

Horizontal distribution of tintinnids in the open waters of the South Adriatic (Eastern Mediterranean)*

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SUMMARY: The horizontal distribution of oceanic tintinnids was studied in the South Adriatic Sea during 11 cruises undertaken between 1980 and 1990. Of the 70 species identified, there were 47 surface, 16 subsurface, 4 mid-water, and 3 deep-sea species. The dominant surface and subsurface species were *Dictyocysta mitra* and *Codonella aspera*. *Undella claparedei*. *Parundella lohmanni* predominated in the mid-water layers and *Xystonellopsis scyphium* in the deep-sea layers. Ingression of water masses from the Ionian Sea and the formation of a cyclonic gyre are important in determining the horizontal distribution of tintinnids in the South Adriatic. Periods of strong advection of waters from the Ionian Sea impose a longitudinal type of distribution on tintinnids, characterized by high species diversity, low abundance, and the transport of southern species to the Middle and North Adriatic. This differs from "eddy type" distribution, in which species diversity is lower, population density is greater in all layers, and the transport of species northward ceases. It may be assumed that mesopelagic and deep-sea tintinnids depend on food resources transported by sinking Middle Adriatic dense waters (MadDW).

Keywords: ciliates, tintinnids, distribution, Adriatic Sea.

RESUMEN: DISTRIBUCIÓN HORIZONTAL DE TINTÍNIDOS EN AGUAS DEL SUD-ADRIÁTICO (MEDITERRÁNEO ORIENTAL). – La distribución horizontal de los tintínidos oceánicos fue investigada en el Sur del Mar Adriático en 11 campañas oceanográficas realizadas entre 1980 y 1990. De las 70 especies identificadas, 47 se encontraron en la superficie, 16 en la subsuperficie, 4 en profundidades medias y 3 en aguas profundas. Las especies dominantes en aguas superficiales y subsuperficiales eran *Dictyocysta mitra*, *Codonella aspera*, y *Udenella claparedei*. *Parundella lohmanni* predominaba en capas medianamente profundas y *Xystonellopsis scyphium* en aguas profundas. La intrusión de masas de agua provenientes del Mar Jónico y la formación de un remolino ciclónico son importantes en la determinación de la distribución horizontal de los tintínidos en el Sud-Adriático. Períodos de fuerte advección de aguas del mar Jónico impone un tipo de distribución longitudinal de tintínidos, caracterizados por una alta diversidad de especies, baja abundancia y transporte de especies del Sur al Centro y Nor-Adriático. Esta difiere del tipo de la distribución típica de remolinos, en los cuales la diversidad de especies es baja y la densidad de la población es más alta en todas las profundidades y el transporte de especies hacia el Norte cesa. Está asumido que los tintínidos mesopelágicos y de aguas profundas dependen de las fuentes de substrato transportados por sedimentación desde las aguas medianamente profundas.

Palabras clave: ciliados, tintínidos, distribución, mar Adriático.

INTRODUCTION

Loricated ciliates or tintinnids are important members of the plankton in all marine habitats, but most

work so far has focused on coastal ecosystems (Hargraves, 1981; Burkill, 1982; Verity and Stocker, 1982; Capriulo and Carpenter 1983; Verity, 1986), in which estuarine and neritic tintinnids are occasionally exceptionally abundant (Paranjape, 1987; Kršinić, 1987; Modigh and Castaldo, 2002). The

*Received January 11, 2005. Accepted June 17, 2005.

role of tintinnids in the oligotrophic waters of tropical and subtropical regions, especially in the Mediterranean, is poorly known. Oceanic tintinnids are less abundant, and many species are quite rare. Adequate sampling methods are a matter of great concern, as the traditional method of using plankton nets has proved to be unsatisfactory for studying their qualitative and quantitative composition.

In the wake of important expeditions carried out at the beginning of the 20th century (Brandt, 1906, 1907; Laackmann, 1910; Jörgensen, 1924), there have been relatively few new data on the biogeography of oceanic tintinnids. Recent authors have reported aspects of their global distribution (Pierce and Turner, 1993), in the North Sea (Cordeiro *et al.*, 1997), south-western Atlantic (Thompson *et al.*, 1999), and the Mediterranean Sea (Dolan *et al.*, 1999; Dolan, 2000; Pitta and Giannakourou, 2000; Pitta *et al.*, 2001; Modigh *et al.*, 2003).

The present paper contributes to the knowledge of oceanic tintinnids in the South Adriatic Sea by analysing data derived from eleven sampling cruises undertaken from 1980 to 1990 aboard the R/V *Andrija Mohorovičić*. Earlier reports on the same data dealt with the population structure and vertical distribution of protozoans and microcopepods (Kršinić, 1998; Kršinić and Grbec, 2002), as well as a more detailed treatment of the vertical distribution of all tintinnids (Kršinić, 1982), and the family Xystonellidae (Kršinić, 1988). This contribution analyzes the data to elucidate features of the qualitative composition, horizontal distribution, and numerical abundance of tintinnids in the South Adriatic and the Palagruža Sill. Research on the horizontal distribution of oceanic tintinnids has generally involved samples taken during a single cruise, where samples were taken most frequently from the surface layer. This research reveals data on the horizontal distribution of oceanic tintinnids in the broadest and deepest regions of the Adriatic Sea, as well as the vertical distribution and seasonal changes in taxonomic composition and abundance.

MATERIAL AND METHODS

Samples were collected during 11 cruises aboard the R/V *Andrija Mohorovičić* (Fig. 1), along all three transects in August 1986, April 1987, November 1989, March 1990 and May 1990; the transects Dubrovnik – Bari and the southern-

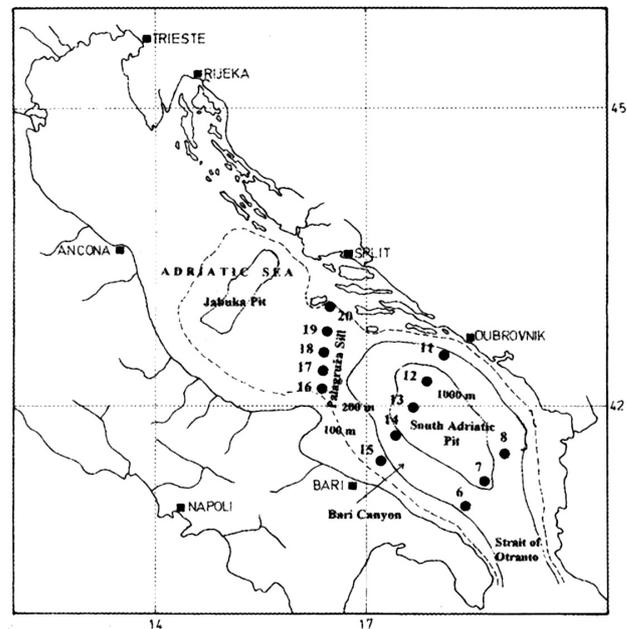


FIG. 1. – Research area and sampling stations.

most transect in January 1980 and April 1986; the transects Dubrovnik – Bari and Palagruža Sill in October 1985, June 1988, September 1988 and July 1989.

