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Temporal variability in abundance and biomass of ciliates and copepods in the eutrophicated part of Kaštela Bay (Middle Adriatic Sea)

Abstract Seasonal variations in abundance and carbon biomass of ciliated protozoa and micrometazoa were studied from May 1998 to November 1999 in the eutrophicated area of Kaštela Bay (Middle Adriatic Sea). Ciliates showed peaks in spring and autumn, primarily due to changes in the abundance and biomass of tintinnines, which participated in total ciliate abundance and biomass with 40.48 and 60.02%, respectively. The highest tintinnine density was 4,278 ind. l^{-1}, while their average biomass varied from 0.611 to 26.557 µgC l^{-1}. Maximal average density and biomass of non-loricates were 1,430 ind. l^{-1} and 3.925 µgC l^{-1}, respectively. The micrometazoa community was dominated by copepod nauplii, especially during the summer and autumn. The copepod biomass ranged between 3.47 and 26.75 µgC l^{-1}. High abundance and biomass values of the investigated zooplankton groups point to an important role of these organisms in the secondary production in the Bay, indicating that they may be (1) a crucial factor in controlling the populations of nano-/pico-phytoplankton and heterotrophic nanoflagellates, and (2) a significant prey for larger micrometazoans.

Keywords Abundance · Adriatic Sea · Biomass · Ciliated protozoa · Micrometazoa

Introduction

Protozoans and micrometazoans play an important role in transferring organic matter from bacteria and phytoplankton to large-dimensional zooplankton, benthic

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invertebrates, and fish larvae (Bernard and Rassoulzadegan 1993; James and Hall 1995; Gonzàlez 1999). Some studies show that ciliates, dinoflagellates and microflagellates larger then 50 µm^3 can consume up to 100% of the daily primary production (Beers and Stewart 1971; Verity et al. 1993), and also an important part of the bacterial production. For example, ciliated protozoans alone can graze about 20% of the bacterial production (Sanders et al. 1989; Šolić and Krstulović 1995). In recent decades, the classic food chain concept has been replaced by the concept of a complex food web, and it has been shown that the relationship between primary producers and primary consumers is not simply one way (Azam et al. 1983; Stone and Berman 1993; Legendre and Rassoulzadegan 1995). Metabolic products, released during remineralisation processes, increase the primary production (Revelante and Gilmartin 1983), and zooplankton excretion products and detritus are suitable media for bacterial growth. In addition, the short generation time of small zooplankton allows these organisms to adapt rapidly to ecosystem changes, stabilising their communities and preventing energy losses (Heinbokel 1978; Capriulo and Carpenter 1980). In such circumstances, ciliates and micrometazoans may act as important links between the microbial food web and the classic food chain.

There are still very few studies in the Adriatic Sea on temporal changes in abundance and biomass of ciliated protozoans and micrometazoa. Previous studies conducted in Kaštela Bay (Kršinić 1980a, 1982; Bojanić 2001; Bojanić et al. 2001) have indicated that this area is ideal for analysing the impact of eutrophication on the abundance and community structure of ciliated protozoa and micrometazoa. The aim of the present study was to investigate the composition of the ciliates and micrometazoa assemblages in the eutrophicated part of Kaštela Bay, to estimate ciliate and copepod biomass, and to evaluate their role in marine food web dynamics. In addition, relationships between zooplankton components and both abiotic and biotic factors were analysed.

Methods

Study area

Samples were collected at the station Vranjic in the eastern part of Kaštela Bay (43°31.9′N, 16°27.2′E) (Fig. 1). Kaštela Bay is a semi-enclosed shallow system (average depth 23 m) located in the eastern part of the Middle Adriatic Sea. The most important influx of fresh water is the river Jadro, which discharges into the Bay near the sampling station. Several submarine springs and the brook Pantan, located along the southeastern and northwestern part of the Bay, are of lower significance. The investigated area of the Bay also receives large quantities of untreated municipal and industrial effluents. An agricultural area extends along the northern coast, so precipitation waters also carry considerable quantities of nutrients. Geographical characteristics of the Bay, vicinity of land and anthropogenic impact result in marked oscillations of hydrographic parameters. Water circulation in the Bay is generated mostly by the local wind. Hydrographic properties indicate strong continental influences on the eastern part of the bay which shows considerably lower water exchange than the western one (Zore-Armanda 1980).

Sampling methods and measurement techniques

Microzooplankton samples were collected on a monthly basis from May 1998 to November 1999, at 5-m depth intervals, between surface and bottom (17 m), using 5 l Niskin bottles. Organisms were preserved in buffered formaldehyde (final concentration 2.5%). Samples were sedimented in the laboratory for 2 days in plastic containers and were decanted down to a volume of approximately 2 l. The remainder was poured into a

Fig. 1 Study area (Kaštela Bay) with the sampling station

cylinder and sedimented for the following 48 h. The excess volume was reduced to 200 ml. Decanting was carried out using a vacuum pump and curved glass pipette that removed water from the surface (Kršinić 1980b). After 24 h, the volume was reduced down to 20 ml for microscopical studies. Counting and identification of the species were performed in a glass chamber (76×47×6 mm) with 'Olympus' inverted microscopes IMT−2 and CK40 at 100× and 400× magnification.

For a quantitative analysis of non-loricate ciliates, we also used a 100-ml aliquot volume, and counting was made at 200× magnification. The organisms were fixed with formaldehyde in the same way as tintinnines and micrometazoans. Formaldehyde was chosen instead of acid Lugol because it does not stain detritus that can be abundant in the eastern part of Kaštela Bay. Since formaldehyde causes cell loss of the naked ciliates (Leakey et al. 1994), our data for ciliates may be somewhat underestimated.

The biovolume of non-loricates was calculated from the aliquot volume of 100 ml by comparing the shape of plasmatic body of each individual organism to one or more geometrical bodies (Edler 1979). After measurement of dimension, cells were divided into four size categories: (1) biovolume $< 10^3$ μm^3; (2) biovolume $10^3 - 10^4$ μm^3; (3) biovolume $10^4 - 10^5$ μm^3; and (4) biovolume $> 10^5$ μm^3 . The biovolume of tintinnines was estimated separately for each species, by measuring linear dimensions of the lorica.

The geometrical method was also applied to determine the biovolume of copepod nauplii and postnaupliar copepods. The biovolume of copepod nauplii was calculated according to the modified formula for the biovolume of rotifers (Ruttner-Kolisko 1977). The body of almost all copepods may be equated to two geometrical forms: cephalothorax to the ellipsoid, and abdomen to the cylinder (Shmeleva 1965). For the determination of length and diameter, 20–150 organisms were measured microscopically at 200× and 400× magnification with a calibrated ocular micrometer. Unlike the biovolumes of ciliates that were calculated from all collected samples, the biovolume of copepods was evaluated by measuring the dimensions of organisms in one sample every month.

Conversion factors used to transform these biovolumes into carbon biomass values were: for non-loricate ciliates 0.14 pgC μm^{-3} (Putt and Stoecker 1989), for nauplii and postnaupliar copepods 0.08 pgC μm^{-3} (Beers and Stewart 1970; Monti and Fonda Umani 1999), and the formula of 444.5 pgC + (lorica volume in μm^{-3}×0.053 pgC) per cell for tintinnines (Verity and Langdon 1984).

