

# Seasonal distribution of the ciliated protozoa in Kaštela Bay

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Seasonal distribution of the ciliated protozoa was studied in the west part of Kaštela Bay during 1995. These are the first data of the annual distribution of four size categories of non-loricate ciliates and tintinnines in the coastal area of the central Adriatic Sea. The maximum densities of ciliated protozoa were recorded during the spring and autumn, when they could act as important factors of 'top-down' control. Contributions of non-loricate ciliates and tintinnines to the total of ciliated protozoa were 72 and 28%, respectively. The highest density of non-loricate ciliates was registered at the surface in September (1400 ind l<sup>-1</sup>). Annual variability of the non-loricates density was mostly influenced by changes in numbers of the second (10<sup>3</sup>–10<sup>4</sup> μm<sup>3</sup>) and third (10<sup>4</sup>–10<sup>5</sup> μm<sup>3</sup>) size categories and they constituted 86% of the total non-loricate counts. Non-loricates with biovolume <10<sup>3</sup> μm<sup>3</sup> were the most abundant during the colder part of the year while those with biovolume >10<sup>5</sup> μm<sup>3</sup> dominated during the summer. The highest density of tintinnines (718 ind l<sup>-1</sup>) was recorded at 5-m depth in May. Quantitatively, the most important tintinnin species was *Helicostomella subulata*. The results suggest a complex influence of biotic and abiotic factors on the annual distribution of ciliated protozoa.

## INTRODUCTION

Protozoans are an important part of the food web of marine ecosystems, because they participate in transfer of organic matter from bacterioplankton and phytoplankton to large-dimension zooplankton fractions, benthic invertebrates and fish larvae (Bernard & Rassoulzadegan, 1993). The data from the earlier scientific studies show that a fraction of zooplankton, which consist of ciliates, dinoflagellates, microflagellates >50 μm<sup>3</sup> and nauplii, might be consuming as much as 100% of the daily phytoplankton organic-carbon production (Beers & Stewart, 1971; Verity et al., 1993) and the major part of bacterial production as well (Sherr et al., 1986; Krstulović et al., 1995). In addition, as a result of the ciliates rapid generation time, they can respond almost instantaneously to various environmental fluctuations and can act as stabilizers of the water-column community (Capriulo & Carpenter, 1980). Therefore, ciliated protozoa are a very important component in the flow of energy and photosynthetically fixed carbon. Dissolved organic matter, released by phytoplankton, is returned to the main food chain via the 'microbial loop' of bacteria–flagellates–microzooplankton (Azam et al., 1983; Hagström et al., 1988).

The first qualitative and quantitative investigations of tintinnines in the coastal area of the middle Adriatic were organized during four seasonal cruises in 1973 and 1974 (Kršinić, 1980a). The author analysed the data on numerical abundance of tintinnines, their taxonomic composition, seasonal and vertical distribution, dimension of their lorica and hydrographical parameters, which affect the distribution. Seasonal and horizontal distribution of non-loricate ciliates, copepods and their developmental stages and other micrometazoans were also studied (Kršinić,

1982). During these earlier studies some scarce tintinnine species were found in Kaštela Bay, suggesting the particularity of the bay in relation to other unpolluted areas. Since all the earlier studies of microzooplankton in Kaštela Bay were carried out from time to time, methodical observation of the ciliate protozoa abundance appeared necessary. This is the first estimation of annual distribution of tintinnines and four size categories of non-loricate ciliates in the coastal area of the central Adriatic.

## MATERIALS AND METHODS

Sampling was performed on a monthly basis throughout 1995 in the west part of Kaštela Bay (43°31'N 16°19'30"E) (Figure 1). Samples were collected at 5 m depth intervals, between the surface and bottom (20 m) using 5-l Niskin bottles for sampling tintinnines and micrometazoans. The planktonic material was preserved in formaldehyde, final concentration 2.5% previously neutralized with CaCO<sub>3</sub>. Samples were sedimented in the laboratory for 24 h in plastic containers and decanted down to a volume of ~2 l. The remainder was poured into a glass cylinder following the 24 h sedimentation. The excess volume was reduced to approximately 200 ml. Decanting was carried out using a vacuum pump and a slightly curved pipette that removed water from the surface. After 72 h the volume had been reduced from 5 l to 20 ml for microscope studies (Kršinić, 1980b). The organisms were counted in the glass chamber (76×47×6 mm). The material was analysed using an 'Olympus' IMT-2 inverted microscope, under ×100 magnification. The tintinnine species were divided in coastal water and open-sea species as indicated by Kršinić (1980a).

