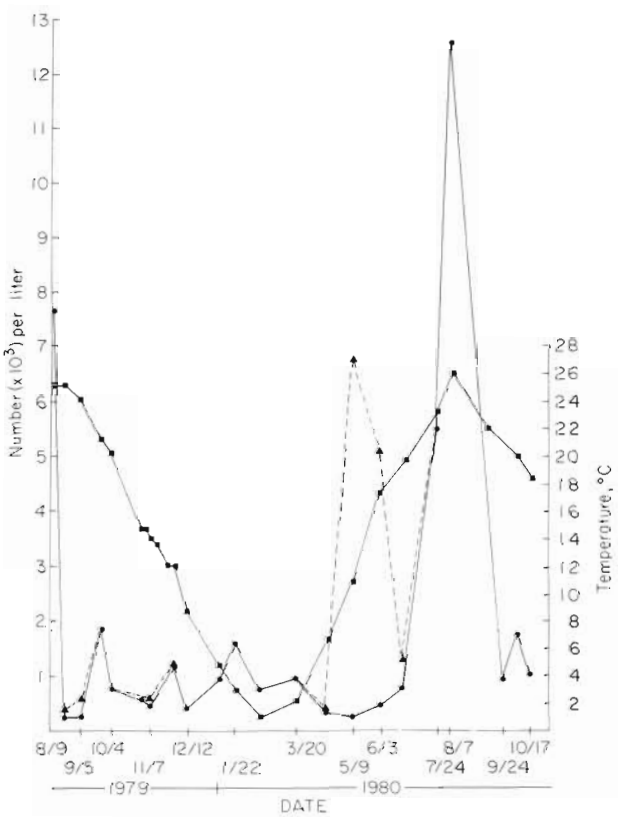

Fig. 2. Profile of total tintinnid abundance (solid circles), total ciliate abundance (solid triangles) and surface-water temperature (solid squares) at Station A in Long Island Sound (August 1979 to October 1980)

Phytoplankton Species Abundance and Composition

The seasonally shifting particle spectrum (Fig. 3) and corresponding phytoplankton species composition (Table 2) show the succession of both food size and type at Station A. The less than 10 μm material for all sampling dates was composed predominantly of various monads (cryptomonads, calycomonads, chroomonads) and other small flagellates. Concentrations of phytoplankton varied from 8×10^4 cells l^{-1} to 4×10^6 cells l^{-1}. Phytoplankton succession followed a general pattern similar to that described by Conover (1956) for Long Island Sound. Diatoms were found through much of the year but attained their highest concentrations in January through April and again in September through October. Dinoflagellates peaked in June and persisted into August. The nanoplankton reached their highest concentrations from May through August with peaks also occurring in winter (Table 2).

Correlation Between Tintinnid and Phytoplankton Abundance

Tintinnid density (Fig. 4) and size (Fig. 5) were found to be unrelated to the size of the food material comprising the biomass peaks. Since food must first pass through the oral opening of a lorica before it is ingested, the oral diameter measurement (a conservative property of a tintinnid which varies little within a species) was used to represent size for this analysis.

Although there was some correlation between tintinnid density and phytoplankton density the relationship was weak both when tintinnid abundance was compared to the total concentration of phytoplankton (correlation coefficient r = .31) and when compared to concentration of ≤ 20 μm nanophytoplankton (correlation coefficient r = .20) (Fig. 6). Nanoplankton were present in variable concentration throughout most of the year (Table 2). Analysis of Tables 1 and 2 and Fig. 2 indicates that highest tintinnid concentrations always occurred when nanoplankton were present in high numbers (≥ 1.3×10^5 cells l^{-1}; August 9, 1979, January 22, July 24 at 1 m depth, August 7 at 1 m depth, October 7 and October 17, 1980). However, equivalent concentrations of nanoplankton at other times were not accompanied by high tintinnid densities. The occurrence of small food alone, therefore, while necessary is not a sufficient condition for high tintinnid abundance. Analysis of Tables 1 and 2 indicates that the type of