Samples for bacterial and heterotrophic nanoflagellates (HNF) counts and for chlorophyll *a* measurements were collected in parallel with microzooplankton sampling. Samples were poured into sterile acid washed glass bottles, fixed with formaldehyde (final concentration 2%). Chlorophyll *a* content was measured on a Turner 112 fluorometer after aceton extraction (Strikland and
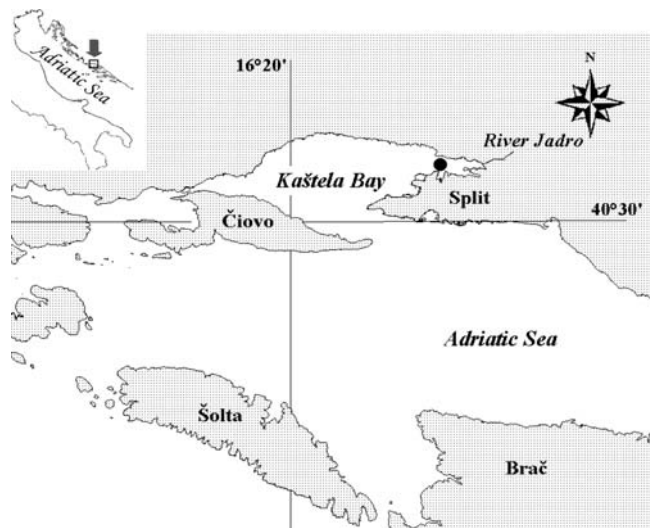
Parsons 1972). Samples were filtered through a plankton net (net mesh diameter 10 μm) and separated in two size categories: microphytoplankton (>10 μm,) and nano-/pico-fraction (<10 μm). Enumeration of bacteria and HNF were made by epifluorescence microscopy using the standard acridine orange direct counting technique (Hobbie et al. 1977) for bacteria, and proflavine staining technique for HNF (Haas 1982). For biovolume estimates, length and width of bacterial and HNF cells were measured with an eyepiece graticule (New Portion G12, Graticules, UK). Biovolume was converted to carbon biomass, assuming 0.220 pgC μm^{-3} for bacteria (Bratbak and Dundas 1984) and HNF (Borsheim and Bratbak 1987).

Vertical temperature and conductivity profiles were measured with a CTD multiparameter probe.

Principal component analysis

In order to extract the main patterns of seasonal changes in abundance and biomass, the principal component analysis (PCA) was carried out. The data input to each analysis consisted of a set of variables representing seasonal fluctuations in abundance and biomass. The Varimax rotation of extracted PC components was used in order to obtain a better insight into the behaviour of observation variables.

Results

Environmental variables and biotic parameters

With respect to the vertical temperature gradient, two annual periods can be distinguished: the colder part of the year, when the entire water column had a similar temperature, and the rest of the year when there was a distinct vertical temperature gradient (Fig. 2a). In the
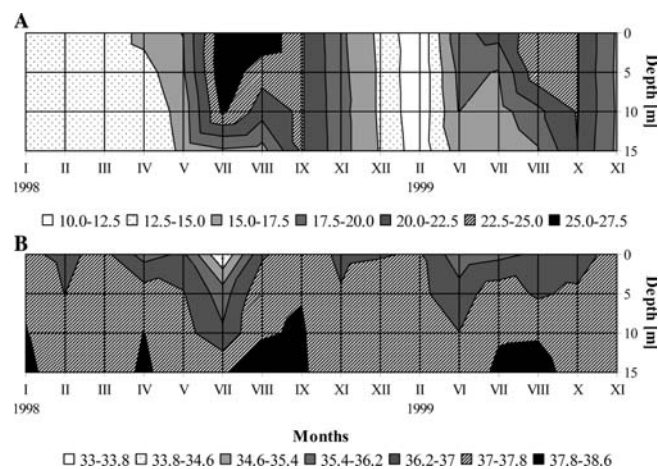

Fig. 2 Seasonal changes of temperature (°C) (bfa) and salinity (PSU) (**b**) in the eastern part of Kaštela Bay

eastern part of Kaštela Bay the water column average temperature values ranged from 10.60°C (February 1999) to 24.00°C (July 1998). The maximal temperature of 27.16°C and the highest vertical gradient of 10.69°C occurred in August 1998.

Throughout the year, salinity ranged from 33.81 to 38.18 PSU (Fig. 2b). Both values were observed in summer 1998, in the surface layer in July and in the bottom layer in August, respectively. Salinity increased with depth, while its seasonal changes decreased with depth. During the colder part of the year all layers had almost the same average salinity of ~37.5 PSU.

The phytoplankton biomass increased during the warmer period of the year. The highest average chlorophyll *a* concentration of 9.16 ± 4.97 μg Chl a l^{-1} was noticed in July 1998, with a maximal value of as high as 15.65 μg Chl a l^{-1} at the surface. Fluctuations of phytoplankton biomass resulted from almost equal changes in both size fractions. The highest average concentration of the microphytoplankton was recorded in June 1999 (6.27 ± 7.73 μg Chl a l^{-1}), and of the nano-/pico-fraction in July 1998 (5.54 ± 7.16 μg Chl a l^{-1}).

The bacterioplankton showed a summer-autumn peak in density and biomass with highest mean values in August 1998 ($3.78 \pm 1.48 \times 10^{6}$ cells ml^{-1} and 78.93 ± 30.94 μgC l^{-1}). During the summer, high values of HNF abundance and biomass were also recorded. The maximal average density of $28.09 \pm 18.78 \times 10^{3}$ cells ml^{-1} and biomass of 122.55 ± 81.94 μgC l^{-1} were found in July 1998 (unpublished data).

Microzooplankton composition and variations in density and biomass

The density of ciliated protozoans in the eastern part of Kaš tela Bay showed peaks in spring and autumn, with average values of $2,711 \pm 2,460$ ind. l^{-1} in April 1999, and $3,200 \pm 1,219$ ind. l^{-1} in September 1998 (Fig. 3a). Ciliate abundance in the remainder period of the year was lower. This oscillation was primarily due to changes in the seasonal distribution of tintinnines ($r = 0.80$, $n = 44$, $P <$ 0.0001). However, tintinnines contributed to the assemblage of ciliated protozoans less then non-loricates (the mean contribution of 40.48%). The periods of tintinnine dominance were relatively short, alternating with those showing a dominance of non-loricates. In total ciliate biomass tintinnines participated with 60.02% (Fig. 4). The biomass of both ciliate assemblages together varied from 0.78 ± 0.32 to 28.44 ± 12.40 μgC l^{-1}, with a mean of 6.69 ± 1.25 μgC l^{-1}.

Seasonal oscillations of micrometazoan density were considerably lower than those of ciliates (Fig. 3b). The lowest density was noted in February 1999 (68 ± 20 ind. l^{-1}). During the warmer season, the values increased by the factor 2–3, with a maximum of 431 ± 208 ind. l^{-1} in July 1998. The micrometazoa community was largely dominated by nauplii of copepod and the non-system-
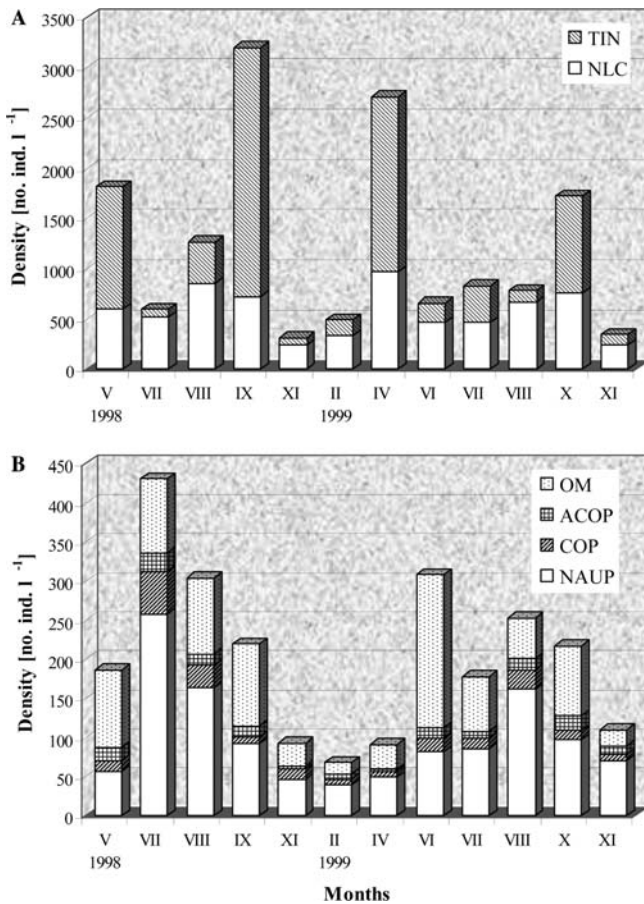
Fig. 3 Seasonal distribution (density) of ciliated protozoans (**a**) and micrometazoans (**b**) in the eastern part of Kaštela Bay (*NLC* non-loricate ciliates; *TIN* tintinnines; *NAUP* copepod nauplii; *COP* copepodites; *ACOP* adult small copepods; *OM* other micrometazoans)