Samples were taken with a 53- μ m Nansen net (45 cm diameter) equipped with a closing system at a hauling speed of 0.5 m s⁻¹ within the following layers: A (0-50 m), B (50-100 m), C (100-200 m), D (200-300 m), E (300-400 m), F (400-600 m), G (600-800 m), H (1000-800 m). Organisms were preserved in a neutrally buffered formaldehyde-seawater solution at a final concentration of about 2.5%. Counting and species identification were performed with an Olympus inverted microscope at magnifications of 100x and 400x. One-sixteenth of each sample was analyzed for common species, while the entire catch was examined for rare species. A GeneralOceanics, Inc. R2 Flowmeter (Model 2030) was used to estimate the volume of filtered seawater.

Tintinnid identifications were based on lorica morphology using the taxonomic references of Daday (1886, 1887), Entz (1904, 1909), Brandt (1906, 1907), Laackmann (1913), Jörgensen (1924), Kofoid and Campbel (1929, 1939), and Balech (1959, 1968, 1975). Only typical forms for the species were considered based on the author's experience in the morphological variability of lorica in the Adriatic Sea. For this reason, we were critical when identifying the species based only on Kofoid and Campbel (1929), as previously recommended

by Laval-Peuto (1981), and Laval-Peuto and Brownlee (1986). Only complete lorica or those with plasmatic body parts were considered for the quantitative analysis, as the empty lorica of surface and subsurface species can contribute to interpreting the horizontal and vertical distribution of tintinnids incorrectly. According to the above-mentioned literature and Kršinić (1980), the species are considered as oceanic or neritic-coastal.

Temperature was measured with Richter-Wiese reversing thermometers and salinity was determined with an Autolab 601-MK III inductive salinometer. During cruises in March 1990 and May 1990, vertical temperature and conductivity profiles were measured with a SBE (Sea Bird Electronic) CTD multi-parameter probe. Temperature and salinity data were obtained from the database of the Hydrographic Institute of the Republic of Croatia (Split).

Cluster analysis (Single linkage, Euclidean distances) was used to identify the similarities between tintinnid communities in all stations during each cruise. Numerical abundance was used for analysing all registered species at both surface and subsurface layers at stations where samples were taken. Statistical analysis and graphical presentations were solved with STATISTICA for Windows (StatSoft, 2000). In order to identify areas (stations) with a similar abundance of tintinnids, the principal component analysis (PCA) was performed on the correlation matrix of the total abundance collected during 6 cruises with complete sets of samples (August 1986; April 1987; June and September 1988; November 1989; May 1990) across the Dubrovnik-Bari and Palagruža Sill transects at 10 stations at both surface and subsurface layers. PCA was performed following procedures already done at a small zooplankton distribution in the Otranto Strait (Kršinić and Grbec, 2002). The Varimax rotation (Richman, 1986), of significant PC components was used in order to obtain a better insight into the biological behaviour of the area in the central part of the southern Adriatic and Palagruža Sill.

RESULTS

Study area

The Adriatic Sea can be divided into two quite separate geo-morphological regions: the South Adriatic, and the Middle with the North Adriatic. In

the South Adriatic, the central area is a deep pit with a maximum depth of 1230 m. A shallow continental shelf less than 100 m in depth is located north of the Palagruža Sill, except in the Jabuka Pit region where the greatest depth is 270 m, as well as the 150 m deep canyon that connects these depressions. The South Adriatic covers 41% of the total surface area of the Adriatic Sea. The South Adriatic is influenced on one side, across the Strait of Otranto for about 70 km at depths of 800 m, by water masses from the Ionian Sea, eastern Mediterranean ISW (Ionian surface water) and LIW (Levantine intermediate waters), (Zore-Armanda, 1963; Buljan and Zore-Armanda, 1976). On the other side, it is influenced by the shallow Middle and North Adriatic, where NadDW (North Adriatic dense waters) and MadDW (Middle Adriatic dense waters) water masses are formed (Vilibić and Orlić, 2002).

The surface circulation over the South Adriatic Pit is influenced by a topographically controlled cyclonic gyre (Orlić *et al.*, 1992). An inflowing current prevails along the eastern Adriatic coast, and an outgoing current prevails along the western coast (Zore-Armanda, 1968).

A minimum salinity was found in August 1986 (38.54 ± 0.18 psu) and a maximum in November 1989, 38.91 ± 0.09 psu. A typical thermocline formed in the surface layer during warmer months. A maximum temperature, 26.32°C , was found in August 1986. Average temperatures below 100 m were within a narrow range, from $13.20 \pm 0.19^\circ\text{C}$ in April 1986 to $13.55 \pm 0.38^\circ\text{C}$ in November 1989. Oxygen hyper-saturation was typical for the surface zone, while an oxygen minimum occurred between 100 and 300 m (range 69-88 %, minimum 51.9 % at 100 m P-12 in May 1990). A more detailed presentation of hydrographic data for the South Adriatic Pit during Mohorovičić cruises are found in Bićanić (1993), and Vilibić and Orlić (2001, 2002).

Qualitative composition

A total of 70 species of tintinnids representing 12 families were recorded. See Table 1 for a list of species. In terms of vertical occurrence, 47 were found in the surface layer, 16 in the subsurface layer, 4 were mesopelagic, and 3 were deep-sea species. Only three species were neritic-coastal (*Tintinnopsis radix*, *Stenosemella ventricosa*, and *Codonellopsis schabi*), while the rest were oceanic.

Fifty species were found during October 1985, but significantly fewer were found subsequently:

TABLE 1. – List of species; surf.= surface species; subsurf. = subsurface species; mezop.=mezopelagic species, deepsea= deep-sea species.