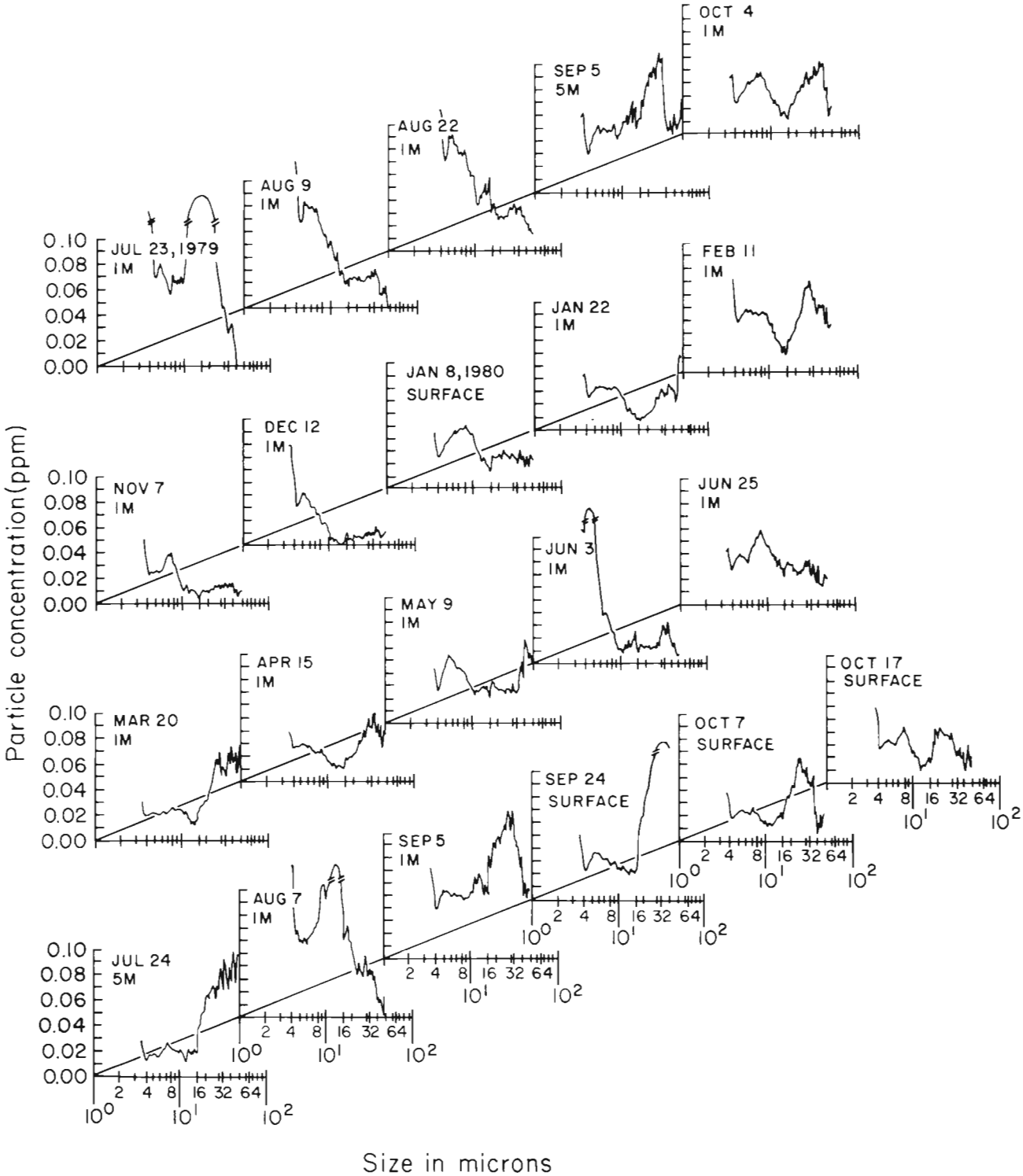

Fig. 3. Particle-size/biomass spectra at Station A from July 1979 through October 1980. Biomass is presented in units of parts per million (ppm) which is equivalent to a particle volume of 1μm^3 m^{-3} of seawater. Samples taken from surface, 1 m or 5 m water depth

Table 2. Abundance and composition of phytoplankton species at Station A in Long Island Sound from July 1979 through October 1980. Total number per liter presented at top, with percentage of total by species in the columns for each cruise date. Total counts ± approximate 95 % confidence intervals