atic category of other micrometazoans (Fig. 3b). Their contribution to the total number of micrometazoa was 49.72 and 35.27%, respectively. The latter assemblage
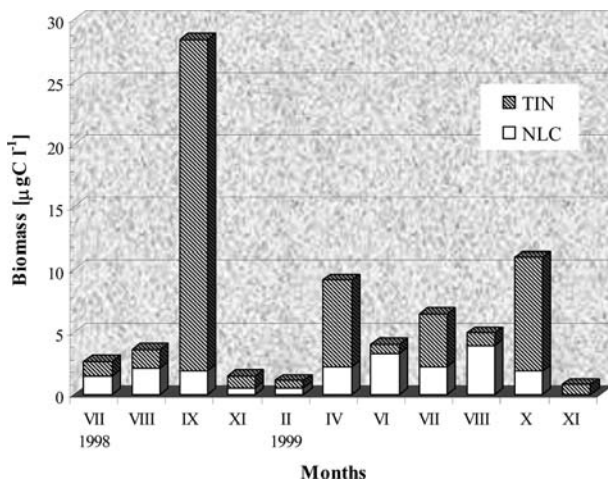

Fig. 4 Seasonal distribution of ciliate biomass in the eastern part of Kaštela Bay (*NLC* non-loricate ciliates; *TIN* tintinnines)

comprised the Rotifera, Cladocera, Pteropoda, Chaetognatha, as well as the larvae of Echinodermata, Polychaeta, and Bivalvia. Their seasonal distribution was characterised by a wide range of abundances, from 14 ± 5 ind. l^{-1} in February 1999 to 195 ± 261 ind. l^{-1} 4 months later, when rotifers dominated.

Non-loricate ciliates

The seasonal abundances of the four size categories of non-loricates (NLC) are shown in Fig. 5a. High NLC abundance was recorded in July and August 1998 (maximum $1,430 \pm 1,348$ ind. l^{-1}), followed by low abundances from September to February. Another smaller NLC peak abundance was observed in the period April–June 1999. The first maximum was particularly due to NLC of the second size category (NLC II, biovolume 10^3–10^4 μm^3) with an average density of $1,220 \pm 1,226$ ind. l^{-1} in July

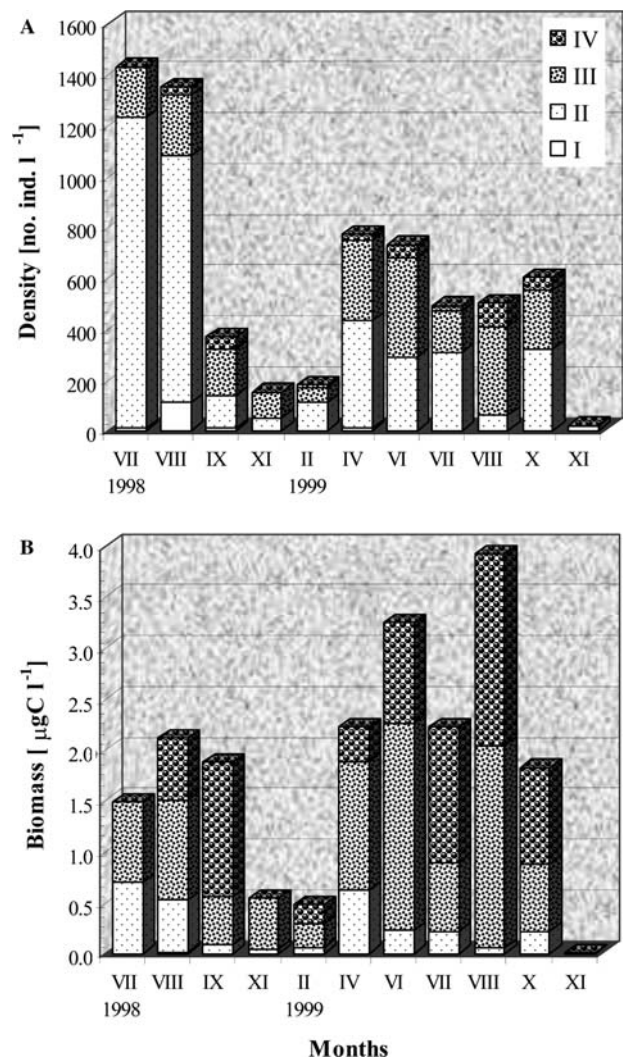**Fig. 5** Seasonal distribution of density (**a**) and biomass (**b**) of four size categories of NLC (*I* $< 10^3$ μm^3; *II* 10^3–10^4 μm^3; *III* 10^4–10^5 μm^3; *IV* $> 10^5$ μm^3)

1998 and a contribution to the total NLC number of 85.92%. In 1999, however, NLC of the second and those of the third size category (NLC III, biovolume 10^4–10^5 μm^3) participated almost equally in the total NLC number (Fig. 5a). The two remaining categories of NLC with biovolumes $< 10^3$ and $> 10^5$ μm^3 formed only 6.66% of the total NLC number. The high summer density in 1998 coincided with proliferation of NLC I and II in the layers above 5 m depth, with maxima of 440 ind. l^{-1} (August, 0 m depth) and 2,560 ind. l^{-1} (July, 5 m depth). In 1999, NLC also concentrated near the surface with the abundances of 880 ind. l^{-1} (NLC II) and 1,120 ind. l^{-1} (NLC III) in June at 0 m depth. Consequently, the majority of organisms (75.87%) remained in the layer above 5 m depth.

Corresponding biomass data are given in Fig. 5b. The biomass was high particularly in summer, with an average of 2.12 ± 0.95 μgC l^{-1} in August 1998 and as high as 3.92 ± 5.09 μgC l^{-1} in the same month 1 year later. The lowest values were recorded during the winter. Just as with the abundance, the biomass was highest at the sea surface with an average of 2.90 ± 3.43 μgC l^{-1}. The biomass of organisms found in this layer formed 39.88% of the total NLC biomass. Changes in biomass data were largely due to changing contributions of NLC III and IV. The highest contribution of NLC III to the total NLC biomass (62.77%) was noticed in summer, with a water column mean of 2.04 ± 2.45 μgC l^{-1} in June 1999 and a maximum of 5.69 μgC l^{-1} at the surface. The highest contribution of NLC IV (47.79%) was in August 1999 with a water column mean of 1.88 ± 2.63 μgC l^{-1}, and a maximum of 5.76 μgC l^{-1} at the surface.

Tintinnines

The vertical distribution of tintinnines varied considerably with respect to year and sampling season (Fig. 6a). An irregular vertical distribution with the highest density at the surface (2,261 ind. l^{-1}) was noticed only in May 1998. In the summer months, the number of organisms were considerably lower. Intensive propagation of tintinnines started again in autumn. In September 1998, 3,584 ind. l^{-1} were found at 10 m depth. The maximal abundance was recorded at the same depth in April 1999 (4,278 ind. l^{-1}). The small density peak in October 1999 was characterised by a largely homogenous vertical distribution.