Non-loricate ciliates were sampled with a 1.7 l Nansen bottle. A 100 ml aliquot was used for the analysis. Counting was made under  $\times 200$  magnification. Size of individuals was measured using an ocular micrometer under  $\times 400$  magnification. Non-loricates were also fixed with formaldehyde in the same way as the tintinnines and micrometazoans. The biovolume of non-loricates was calculated by comparing the shape of the plasmatic body of each individual organism to one or more geometrical bodies. After measurement of dimensions, non-loricate ciliates were divided into four size categories: I, biovolume  $< 10^3 \mu\text{m}^3$ ; II, biovolume  $10^3\text{--}10^4 \mu\text{m}^3$ ; III, biovolume  $10^4\text{--}10^5 \mu\text{m}^3$ ; and IV, biovolume  $> 10^5 \mu\text{m}^3$ .

Seawater temperature was measured with a reversible thermometer attached to a Nansen bottle. Salinity was determined in the laboratory by an inductive salinometer (model RS10).

#### Principal component analysis (PCA)

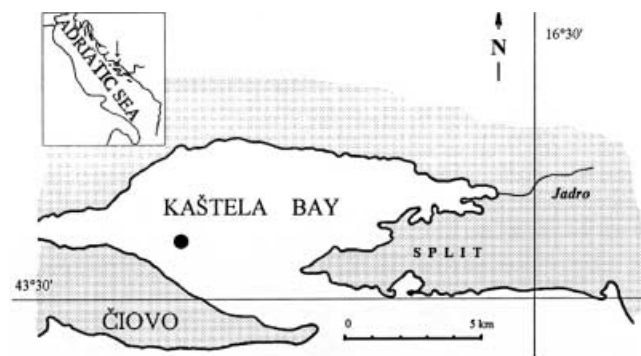
Principal component analysis was used to extract the main patterns of seasonal changes in abundance of ciliated protozoa and some micrometazoan groups. The data input for each analysis consisted of a set of variables representing seasonal fluctuations in abundance. The analyses were all based on correlation matrices involving the standardization of each variable to zero mean and unit variance. The purpose of this is to eliminate differences in abundance between studied groups, leaving only the relative month-to-month changes in abundance.

## RESULTS

### Hydrography

The entire winter period was characterized by homothermy and a gradual temperature increase from 10.4 to 13.5°C. A vertical temperature gradient appeared in May, while the highest temperature gradient of 9.3°C occurred in July. The thermocline disappeared in September when the entire water column had a temperature of 21.8°C. The rest of the year was characterized by decreasing and inversion of temperature (the surface layer had a lower temperature than the bottom layer) (Figure 2A).

Throughout the year, salinity ranged from 33.9 to 38.2 psu. Salinity increased with depth, while the annual fluctuation of salinity for each layer decreased with depth.



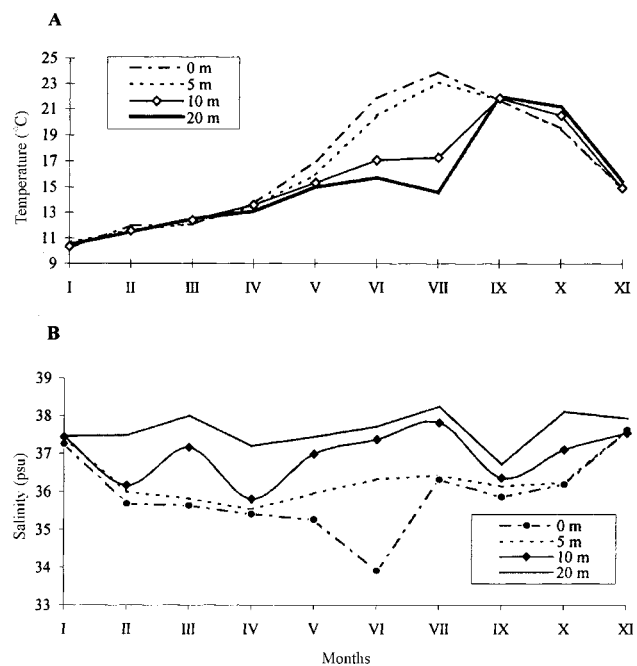
**Figure 1.** Study area (Kaštela Bay) with the sampling station—Trogir.

In November and January all the layers showed almost the same average salinity values between 37.4 and 37.7 psu (Figure 2B). From February on, salinity of the surface layers dropped and in June the highest vertical gradient of salinity of 3.8 psu was recorded.

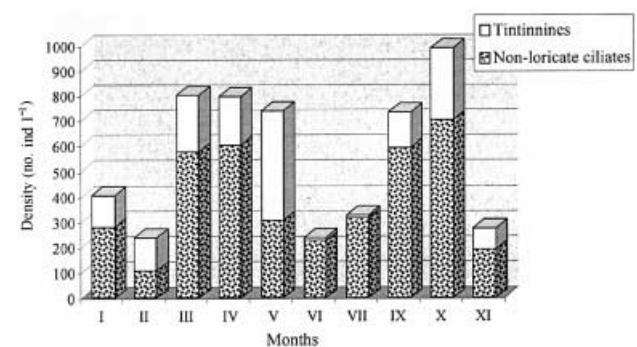
The hydrographic characteristics of Kaštela Bay were affected by the fresh water sources, such as the Jadro River runoff in the eastern part of the bay, the small brook Pantan and submarine springs in the western part of the bay.