Date and total abundance	Jul 23 1979 4.22 × 10^6	Aug 9 1m 1.03 × 10^6	Aug 22 1m 4.38 × 10^5	Sep 5 Surf 4 81 × 10^5	Oct 4 1m 1 16 × 10^5	Nov 7 1m 1.53 × 10^5	Dec 12 1m 1.58 × 10^5	Jan 8 1980 7.92 × 10^4	Jan 22 1m 3.54 × 10^5	Feb 11 1m 4.44 × 10^5	Mar 20 1m 2.51 × 10^5	Apr 15 1m 2.96 × 10^5	May 9 1m 3.01 × 10^5	May 9 5m 3.80 × 10^5	Jun 25 1m 2 72 × 10^5	Jun 25 5m 2 59 × 10^5	Jul 24 1m 2.90 × 10^5	Jul 24 5m 3 64 × 10^5	Aug 7 Surf 4.17 × 10^5	Aug 7 1m 5.54 × 10^5	Aug 7 5m 4.65 × 10^5	Sep 5 1m 1.15 × 10^6	Sep 5 5m 1 62 × 10^6	Sep 24 Surf 1.46 × 10^6	Oct 7 Surf 7.50 × 10^5	Oct 17 Surf 3.91 × 10^5
Phytoplankton species	±8%	±18%	±22%	±21%	±32%	±26%	±23%	±32%	±19%	±22%	±21%	±20%	±20%	±19%	±20%	±29%	±25%	±23%	±22%	±22%	±22%	±20%	±15%	±15%	±19%	±22%
Prorocentrum redfieldi															16.5	32.7	1.8		6.3	2.9	2.2		0.3			1.4
Prorocentrum micans	81.8	0.5	8.4														1.8				8.0	0.5	0.3			
Prorocentrum minimum	1.4	2.1	19.2	11.0		1.7									9.7	10.2			36.7	40.0	1.1	0.9	0.3	0.7		
Prorocentrum scutellum	0.2			3.3	4.5	1.7																				
Dinophysis sp.										1.2																
Dinophysis acuminata												0.9						4.3								
Dinophysis ovata											1.1											1.3				1.4
Peridinium triquetum	0 1														7.8	24.5										
Peridinium sp.												0.9											1.6			
Peridinium trochoideum															3.9	4.1						0.9				2.7
Gyrodinium estuariale																	5.5	4.3	3.8	1.0						
Gyrodinium sp.	0.1	1.5															5.5			7.6						5.4
Gyrodinium spirale															1.0											
Gyrodinium dominans					2.3																			0.4		
Gymnodinium sp. (20 × 20 µm)													0.9		2.9						3.4					
Gymnodinium nelsoni																									0.7	
Katodinium rotundatum		0.5							4.5				0.9	0.7						1.0						
Unidentified dinoflagellate																			6.3							
Gyrosigma sp.																					3.4			0.4		
Polykrikos sp. (35 × 35 µm)									0.7				0.9													
Pleurosigma sp. (60 × 20 µm)																						0.9	1.0			
Eutreptia sp.						1.7																				4.1
Olisthodiscus lutens		6.7		2.2	19.9				0.7							4.1		2.9			17.0					
Olisthodiscus sp. (14 × 8 µm)																			8.9							
Asteromphalis sp. (75 µm)																							0.3			
Guinardia flaccida																							0.3			
Actinoptychus sp. (55 µm)										1.2																
Thalassionema nitzschioides		1.0				32.8	10.0	62.2	47.8	50.0	21.1	17.9	17.5	15.3		2.0	5.5	7.2	8.9	6.7	28.4	10.1				
Thalassiosira decipiens																						1.3				
Thalassiosira sp. (18 × 10 µm)									5.2		44.2												1.0			8.1
Thalassiosira nordenskioldii										1.2																
Thalassiosira rotula															4.9			1.4								
Thalassiosira nana																		4.3								1.4
Thalassiosira pseudonana						3.4			0.7			0.9			2.9		9.1			1.0	14.8					0.7	
Skeletonema menzilii				59.3	13.6					10.7																
Skeletonema costatum										2.4							5.5					77.4	83.4	2.9	47.9	
Coscinodiscus lineatus		1.0						4.4		5.9						2.0					1.1	1.3	1.6	0.4		
Rhizosolenia delicatula							8.3		3.0		11.6	7.1	0.9		8.7	8.2					3.4				0.7	