TINTINNINA Kofoid and Campbell, 1929			
CODONELLIDAE Kent, 1881			
1. <i>Tintinnopsis angulata</i> Daday, 1887	(surf.)	35. <i>Xystonellopsis aciculifera</i> (Jørgensen) Balech, 1968	(deepsea)
2. <i>Tintinnopsis radix</i> (Imhof) Brandt, 1907	(surf.)	UNDELLIDAE Kofoid and Campbell, 1929	
3. <i>Codonella aspera</i> Kofoid and Campbell, 1929	(surf.)	36. <i>Undella clevei</i> Jørgensen, 1924	(surf.)
4. <i>Codonella galea</i> Haeckel, 1873	(subsurf.)	37. <i>Undella hyalina</i> Daday, 1887	(surf.)
5. <i>Codonella amphorella</i> Biedermann, 1893	(subsurf.)	38. <i>Undella claparedei</i> (Entz) Daday, 1887	(subsurf.)
6. <i>Codonella apicata</i> Kofoid and Campbell, 1929	(surf.)	39. <i>Undella biangulata</i> Kofoid and Campbell, 1929	(surf.)
7. <i>Codonaria cistellula</i> (Fol) Kofoid and Campbell, 1939	(surf.)	40. <i>Undella pentagona</i> (Jørgensen) Balech, 1975	(surf.)
8. <i>Poroecus apiculatus</i> (Cleve) Cleve, 1902	(surf.)	41. <i>Undella subcaudata acuta</i> (Jørgensen) Balech, 1975	(surf.)
9. <i>Poroecus tubulosus</i> Balech, 1968	(surf.)	42. <i>Undella subcaudata subcaudata</i> (Jørgensen) Balech, 1975	(subsurf.)
CODONELLOPSIDAE Kofoid and Campbell, 1929		43. <i>Amplectella collaria</i> (Brandt) Kofoid and Campbell, 1929	(surf.)
10. <i>Stenosemella ventricosa</i> (Clap. and Lach.) Jørgensen, 1924	(surf.)	44. <i>Amplectella tricollaria</i> (Laackmann) Balech, 1975	(surf.)
11. <i>Codonellopsis orthoceras</i> (Haeckel) Jørgensen, 1924	(surf.)	45. <i>Undellopsis marsupialis</i> (Brandt) Kofoid and Campbell, 1929	(subsurf.)
12. <i>Codonellopsis schabi</i> (Brandt) Kofoid and Campbell, 1929	(surf.)	DICTYOCYSTIDAE Haeckel, 1873	
METACYCLIDIDAE Kofoid and Campbell, 1929		46. <i>Dictyocysta elegans</i> Ehrenberg, 1854	(surf.)
13. <i>Climacocylis scallaroides</i> Kofoid and Campbell, 1929	(surf.)	47. <i>Dictyocysta lepida</i> Ehrenberg, 1854	(surf.)
CYTTAROCYLIDIDAE Kofoid and Campbell, 1929		48. <i>Dictyocysta muelleri</i> (Imhof) Jørgensen, 1924	(subsurf.)
14. <i>Cyttarocylis eucecryphalus</i> (Haeckel) Kofoid, 1912	(subsurf.)	49. <i>Dictyocysta mitra</i> Haeckel, 1873	(subsurf.)
15. <i>Cyttarocylis cassis</i> (Haeckel) Fol, 1881	(subsurf.)	50. <i>Dictyocysta entzi</i> Jørgensen, 1924	(subsurf.)
16. <i>Petalotricha ampulla</i> (Fol) Kent, 1882	(subsurf.)	TINTINNIDAE Claparede and Lachmann, 1858	
PTYCHOCYLIDIDAE Kofoid and Campbell, 1929		51. <i>Stenstrupiella stenstrupii</i> (Clap. and Lach.) Kofoid and Campbell, 1929	(surf.)
17. <i>Favella azorica</i> (Cleve) Jørgensen, 1924	(surf.)	52. <i>Daturella</i> spp.	(subsurf.)
EPILOCYLIDIDAE Kofoid and Campbell, 1939		53. <i>Ormosella trachelium</i> (Jørgensen) Kofoid and Campbell, 1929	(deepsea)
18. <i>Epiplocyliis undella</i> (Ostenfeld and Schmidt) Balech, 1962	(surf.)	54. <i>Ascampbeliella acuta</i> (Kofoid and Campbell) Corliss, 1960	(surf.)
19. <i>Epiplocyliis acuminata</i> (Daday) Jørgensen, 1924	(surf.)	55. <i>Albatrosiella agassizi</i> Kofoid and Campbell, 1929	(surf.)
ASCAMPBELLIELLIDAE Corliss, 1960		56. <i>Amphorides amphora</i> (Clap. and Lach) Kofoid and Campbell, 1929	(surf.)
20. <i>Craterella armilla</i> Kofoid and Campbell, 1929	(surf.)	57. <i>Amphorides tetragona</i> Jørgensen, 1924	(mezop.)
RHABDONELLIDAE Kofoid and Campbell, 1929		58. <i>Amphorides quadrilineata</i> (Clap. and Lach) Jørgensen, 1924	(surf.)
21. <i>Rhabdonella spiralis</i> (Fol) Brandt, 1907	(surf.)	59. <i>Amphorides quadril.</i> var. <i>minor</i> Jørgensen, 1924	(surf.)
22. <i>Rhabdonella elegans</i> Jørgensen, 1924	(surf.)	60. <i>Amphorides laackmanni</i> Jørgensen, 1924	(surf.)
23. <i>Rhabdonella amor</i> (Cleve) Brandt, 1906	(surf.)	61. <i>Dadayiella ganymedes</i> (Entz) Kofoid and Campbell, 1929	(surf.)
XYSTONELLIDAE Kofoid and Campbell, 1929		62. <i>Dadayiella pachytoecus</i> (Jørgensen) Kofoid and Campbell, 1929	(surf.)
24. <i>Parundella lohmanni</i> (Jørgensen) Kofoid and Campbell, 1929	(mezop.)	63. <i>Eutintinnus fraknoi</i> (Daday) Kofoid and Campbell, 1939	(surf.)
25. <i>Parundella messinensis</i> (Brandt) Jørgensen, 1924	(mezop.)	64. <i>Eutintinnus lusus-undae</i> (Entz) Kofoid and Campbell, 1939	(surf.)
26. <i>Parundella caudata</i> (Ostenfeld) Cleve, 1900	(subsurf.)	65. <i>Eutintinnus latus</i> (Jørgensen) Kofoid and Campbell, 1939	(surf.)
27. <i>Parundella aculeata</i> Jørgensen, 1924	(subsurf.)	66. <i>Eutintinnus elegans</i> (Jørgensen) Kofoid and Campbell, 1939	(surf.)
28. <i>Xystonella longicauda</i> (Brandt) Laackmann, 1911	(surf.)	67. <i>Eutintinnus tubulosus</i> (Ostenfeld) Kofoid and Campbell, 1939	(surf.)
29. <i>Xystonella lohmanni</i> (Brandt) Kofoid and Campbell, 1929	(surf.)	68. <i>Eutintinnus apertus</i> Kofoid and Campbell, 1929	(surf.)
30. <i>Xystonella treforti</i> (Daday) Laackmann, 1909	(subsurf.)	69. <i>Salpingella glockentoegeeri</i> (Brandt) Kofoid and Campbell, 1929	(surf.)
31. <i>Xystonellopsis brandti</i> (Laackmann) Jørgensen, 1924	(surf.)	70. <i>Salpingella decurtata</i> Jørgensen, 1924	(surf.)
32. <i>Xystonellopsis paradoxa</i> (Cleve) Jørgensen, 1924	(subsurf.)		
33. <i>Xystonellopsis scyphium</i> Jørgensen, 1924	(deepsea)		
34. <i>Xystonellopsis cymatica</i> (Brandt) Jørgensen, 1924	(mezop.)		