### Ciliated protozoans

Annual fluctuations of the ciliated protozoan abundance in the western part of Kaštela Bay showed the highest density from March to May. Another ciliate peak was observed in September and October (Figure 3). During the spring the density value ranged from 205 to 1358 ind l<sup>-1</sup> (in May at 20 and 5 m) with a mean value of  $735 \pm 424$  ind l<sup>-1</sup>, while the values in autumn varied from 292 to 1666 ind l<sup>-1</sup> (in September at surface and 15 m), with mean of  $733 \pm 560$  ind l<sup>-1</sup>. The mean abundance



**Figure 2.** Seasonal changes of temperature (A) and salinity (B) at sampling station in 1995.



**Figure 3.** Seasonal distribution of density of non-loricate ciliates and tintinnines in 1995.

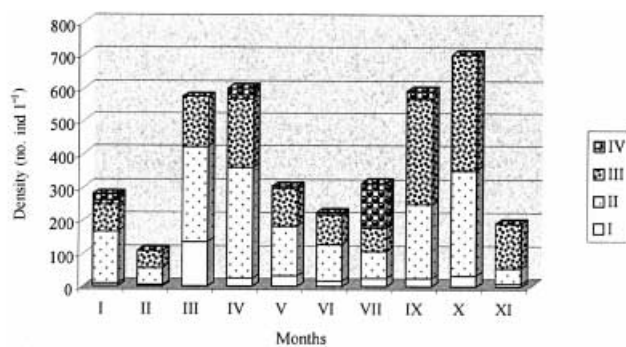
represent average density from all depths. On the other hand, ciliate abundance in the remainder period of the year was lower. Non-loricates were qualitatively more important than tintinnines and their mean contribution throughout the year to the total number of ciliated protozoa was 72 and 28%, respectively. However, tintinnines achieved a greater share, more than 55% of the total ciliate number, in February and May.

*Non-loricate ciliates*

Seasonal distribution of four size categories of non-loricate ciliates is shown in Figure 4. During the colder part of the year the average density of non-loricates was low, especially in February. With the increase in seawater temperature the number of non-loricates increased and in April the first maxima of  $600 \pm 265 \text{ ind l}^{-1}$  was recorded. The spring peak was particularly affected by non-loricate ciliates of the second size category (biovolume  $10^3\text{--}10^4 \mu\text{m}^3$ ) with an average density of  $336 \pm 161 \text{ ind l}^{-1}$ . Their contribution to the total number of non-loricates was 56%. The organisms were dispersed uniformly in the whole water column with a peak density of  $560 \text{ ind l}^{-1}$  at 10 m depth (Figure 5). During the summer the number of non-loricate ciliates dropped and in June was recorded at  $224 \pm 119 \text{ ind l}^{-1}$ . The majority of organisms (71%) remained in the layer above the thermocline. However, the most numerous non-loricates in July were those with a biovolume  $>10^5 \mu\text{m}^3$ , their maxima number of  $640 \text{ ind l}^{-1}$  occurring at the bottom (14.6°C, 38.2 psu) when they formed 43% of the total counts of ciliated protozoa (Figures 4 & 5). The average density of non-loricates increased threefold from July to October when the second maxima of  $702 \pm 540 \text{ ind l}^{-1}$  was recorded. The organisms were the most abundant at the surface in September, with a density of  $1400 \text{ ind l}^{-1}$  (21.7°C, 35.9 psu). During the autumn non-loricates from the third size category (biovolume  $10^4\text{--}10^5 \mu\text{m}^3$ ) prevailed with an average density of  $350 \pm 247 \text{ ind l}^{-1}$  in October. Their highest contribution, 54% of the total non-loricate ciliates count was found in September, with  $640 \text{ ind l}^{-1}$  in the surface layer.