Seasonal and vertical changes of tintinnine biomass were almost identical to those in tintinnine abundances ($r = 0.86$, $n = 48$, $P < 0.0001$). However, for comparison of different planktonic groups it is more appropriate to use biomass data instead of numbers. Therefore, temporal and vertical distributions of tintinnine biomass are shown in detail in Figs. 4 and 6b. The biomass values ranged from 0.24 μgC l^{-1} (August 1999 in the bottom layer) to 39.46 μgC l^{-1} (September 1998 at 10 m depth). The mean value for the entire investigated period was 4.88 ± 7.99 μgC l^{-1}.
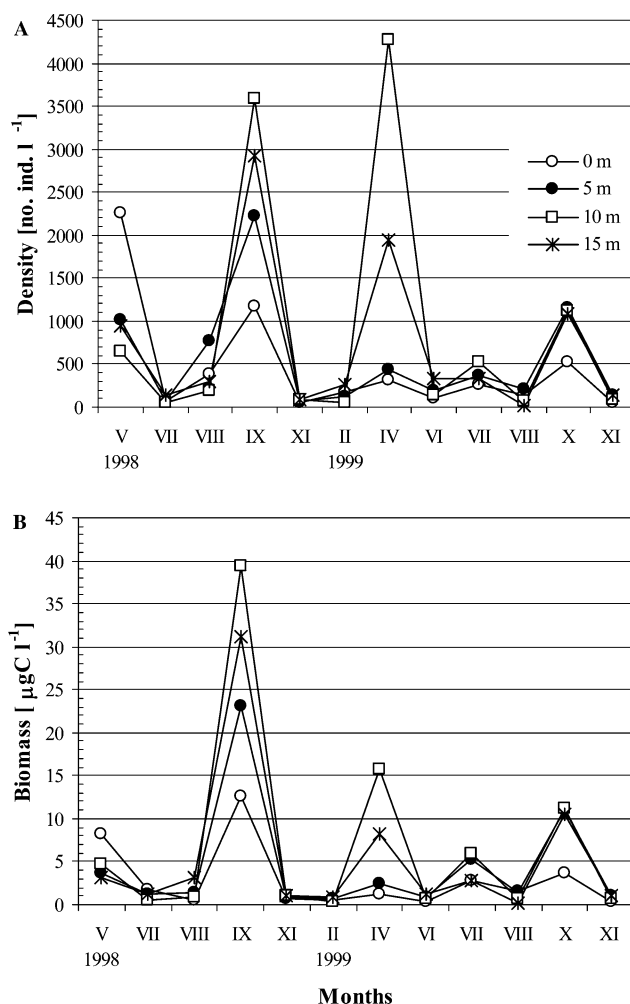

Fig. 6 Vertical distribution of tintinnine density (a) and biomass (b) in the eastern part of Kaštela Bay

We determinated 36 tintinnine species: 21 neritic-estuarine and 15 open-sea species. The greatest diversity was recorded in October 1999 when 75% of all tintinnine species were present. Coastal water species prevailed during the whole period of investigation. Their contribution to the total number of tintinnine species varied between 62.96% (October 1999) and 91.67% (February 1999), when 17 and 11 species were noticed, respectively. The two quantitatively dominant species were *Helicostomella subulata* and *Codonellopsis schabi*, which presented 79.60% of all loricate ciliates. Other species participated in the tintinnine assemblage with less then 5% each. The statistical analysis showed that the seasonal changes in the abundance and biomass of tintinnines can be described by those of the two dominant species ($r = 0.99$, $n = 48$, $P < 0.0001$; and $r = 0.98$, $n = 48$, $P < 0.0001$).

Copepod nauplii

In the colder part of the year the density of copepod nauplii was low, while in the warmer part of the year a

rapid proliferation was recorded (Fig. 7a), resulting in high naupliar abundance with an average of 258 ± 141 ind. l^{-1} in July 1998. Another density peak in August 1999 was less marked. During these months, copepod nauplii participated in the total number of micrometazoans with 59.90% (July 1998) and 63.83% (August 1999). During the cold period of the year, nauplii were found distributed homogenously in the water column. However, a stratification was noticed during the summer. Approximatively 87% of copepod nauplii concentrated in the layers from 0 to 10 m depth. The maximal number of 349 ind. l^{-1} was recorded in July 1998 at the surface, when naupliar densities in the layers of 5 and 10 m depths were also high (>300 ind. l^{-1}).

The naupliar biomass varied considerably depending on sampling season (Fig. 7b). Biomass was maximal (6.09 μgC l^{-1}) in July 1998, and decreased gradually towards the end of the year. High values were also recorded in June, August and October 1999, ranging from 2.94 to 3.19 μgC l^{-1}. However, a special feature of the investigated area was a winter maximum of 3.79 μgC l^{-1}, recorded in February 1999. The described changes in biomass were due not only to changes in the abundance ($r = 0.79$, $n = 12$, $P < 0.01$) but also by those in the biovolume of copepod nauplii. While small nauplii with volumes ranging from 0.23 to 0.48×10^6 μm^3 ind.$^{-1}$ dominated over the entire period of investigation, the mean biovolume of copepod nauplii in February 1999 was 1.21×10^6 μm^3 ind.$^{-1}$.

Copepodites

Like the nauplii, copepodites were most numerous in the summer. The average density varied between 7.75 ± 2.06 ind. l^{-1} in April 1999 and 55.00 ± 35.50 ind. l^{-1} in July 1998, when these organisms accounted for 8.52 and 12.77% of the total micromezatoans, respectively (Fig. 7a). During the summer, organisms concentrated above the thermocline. Maximal abundance of 88 ind. l^{-1} was found in July 1998 at 10 m depth, contributing 40.00% to the total copepodite number. However, a similar number of copepodites was found at the surface. When seawater temperature decreased, copepodites migrated downward and stayed near the bottom until the vertical temperature became re-established. Regarding the taxonomic structure, calanoid copepodites dominated the copepodite populations (44.68%). Their number was highest in August 1998 with a mean value of 18.25 ± 7.89 ind. l^{-1}, a density of 25 ind. l^{-1} at the surface, and a contribution of 61.34% to the total number of copepodites. Copepodites of the cyclopoid genus *Oithona* (contribution 39.86%) prevailed in the plankton during the summer. For example, in July 1998, their mean density was 37.25 ± 29.02 ind. l^{-1}, their density at the sea surface 66 ind. l^{-1}, and their contribution to the total number of copepdites 37.73%.

Seasonal changes in copepodite numbers corresponded with changes in their biomass ($r = 0.90$, $n = 12$, $P < 0.0001$). As presented in Fig. 7b, extremely high biomass values were recorded in July and August 1998,

Fig. 7 Seasonal distribution of densities (**a**) and biomasses (**b**) of nauplii and post naupliar copepods in the eastern part of Kaštela Bay (*NAUP* copepod nauplii; *COP* copepodites; *ACOP* adult small copepods)
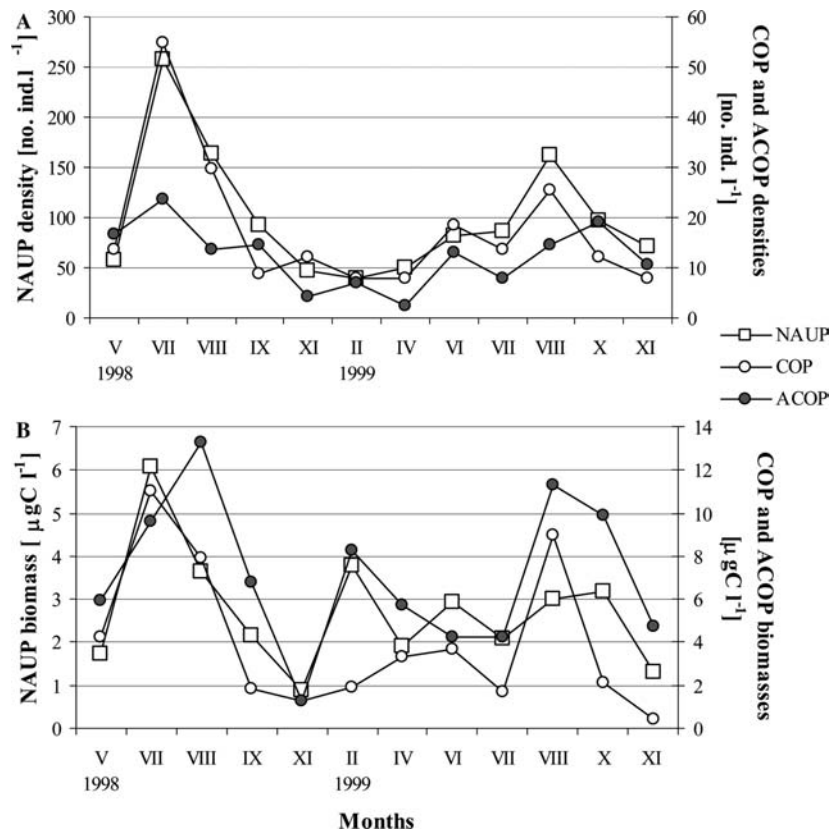
and in August 1999 (11.05, 7.94, and 9.01 μgC l^{-1}, respectively). During the other periods of the year, copepodite biomass varied from 0.46 to 4.23 μgC l^{-1}.

