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Quantitative variability of the copepod assemblages in the northern Adriatic Sea from 1993 to 1997

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Abstract

Quantitative variability of the copepod assemblages in the northern Adriatic Sea was investigated at two stations, during 43 cruises, from January 1993 to October 1997. Samples were taken at 0.5, 10, and 20 m, as well as near the bottom, using 5-l Niskin bottles. For inter-annual variation in the density of copepod assemblages data were presented as total number of nauplii and copepodites with adult copepods of the following groups: Calanoida, Cyclopoida-oithonids, Cyclopoida-oncaeids and Harpacticoida. Moreover, hydrographic conditions, both fractions of phytoplankton, non-loricate ciliates and tintinnids were taken into consideration. Nauplii are the most numerous fraction at both stations with an average over 74% in the total number of all copepod groups. Their numbers were significantly higher at the western eutrophic station, while at the eastern oligotrophic station, an absolute maximum of 693 ind. l^{-1} was noted. The maximum values of calanoids and oithonids occur generally during summer and these copepods are always more numerous at the western station: 33–50% and 50–63%, respectively. The most abundant taxa identified were the calanoid *Paracalanus parvus* and the cyclopoid *Oithona nana*. Oncaeid species *Oncaea waldemari* and *Monothula subtilis* dominated during late autumn and winter. An atypical increase in the abundance of oncaeids during the summer of 1997 could be related to an invasion and mass occurrence of the calycophoran siphonophore *Muggiaea atlantica*. It can be concluded that these dominant copepods are responsible for the stabilization of very complex processes. Atypical appearances of major copepod groups and disturbances in the copepod population structure itself can significantly influence changes in the ecosystem of this very sensitive region.

Keywords: phytoplankton; zooplankton; copepods; Adriatic; northern Adriatic

1. Introduction

The northernmost part of the Adriatic Sea is located between the western coast of the Istrian Peninsula (Croatia) and the northeastern coast of Italy. The area is estuarine in character and is shallow with depths between 20 and 40 m. The western part of this area is strongly influenced by the Po River and is therefore highly eutrophic (Degobbis et al., 1995). Productivity in the eastern part of the basin is much lower due to incoming southern currents carrying oligotrophic water masses from the central and southern Adriatic (Orlić et al., 1992). Phytoplankton blooms, which have inspired numerous investigations, were frequently observed in the last 30 years in the Adriatic, as summarized by Fonda-Umani (1996). Amorphous mucous aggregates have appeared during the summer months with very strong intensities during 1988, 1989, 1991, 1997 and 2000–2002 (Herndl and Peduzzi, 1988; Degobbis et al., 1991; Kaltenböck and Herndl, 1992; Precali et al., 2005).

Zooplankton assemblages have received less attention, though they are important for the knowledge of pelagic ecosystems. Copepods, as the dominant organisms in any marine habitat, are naturally very important to the overall grazing potential

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of the northern Adriatic. The first data on the qualitative content of copepods in the northern Adriatic originate from the last decades of the 19th century and the first decades of the 20th century. More recently, studies have been made on the distribution of copepods in the northern Adriatic (Hure and Scotto di Carlo, 1969; Hure and Kršinić, 1998), their seasonal and inter-annual variability (Mozetič et al., 1998; Fonda-Umani et al., 2005), as well as the distribution or population densities of their early development stages (Revelante and Gilmartin, 1983; Kršinić et al., 1988; Kršinić, 1995). Nauplii and earlier copepodites were included in the micro-zooplankton category, and they were not considered in the evaluations of total copepod populations. Comparison of the results of many years of research conducted on all copepod groups found in the open waters of the northern Adriatic which had previously been studied presented problems, primarily because of the variety in sampling methods used for different groups. In early copepod research, it was common to use a 250 μm (Hure and Kršinić, 1998) or 200 μm plankton net in vertical hauls from the bottom to the surface (Mozetič et al., 1998; Fonda-Umani et al., 2005). Such samples are not quantitatively relevant, as they allow almost all small copepods and their developmental stages to pass through (Kršinić and Lučić, 1994). In addition, during phytoplankton blooms and when gelatinous matter is present in large quantities, the mesh aperture becomes blocked, and the net loses its filtration capacity.

The objective of this paper is to determine the quantitative aspect of the population structure, seasonal abundance and vertical variability of all copepod assemblages based on identical methods at two characteristic stations in the northern Adriatic Sea between 1993 and 1997.

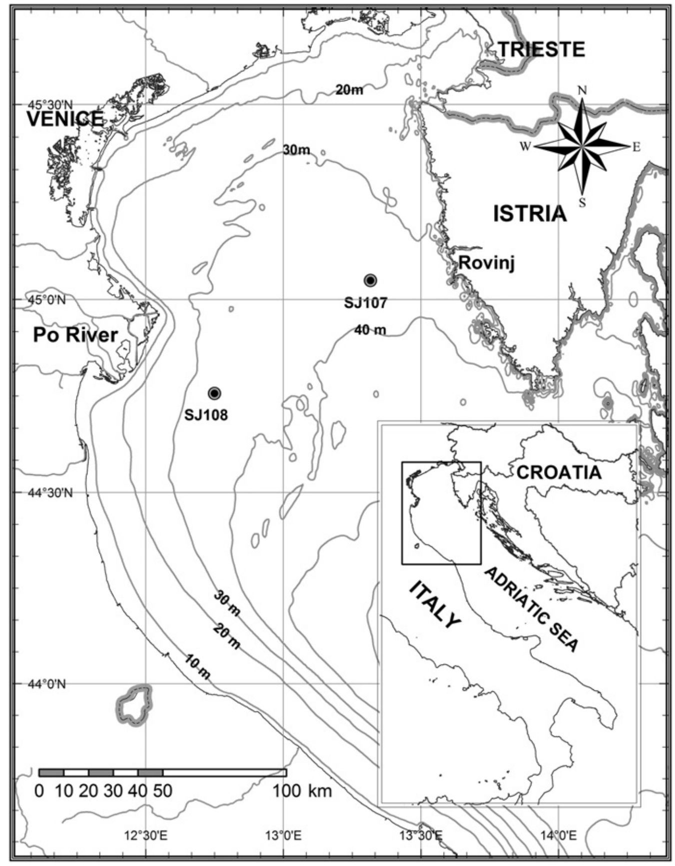

Fig. 1. Map of the northern Adriatic Sea with location of sampling stations.