Melosira sulcata								33.3					4.4													
Cyclotella sp.					52.3		3.3									6.1	9.1					0.9				
Cyclotella closterium																	5.5	13.0			2.2	1.8	0.3	0.4	0.7	
Nitzschia seriata																								10.1	0.7	
Asterionella japonica												3.6			1.0			1.4								
Stephanopyxis turris																							1.0	3.3		
Chaetoceros sp. (20×10 μm)																6.1		1.4						77.5	20.4	
Ditylum brightwellii																	7.3	17.4								
Leptocylindrus minimus																		2.9								
Leptocylindrus danicus																		2.9				0.5	0.3			
Lithodesmium undulatum																						1.3				
Pseudopedinella pyriformis										1.2		30.4														2.7
Unidentified pennate (5×30 μm)																							2.3			
3–6 μm chlorophytes							75.0											13.0								
1 μm small forms																		4.3								
Chroomonas amphioxeia		0.5							26.1				37.7	41.7				1.4			9.1	0.5	5.5		11.6	47.3
Chroomonas minuta												5.4	36.8	40.3			3.6			1.9			1.0	4.0	10.6	13.5
Cryptomonads (5×20 μm)		24.6	4.8	9.9	11.4	55.2	3.3		1.4	14.3	3.2	5.4			22.3		36.4	15.9	13.9	14.3	5.7					
Calycomonas ovalis			48.2	14.3							18.9															
3–10 μm flagellates	16.3	61.0	16.9			3.4			4.5	11.9		27.7		2.1	13.6				15.2	23.8					2.1	
Ochromonas oblongata									5.2																	
Pyramimonas sp. (20×20 μm)															4.9		3.6	1.4								12.1

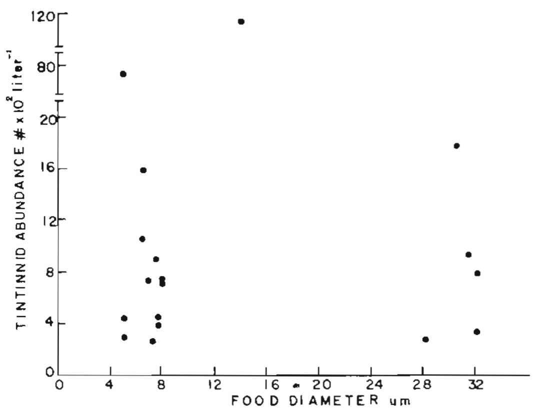

Fig. 4. Tintinnid abundance (number $\times 10^2$ cells l^{-1}) as a function of the size (equivalent spherical diameter) of the natural food-biomass peak

small food does not appear to be critical for high tintinnid densities, since several food spectra, dominated by different nanoplankters, all supported tintinnid densities in the 10^3 l^{-1} range.

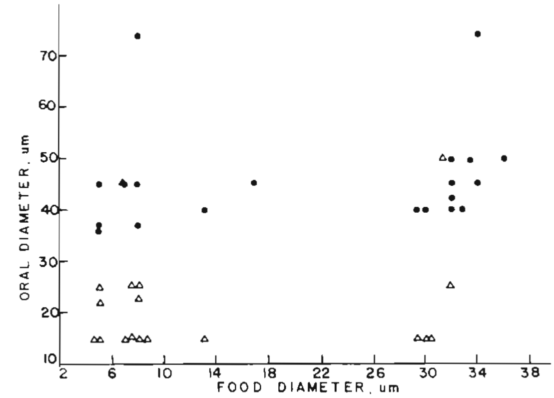

Fig. 5. Tintinnid oral diameter as a function of the size of the natural food-biomass peak (circle: largest, triangle: most abundant tintinnid species)

DISCUSSION

Phytoplankton and Tintinnid Species Abundance and Composition

The gross pattern of phytoplankton succession observed in this study is similar to that pattern described for central Long Island Sound by Conover (1956) in her earlier study of Long Island Sound phytoplankton. In general there is a characteristic spring diatom bloom (January or February) followed by nanoplankton and later (June and July) dinoflagellate blooms, with an additional fall (September through October) diatom bloom.