Adult small copepods

The density of adult small copepods in Kaštela Bay oscillated between low values during the colder, and high values during the warmer period of the year (Fig. 7a). Besides the summer peak, an autumn increase in abundance was recorded, but its intensity differed depending on sampling year. In 1998, the highest average value of 23.75 ± 11.15 ind. l^{-1} was measured in July, while in 1999, the highest value of 19.00 ± 9.49 ind. l^{-1} was recorded in October. The minimal average value of 2.50 ± 1.91 ind. l^{-1} was noted in April 1999. The contribution of adult small copepods to the fraction of micrometazoa varied between 2.75 (April 1999) and 10.29% (February 1999). These values were mainly conditioned by the changing quantity of other micrometazoan species. In the eastern part of the Bay, 58% of copepods occurred in the 5–10 m depth layer. In that layer, from May to September 1998, and from June to October 1999, high densities were recorded with a maximum of 40 ind. l^{-1} in July 1998 at 10 m depth. From October 1998 to April 1999, organisms showed a tendency to concentrate in the bottom layer. Among the adult small copepods in Kaštela Bay, copepods of the order Cyclopoida were dominant (41.63%). In July 1998 adult cyclopoids had an average abundance of 12.50 ± 5.97 ind. l^{-1}. The most abundant cyclopoid species was *Oithona nana*, with a maximal density of 16 ind. l^{-1} at 10 m depth in the same month. Copepods of the order Harpacticoida were the second most important, participating with 31.77% in the total number of copepods. In the plankton of the neritic sea, individuals were numerous in the summer–autumn period when the species *Euterpina acutifrons* dominated.

Unlike the biomasses of nauplii and copepodites, the biomass of adult small copepods was not significantly correlated with their numbers. In both 1998 and 1999, the values were highest in August (13.29 and

11.31 μgC l^{-1}); a special feature was the winter maximum of 8.29 μgC l^{-1} recorded in February 1999 (Fig. 7b).

Between-group analysis

The correlation matrix for the abundances of NCL, tintinnines, and micrometazoan groups is given in Table 1. High coefficients of correlation point to a statistically significant connection between copepod nauplii and copepodites ($r = 0.82$) and between copepodites and adult small copepods ($r = 0.60$). Coefficients of correlation for protozoans were less pronounced. Statistically significant positive correlations were found only between NLC II and nauplii, and between NLC III and other micrometazoans. It is interesting to note that tintinnines showed no significant correlation with any other assemblage.

A PCA was carried out on the sets for non-loricates, tintinnines and micrometazoans. The analysis extracted three clusters enclosing zooplankton groups with similar patterns of seasonal variability. The first cluster comprised all copepods, the second cluster consisted of tintinnines and the third contained NCL and other micrometazoans (Fig. 8).

Relation to biotic and abiotic parameters

Pearson's correlations also showed relationships between biomass data of ciliated protozoans and several abiotic and biotic parameters (Table 2). High and statistically significant correlations were recorded between temperature and NLC II, and between salinity and NLC II. Furthermore, statistically significant correlations were found between nano-/pico-phytoplankton and NLC II, between microphytoplankton and NLC III, between bacteria and NLC I and between HNF and both NLC I and II.

Abiotic parameters such as temperature and salinity showed stronger correlations with the abundance data

Table 1 Pearson's correlation coefficients for the densities of principal groups of ciliated protozoa and micrometazoa. *NLC* non-loricate ciliates; *TIN* tintinnines; *NAUP* copepod nauplii; *COP* copepodites; *ACOP* adult small copepods; *OM* other micrometazoans

	Zooplankton groups								
	NLC I	NLC II	NLC III	NLC IV	TIN	NAUP	COP	ACOP	OM
NLC I	1.00								
NLC II	0.51**	1.00							
NLC III	−0.09	0.29	1.00						
NLC IV	−0.08	−0.09	0.51**	1.00					
TIN	0.00	−0.03	0.07	0.17	1.00				
NAUP	0.27	0.65***	0.29	0.24	−0.14	1.00			
COP	0.19	0.46*	0.16	0.07	−0.23	0.82***	1.00		
ACOP	−0.11	0.14	0.10	0.13	0.01	0.54**	0.60***	1.00	
OM	0.04	0.32*	0.66***	0.12	0.07	0.24	0.23	0.20	1.00

$*P < 0.05$, $**P < 0.001$, $***P < 0.0001$, $n = 44$

Fig. 8 Ordering of densities of microzooplankton groups obtained by PCA (*NLC* non-loricate ciliates; *TIN* tintinnines; *NAUP* copepod nauplii; *COP* copepodites, *ACOP* adult small copepods, OM other mikrometazoa)
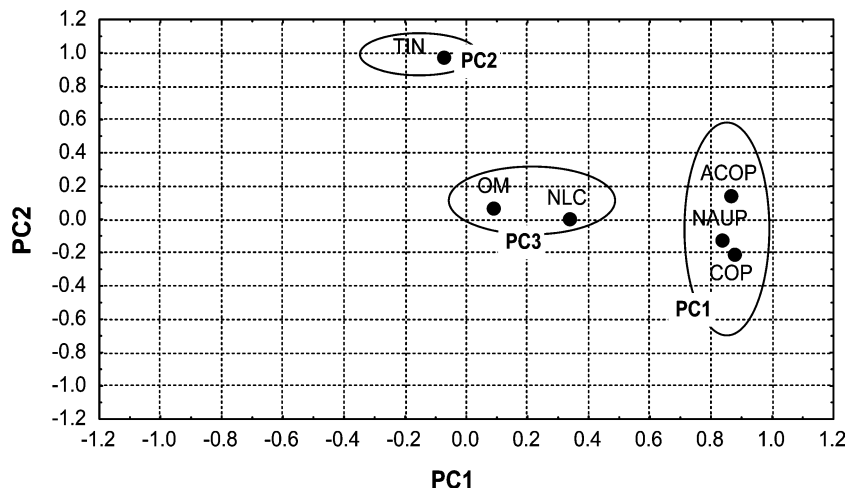
Table 2 Pearson's correlations for biomass data of four size categories of NLC, TIN and abiotic and biotic factors

Factor	Ciliated protozoans				
	NLC I	NLC II	NLC III	NLC IV	TIN
Temperature	0.45	0.60*	0.29	0.29	0.31
Salinity	−0.12	−0.78**	−0.51*	−0.07	0.24
Nano-/pico- phytoplankton	0.10	0.80***	0.35	−0.07	−0.16
Microphytoplankton	0.07	0.51*	0.65*	−0.04	−0.17
Bacteria	0.55*	0.46	−0.09	−0.11	−0.10
Heterotrophic nanoflagellates	0.63*	0.93***	0.14	−0.08	−0.20

*$P < 0.05$, **$P < 0.01$, ***$P < 0.0001$, $n = 18$

of copepod nauplii and copepodites than with their biomass data (Table 3). A clear negative correlation was found between temperature and the average dimension of copepod nauplii ($r = -0.72$, $n = 11$, $P < 0.05$). Similarly, correlations were found for phytoplankton assemblages. An especially high and positive correlation of 0.87 was noticed between the densities of copepodites and nano-/pico-phytoplankton. However, the microphytoplankton was better correlated with the density of other micrometazoans ($r = 0.92$) than with that of copepodites. In addition, high coefficients of correlations were found between the densities and biomasses of

copepod nauplii and copepodites on the one hand, and HNFs on the other (Table 3).

A PCA analysis extracted four clusters: the first one comprised both phytoplankton fractions, NLC II and HNF; the second cluster contained bacteria and NLC I; the third consisted of NLC $> 10^4$ μm³; and the fourth cluster contained copepod nauplii, copepodites and adult small copepods (Fig. 9). The most significant correlations between number or biomass of some microzooplankton groups and biotic parameters are shown in Figs. 10 and 11.