2. Materials and methods

The copepod assemblages in the northern Adriatic Sea were investigated at two stations (Fig. 1) during 43 cruises (mainly monthly sampling), in the period from January 1993 to October 1997. Samples were taken at 0.5, 10, and 20 m depth, as well as near the bottom, using 5-l Niskin bottles aboard the vessel "Vila Velebita" from the Center for Marine Research in Rovinj (CMR).

Zooplankton samples were preserved with a 2.5% final concentration of formaldehyde neutralized with $CaCO_3$. Samples were sedimented for 24 h in plastic containers in the laboratory, from which about 3/4 of the water was decanted. The remainder was poured into a glass cylinder (10 cm diameter), and was sedimented for a further 24 h after which the superfluous volume was decanted. This process reduced the original volume of 5 l to 30 ml in 72 h. Decanting was accomplished using a vacuum pump and a slightly curved pipette. The organisms were counted by means of an inverted microscope (Olympus IMT-2) at a magnification of 100 and 400×. Samples were counted in a glass cell, dimensions 7 × 4.5 ×0.5 cm.

Temperature was measured using reversing thermometers, while salinity was measured with a Yoo Kal MKII high precision salinometer. The hydrographic samples were collected at standard hydrographic levels. For details, see Degobbis et al. (1995).

Samples (200 ml) for micro-phytoplankton (cells >20 μm) and nano-phytoplankton (cells 2–20 μm) enumeration were preserved with Lugol's solution buffered with sodium acetate (2% final concentration). Micro-phytoplankton species identification and micro-phytoplankton and nano-phytoplankton cell count were conducted with a Zeiss inverted microscope, following the Ütermöhl settling technique of random fields (Ütermöhl, 1958). Autotrophic and heterotrophic nano-phytoplankton were not discriminated in this study.

The non-parametric Spearman correlation coefficient (R_s) was used for correlations between all variables. Parameters were compared between stations using the *t*-test; all data were log transformed. Non-parametric multivariate analysis (Clarke, 1993; Clarke and Warwick, 1994) based on zooplankton communities was performed. Classification (group average sorting of the Bray–Curtis similarity measures based on 4th root transformed relative seasonal abundance data) and ordination (multi-dimensional scaling (MDS) on the above similarity matrices) methods were used. MDS analysis would be considered unsuccessful if the stress values were >0.3 (Clarke, 1993). Similarity percentage analysis (SIMPER) was used in order to reveal the contribution of single groups of copepods to dissimilarities between stations. Multivariate statistical analyses (MDS) and SIMPER were performed using PRIMER software (version 5.0; Clarke and Gorley, 2001).

3. Results

3.1. Hydrography

During the period 1993–1997, temperature in the investigated area ranged from 7.40 to 28.93 °C, and salinity from 21.00 to 38.77 (Table 1). The larger temperature range and minimal salinity range were observed at station SJ108, which is close to the Po River and is therefore directly influenced by its freshwater (Degobbis et al., 2000). The highest salinity was observed (Table 1) at station SJ107 at the opposite side of the basin, which is more influenced by the southern currents that import saltier waters to the area (Artegiani et al., 1997).

The investigated period was characterized by two events. The first event occurred in the autumn of 1993 when an extreme freshwater discharge from the Po River flooded the northern Adriatic, and was mainly limited to the upper part of the water column (Kršinić and Precali, 1997). The second event was at the end of the winter of 1996, when a pronounced intrusion of saltier and warmer water from the south occurred in the whole area. This event probably contributed to the lack of circulation in the northern Adriatic during the last year of the investigated period.

3.2. Phytoplankton

Abundances of micro-phytoplankton (Fig. 2a) were lower by 40–70% and those of nano-phytoplankton (Fig. 2b) were lower by 10–30% at the eastern (SJ107) than at the western station (SJ108) and both decreased with depth. Micro-phytoplankton abundances at the eastern station (SJ107) were approximately 50% lower than at the western station (SJ108). Three micro-phytoplankton blooms occurred yearly: highest in spring (February–April), followed by two less abundant blooms, one in summer (July) and the other in autumn (September/October). The blooms (10^7 cells l^{-1}) occurred in the spring of 1993 and summer of 1997 at the western station (SJ108) and in October 1993 at the eastern station (SJ107). A spring bloom of considerably lower magnitude occurred at the western station (SJ108) during 1994. 1995 differed from other years, with micro-phytoplankton spring bloom at the western station at 10 m, rather than at the surface as occurs usually, and an unusually high micro-phytoplankton bloom in June at the eastern station (SJ107), followed by only one another in November, which was smaller than other autumn blooms. Nano-phytoplankton abundances showed fewer oscillations during the year, with regular spring increase, which was rather high in 1993 and 1997 at the western station (SJ108).

Table 1
Annual statistics (N – number of data, Avg – average, Min – minimum, Max – maximum) for temperature (t) and salinity (S) at the analyzed stations in the period 1993–1997

Station	Year	N	t_{Avg}(°C)	t_{Min} (°C)	t_{Max} (°C)	$S_{Avg} \cdot 1$	$S_{Min} \cdot 1$	$S_{Max} \cdot 1$
SJ108	1993	55	15.15	7.40	28.93	36.33	21.89	38.42
	1994	55	14.86	8.05	28.30	35.94	21.00	38.05
	1995	40	14.80	8.52	26.17	36.73	29.25	37.81
	1996	55	16.68	7.68	25.40	36.35	25.63	38.54
	1997	74	16.79	8.20	26.77	35.21	24.28	38.01
SJ107	1993	76	14.17	8.33	26.02	37.67	28.98	38.50
	1994	72	15.49	10.15	26.80	37.40	34.86	38.17
	1995	48	14.91	10.04	25.66	37.41	31.94	38.10
	1996	46	15.93	8.23	24.25	37.71	35.39	38.77
	1997	74	17.29	10.30	26.29	36.37	29.63	38.45

3.3. Ciliated protozoans

Non-loricate ciliates were occasionally the dominant zooplanktonic organisms in the northern Adriatic. In general, two annual peaks of abundance were registered, lower in the spring and higher in the summer (Fig. 2c). In contrast to the abundance in 1993, 1996 and 1997, non-loricates were exceptionally numerous at both stations in 1994 and 1995. Maximum concentrations at the western station SJ108 were observed in July 1994 at the surface (6560 ind. l^{-1}) and at the eastern station SJ107 in August 1995 at a 10 m depth (4880 ind. l^{-1}). In 1993, very low values were noted at both stations, generally under an average of 200 and 20 ind. l^{-1}, respectively. Tintinnids were scarce during the entire investigation period at station SJ107 (Fig. 2d). However, they dominated at station SJ108 in March 1994 (1587 ind. l^{-1} at surface) and June 1995 (5732 ind. l^{-1} at surface) when the species *Tintinnopsis minuta* comprised 97% of the total abundance.