A finer scale comparison of species composition also

shows strong similarities. Similar patterns of occurrence were observed for *Rhizosolenia delicatula, Thalassiosira decipiens, Melosira sulcata, T. nordenskioldii, Asterionella japonica, Thalassionena nitzschioides, Peridinium trochoideum* and *Prorocentrum scutellum*. However, many of the species clas-

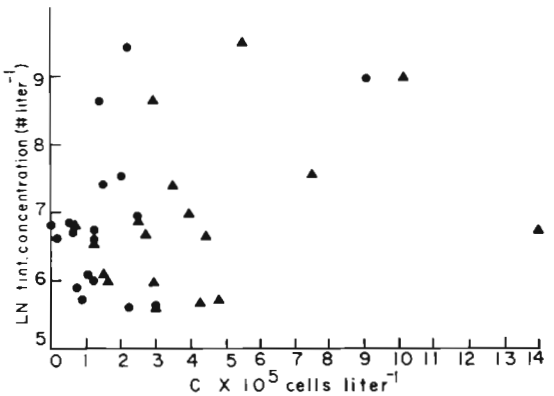

Fig. 6. Natural logarithm of tintinnid abundance (no. l^{-1}) versus total phytoplankton (solid triangles) and less than or equal to 20 μm phytoplankton (solid circles) concentration (C) in units of 10^5 cells l^{-1} Correlation coefficients for the 2 relationships are r = .31 and r = .20, respectively

sified by Conover as major species were not encountered in this study. For example, *Cerataulina pelagica*, several species of *Chaetoceros, Asterionella formosa, Corethron criophilum, Lauderia borealis, Rhizosolenia fragilissima, Schroderella delicatula, Thalassiosira gravida, Nitzschia longissima, Exuviella apora* and *Peridinium elongatum* were not observed.

The seasonal pattern of tintinnid abundance reported here, with a range of 2.68×10^2 to 1.26×10^4 tintinnids l^{-1}, is similar to that found in Narragansett Bay (Hargraves, 1981). In all, 28 species (4 additional species, *Tintinnopsis dadayi, T. levigata, Tintinnus pectinis* and *Proplectella* sp., were also found in Long Island Sound at times not covered by this study) have been encountered. This compares with 32 species reported for Narragansett Bay (Hargraves, 1981) and 34 species for the New York Bight (Gold and Morales, 1975). The greatest species diversity for the New York Bight was found in October with high diversity, with the exception of December, occurring from late September through May. These findings are similar to those of this study where diversity was high between September and April. This contrasts with Hargrave's findings of highest diversity in summer (July and August) in Narragansett Bay. *Tintinnopsis minuta* was the dominant tintinnid in July and August for all 3 study areas. This species persisted through October and November, although in reduced numbers, for both Long Island Sound and Narragansett Bay, while being observed only through August in the New York Bight.

The species encountered in Long Island Sound were similar to those of the New York Bight and Narragansett Bay regions. *Stenosemella ventricosa, Tintinnopsis kofoidii, T. platensis* and *T. undella* were found both in the New York Bight and Narragansett Bay but not in Long Island Sound. In addition, *T. fimbriota, T. sufflata* and *Helicostomella fusiformis* were found in Narragansett Bay and *Favella arcuata, Metacylis angulata, Ptychocylis obtusa, Parafavella gigantea, P. parumdentata, Parundella* sp. and *Coxliella* sp. in New York Bight but not in Long Island Sound. The same 5 species (*Stenosemella nivalis, Tintinnopsis incurvata, T. nana* and *Proplectella* sp.) were present in Long Island Sound samples but not in either the New York Bight or

Table 3. Yearly volume ingestion rates for copepods of central Long Island Sound. Copepod abundance taken from Figs. 3 and 5 of Deevey (1956). Ingestion rates assigned as described in text. A copepod abundance (# m^{-3}); I ingestion rate × 10^6 μm^3 copepod^{-1} d^{-1}; V average daily ingestion rate × 10^{10} μm^3 by species for the appropriate season. Winter = December, January, February (90 d); spring = March, April, May (92 d); summer = June, July, August (92 d); fall = September, October, November (91 d)

Copepod species	Winter			Spring			Summer			Fall		
	A	I	V	A	I	V	A	I	V	A	I	V
Acartia clausi	4,920	19	9.35	23,914	20	47.8	9,900	28	27.70	0	0	0
Acartia tonsa	3,693	9	3.32	300	40	1.2	18,500	40	74.00	13,393	9	12.00
Temora longicornis	1,653	18	2.97	8,116	30	24.0	11,400	50	57.00	0	0	0
Pseudocalanus minutus	2,897	12	3.48	2,003	17	3.4	200	14	0.28	0	0	0
Paracalanus crassirostris	1,540	5	0.77	0	0	0	16,500	6	9.90	13,793	6	8.23
Oithona sp.	4,297	5	2.15	0	0	0	3,500	6	2.10	18,814	6	11.30
Total seasonal ingestion		1.98 × 10^{13}			7.03 × 10^{13}			1.57 × 10^{14}			2.87 × 10^{13}	