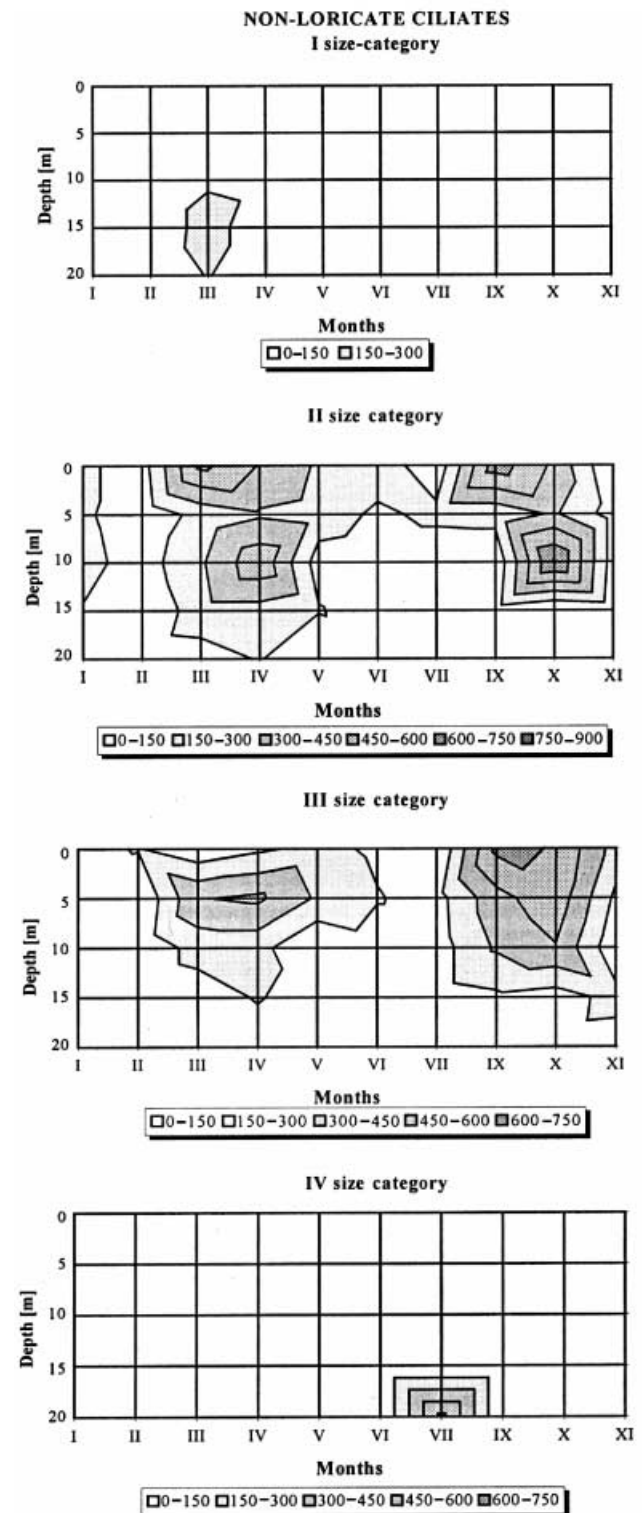
*Tintinnines*

In the investigated part of Kaštel Bay a total number of 35 tintinnine species were found: 18 coastal water and 17 open-sea tintinnine species. The greatest number of 22 species was noted in May and in the autumn, while the



**Figure 4.** Seasonal distribution of density of four size categories of non-loricate ciliates in 1995 (I,  $<10^3 \text{ m}^3$ ; II,  $10^3\text{--}10^4 \text{ m}^3$ ; III,  $10^4\text{--}10^5 \text{ m}^3$ ; IV,  $>10^5 \text{ m}^3$ ).

lowest value of six species was recorded in June. Coastal water species prevailed over most of the year, whilst the open-sea species were numerous in June, July and October. High and statistically significant correlation was established between the number of coastal water species and tintinnine density ( $r=0.76$ ).



**Figure 5.** Vertical distribution of density of four size categories of non-loricate ciliates in 1995 (I,  $<10^3 \text{ m}^3$ ; II,  $10^3\text{--}10^4 \text{ m}^3$ ; III,  $10^4\text{--}10^5 \text{ m}^3$ ; IV,  $>10^5 \text{ m}^3$ ).

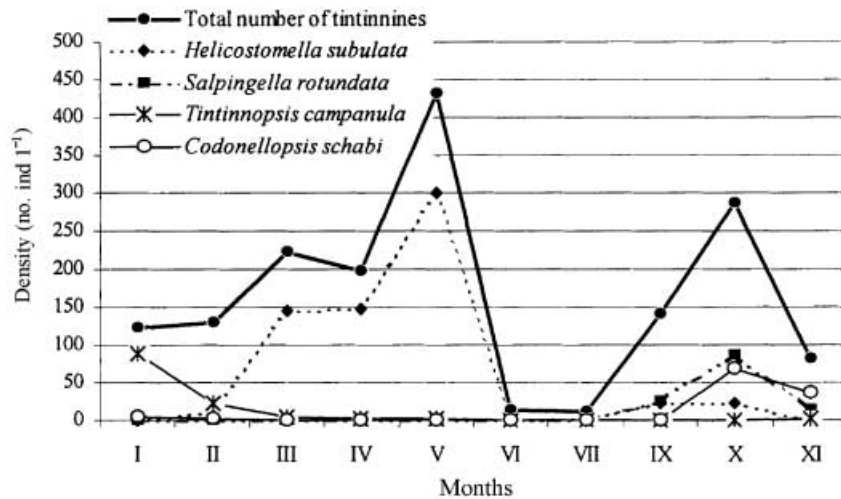


Figure 6. Seasonal distribution of the most qualitatively important tintinnine species in 1995.