3.4. Copepod assemblages

3.4.1. Nauplii

Inter-annual variation in the density of copepod nauplii at both stations generally showed a summer maximum (Figs. 3a and 4a). Significant differences in naupliar abundance between stations were found (t-test, $p < 0.01$, $n = 172$). The highest differences in nauplii abundance between stations were found in 1996 when the density was greater on average by 55% or 67% at the western station. Values of nauplii were under 200 ind. l^{-1} throughout 1994 and 1995. However, nauplii were more abundant in the upper layers at station SJ108 in August 1993, June and September 1996, and July and September 1997 at 20 m depth. In August 1997, minimum values were observed at all layers at station SJ108, while at the same time, the density of nauplii reached 693 ind. l^{-1} at station SJ107 at 10 m. The contribution of nauplii to the total number of copepods at station SJ108 was lower during 1994 and 1995 at only 63%, while in other years the contribution was between 74%, in 1993, and 80%, in 1997. However, nauplii contributed between 67% (in 1995) and 84% (in 1997) at the eastern station, SJ107. A significant correlation ($p < 0.001$) was observed throughout the investigated period between nauplii abundance and all copepod groups at station SJ107 and at station SJ108 for calanoids and oithonids (Table 2). The correlation between nauplii and non-loricate ciliates was significant ($R_s = 0.627$, $p < 0.0001$) at the western station and ($R_s = 0.450$, $p < 0.0001$) at the eastern station. A significant correlation between nauplii and micro-phytoplankton and nano-phytoplankton occurred at both stations (Table 2).

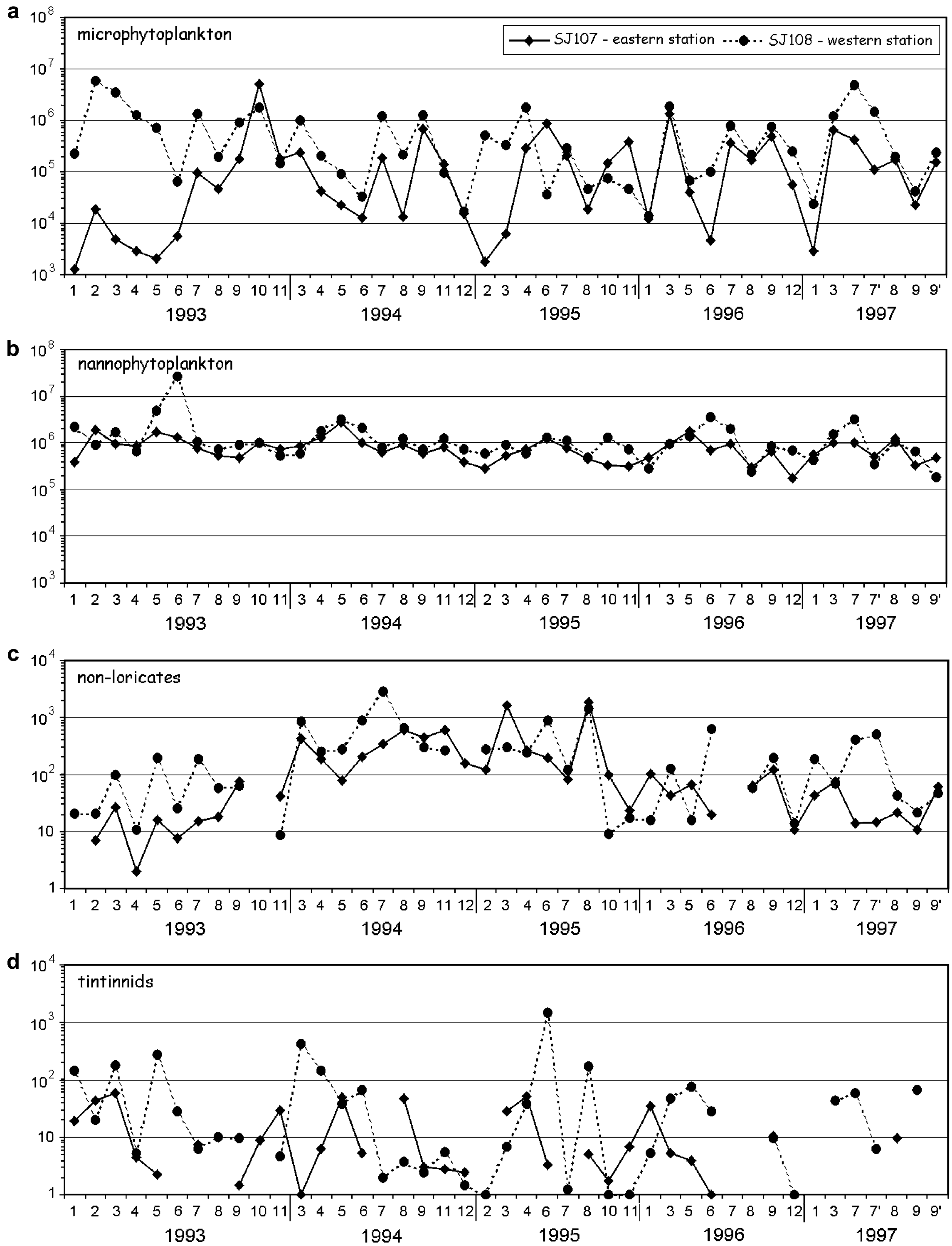

Fig. 2. Inter-annual variability of (a) micro-phytoplankton, (b) nano-phytoplankton, (c) non-loricates and (d) tintinnids at two sampling stations presented on logarithmic scale.