Year total = 2.76×10^{14}

Table 4. Yearly volume ingestion rates for tintinnids of central Long Island Sound. Tintinnid abundance from present study. Ingestion rates from regression equation of Fig. 21, Capriulo (1982). A tintinnid abundance (# m^{-3}); I ingestion rate × 10^6 μm^3 tintinnid^{-1} d^{-1}; V average daily ingestion rate × 10^{10} μm^3 by species for the appropriate season. Seasons divided as in Table 3

Tintinnid species	Winter			Spring			Summer			Fall		
	A	I	V	A	I	V	A	I	V	A	I	V
Stenosemella oliva	151,569	0.42	6.37	72,393	0.42	3.04	16,173	0.42	0.68	38,956	0.42	1.64
S. steini	71,634	0.35	2.51	5,260	0.35	0.18	0	–	–	4,197	0.35	0.15
Tintinnopsis acuminata	101,947	0.05	0.51	62,053	0.05	0.31	46,320	0.05	0.23	144,982	0.05	0.72
T. beroidea	156,192	0.34	5.31	66,831	0.34	2.27	44,459	0.34	1.51	60,725	0.34	2.06
T. minuta	59,782	0.23	1.38	68,069	0.23	1.60	4.1×10^6	0.23	94.30	498,863	0.23	11.47
T. nana	29,544	0.23	0.68	11,073	0.23	0.25	4,396	0.23	0.10	44,179	0.23	1.02
T. rapa	36,848	0.38	1.40	10,643	0.38	0.40	0	–	–	6,947	0.38	0.26
T. vasculum	0	–	–	94,684	0.08	0.76	0	–	–	0	–	–
T baltica	37,875	0.37	1.40	22,471	0.37	0.83	22,917	0.37	0.85	12,365	0.37	0.46
T. parva	76,081	1.30	9.90	67,466	1.30	8.77	35,913	1.30	4.67	35,413	1.30	4.60
T. tubulosa	43,336	0.37	1.60	0	–	–	3,311	0.37	0.12	25,248	0.37	0.93
T. tubulosoides	9,393	0.38	0.36	5,985	0.38	0.23	0	–	–	7,784	0.38	0.30
T. ventricosoides	69,955	0.38	2.66	11,881	0.38	0.45	15,540	0.38	0.59	24,794	0.38	0.94
Unid. tint.	46,400	0.28	1.30	50,202	0.28	1.41	3,382	0.28	0.09	2,574	0.28	0.07
Metacylis annulifera	0	–	–	5,985	0.34	0.20	4,395	0.34	0.15	0	–	–
Unid. hyaline tint.	0	–	–	5,985	0.14	0.08	21,438	0.14	0.30	1,800	0.14	0.03
Favella ehrenbergii	0	–	–	0	–	–	10,000	0.17	0.17	0	–	–
Helicostomella subulata	0	–	–	0	–	–	3,383	0.81	0.27	0	–	–
Stenosemella nivalis	0	–	–	0	–	–	0	–	–	3,056	0.34	0.10
Tintinnopsis incurvata	0	–	–	0	–	–	0	–	–	2,261	0.39	0.09
Tintinnopsis nucula	0	–	–	0	–	–	0	–	–	5,317	0.38	0.20
Tintinnopsis urnula	0	–	–	0	–	–	0	–	–	4,993	0.37	0.18
Tintinnopsis karajacensis	0	–	–	0	–	–	0	–	–	1,767	0.39	0.07
Total seasonal ingestion	3.18×10^{13}			1.91×10^{13}			9.57×10^{13}			2.30×10^{13}		
Year total = 1.7×10^{14} μm^3												

Narragansett Bay. Also, *T. levigata* was found in Long Island Sound and not in Narragansett Bay. Only 1 specimen of *T. incurvata* was observed and therefore the identification cannot be considered conclusive. *Ptychocyles, Coxliella* and *Parundella* are typical coastal forms and their absence from an estuary is not unusual. The boundaries between species are sometimes very ambiguous. *Helicostomella subulata* and *H. fusiformis* are considered by some to be synonymous (Hargraves, 1981). In addition, *T. beroidea, T. minuta, T. nana, T. parvula* and *T. rapa* may be variations of the same species (Baker and Phaff, 1976), as may be the case for *T. lobiancoi, T. tubulosa, T. karajacensis* and *T. tubulosoides*. Similar problems of identification are encountered in the genera *Favella* (Laval-Peuto, 1981) and *Ptychocylis* (Davis, 1981). These problems in taxonomy may account for some of the differences in species lists from different areas.