Discussion

Recent studies on NLC densities in Kaštela Bay revealed higher values than primarily estimated (Kršinić 1982), but peaks varied considerably on spatial and temporal scales (Bojanić 2001; Bojanić et al. 2001). In the eutrophicated part of Kaštela Bay, favourable conditions for proliferation of NLC were in the spring–summer period (Figs. 3a and 5a). These results suggest different roles of NLC in the microbial food web depending on the trophic status of the investigated area. Considering only seasonal variations of NLC in the coastal part of the Adriatic Sea, highest similarities were found between Kaštela Bay and the Bay of Mali Ston as well as Kotor

Table 3 Pearson's correlations for the abundances of micrometazoans and biomasses of copepods, respectively, and abiotic and biotic factors; $n = 18$ for abundances, $n = 11$ for biomasses. *NAUP* copepod nauplii; *COP* copepodites; *ACOP* adult small copepods; *OM* other micrometazoans

Factor	Abundance of micrometazoans				Biomass of copepods		
	NAUP	COP	ACOP	OM	NAUP	COP	ACOP
Temperature	0.76**	0.54*	0.35	0.22	0.32	0.52	0.42
Salinity	−0.75**	−0.78**	−0.36	−0.39	−0.62*	−0.51	0.03
Nano-/pico-phytoplankton	0.71*	0.87***	0.30	0.41	0.76*	0.68*	0.15
Microphytoplankton	0.09	0.16	0.02	0.92***	0.46	0.33	−0.08
Bacteria	0.35	0.22	0.46	−0.10	0.19	0.17	0.46
Heterotrophic nanoflagellates	0.82***	0.88***	0.18	0.19	0.76*	0.84*	0.46

*$P < 0.05$; **$P < 0.001$; ***$P < 0.0001$

Fig. 9 Ordering of biomasses of phytoplankton, bacteria, HNF, ciliates and copepods obtained by PCA (*Phy N P* nano-/pico-phytoplankton; *Phy M* microphytoplankton; *B* bacteria; *HNF* heterotrophic nanoflagellates; *NLC* non-loricate ciliates; *NLC I* $< 10^3$ μm^3; *NLC II* 10^3–10^4 μm^3; *NLC III* 10^4–10^5 μm^3; *NLC IV* $> 10^5$ μm^3; *TIN* tintinnines)
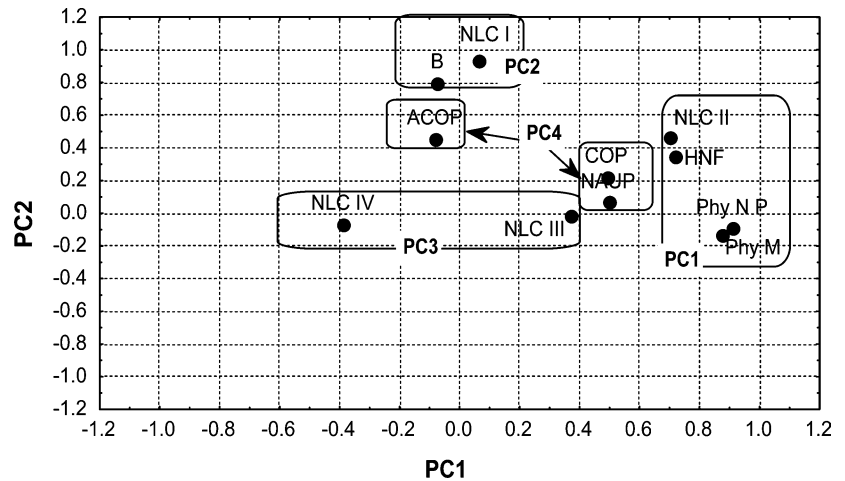
Bay, located in the south Adriatic (Kršinić and Mušin 1981; Kršinić and Viličić 1989). However, the maximal NLC abundance in Kaštela Bay was approximately 5 and 4 times higher, respectively, than at those locations. On the other hand, considerably higher NLC densities were noticed in the northern Adriatic Sea (Revelante and Gilmartin 1983; Revelante et al. 1985; Mozetić et al. 1998). The pattern of NLC temporal variability in Kaštela Bay resembles those in other neritic sea areas such as the Chesapeake Bay, the Nueces Estuary or the Gulf of Maine, but differences are obvious in the intensities of those changes (Sanders 1987; Dolan and Coats 1990; Buskey 1993). It is possible that low values of NLC abundance recorded in this study are somewhat influenced by the fixation method used.

A study of Montagnes et al. (1988) on ciliates in the Gulf of Maine confirmed the importance of population size structure for a better understanding of seasonal oscillations. During the summer, ciliates with a cell volume between 10^2 and 10^3 μm^3 reached a higher abundance than any other size class. Ciliates in the 10^3–10^4 μm^3 size class were most abundant in autumn and winter, while those in the 10^4–10^5 μm^3 size class were abundant in late winter and spring. Ciliates in the $> 10^5$ μm^3 size class never represented more than 4% of total numbers (Montagnes et al. 1988). Our results are in general agreement with these findings (Fig. 5a). Differences were observed for the NLC $< 10^3$ μm^3 size class which in the eastern part of Kaštela Bay formed less than 2%. Quantitatively the most important size category was NLC II, especially in summer, while during other seasons the number of NLC III was increased.

In the eastern part of Kaštela Bay, tintinnine densities were one order of magnitude higher than in other parts of Kaštela Bay during the same period (Bojanić, unpublished data) and were similar to those recorded in the eutrophicated northern Adriatic (Kršinić 1995). Besides seasonal changes in total abundance of tintinnines, it is also important to understand changes in their taxonomic structure. Quantitatively dominant tintinnine species in the Vranjic Basin were *H. subulata* and *C. schabi*, which presented 80% of the total loricate

number. These species thus may have an exceptional importance in the microbial food web of coastal ecosystems, particularly during periods of their highest abundance. *H. subulata* was the most abundant species in spring. Favourable environmental conditions and probably the trophic state of the investigated area may be relevant in this context (Verity 1987; Kršinić et al. 1988; Cordeiro et al. 1997).