3.4.2. Calanoida copepodites and adults

Inter-annual variation in the density of post-nauplii calanoids was observed at both stations, with a summer maximum usually occurring from June to August (Figs. 3b and 4b). Significant differences in calanoid abundance between stations were found (t-test, $p < 0.001$, $n = 172$). At the western station, the average annual values were 33–50% greater than at the eastern station. Variations at the eastern station were lower in intensity, with maximum values under 20 ind l^{-1}. There was a marked difference in the year-to-year variation of calanoids at the western station. Usually, most of the population was at the surface or at a depth of 10 m. Very high values

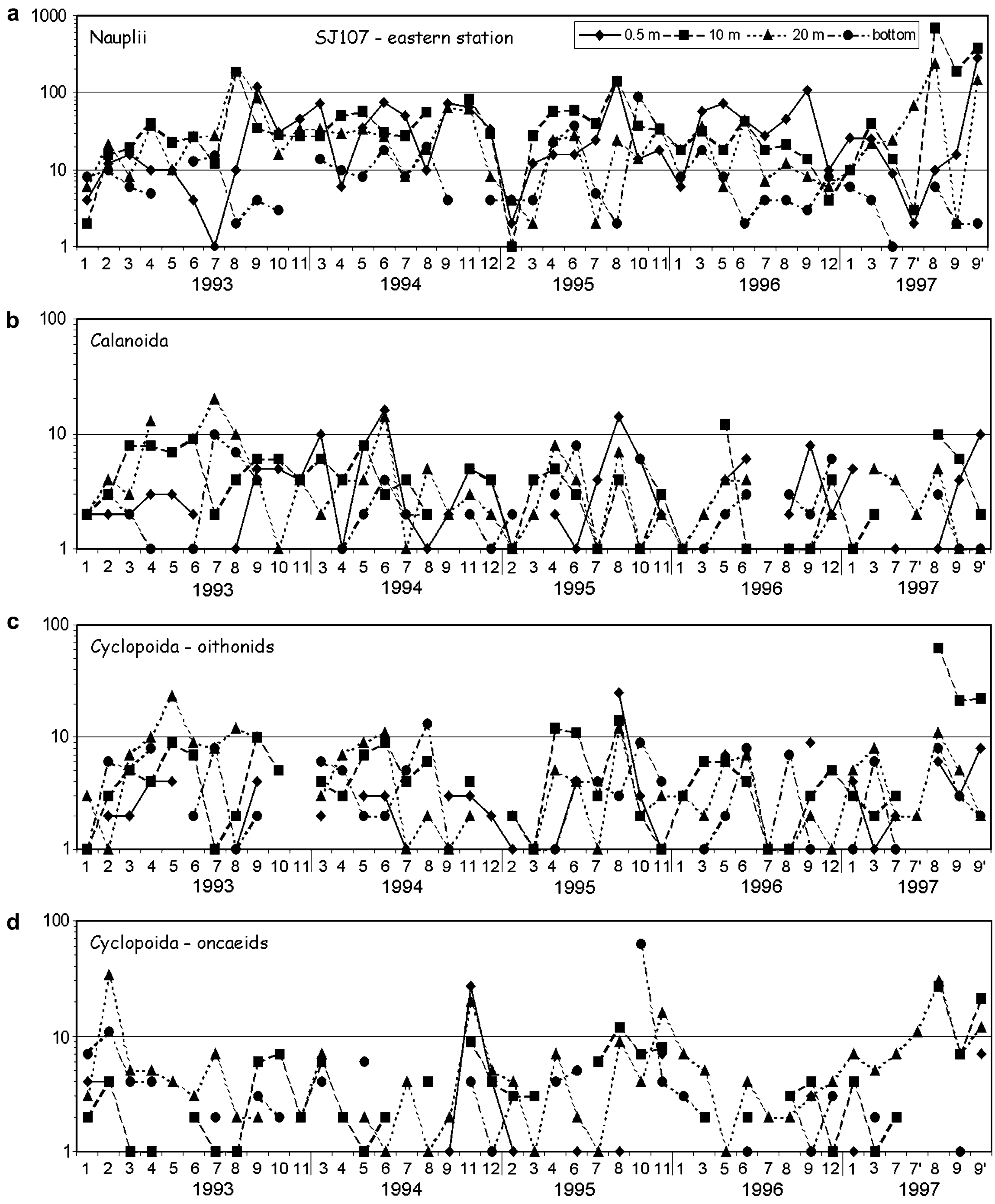

Fig. 3. Inter-annual variability of copepod population densities for different depths at the eastern station SJ107 presented on logarithmic scale; (a) Nauplii, (b) Calanoida, (c) Cyclopoida-oithonids and (d) Cyclopoida-oncaeids.

were registered in 1993, with a summer maximum of 109 ind. l^{-1} at the surface in August and a predominance of copepodites and adult individuals of *Paracalanus parvus*, and also in November, when copepodites of *Acartia clausi* dominated with 35 ind. l^{-1}. Calanoids contributed to the annual average at both stations, making up 18–38% of the total number of copepods. Of the 20 calanoids identified to the species level, the following were quantitatively significant: *Ctenocalanus vanus*, *Temora stylifera*, *Temora longicornis* and *Centropages typicus*. The remaining species accounted for less than 3% of the total number of calanoids. Significant correlations between calanoids and nano-phytoplankton, as with non-loricate ciliates at both stations were noted (Table 2).

3.4.3. Cyclopoida-oithonid copepodites and adults

Inter-annual variation in the density of oithonids was higher at the western station than at the eastern station. Significant differences in oithonid abundances between stations