This study, along with those of Vitiello (1964), Beers and Stewart (1967), Heinbokel and Beers (1979), Capriulo and Carpenter (1980), Hargraves (1981) and Margalef (1982), demonstrates that the concentrations of tintinnids found in the coastal zone are substantially higher than those reported for the open ocean. One reason for this difference may be cell sinking. The tintinnid lorica (particularly agglutinated types which have large amounts of attached nonbiogenic and biogenic particles; Gold and Morales, 1976) adds substantial weight to these organisms (Margalef, 1982) thus increasing their sinking rates (increased weight and associated sinking may represent an evolutionary adaptation affording tintinnids a means of escape from predation, Capriulo et al., 1982). It is possible that the high advective energy associated with coastal waters counteracts sinking to some extent by keeping tintinnids in suspension for longer periods of time than would be possible in less turbulent open ocean waters. In this way, tintinnids may survive better by remaining in the euphotic zone with the phytoplankton on which they feed. Since decreases in tintinnid abundance offshore are accompanied by decreases in phytoplankton concentrations (Beers et al., 1980) the above hypothesis cannot yet be confirmed. Verification awaits an analysis of the ratio of aloricate ciliate concentration to tintinnid concentration as a function of water column mixing intensity. Since aloricate ciliates are not as dependent on turbulence for maintenance of water column position as are their heavier relatives, their abundance should increase relative to the tintinnids, in low turbulence environments.

Table 5. Measurements of width (oral diameter, OD) and length (μm) for all tintinnids encountered in this study. Lorica volume calculated assuming a half ellipsoid shape. Animal volume assumed to be equal to half the lorica volume with a specific weight of 1 (Beers and Stewart, 1969; Hedin, 1976). Dry weight assumed to equal 20 % wet weight (Cushing et al., 1958)

Tintinnid species	OD (μm)	L (μm)	Lorica volume (μm^3)	Animal volume (μm^3)	Wet wt. (μg)	Dry wt. (ng)
Favella ehrenbergii	75	200	5.89×10^5	2.9×10^5	.290	58.0
Helicostomella subulata	22	250	6.33×10^4	2.1×10^4	.021	4.2
Metacylis annulifera	21	40	9.20×10^3	4.6×10^3	.005	1.0
Stenosemella nivalis	21	40	9.20×10^3	4.6×10^3	.005	1.0
S. oliva	25	50	1.64×10^4	8.2×10^3	.008	1.6
S. steini	25	60	6.08×10^4	3.0×10^4	.030	6.0
Tintinnidium fluviatile	45	95	1.00×10^5	5.0×10^4	.050	10.0
Tintinnopsis acuminata	22	35	8.90×10^3	4.4×10^3	.004	0.8
T. baltica	36	60	4.10×10^4	2.1×10^4	.021	4.2
T. beroidea	23	34	9.40×10^3	4.7×10^3	.005	1.0
T. incurvata	24	90	2.70×10^4	1.4×10^4	.014	2.8
T. karajacensis	25	100	3.30×10^4	1.6×10^4	.016	3.2
T. minuta	15	30	3.50×10^3	1.8×10^3	.002	0.4
T. nana	16	24	3.20×10^3	1.6×10^3	.002	0.4
T. nucula	29	45	2.04×10^4	1.0×10^4	.010	4.0
T. parva	25	38	1.20×10^4	6.0×10^3	.006	1.2
T. rapa	25	50	1.60×10^4	8.0×10^3	.008	1.6
T. tubulosa	37	60	4.30×10^4	2.1×10^4	.021	4.2
T. tubulosoides	37	46	3.30×10^4	1.7×10^4	.017	3.4
T. urnula	42	50	4.60×10^4	2.3×10^4	.023	4.6
T. vasculum	48	60	7.20×10^4	3.6×10^4	.036	7.2
T. ventricosoides	38	50	3.80×10^4	1.9×10^4	.019	3.8
Unid. tint.	22	24	6.00×10^3	3.0×10^3	.003	0.6
Unid. hyaline tint	15	19	2.20×10^3	1.1×10^3	.001	0.2