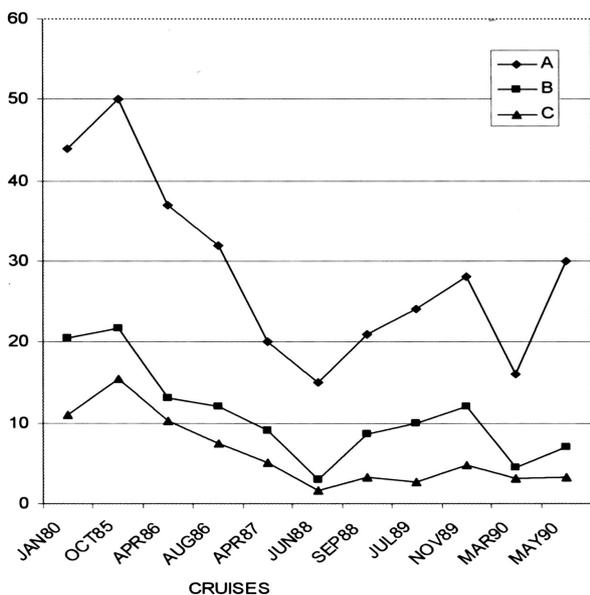


FIG. 2. – Variability of the total number of species from 100 m to the surface for cruises at all stations (line A); the number of species only for stations S7, 8, 12-14 (line B) and only for stations S6, 11, 15-20 (line C).

only 15 species were collected in June 1988 (Fig. 2, line A). The number of species increased again from September 1988, except during March 1990. The pattern of the total number of species is similar to that of the number of species in the 0 - 100 m layer for stations S 7, 8, and S12-14 (Fig. 2, line B); and for stations S6, 11, and S15-20 (Fig. 2, line C). In general, tintinnid species were poorly represented at stations near the shoreline and at the Palagruža Sill.

Horizontal distribution in surface and subsurface layers

As a rule, a maximum density was found at one or two stations in the central area of the South Adriatic Pit, in surface or subsurface layers with higher values as presented in Table 2. The minimum, maximum and median values for four groups of stations, excluding extremes, as well as for both

TABLE 2. – Range numerical abundance of tintinnids (No. m⁻³) for two groups of stations during 11 cruises in the open waters of the South Adriatic (A= 50 – 0 m; B= 100 – 50 m; n= number of samples).

	Layers	n	Stations 12-14, 6-8 Range	Station with maximum	n	Stations 11, 15-20 Range	Station with maximum
January 1980	A	6	58 - 517	S8	3	121 - 1111	S11
	B	6	108 - 392	S7	3	55 - 502	S11
October 1985	A	3	2086 - 3914	S13	6	244 - 1166	S11
	B	3	1680 - 3970	S12	6	134 - 410	S15
April 1986	A	6	60 - 3778	S14	2	78 - 644	S15
	B	6	757 - 2620	S14	2	288 - 408	S15
August 1986	A	5	356 - 1014	S13	7	14 - 452	S11
	B	5	634 - 1568	S12	7	16 - 771	S15
April 1987	A	5	48 - 227	S14	6	67 - 324	S19
	B	5	206 - 348	S12	6	32 - 896	S15
June 1988	A	3	132 - 8196	S12	7	13 - 120	S15
	B	3	1632 - 33574	S14	7	13 - 48	S11
September 1988	A	3	288 - 1456	S12	7	14 - 460	S11
	B	3	488 - 2484	S12	7	0 - 82	S20
July 1989	A	3	1006 - 6000	S13	5	36 - 60	S15
	B	3	221 - 1217	S12	5	0 - 78	S20
November 1989	A	6	161 - 799	S12	7	102 - 369	S11
	B	6	15 - 134	S12	7	18 - 198	S15
March 1990	A	6	6 - 137	S13	7	9 - 528	S11
	B	6	85 - 185	S12	7	15 - 369	S20
May 1990	A	6	16 - 7438	S7	7	12 - 192	S15
	B	6	17 - 3104	S7	7	0 - 1092	S15

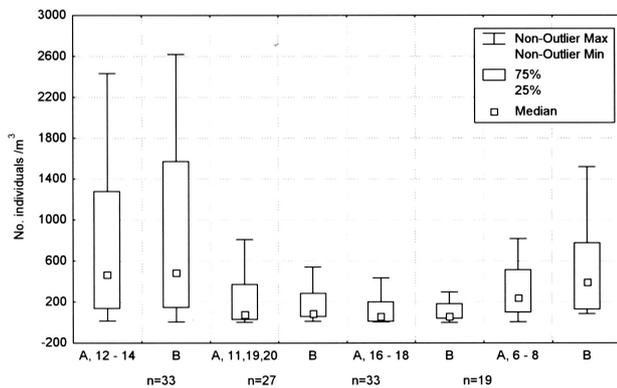


FIG. 3. – Box diagram of non-transformed data for the total number of tintinnids in layers A, 0-50 m; B, 50-100 m for four different areas.

surface and subsurface layers are presented in Figure 3. The lowest values were noted at perimeter stations towards the shoreline (S11, 19, 20) and in the area of the Palagruža Sill (S16, 17, 18). The most common type of tintinnid horizontal distribution was characterized by a core of pronounced abundance in the central area of the South Adriatic Pit, which included stations S12, 13, 14, and 7 (October 1985; April and August 1986; June and September 1988; July 1989). For the mentioned cruises, these stations stand out from others when displayed in dendrograms, Figure 4. The second type of horizontal distribution is presented by longitudinal isopleths of abundance in one or both layers (January 1980; November 1989; March and May 1990). Differences in population density

between layers were usually very low. The cluster analysis showed a similarity between most stations during these cruises (Fig. 4). Based on the PC analysis performed on total tintinnid abundance, three significant eigenvectors (according to the rule N) were extracted, which accounted for 71% of the total variance. After Varimax rotation, and based on the distribution of PC loadings, it was possible to separate three different areas in the Middle Adriatic Sea, as can be seen in Figure 5.