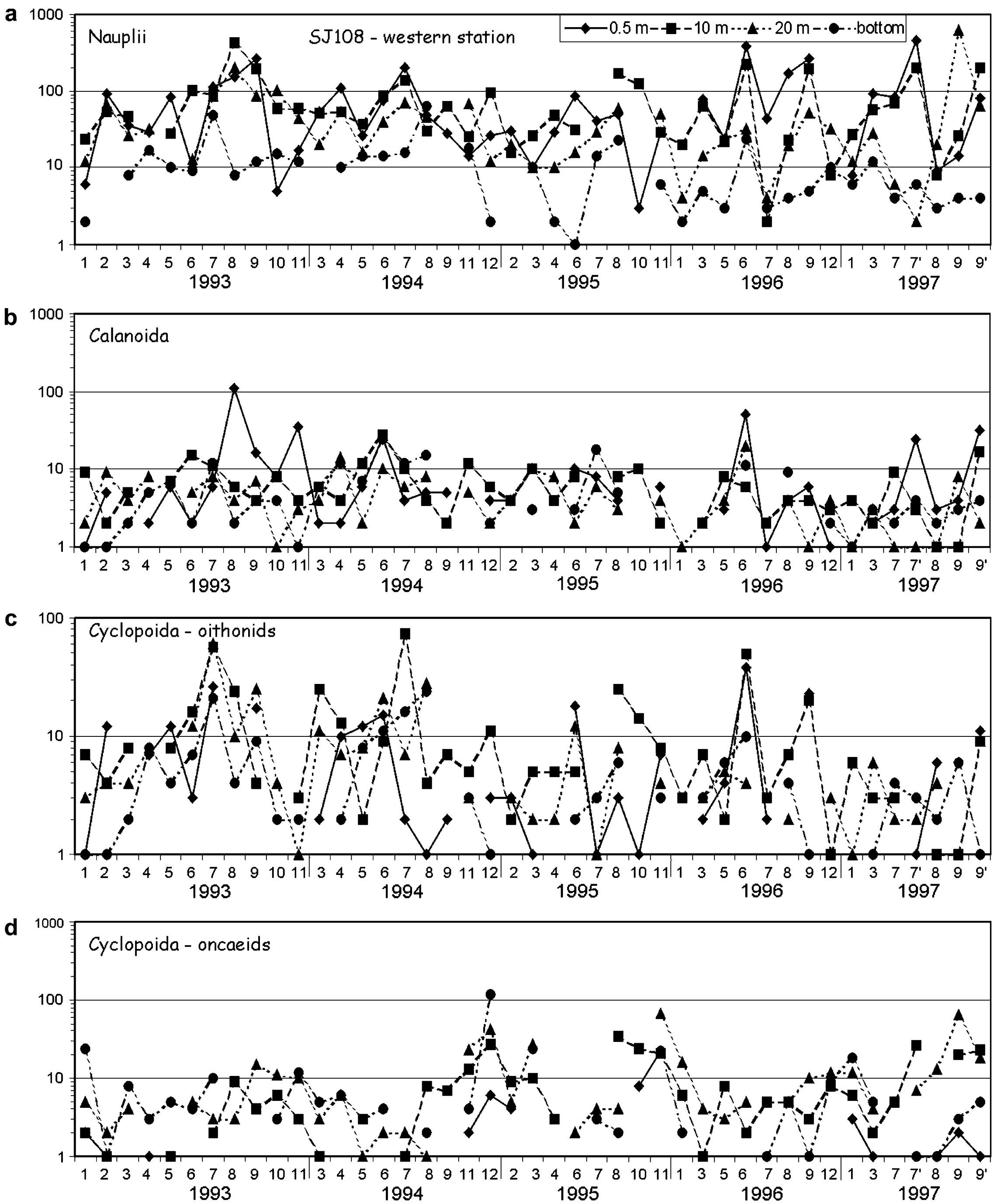

Fig. 4. Inter-annual variability of copepod population densities for different depths at the western station SJ108 presented on logarithmic scale; (a) Nauplii, (b) Calanoida, (c) Cyclopoida-oithonids and (d) Cyclopoida-oncaeids.

were found (t-test, $p < 0.05$, $n = 172$). The highest differences between stations were found in 1993 and 1994, when the average density at the western station was 50–64% higher on average. The highest densities of oithonids rarely occurred at the surface, while the population core was generally found at 10–20 m depth. Maximum values occurred at SJ107 in August 1997 at 10 m depths (62 ind. l^{-1}); otherwise, the density was under 20 ind. l^{-1}. At the western station, summer maximum was absent in 1997. Relatively high values were noted in July 1993, 1994, and in June 1996 (Figs. 3c and 4c), with values between 49 and 74 ind. l^{-1}; *Oithona* copepodites and adults of *Oithona nana* predominated. The species *Oithona similis* is quantitatively important, and is generally found in the bottom layer with average values of up to 34% of the total number of adult oithonids. The species *Oithona plumifera* was observed sporadically, with few specimens. The annual average contribution of oithonids to the total number of copepods was 20–47% at both stations. At both the stations, a significant correlation of oithonids with calanoids was noted (Table 2), while at the western station significant

Table 2
Spearman rank correlation coefficient between copepod assemblages and nano-phytoplankton, micro-phytoplankton, non-loricate ciliates and tintinnids ($n = 172$, $p < 0.01$*, $p < 0.001$**, $p < 0.0001$***)

	Nano-phytoplankton	Micro-phytoplankton	Non-loricates	Tintinnids	Nauplii	Calanoids	Cyclopoida-oithonids
Station SJ108							
Nauplii	0.313***	0.327***	0.627***	0.197			
Calanoids	0.247*	0.063	0.328***	0.135	0.537***		
Cyclopoida-oithonids	0.257**	0.007	0.346***	0.253**	0.522***	0.538***	
Cyclopoida-oncaeids	−0.252**	−0.280**	−0.206*	−0.132	0.051	0.045	0.089
Station SJ107							
Nauplii	0.416***	0.429***	0.450***	0.144			
Calanoids	0.289**	0.076	0.215*	0.167	0.547***		
Cyclopoida-oithonids	0.120	−0.105	0.081	0.075	0.386***	0.449***	
Cyclopoida-oncaeids	−0.060	0.060	0.057	0.177	0.258**	0.140	0.231*

correlations were noted with non-loricate ciliates, tintinnids and nano-phytoplankton.

3.4.4. Cyclopoida-oncaeid copepodites and adults

Oncaeids were consistently present at both stations, and maximal values were reached in the autumn/winter period, except in the summer of 1997 (Figs. 3d and 4d). Significant differences in oncaeid abundance between stations were found (t-test, $p < 0.01$, $n = 172$). During 1993 and 1996, lower values were recorded at both stations. A maximum of 118 ind. l^{-1} was observed just above the bottom in December 1994 at SJ108 (86 ind. l^{-1} copepodites and 32 ind. l^{-1} adult *Oncaea waldemari*). At the same station in early September 1997, a maximum of copepodites (45 ind. l^{-1}) and *Monothula subtilis* (19 ind. l^{-1}) were found at 20 m depths. Lower densities were registered at the surface of both stations, while the greatest densities were noted in general at 20 m or above the bottom. During winter, individual specimens of the species *Oncaea media* and *Oncaea zernovi*, as well as representatives from the *Corycaeus*, were observed in the bottom layers. The annual average contribution of oncaeids to the total number of copepods was 25–40% at station SJ107 and 18–53% at SJ108 (in 1997). A significant correlation with negative low coefficients between oncaeids and phytoplankton and non-loricates at SJ108 was noted (Table 2).