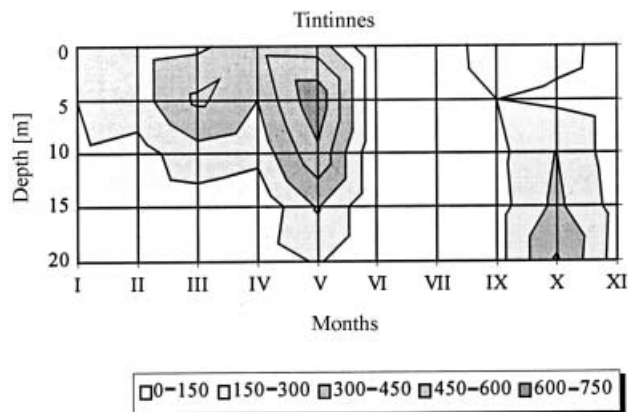


Figure 7. Vertical distribution of tintinnine density in 1995.

Based on seasonal distribution of each tintinnine, the cluster analysis extracted dominant species *Helicostomella subulata*, *Tintinnopsis campanula*, *Codonellopsis schabi* and *Salpingella rotundata*. Those species accounted an average of 62% of the total tintinnine counts. The coastal water species *H. subulata* was qualitatively the most important tintinnin in Kaštela Bay and comprised 39% of the total number of tintinnines. The share for the species *S. rotundata* and *T. campanula* was 8% and for *C. schabi* was 7%. The statistical analysis showed that the seasonal distribution of the tintinnines could be described by succession of these four tintinnine species with coefficient correlation of 0.95 ( $N=10$ ;  $P<0.05$ ) (Figure 6).

The seasonal distribution of tintinnine abundance was distinguished by two peaks, the first in May with a mean value of  $431 \pm 216 \text{ ind l}^{-1}$  and a tintinnine contribution of 59% of the total number of ciliated protozoa (Figure 3). The second, autumn peak was less intensive than the first with a mean value of  $286 \pm 132 \text{ ind l}^{-1}$  in October and a tintinnine contribution of 29%. The minimum density was attained during the summer and the abundance varied from 7 to  $22 \text{ ind l}^{-1}$ .

The vertical distribution of these organisms is shown in Figure 7. An average of 53% of the tintinnine population was restricted to the upper 5 m from the surface. During

Table 1. Correlation coefficients between principal groups of ciliated protozoa and micrometazoa. (Statistically significant values of correlation coefficients are printed in bold;  $P<0.05$ ;  $N=50$ ).

	Zooplankton groups					
	NLC	TIN	NAUP	COP	ACOP	OM
NLC	1.00					
TIN	<b>0.32</b>	1.00				
NAUP	0.22	0.11	1.00			
COP	-0.06	-0.05	<b>0.57</b>	1.00		
ACOP	0.15	-0.08	<b>0.59</b>	<b>0.53</b>	1.00	
OM	<b>0.43</b>	0.24	<b>0.65</b>	<b>0.54</b>	<b>0.53</b>	1.00

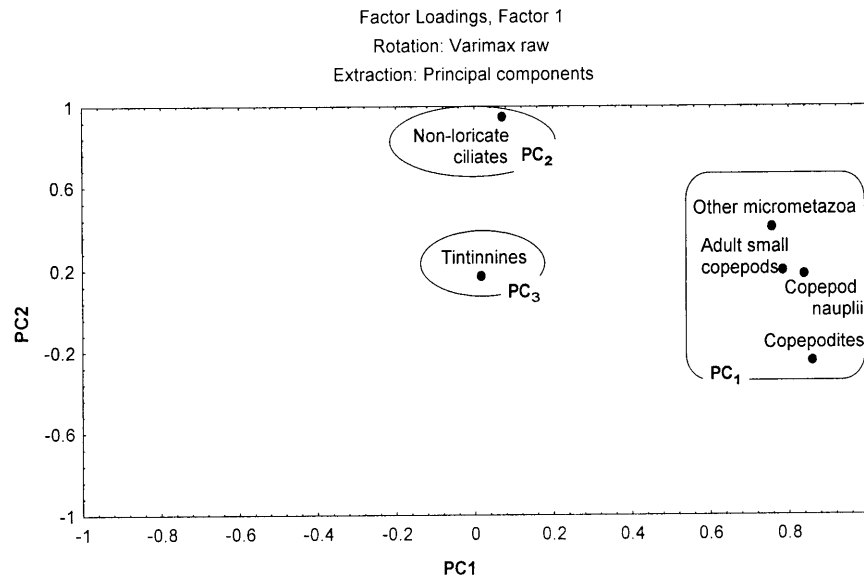
TIN, tintinnines; NLC, non-loricate ciliates; NAUP, copepod nauplii; COP, copepodites; ACOP, adult small copepods; OM, other micrometazoans.