Horizontal distribution in mesopelagic and deep-sea layers

The total tintinnid abundances in the mesopelagic layer, especially between 100-200 m, were influenced greatly by the subsurface layer, so that this layer showed the greatest variability (Fig. 6). The lowest value (10 ind m⁻³) was found at S13 in March and at S14 in November. Maximum values frequently occurred at S14, with 3048 ind m⁻³ in September 1988; 1269 ind m⁻³ in April 1986; 758 ind m⁻³ in June 1988; and at S13 (1218 ind m⁻³) in October 1985; and S12 (783 ind m⁻³) in August 1986. Values were lower and more uniform at 200-300 m; a maximum of 818 ind m⁻³ was noted at S14 in April 1986. Tintinnid abundance was low and uniform in all deeper layers (Fig. 6), but increased occasionally in the deepest layers (800-1000 m) of the South Adriatic Pit.

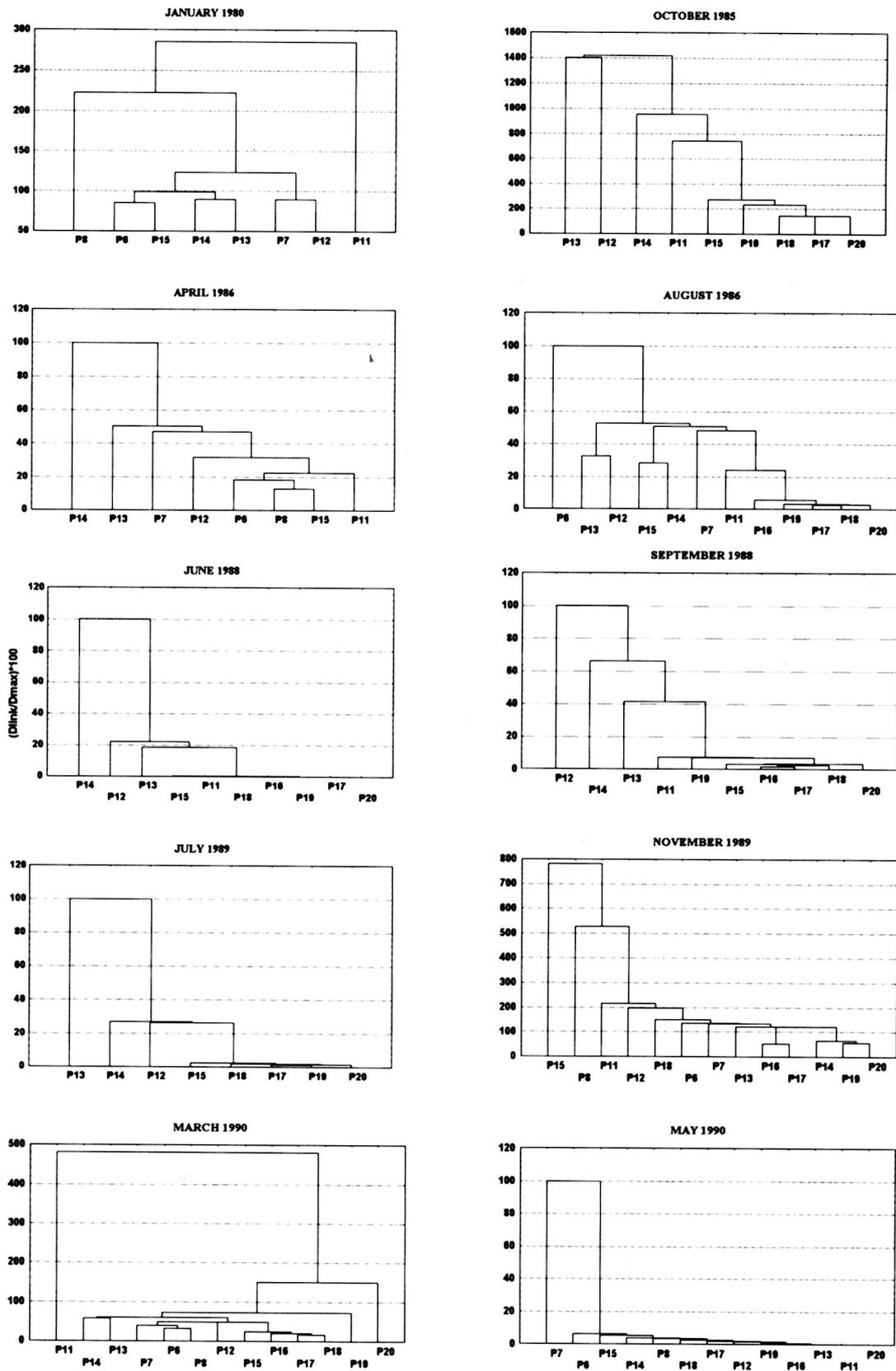


FIG. 4. – Cluster analysis for each cruise based on total tintinnids abundance.

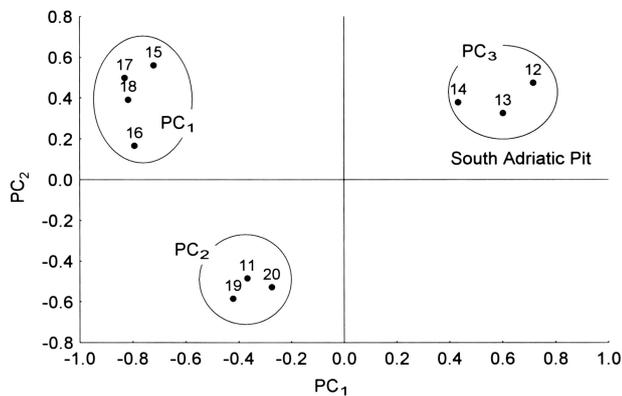


FIG. 5. – Spatial representation (in coordinate PC frame) of factor loadings of three significant PCs. The total tintinnid abundances were used. The number above the circles indicates the station number.