3.4.5. Harpacticoida copepodites and adults

Euterpina acutifrons and *Microsetella norvegica* represented planktonic harpacticoids during warmer periods at both stations, with highest values occurring in autumn. Average values were usually under 3 ind. l^{-1}. Only in 1997 did the average density increase substantially, reaching 5 ind. l^{-1} in August at SJ107 and in September at SJ108.

3.5. Statistical analysis

Zooplankton assemblages were determined for both, eastern and western, stations according to their relative seasonal abundances for the entire 5-year investigated period. Encircled groups on MDS plots (Figs. 5b and 6b) are defined as a result of hierarchical clustering displayed in dendrograms (Figs. 5a and 6a).

The same grouping pattern can be noticed for both stations. Calanoids, oithonids and oncaeids form the same group (group A). Oncaeid values slightly differ so they are forming A2 subset; at the eastern station values from years 1993, 1994, and 1996 and from years 1994 and 1995 at the western one. Non-loricates form group C at both stations because of their high values during 1994 and 1995. Other non-loricates belong to group B with nauplii and, only at the western station, tintinnids. Separation of group D at both stations is caused by lack of tintinnids in 1997.

The similarity percentage (SIMPER) analysis was used to identify the groups of copepods that contributed most to the differences between stations SJ107 and SJ108. Nauplii contributed to 33% of those differences, while oncaeids, oithonids and calanoids contributed to 24.3%, 22.9% and 19.8%, respectively.

4. Discussion

The 5-l volume that we used during our research is representative for the eutrophic and mesotrophic regions of the Adriatic (Kršinić, 1980). However, it does not meet the needs of adult calanoid copepods during the colder months, when their population density is low, with values of less than 1 ind. l^{-1}. In addition, we identified only 50% of the known calanoid species in the northern Adriatic (Hure and Scotto di Carlo, 1969; Hure and Kršinić, 1998). On the other hand, small oncaeid species were not registered. For example, *Oncaea waldemari* was determined for the first time in the northern Adriatic according to Böttger-Schnack (2001). It was probably previously classified as *Oncaea media*, which is considered a rare species and an immigrant from the Middle Adriatic. Accordingly, other quantitative methods must be used for qualitative and quantitative research work in this shallow and eutrophic region of the Adriatic Sea, such as Niskin bottles of great volume or the sampler «Adriatic» (Kršinić, 1990).

During the entire investigated period, the phytoplankton abundance was higher in the western compared to the eastern region of the northern Adriatic (Revelante and Gilmartin, 1983, 1992; Degobbis and Gilmartin, 1990). However, the phytoplankton higher density did not always result in a higher density of all copepod groups (Revelante et al., 1985;

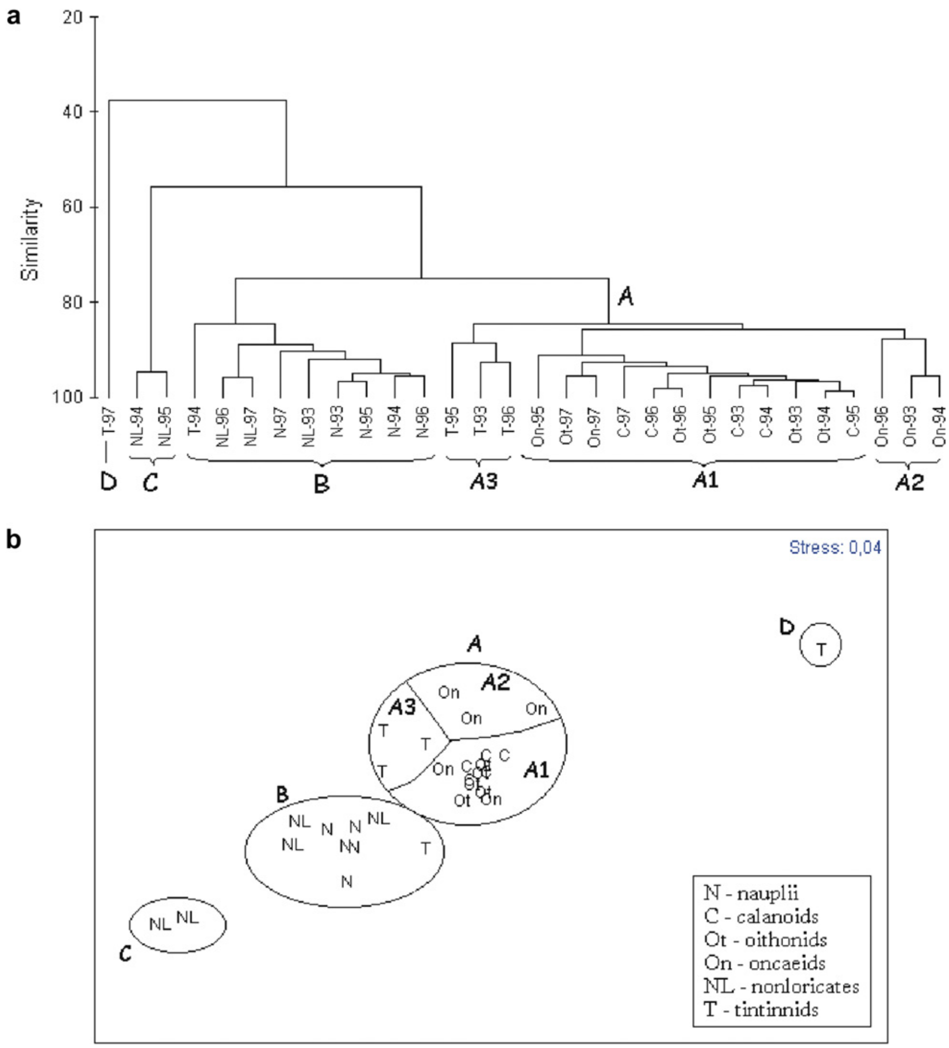

Fig. 5. Copepod assemblages at the eastern station SJ107. (a) Cluster and (b) MDS analyses based on Bray–Curtis similarity matrices.