Table 2. Pearson correlations between four size categories of non-loricate ciliates and tintinnines and individual abiotic and biotic factors ( $N=40$  for temperature and salinity,  $N=50$  for other parameters).

Factor	NLC I	NLC II	NLC III	NLC IV	TIN
Temperature	-0.09	0.12	0.34*	-0.06	-0.10
Salinity	0.02	-0.44**	-0.37*	0.18	-0.30
TIN	0.17	0.34*	0.29*	-0.10	1.00
NAUP	-0.06	0.20	0.31*	-0.10	0.11
COP	-0.00	-0.07	0.01	-0.11	-0.05
ACOP	-0.02	0.12	0.12	0.10	-0.08
OM	0.23	0.40**	0.45**	-0.17	0.24

\*,  $P<0.05$ ; \*\*,  $P<0.01$ ; NLC, non-loricate ciliates; I,  $<10^3 \mu\text{m}^3$ ; II,  $10^3-10^4 \mu\text{m}^3$ ; III,  $10^4-10^5 \mu\text{m}^3$ ; IV,  $>10^5 \mu\text{m}^3$ ; TIN, tintinnines; NAUP, copepod nauplii; COP, copepodites; ACOP, adult small copepods; OM, other micrometazoans.

the winter, the most numerous species was *T. campanula* with a density of  $123 \text{ ind l}^{-1}$  at the surface in January. In the period from February to May the highest tintinnine abundance was established in the upper 5 m reaching a maximum of  $718 \text{ ind l}^{-1}$  in May at 5 m depth, with



**Figure 8.** Grouping of ciliated protozoa and micrometazoan groups obtained by principal components analysis.

temperature and salinity of 16.0°C and 36.0 psu, respectively. The spring maximum of total tintinnines matched with the distribution of the species *H. subulata*. This species was abundant during the whole spring with a maximum density (528 ind l<sup>-1</sup>) in May at 5 m depth. With the disappearance of the thermocline from September on, vertical distribution of tintinnines became more uniform and they were mostly retained in the layer below the 10 m depth. That distribution was mainly due to two autumn species, *S. rotundata* with a density of 146 ind l<sup>-1</sup> at 10 m depth in October and *C. schabi* with a density of 160 ind l<sup>-1</sup> at 15 m depth in October, as well.

#### Analysis

The correlation matrix between non-loricate ciliates, tintinnines and micrometazoan groups is given in Table 1. A high coefficient of Pearson correlation indicates a similar annual cycle of some studied groups. This particularly applies to copepods and their developmental stages.

The highest and statistically significant correlation coefficients in the range of 0.53–0.65 were recorded between the number of micrometazoan groups (copepod nauplii, copepodites, adult small copepods and other micrometazoans). Positive correlation was also established between non-loricates and tintinnines ( $r=0.32$ ) and non-loricates and other micrometazoans ( $r=0.43$ ) as well.

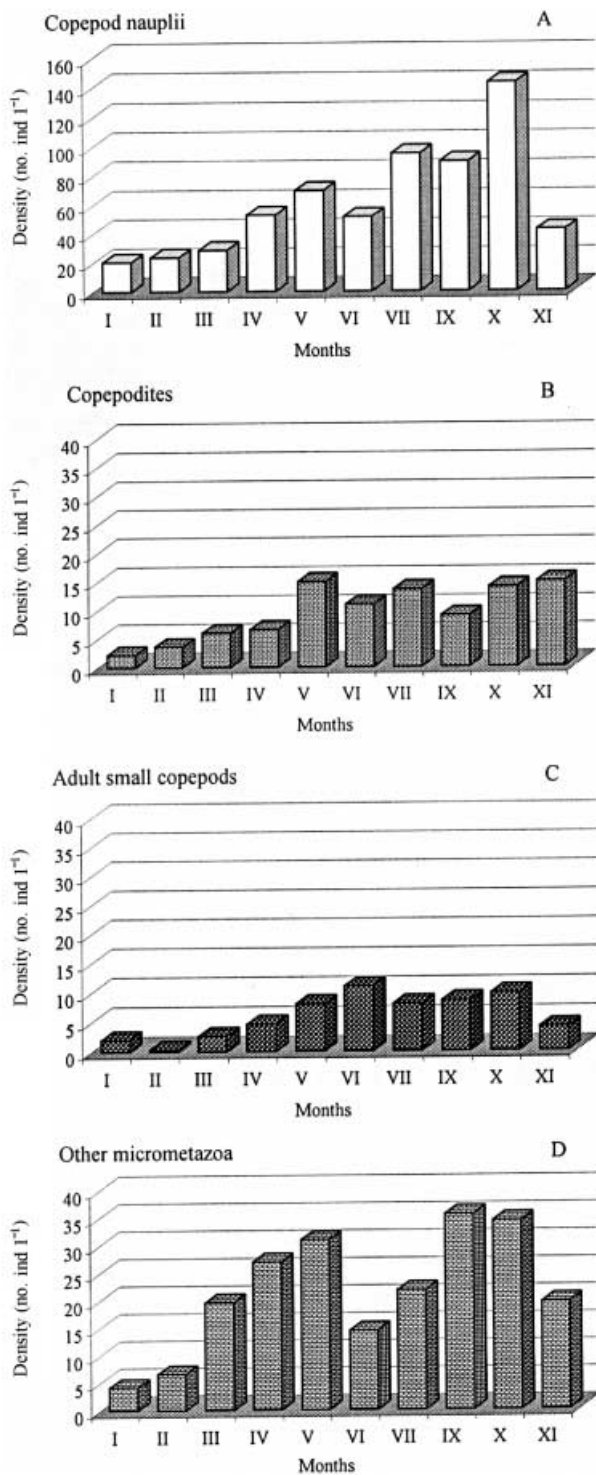
Principal component analysis was carried out on an array consisting of the data sets for non-loricate ciliates, tintinnines, and micrometazoa groups. All time series were standardized (zero mean, unit variance). Principal component analysis extracted three clusters enclosing zooplankton groups with similar patterns of seasonal distribution. The first cluster comprised all micrometazoan groups: nauplii, copepodites, adult small copepods and other micrometazoans, the second cluster consisted of non-loricate ciliates and the third of tintinnines (Figure 8).