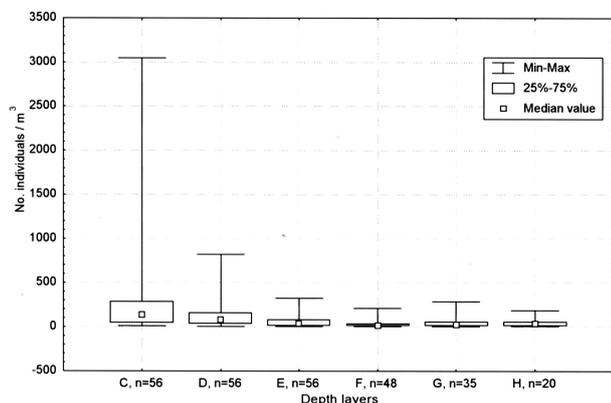


FIG. 6. – Box diagram of non-transformed data for the total number of tintinnids in different layers (C, 100-200 m; D, 200-300 m; E, 300-400 m; F, 400-600 m; G, 600-800m; H, 800-1000 m).

Dominant species in surface and subsurface layers

Figure 7 shows the percentage contribution of the three dominant species, *Dictyocysta mitra*, *Codonella aspera*, and *Undella claparedei* (*syn. Proplectella*, see the revision of the family

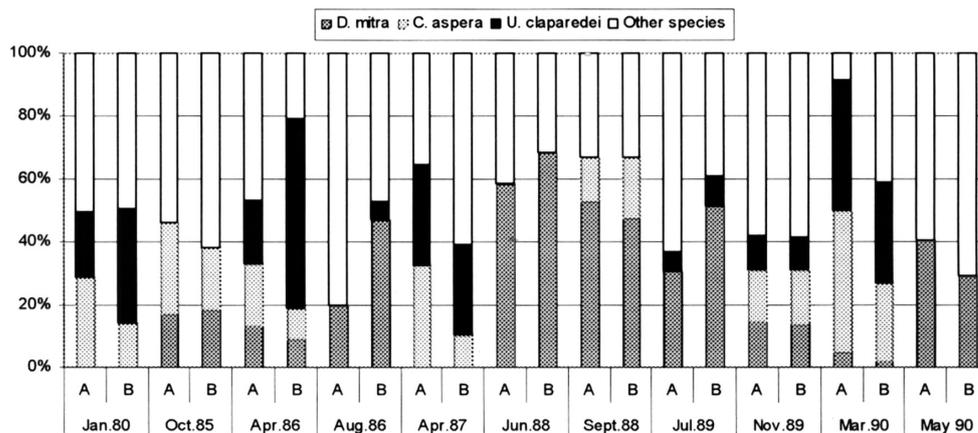


FIG. 7. – Percent contribution of dominant species to the total number of tintinnids in 0-50 m layer (A), and 50-100 m layer (B).

Undellidae, Balech, 1975), within surface and subsurface layers, as well as their relationship to other species. In the surface layer, these species accounted for 20-91% (average: 51.8%) of the total tintinnid abundance; in the subsurface layer, this figure ranged from 29 to 79% and averaged 52.9%. *D. mitra* was markedly predominant in June 1988, accounting for 68.4% of the total tintinnids in the subsurface layer. A maximum of 33,024 ind m⁻³ was found at station S14. *C. aspera* predominated in March 1990, accounting for 45.3% of tintinnids in the surface layer; but the highest density (860 ind m⁻³) was noted in October 1985 (S13). *U. claparedei* accounted for 60.5% of subsurface specimens in April 1986, with a maximum of 1960 ind m⁻³ at S14. In addition to the three species mentioned above, 10 additional species accounted for over 5% of the total tintinnids at one time or another. *Tintinnopsis angulata*, for example, was 43% of the total numbers in August 1986; and *Xystonella lohmanni* was 46% (2816 ind m⁻³) of tintinnids in the surface layer in July 1989 at S13.

Dominant species in mesopelagic layers

D. mitra and *U. claparedei* were always present from 100 to 400 m (layers C, D and E), namely at stations located at over 400 m. Higher contributions of these species to the population of deep-sea tintinnids occurred only when they were dominant in surface layers (Fig. 8). *D. mitra* accounted for 53% of all species in these layers in June 1988; *U. claparedei* accounted for 69% of this group in April 1996. The characteristic mesopelagic species *Parundella lohmanni* was constantly present at 1-83%, with an average of 35.7%. This species was especially abundant in August 1986 and September 1988, with the

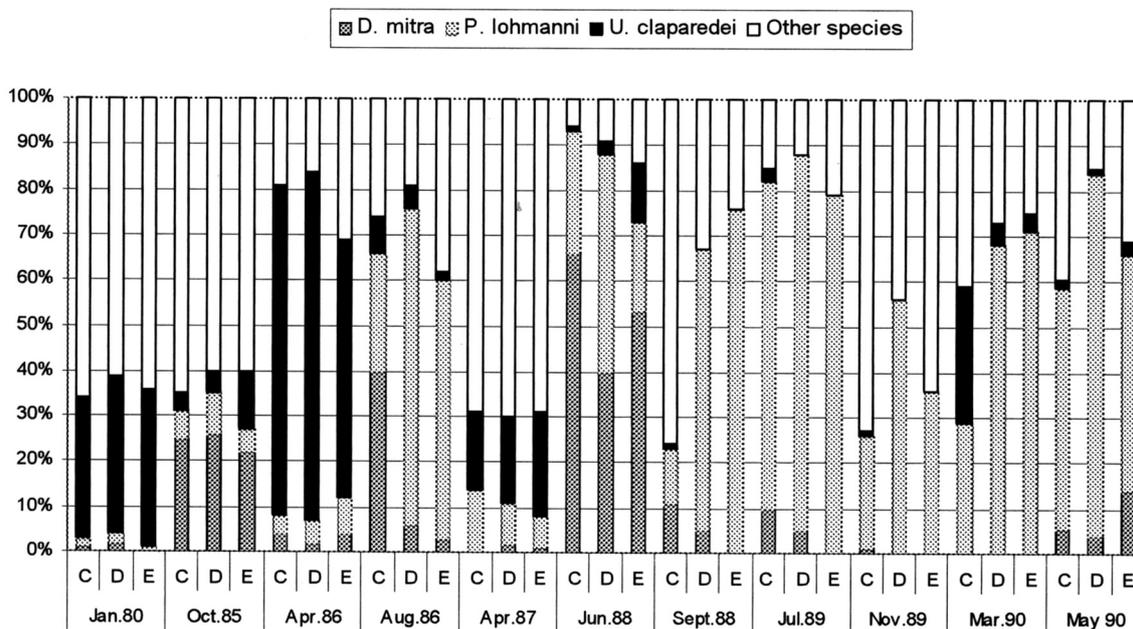


FIG. 8. – Percent contribution of dominant species to the total number of tintinnids in 100-200 m layer (C); 200-300 m layer (D); 300-400 m layer (E).

highest density, 280 ind m⁻³, at station S12 from 300 to 100 m. *Xystonellopsis cymatica* accounted for 6 to 10% of tintinnids in August 1986, November 1989, and May 1990. The species *Codonella amphorella* occurred with a frequency of 28 to 32% in April 1987. *Petalotricha ampulla* was 45% of the total tintinnine community (2265 ind m⁻³) from 100 to 200 m only in September 1988.