Kršinić et al., 1988). Nauplii were the most numerous fraction of copepods at both stations. Moreover, the percentage of nauplii in the total number of all copepod groups was very high, and on average was greater than 74% (Revelante et al., 1985; Kršinić et al., 1988; Kršinić, 1995). The highest difference in nauplii density between stations was noted during 1993 and 1996, when there were 55% or 67% more nauplii on average at the western station. Therefore, nauplii contributed to 33% of the differences between stations (SIMPER). However, at the eastern, oligotrophic station (SJ107), an absolute maximum of nauplii was noted for the northern Adriatic. It should be noted that the highest values of 450 ind. l^{-1} in October 1988 (Kršinić, 1995) were observed earlier at this station. Along the eastern coast of the Adriatic, nauplii values greater than 500 ind. l^{-1} were noted only in peripheral zones influenced by eutrophication, the central part of Kaštela Bay and the estuary of the Krka River (Kršinić, in preparation), as well as in the small meromyctic Lake Rogoznica, where only one species of calanoid copepod exists (Kršinić et al., 2000). During the summer of 1997, we registered an atypical horizontal distribution of the nauplii population with a shift in the main bulk away from the western station towards the eastern one and back, which could be related to specific summer currents in the northern Adriatic (Brana and Krajcar, 1995; Kršinić and Njire, 2001).

The maximum values of calanoids and oithonids generally occurred during the summer months at both stations, mainly more numerous at the western station, and the density differences between stations for these copepod groups were significant. In general, there were two peaks of abundance each year, occurring at differing times between June and September. Among summer abundance peaks, the eastern station stood out with its markedly decreased densities in July between 1994 and 1997. Annual peaks with increased values were noted for both groups, either simultaneously or one month apart (Fig. 7). The fact remains that the process of mucilage formation was not noted from 1993 to 1996 (Precali et al., 2005). It may be concluded that the two dominant species, small calanoid *Paracalanus parvus* (filter feeding behavior) and oithonid *Oithona nana* (omnivorous feeding), were very important for the regulation of phytoplankton production levels during the summer period. The low correlations for both

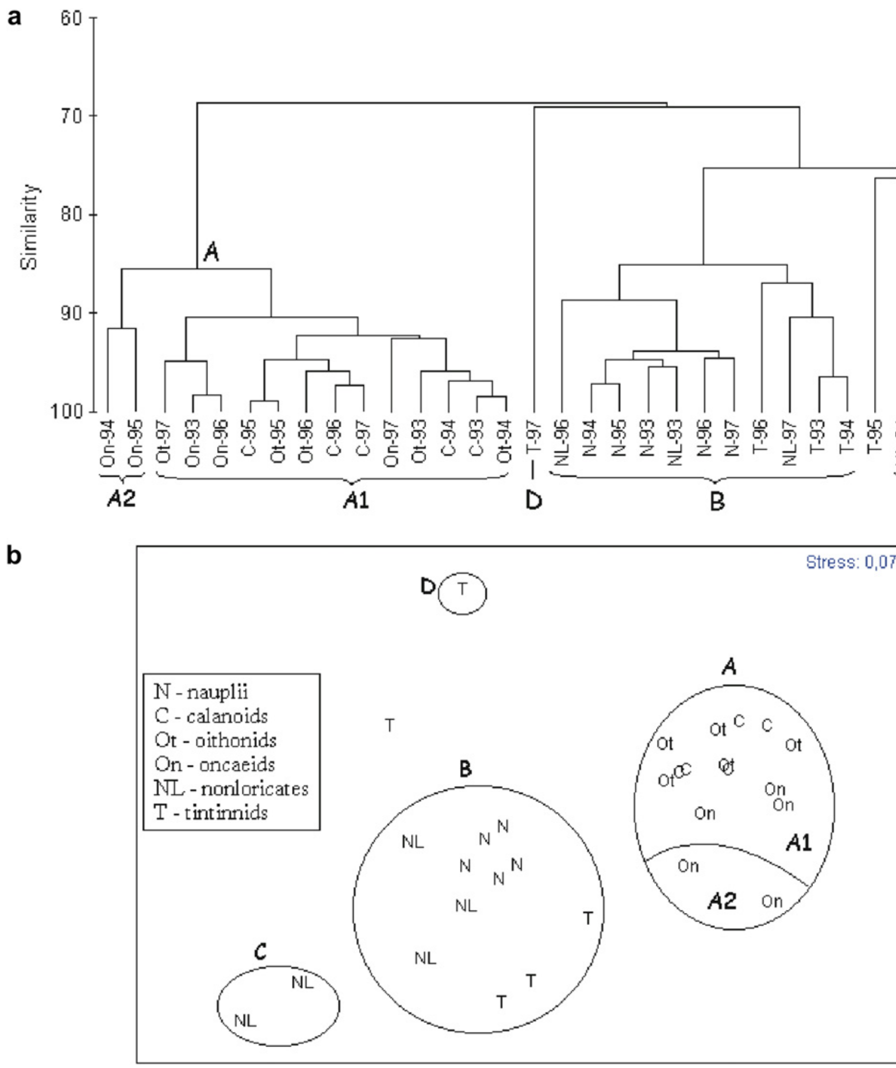

Fig. 6. Copepod assemblages at the western station SJ108. (a) Cluster and (b) MDS analyses based on Bray–Curtis similarity matrices.

phytoplankton fractions and fractions of these copepods were determined due to very fast pelagic changes in the northern Adriatic, which cannot be analyzed by monthly samplings, particularly under stratification conditions. However, the graph that depicts the relative succession of calanoids, oithonids and micro-phytoplankton shows that there is usually a phytoplankton minimum when these copepods are dominant (Fig. 7). For example, in August of 1994, an annual minimum of phytoplankton pigments was determined (Ahel and Terzić, 1998), which came after the annual maximum of nauplii, *P. parvus* and *O. nana*. Davis (1984) states that *P. parvus* is the major producer of copepod biomass in Georges Bank. In terms of secondary production, the combined annual production of these small species is nearly twice that of *Calanus finmarchicus*. The species *O. nana*, has the ability to adapt to different food sources because it consumes a much wider range of food than the other copepods (Lampitt and Gamble, 1982), and is very important in many neritic regions that are exposed to eutrophication (Richard and Jamet, 2001). According to Williams and Muxagata (2006) it achieves a density of 48 ind. l^{-1} in the Southampton Waters, and its annual production represents 18% of the total copepod production. For the Gulf of Trieste, it was found (Fonda-Umani et al., 2005) that *Acartia clausi* is present throughout the year and can represent up to 90% of the whole copepod population. Considering that the authors used a 200 μm net, it is obvious that an important population of small copepods was lost (Kršinić and Lučić, 1994; Gallienne and Robins, 2001; Paffenhöfer and Mazzocchi, 2003).