Biomass data are essential for a better understanding of the ecology of ciliated protozoa and micrometazoa. Temporal changes in ciliate biomass are well known from many marine environments, but relatively little is known for the Adriatic Sea (Revelante and Gilmartin 1983; Revelante et al. 1985; Lipej 1992; Cataletto et al. 1993; Fonda Umani and Beran 2003). Revelante and Gilmartin (1983) studied the distribution of ciliate biomass in the northern Adriatic in the summer stratified and the winter mixed periods. They indicated a dominant role of naked oligotrichous ciliates, except for the summer stratified period when these ciliates contributed as much to the protozoan biomass as tintinnines. A quite different situation was found in our study, where tintinnines participated in the ciliate biomass with an average of 60% (Fig. 4). In September 1998 and November 1999 their contributions were even higher (93.39 and 98.41%, respectively). Suzuki and Taniguchi (1998) speculated that tintinnines might possess a higher adaptability to eutrophic environments than other ciliates. A comparison of those results with data from Kaštela Bay (Bojanić et al. 2001; Bojanić, unpublished data) indicates that eutrophication and the ciliate biomass increase proportionally, and that eutrophication also affects the structure of populations and their seasonal variability. This points to a special character of the Vranjic Basin, because the differences in the succession of ciliate biomass necessarily affect the energy flow in the marine food web. Ciliate biomass values from Kaštela Bay and the Gulf of Trieste were largely similar with respect to NLC populations. Average biomass of NLC in the Gulf of Trieste ranged between 0.017 and 3.26 μgC l^{-1} (Lipej 1992), compared to 0.012 and 3.925 μgC l^{-1} in Kaštela Bay. However, tintinnine bio-
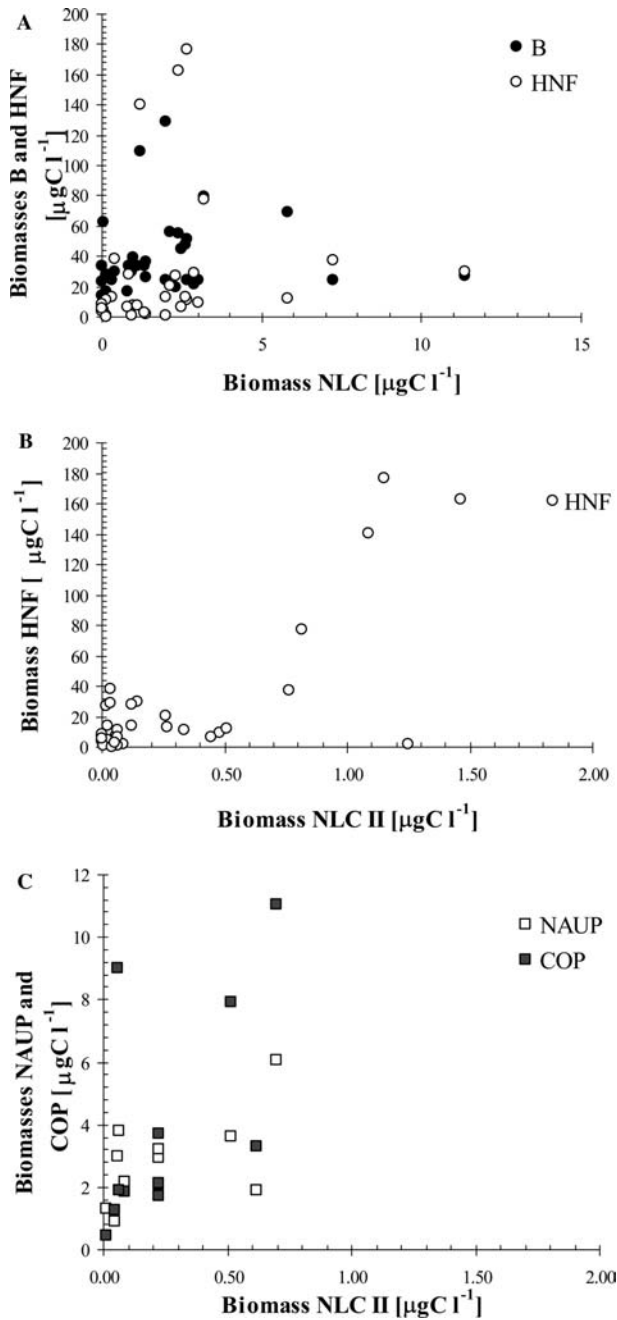
Fig. 10 Relationships between biomasses of bacteria, HNF, and NLC (**a**), HNF and NLC II (**b**) and NLC II, copepod nauplii and copepodites (**c**) illustrated by scatter plots (*B* bacteria; *HNF* heterotrophic nanoflagellates; *NLC* II non-loricate ciliates of the second size category 10^3–10^4 μm^3; *NAUP* copepod nauplii; *COP* copepodites)

Fig. 11 Relationships between the abundance of NLC II and nano-/ pico-phytoplankton (*a*) and abundances of NLC III, micrometazoans, and micro-phytoplankton (*b*) illustrated by scatter plots (*Phy N P* nano-/ pico-phytoplankton; *Phy M* microphytoplankton; *NLC II* non-loricate ciliates 10^3–10^4 μm^3; *NLC III* non-loricate ciliates 10^4–10^5 μm^3; *M* micrometazoans)

mass was markedly different. In the northern Adriatic, it varied from 0.001 to 1.648 μgC l^{-1}, while in Kaštela Bay the mean value in September 1998 was 25 μgC l^{-1}, with a maximum of 39.46 μgC l^{-1} at 10 m depth (Figs. 4, and 6b). The values of ciliate biomass in different marine areas are shown in Table 4.

Among the micrometazoans, copepod nauplii were quantitatively the most important (Fig. 3b). In the
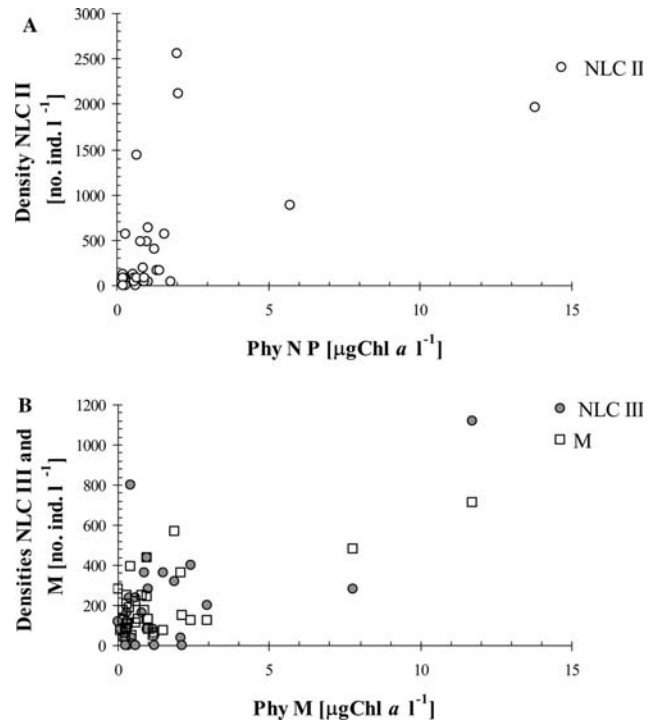
eutrophicated part of the Bay their share of micrometazoans was 49.72%, which was affected by high numbers of rotifers and Bivalvia larvae. In the northern Adriatic, copepod nauplii participated in the micrometazoan group with more than 60% (Revelante et al. 1985). Investigations in Boston harbour, Massachusetts and Cape Cod Bays also showed a dominance of copepods and their developmental stages contributing to metazoans with an average of even 83.2% (Turner 1992). In Kaštela Bay, the highest density of copepod nauplii (816 ind. l^{-1}) was found in July 1982, at 1 m depth (Kršinić, unpublished data). However, such high abundance was scarce even in the eutrophicated part of the Adriatic Sea. For example, in the Vranjic Basin the maximal number was 349 ind. l^{-1}, while in the Gulf of Trieste and the northern Adriatic the maxima were 358 and 427 ind. l^{-1}, respectively (Milani et al. 1991/1994; Lučić et al. 2003). The annual variability in nauplii number in the Adriatic Sea is similar to those recorded for other marine areas (Sanders 1987; Dagg and Whitledge 1991).

Maximum density of nauplii was recorded in the summer-autumn period when small organisms with a biomass of ~0.02 μgC ind^{-1} prevailed, indicating that many copepods show a hatching peak at that time (Fig. 3b). The summer increase in copepod number was mostly affected by *O. nana* as dominant species. This species is cosmopolitan and occurs from estuaries to the

Table 4 Ranges of ciliate biomass as reported for different marine regions

Area	Biomass of ciliated protozoans (µg C l^{-1})	Authors
Gulf of Maine	< 1–5.7	Montagnes et al. 1988
Norwegian Fjord	< 1–~12	Andersen and Nielsen 2002
		Nielsen and Andersen 2002
Chesapeake Bay	5–12	Dolan and Coats 1990
Southern part of Biscay Bay	0.7–13.3	Quevedo and Anadón 2000
Laizhou Bay	0–24.52	Zhang and Wang 2000
Kaštela Bay (Vranjic)	0.78–28.44	This paper
Damariscotta Estuary	0.4–33	Revelante and Gilmartin 1987
North Adriatic	0.02–37	Revelante and Gilmartin 1983
		Revelante et al. 1985
Kiel Bight	1–56	Smetacek 1981

open ocean and from tropical to polar regions (Paffenhöfer 1993; Nielsen and Sabatini 1996). Their relatively low rate of feeding, growth, reproduction, and mortality suggest that cyclopoids contribute significantly to the stability of planktonic communities. Their populations increase and decrease relatively slowly and are able to survive unfavourable conditions (Paffenhöfer 1993). *Oithona* spp. feed on particles which are within the lower range of the food size spectrum of copepods, and Nielsen and Sabatini (1996) thus speculated that *Oithona* might act as a link between smaller phytoplankton and/or small protozooplankton on the one hand, and larger zooplankton and fish larvae on the other hand. Statistically significant correlations, which we found between the genus *Oithona* and the small size fraction of phytoplankton, HNF, and NLC II, support this hypothesis.