Dominant species in deep-sea layers

Xystonellopsis scyphium was encountered regularly between 400 to 1000 m (layers F, G and H). This included those stations at which the total depth exceeded 600 m. It was the dominant deep-sea tintinnid (53 to 79%) in August 1986, and from June 1988 to May 1990 (Fig. 9). The two highest densities were 150 ind m⁻³ at station S7 in August 1986

between 600 to 800 m; and 180 ind m⁻³ at S13 between 800 to 1000 m. The other important deep-sea species, *Xystonellopsis aciculifera*, was also most abundant in August 1986, with 7% of the tintinnid population and with a maximum value of 14 ind m⁻³ at S13 from 400 to 600 m depths. *Parundella lohmanni* and *Undella claparedei* are also important in deep-sea layers when they are most abundant in the mesopelagic or sub-surface layer. Furthermore, in April 1987 *Codonella amphorella* averaged 40% of the total deep-sea tintinnids.

DISCUSSION

The plankton net used in this work was suitable for evaluating the larger individuals of tintinnid populations, but no estimates could be done to quantify small species, such as *Dadayiella ganymedes*, which passed through the net. Nevertheless, studies on these smaller species using the 250-1 plankton trap “Adriatic” (Kršinić, 1990; Kršinić, unpublished data), have demonstrated that many of these are rare in the open waters of the South Adriatic. Thus, despite this shortcoming, the present data still permit a valuable quantitative description of the relative abundance relationships of this group over space and time. A comparison between the results of the numerical abundance of open-sea tintinnids presents difficulties due to differences in sampling methods.

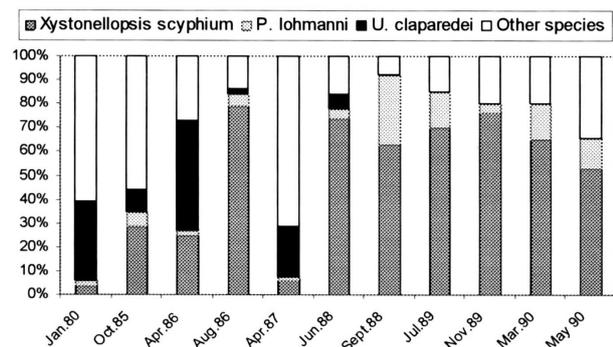


FIG. 9. – Percent contribution of dominant species to the total number of tintinnids in layers between 400 to 1000 m.

In addition, sampling problems for research below 200 m depths are an important reason for the very poor knowledge of deep-sea communities.

An abundance of 33 ind l⁻¹ for only one species, *Dictyocysta mitra*, in the 100 to 50 m layer is especially noteworthy for an oligotrophic oceanic region. A maximum abundance of 35 ind l⁻¹ of total tintinnids in the central area of the South Adriatic was noted in September 1993, using the plankton trap "Adriatic" at 50 m depths (Kršinić, unpublished data). Tintinnid concentrations in open Mediterranean waters are generally 25 ind l⁻¹ (Dolan, 2000), and in the south-western Atlantic Ocean the concentrations only average about 11 ind l⁻¹ with a maximum of 59 ind l⁻¹ (Thompson *et al.*, 1999). In the North Aegean, the dominant species *Codonella galea* exceeds 30 ind l⁻¹ at the surface, but in the South Aegean, tintinnids showed a very low abundance (Pitta and Giannakourou, 2000). Abundance of tintinnines along coastal sites of the western Mediterranean was lower than that found in the Gulf of Naples. In this gulf, open-sea species were present in very high values, for example *Dictyocysta mitra* 120 ind l⁻¹ and *Rhabdonella conica* 200 ind l⁻¹ (Modigh and Castaldo, 2002). Similar to these findings, certain open-sea species were recorded in much higher numbers in the eastern part of the northern Adriatic than in their natural niche, the surface layer of the southern Adriatic. *Amphorides laackmanni*, usually a very rare oceanic species, was present with a maximum of 890 ind l⁻¹ (Kršinić and Precali, 1997).

From about 100 species of tintinnids registered in the Adriatic Sea (Entz, 1904, 1909; Laackmann, 1913; Jörgensen, 1924; Kršinić, 1980), none of the estuarine-neritic species of the genera *Tintinnopsis*, *Stenosemella*, *Metacylis*, *Helicostomella*, *Favella* were found during the present research, which indicates that the central part of the southern Adriatic and the area around the Palagruža Sill are not influenced by coastal waters from the eastern and western Adriatic. The inflow of water masses from the Mediterranean Sea is an important factor that determines the qualitative composition of the distribution of surface and sub-surface tintinnids in the South Adriatic. The highest total number of tintinnid species per cruise occurred in January 1980, October 1985, and November 1989. In each case, this can be related to an intrusion of Levantine Intermediate Water (LIW) (Vilibić and Orlić, 2001). The ingression of LIW was accompanied by a wealth of oceanic tintinnids throughout the entire

region, especially at central deep-sea stations. However, ingressions did not increase species diversity to the same extent. This points to the fact that in April 1987 and June 1988, the whole vertical transect was occupied by a significant fraction of LIW, while tintinnid fauna was very poor. This perhaps is due to the qualitative composition of the species in the source area, the Ionian Sea. According to Dolan *et al.* (1999), the diversity of tintinnids appeared higher in the central and eastern basins, as compared to the west Mediterranean. All mesopelagic and deep-sea species, like the dominant surface and sub-surface species, were permanent inhabitants of the South Adriatic Pit. The advection of inflowing water masses imposed a longitudinal type of horizontal distribution on surface and subsurface tintinnid populations of the South Adriatic. This was characterized by a higher diversity of species and the relatively low abundance in all layers at the central stations. The open-sea tintinnid species in the southern Adriatic are regenerated from time to time with the LIW water mass (Kršinić and Grbec, 2002). The extent of the incursion also affected the distribution of oceanic tintinnids in the Middle and North Adriatic. The highest species diversity in the North Adriatic was observed in 1990, with a maximum of 13 species in October (Kršinić and Precali, 1997).