Relative Importance of Tintinnid and Copepod Ingestion

A first approximate comparison of the yearly ingestion rate of the tintinnids and copepods of central Long Island Sound can be made, using tintinnid abundance data presented in this study (Table 1) and the abundance data for copepods in central Long Island Sound presented by Deevey (1956: Figs. 3 and 5). To accomplish this, a year was broken up into 4 seasons as follows: winter including December, January and February (total of 90 d); spring including March, April and May (total of 92 d); summer including June, July and August (total of 92 d); fall including September, October and November (total of 91 d). Individual species concentrations were averaged over each 3 mo season to give an average season abundance value per species per m^3 (Table 3 for copepods, Table 4 for tintinnids). Ingestion rates were then assigned to each species.

Data on copepod ingestion rates, based on particle volume food concentrations found in this study, were extracted from O'Connors et al. (1976) for *Acartia clausi*, from the data of Capriulo and Ninivaggi (1982) for *Acartia tonsa*, from O'Connors et al. (1980) for *Temora longicornis* and from Mayzaud and Poulet (1978) for *Oithona sp.* and *Pseudocalanus minutus*. Ingestion rates for *Paracalanus crassirostris*, a copepod similar in size to *Oithona similis*, were estimates from rates reported for *O. similis* by Mayzaud and Poulet (1978). Tintinnid ingestion rates were taken from the weight specific ingestion rate versus dry body weight regression equation of Fig. 21 of Capriulo (1982). Tintinnid body weights were taken from the calculated weights of Table 5. It was assumed that dry weight is equal to 20 % wet weight and that specific weight is equal to 1 (Cushing et al., 1958; Beers and Stewart, 1969; Hedin, 1976). Appropriate ingestion rates are presented in Table 3 for copepods and in Table 4 for tintinnids.

Daily ingestion rates for all species studied were summed for each season and then multiplied by the number of days corresponding to that season. Summation of the 4 seasonal totals was then carried out (Tables 3 and 4 for copepods and tintinnids, respectively). Comparison of the yearly totals, 2.8×10^{14} um μm^3 ingested per m^3 for copepods and $1.7\times10^{14}\mu m^3$ per m^3 for tintinnids, demonstrates that both groups are removing the same order of magnitude amount of food and in fact differ by only a factor of 1.6. Conversion of these estimates to units of carbon (using conversion of Parsons et al., 1967) indicates that about 9.2 and 15 g C $m^{-3}yr^{-1}$ are being removed by the tintinnids and copepods of central Long Island Sound. Riley's esti-

mate (1956) of Long Island Sound's primary production (currently the best available estimate) suggests a rate of 34 g C fixed m^{-3} yr^{-1} (assuming a 6 m euphotic zone; Capriulo and Carpenter, 1980). Thus, the tintinnids and copepods of central Long Island Sound are removing about 27 % and 44 % of the annual primary production, respectively.

It should be pointed out that *Tintinnidium fluviatile*, at times during the summer quite abundant, was not included in these calculations since poor preservation prevented estimation of precise numerical abundance. Inclusion of this large-sized species in the above calculations would have raised the yearly ingestion estimate for the tintinnids. Also, naupliar stage copepods were not considered in the above estimates, nor were ciliates other than tintinnids (which at times reach concentrations as high as 50000 l^{-1} in Long Island Sound surface waters; McManus, unpubl). Lastly, differences exist in the methods of collection of the tintinnids and copepods for abundance estimates. Tintinnids were collected in 10-l Niskin bottles while copepods were collected in vertical tows. How these differences in sample collection might alter the above estimates of yearly ingestion is presently unknown. Unpublished data of G. McManus does, however, indicate that tintinnids are approximately uniformly distributed with depth in central Long Island Sound.

These findings demonstrate that tintinnids are a major herbivore group in central Long Island Sound; they confirm, for a yearly cycle, the findings of Capriulo and Carpenter (1980) that ingestion of phytoplankton by tintinnids is significant relative to the copepod ingestion rate.

Acknowledgements. This research was supported in part by a fellowship from the Jessie Smith Noyes Foundation; by a grant from the Lerner Foundation for Marine Research; by MESA (NOAA); and by a grant from the New York State Department of Environmental Conservation. We wish to thank Drs. J. F. Heinbokel, R. Armstrong, K. Gold and R. Malouf for valuable criticism regarding this work.

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This paper was presented by Dr. M. Levandowsky; it was accepted for printing on October 9, 1982