Pearson's correlation showed a relationship of ciliated protozoa with several abiotic and biotic parameters

(Table 2). Statistically significant correlation was recorded between temperature and the third size category of non-loricates. In addition, the second and third size categories of non-loricates were negative and statistically significantly correlated with salinity,  $r=-0.44$  and  $r=-0.37$ . On the basis of the analysis of the relationship between ciliated protozoa and other components of microzooplankton, significant correlations were recorded between non-loricates of the second size category and tintinnines. This category of non-loricates was correlated with number of other micrometazoans, as well. The third size category of non-loricate ciliates was significantly correlated with tintinnines, copepod nauplii and other micrometazoans.

#### DISCUSSION

The earlier investigation of microzooplankton in Kaštela Bay showed that Oligotricha are only important components of plankton in July and February (Kršinić, 1982). The data from this study suggests that non-loricates were the most important protozoans in the Bay with two density maxima during the March–April and September–October periods. A similar variability is found in Kotor Bay where non-loricates are markedly dominant during the same periods with a maximum density of 673 ind l<sup>-1</sup> at the surface in April (Kršinić & Viličić, 1989). In Kaštela Bay non-loricate density was relatively high compared with the values recorded in other parts of the Adriatic Sea. The average number of non-loricates in the Mali Ston Bay ranged from 10 to 50 ind l<sup>-1</sup>, with a maximum value of 560 ind l<sup>-1</sup> (Kršinić & Mušin, 1981). In the Kvarner region non-loricates are of numerical importance during the colder months, especially in February with an abundance of 152 ind l<sup>-1</sup> at the surface (Kršinić, 1979). The oligotrichs are also the most abundant ciliated protozoan group in the northern Adriatic Sea (Revelante et al., 1985). Along the transect from the Istrian Peninsula to the Po delta region, under the stratified conditions, their abundance increases from 1612 ± 1396 to 5997 ± 10092 ind l<sup>-1</sup> (Table 3).



**Figure 9.** Seasonal distribution of density of: (A) copepod nauplii; (B) copepodites; (C) adult small copepods; and (D) other micrometazoa, in the western part of Kaštela Bay during 1995.

The data shows that the seasonal pattern of ciliated protozoa distribution, with the biomass at its highest in the spring and autumn and lowest in the summer and winter, is comparable to the observations in other temperate waters (Sanders, 1987; Nielsen & Kiørboe, 1994). The highest ciliate density of  $17.5 \times 10^3 \text{ ind l}^{-1}$  is recorded in Chesapeake Bay (Dolan & Coast, 1990).

**Table 3.** The maximal non-loricate ciliate density as reported for some Adriatic Sea regions.

Area	Non-loricate ciliates density (no. ind l <sup>-1</sup> )	Author
Kotor Bay	673	Kršinić & Viličić, 1989
Mali Ston Bay	560	Kršinić & Mušin, 1981
Kvarner Region	152	Kršinić, 1979
North Adriatic	$5997 \pm 10092^*$	Revelante et al., 1985
Kaštela Bay	1400	this paper

\*, the sample obtained by pooling 2-l samples collected at five different depths.

Besides the earlier investigations in Šibenik, Gruž and Kotor Bay and in the northern part of the Adriatic Sea, tintinnines are the most abundant during the warmer part of the year (Kršinić, 1979; Revelante et al., 1985) with a maximum of  $5192 \text{ ind l}^{-1}$  (Kršinić et al., 1988). On the other hand in the Bay of Mali Ston tintinnines are qualitatively the most important in the autumn–winter period (Kršinić & Mušin, 1981). The present study emphasizes the peculiarity of Kaštela Bay since the highest values were recorded in May and October, while the lowest were in the summer.