Vučetić (1965, 1969, 1979) and Benović et al. (1984) presented the first data on mesozooplankton biomass in the central Adriatic, but they estimated only the dry weight of net-zooplankton. Shmeleva (1965) reported the first estimations of copepod biomass in the Adriatic Sea by calculating biovolumes. However, only a few data are available on the microzooplankton biomass in the Adriatic Sea. The temporal pattern of microzooplankton biomass (as carbon content) was described only for the Gulf of Trieste, where the microzooplankton biomass was of the same order of magnitude as the net-zooplankton (Cataletto et al. 1993; Fonda Umani 1996) (Table 5). In Kaštela Bay, the highest nauplii biovolume was twice as high as the biovolume reported by Revelante et al. (1985) for the northern Adriatic Sea.

This difference was even more evident for postnaupliar copepods: copepodite and copepod biovolumes in the Vranjic Basin were 6.9 and 8.3 times higher than in the northern Adriatic. These results reflect the high eutrophication level in the eastern part of Kaštela Bay. Studies on copepod nauplii in the northern Adriatic from March 1990 to until November 1993 provided new data on the seasonal distribution of their biovolume. At a station near the northwest cost of the Istrian Peninsula in August 1992, a biovolume of 84.82×10^6 µm^3 l^{-1} was noticed in the bottom layer (Njire 1999), which is quite similar to our data from July 1998. Almost equal biovolumes were recorded in the Lagoon of Venice (Sorokin et al. 1996). Data on microzooplankton biomass for different marine areas are shown in Table 5. Apparently, high values of biomass and biovolume of copepods and their developmental stages are characteristic for shallow neritic areas and estuaries.

As to the impact of abiotic factors on the temporal variability of the investigated zooplankton groups, our results suggest that salinity may be more important than temperature (Tables 2, 3); this is also supported by Andersen and Nielsen (2002). However, a correlation does not automatically implicate a direct causal relationship, and the trophic relationships between microzooplankton groups and biotic parameters are rather complex (Fig. 12). In summer, when the concentration of chlorophyll *a* is maximal, the nano-/pico-phytoplankton participated in the total phytoplankton biomass with more than 50%. Almost identical seasonal fluctuations occurred in bacteria and HNF. These conditions are convenient to promote the

Table 5 Ranges of microzooplankton biomass as reported for different marine regions

Area	Biomass (µgC l^{-1})	Group of organisms	Authors
Laizhou Bay	0–7	Nauplii	Zhang and Wang 2000
Gulf of Trieste	0.54–7.35	Microzooplankton	Cataletto et al. 1993
Southern part of Biscay Bay	2.4–9.3	Microzooplankton	Quevedo and Anadón 2000
	0.4–5.7	Nauplii	
Irish Sea	2–22	Microzooplankton	Edwards and Burkill 1995
Kaštela Bay (Vranjic)	3.47–26.75	Nauplii and postnauplii copepods	This paper
Norwegian Fjord	< 1–60	Nauplii and postnauplii copepods	Andersen and Nielsen 2002
North Sea	5.9–86.5	Metazoa	Fransz et al. 1998

Fig. 12 Schematic representation of statistically significant correlations among bacteria, heterotrophic nanoflagellates, phytoplankton, ciliated protozoans and micrometazoa assemblages in the eutrophicated part of the Kaštela Bay (*NLC* non-loricate ciliates; *NLC I* $< 10^3$ μm^3; *NLC II* 10^3–10^4 μm^3; *NLC III* 10^4–10^5 μm^3; *NLC IV* $> 10^5$ μm^3)
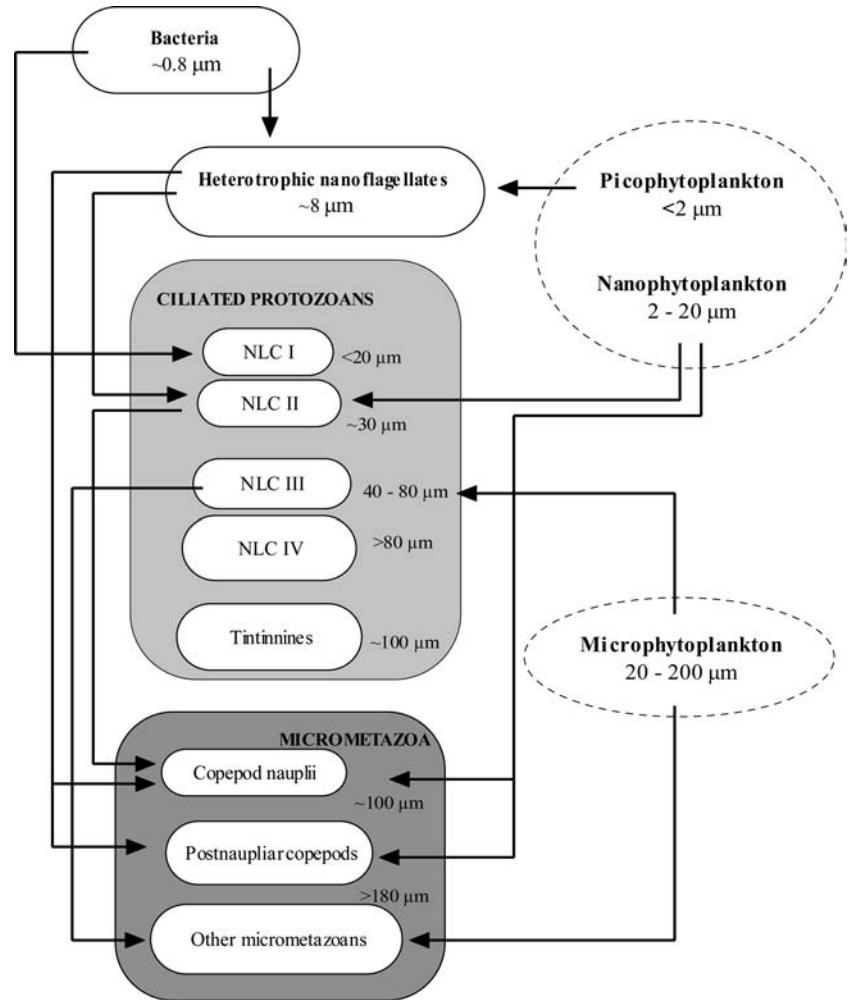
growth of ciliate populations (Fig. 10a, b). Under these circumstances, the NLC assemblage may act as an important factor of "top-down" control. From the middle of the summer, the biomasses of copepod nauplii, copepodites, and ultimately, adult small co-pepods increased. Since most of the copepods were omnivorous organisms from the genus *Oithona*, their predatory activity may play an important role in controlling NLC populations. The proliferation of *C. schabi* in autumn resulted in an increase in tintinnine biomass, which in that period even exceeded the bio-mass of copepods and their developmental stages. Hence it follows that ciliate and copepod grazing be-come more intensive with increasing eutrophication. The correlation between ciliates on the one hand, and phytoplankton, bacterioplankton, and HNF on the other hand, was higher in the Vranjic Basin then in the oligotrophic area of the Split Channel (Bojanić, unpublished data). From such connections between examined parameters, we are reasonably sure that in eutrophicated ecosystems heterotrophic nutrition, i.e. predation, prevailed (Fig. 12), while in trophically poorer environments "bottom-up" control dominated.

According to Capriulo et al. (1991), microzooplank-ton may consume between 5 and 100% of the phyto-plankton production. Although we did not estimate grazing rates, the density and biomass of the small zooplankton fraction, as well as the importance of nano-/pico-phytoplankton in the primary production (Ninević 2000), suggest an exceptional importance of ciliates and micrometazoans in the secondary produc-tion in Kaštela Bay. Our results indicate some important relationships within the microbial food web, stressing the need for the further detailed analyses as to the role of these assemblages in food web dynamics in Kaštela Bay and similar ecosystems.

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