A South Adriatic cyclonic gyre was the result of an inflowing current along the eastern coast, and an outflow along the western coast. Aspects of the bottom topography that separate the Middle Adriatic from Mediterranean influences (Orlić *et al.*, 1992), also appear to play a role in this process. Gyre formation in the central region of the southern Adriatic Pit is responsible for the "eddy type" distribution of surface and subsurface tintinnids. This results in a decrease in the number of species and an increase in population densities in the core of the eddy. It also inhibits the transport of tintinnids towards the Middle and North Adriatic. In addition, the high abundance of tintinnids in the surface or subsurface layers is linked to the tintinnid abundances of the mesopelagic layer. Similarly, the density of specimens in mesopelagic layers was reflected in deep-sea layers. Comments on the vertical distribution and characteristic species of this area are found in previous works (Kršinić, 1988, 1998; Kršinić and Grbec, 2002).

The two above mentioned different types of horizontal distribution of oceanic tintinnines in surface and subsurface layers coincide with two seasons. During the fauna-poor summer and autumn, the

highest abundance of tintinnids was found at central stations. However, the highest species diversity was noted during winter and early spring for the entire area of the southern Adriatic, and the highest abundance at the perimeter stations on the eastern (S11) and western Adriatic coast (S15). The results of this research are in accordance with those previously reported for the eastern coastal area of the Adriatic. In the Dubrovnik coastal area, the oceanic tintinnid fauna was quite diverse from November to mid-March, with an average of 20 species per sample, and a minimum of only 2 species per sample, which occurred from June to August. The highest abundances were noted at the same time, a first maximum of 4300 ind.m⁻³ in November and the second of 2900 ind.m⁻³ in February (Kršinić, 1980). In the period from 1996 to 1997 at the same station off Dubrovnik, the oceanic tintinnids were of qualitative-quantitative importance only from December to February, when a maximum 11300 ind.m⁻³ in mid-December was registered in layers from 50 to 25 m depths (Kršinić, unpublished data).

The outflow of eutrophic North Adriatic waters along the west coast of the Adriatic, and their sinking in the area of the Bari Canyon (Vilibić and Orlić, 2001), encouraged an increase in the population densities of some species of oceanic tintinnids (S14). Therefore, it may be assumed that mesopelagic and deep-sea tintinnids apparently depend on food resources transported by sinking mid-Adriatic waters along the western outer edge of the eddy. This was shown in April and August 1986, September 1988, July 1989, and again in March 1990.

The dramatic change in the qualitative composition of tintinnids makes 1988 stand out as an exceptional year. June 1988 showed the greatest impoverishment of the species in the South Adriatic, accompanied by changes in the qualitative composition and structure of the dominant species. The abundant subsurface species *Undella claparedei* almost disappeared, and *Dictyocysta mitra* increased significantly. In the same year, a nanophytoplankton bloom was noted in the western region of the North Adriatic in late spring and at the beginning of summer; which contributed to high levels of detritus aggregates (Degobbis, 1989). According to Šolić and Krstulović (1991), the number of heterotrophic bacteria at one station in the eastern part of the Palagruža Sill was 7 times greater than the mean value for the period 1968-1979. After 1987, a remarkable change in the deep thermohaline circulation of the eastern Mediterranean occurred as a con-

sequence of the different water exchange regimes between the Ionian and Levantine Basin and the Adriatic Sea (Klein *et al.*, 1999). According to Vilibić and Orlić (2001), in April 1987 dense water sank to the bottom of the South Adriatic Pit and then flowed out to the Ionian Sea. Characteristic small copepod species also sank towards the southern part of the Pit and the Strait of Otranto (Kršinić and Grbec, 2002). It can be assumed that the occurrence of anomalous cooling and mixing at surface and subsurface layers in the South Adriatic Pit in April 1987 could be responsible for the diversity of oceanic tintinnids. This thermohaline stress is perhaps the reason for the negative influence on the immigration of surface and subsurface oceanic tintinnids in the region. In the 1989-1990 cruises, the LIW fraction distribution was similar once more to the situation in 1980 and 1985, which influenced a more similar qualitative composition of the tintinnid population.

According to Buljan (1968), Pucher-Petković (1971) and Vučetić (1973), the South Adriatic Pit is the most impoverished zone of the Adriatic Sea. According to Viličić *et al.* (1998), the South Adriatic is oligotrophic with $< 0.2 \mu\text{mol l}^{-1} \text{PO}_4$ and $< 3 \mu\text{mol l}^{-1} \text{NO}_3$. During April 1987, when a microphytoplankton bloom was registered for the first time in the South Adriatic (Viličić *et al.*, 1989), chlorophyll *a* exceeded 3 mg chl *a* m⁻³ (Marasović *et al.*, 1999). This was accompanied by an atypical distribution of tintinnids, with relatively low abundance in the surface layer. However, in April 1986, a relatively high abundance of tintinnines in both surface layers was noted simultaneously with lower concentrations of chlorophyll *a*, about 0.5 mg chl *a* m⁻³, but with a greater part of the phytoplankton being nanophytoplankton (Marasović *et al.*, 1999). Nanophytoplankton manifested less marked oscillation than microphytoplankton in the central area of the South Adriatic. The nanophytoplankton biomass was generally lower in winter and higher in spring and autumn (Viličić, 1985). During the microphytoplankton bloom, it thus seems likely that conditions for the development of oceanic tintinnids towards the deepest part of the South Adriatic were not optimal as in the post-bloom period, during the re-mineralization process of particular organic matter. The South Adriatic Pit, in contrast with other regions, is characterized by higher particulate organic carbon (POC) and low primary production. This phenomenon is related to the erratic nutrient supply which contains stagnant water in the centre of the gyre (Faganeli *et al.*, 1989).

Accordingly, it seems reasonable to conclude that the horizontal distribution of oceanic surface and subsurface tintinnids in the oligotrophic region of the South Adriatic Pit are influenced by Mediterranean water masses and the formation of a cyclonic gyre. The dense bottom waters from the middle Adriatic reach the western part of the pit and enrich deep layers with organic detritus important for the autochthonous populations of mesopelagic and deep-sea tintinnids.

ACKNOWLEDGEMENTS

Many thanks are due to the personnel of the Hydrographic Institute of the Republic of Croatia in Split for the hydrographical data. We would like to thank anonymous reviewers for their critical reviews and suggestions for improving this paper. The research was supported by the Ministry of Science, Education and Sports of the Republic of Croatia.

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