During 1994 and 1995, which showed conditions of the lowest nauplii density values as well as very high density values for non-loricate ciliates and tintinnids, relatively high annual density averages for calanoids and oithonids were noted. A markedly lower density of phytoplankton was noted for the same period, and the average micro-phytoplankton density values did not exceed 30% of the maximum density in 1993. We can assume that oithonids, ciliates, together with calanoids, contributed significantly to the total zooplankton population in regulating the level of phytoplankton production. Ciliates are certainly important in the food chain both as predators and prey, which should be taken into account when evaluating the overall production relationships in this part of the Adriatic

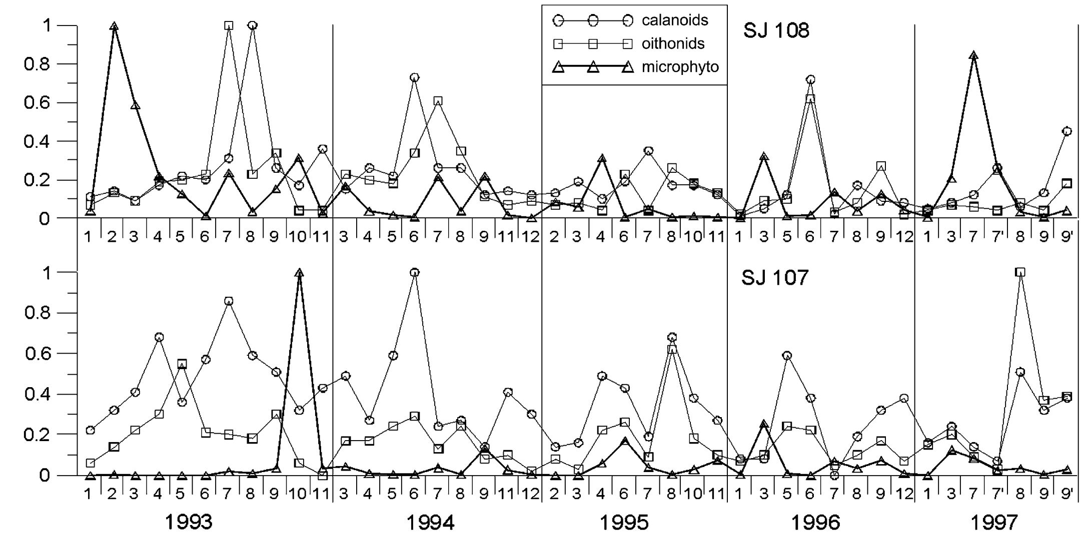

Fig. 7. Inter-annual succession of micro-phytoplankton, calanoids and cyclopoid-oithonids. Values present percentages of an average maximum population density (cells l^{-1}, ind. l^{-1}) for the entire period. Average maximum values are: station SJ108; 5.8×10^6 (microphyto', February 1993); 41 (oithon', July 1993); 31 (calan., August 1993), station SJ107; 5.2×10^6 (microphyto', October 1993); 22 (oithon', August 1997) and 9.3 (calan', June 1994), respectively.

Sea. In this respect, the contribution of ciliates to the daily food intake of copepods could be significant (Calbert and Saiz, 2005; Gismervik, 2006).

Oncaeids, as carnivorous copepods, are consistently present in the northern Adriatic zooplankton community, with maximum densities occurring during late autumn and winter (Hure and Scotto di Carlo, 1969; Kršinić, 1995; Hure and Kršinić, 1998). However, during the summer of 1997, an atypical increase in density of oncaeids could be related to an invasion and mass occurrence of the calycophoran siphonophore *Muggiaea atlantica* at the beginning of summer 1997 in the northern Adriatic (Kršinić and Njire, 2001). It is reasonable to assume that the increase in oncaeid density plays a significant role in the processes of calycophorid decomposition. It is known that oncaeid copepods, due to their feeding behavior (Paffenhöfer, 1993), show a high frequency of association with larger gelatinous organisms (Ohtsuka and Kubo, 1991; Go et al., 1998).

The mucilage event during summer of 1997 in the northern Adriatic followed the phytoplankton bloom at the western station (Precali et al., 2005). This probably affected the copepod population structure, as in earlier years, 1988, 1989 and 1991 (Kršinić, 1995), but also likely lowered their potential in reducing phytoplankton production. Very high nano- and micro-phytoplankton density values were observed at the beginning of July, followed by high nauplii densities at the end of July, and slightly increased calanoid and non-loricate ciliate densities. In addition, very low oithonid densities throughout 1997, and even their minimum values were observed for the entire period of research. Namely, the copepod population was under the heavy grazing pressure of calycophorid *Muggiaea atlantica* colonies in early July, which achieved very high values, 450 nectophores and 730 eudoxids m^{-3} (Kršinić and Njire, 2001). In August, massive deaths and a degradation of the calycophorid colonies contributed to the increase of gelatinous matter.

This research has shown that the fine-scale vertical distribution of copepods should be evaluated, even for shallow eutrophic regions (Paffenhöfer and Mazzocchi, 2003). Almost as a rule, the bulk of main copepod populations are distributed in various layers during conditions of stratification; small calanoid copepods are generally the most numerous in the surface layer up to 10 m of depth, oithonids from 10 to 20 m, while oncaeids are always present in the deepest layers.

5. Conclusions

Based on the 5 years of research presented, which examined the structure and variability of major groups of copepod populations, it can be concluded that nauplii, copepodites and adult copepods, along with ciliates, are the most important organisms of the zooplankton community in the northern Adriatic. Small calanoid and oithonid copepods are responsible for the stabilization of very complex processes and the regulation of phytoplankton production levels during the warmer months. Atypical appearances of major copepod groups and disturbances in the copepod population structure itself can significantly influence changes in the ecosystem of this very sensitive region. Future research must combine other quantitative methods in order to determine patterns in vertical distributions at a finer scale, with sampling conducted at intervals significantly shorter then one month, particularly during the stratification period.

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