In the investigated part of the Bay a total of 35% of known Adriatic tintinnines were recorded. The characteristic species diversity and higher share of estuarine and coastal water species indicated the stronger influence of mainland. Qualitatively, the most important tintinnine species was *Helicostomella subulata*. It suggests that *H. subulata* could have a pivotal role in coastal area food webs, especially in the period from March to May. During that period the first and second size category of non-loricate ciliates ( $<10^4 \mu\text{m}^3$ ) prevailed in the plankton. In other parts of the Adriatic Sea the highest abundance of *H. subulata* was recorded at different times. For example in the Bay of Mali Ston, the peak is recorded in March (Kršinić & Mušin, 1981) and in the western part of the northern Adriatic in June, with a value of  $2376 \text{ ind l}^{-1}$  (Kršinić et al., 1988). This species is one of the most abundant in other particularly eutrophicated areas where it reaches an extremely high concentration of  $10^5 \text{ ind l}^{-1}$  (Paranjape, 1980; Hargraves, 1981). Other tintinnine species in Kaštela Bay were of less importance. In this way *Codonellopsis schabi* occurred at half the abundance recorded by Kršinić (1982). However, the investigations performed throughout 1998 (N. Bojanić, unpublished data) indicated high density of the species, especially in the eastern part of the Bay with an average density of  $2123 \text{ ind l}^{-1}$ . Consequently, it can be supposed that some tintinnine species appear in the plankton in characteristic cycles. Long-term investigations would be valuable to understand their life cycle.

During the colder part of the year ciliated protozoa were distributed homogeneously through the water column, while during the marked summer stratification of the water column they preferred the surface layer. Many earlier studies confirm the pattern of vertical stratification (Revelante et al., 1985; Edwards & Burkill, 1995). Besides specific hydrographic circumstances (James

& Hall, 1995) the vertical distribution of ciliates is influenced by similar distribution of phytoplankton (dinoflagellates) (Stoecker et al., 1984), bacterioplankton and heterotrophic nanoflagellates (HNF) (Krstulović et al., 1995; Šolić et al., 1998). The results of Stoecker et al., (1984) show that sampling time also controls ciliate vertical distribution. So the highest density of non-loricates with biovolume  $>10^5 \mu\text{m}^3$  could be due to the sampling being carried out in the evening.

Based on the results presented in this paper it could be concluded that salinity was, as an abiotic factor, more important than temperature in affecting ciliate distribution. Although salinity was interpreted as a factor possibly affecting non-loricate ( $10^3$ – $10^5 \mu\text{m}^3$ ) populations, following the Pearson correlation coefficient, it is possible that examined factors co-varied with some unmeasured parameters which had more important effects on non-loricate density. Hargraves (1981) confirms that the significant negative correlation is not generally considered to be important from the bottom upward and non-loricates and tintinnines retained in the upper part of the water column, which could be a reason for statistically significant correlations.

Seasonal variations of abundance and biomass of microzooplankton in subtropical estuaries points to the fact that their abundances are partly dependent on food concentration (Buskey, 1993). The time of ciliate proliferation is accompanied by an increase in the concentration of chlorophyll-*a* (Ninčević, 1996). This led to the conclusion that ciliates, particularly non-loricates from the second and the third size category, are the first link in organic matter conversion, namely the primary consumers. Besides phytoplankton, bacterioplankton and HNF are very important food sources for ciliates (Sanders, 1987; Šolić & Krstulović, 1994). The increase of phytoplankton and bacteria biomass in the spring and autumn (Krstulović et al., 1995) is favourable to the non-loricate and tintinnine proliferation. Therefore, ciliate could influence the size of bacterial and HNF populations in that period and could act as important factor of bacterial and HNF 'top-down' control. In the investigated area of Kaštela Bay the 'top-down' control was intensive in September, since the abundance of ciliated protozoa in the surface layer exceeded the density value of  $1600 \text{ ind l}^{-1}$ . The earlier data also suggests that ciliate grazing increases during the colder part of the year (Šolić & Krstulović, 1994).

The density of ciliates in Kaštela Bay could be affected by metazoan grazing, especially in the autumn when other micrometazoan groups prevail in the plankton (N.Bojanić, unpublished data) (Figure 9). The group consisted of Cladocera, Pteropoda, Appendicularia, Chaetognatha as well as the larvae of Echinodermata, Polychaeta and Bivalvia. Pearson correlations between those organisms and non-loricates were statistically significant.

This study indicates that ciliate protozoa are an important component in the neritic eutrophicated ecosystem and gives some new information on their distribution in the coastal part of the middle Adriatic Sea. However, further investigations about the trophic relationships between ciliates and other microbial and metazoan components, as well as the efficiency of carbon transfer

are needed for better understanding of their role in the microbial food web.

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