Gelatinous invertebrate zooplankton of the South Adriatic: species composition and vertical distribution

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The species composition and vertical distribution of gelatinous invertebrate zooplankton were investigated from April 1993 to June 1994 in the 0–1000 m water column at a deep-sea station in the northern part of the South Adriatic Pit. Fifty-seven species were identified: 11 hydromedusae, 13 calycophores, 3 ctenophores, 3 heteropods, 10 pteropods, 8 polychaetes and 9 chaetognaths. The pteropod Desmopterus papilio and the heteropod Protatlanta mediterranea were recorded for the first time in the Adriatic Sea. Data from this study differed from those of previous investigations in the South Adriatic as regards the numerically dominant polychaete and pteropod species. All investigated groups generally were more abundant in the upper 100 m and decreased with depth. Different vertical distributions of life stages were observed for those species that occupy a wide depth range: Persa incolorata, Solmissus albescens, Limacina inflata, Cymbulia peroni, Pelagobia longicirrata, Sagitta lyra and Sagitta decipiens.

INTRODUCTION

The Southern Adriatic basin constitutes the southernmost and the deepest part of the Adriatic Sea. It communicates through the Strait of Otranto with the Eastern Mediterranean and, on the other side, with the Middle and Northern Adriatic basins. In general, Mediterranean waters enter the Adriatic in the intermediate layer, while Adriatic waters enter the Mediterranean in the surface and bottom layers (Orlić *et al.*, 1992). This part of the Adriatic is thus very interesting from both the hydrological and the biological points of view. From a biological standpoint, changes in production, phytoplankton species composition, biomass and the composition of zooplankton have been observed throughout the Adriatic and related to stronger inflow of Mediterranean water (Vučetić, 1970; Pucher-Petković *et al.*, 1971). Recent research has focused on the influence of newly documented changes in the thermohaline circulation in the Eastern Mediterranean (referred to as Eastern Mediterranean Transient) on the South Adriatic (Civitarese and Gacic, 2001). This raises questions on the implications of this phenomenon for zooplankton in this part of the Adriatic.

Zooplankton data from this area are not numerous and mainly refer to copepods (Hure and Kršinić, 1998), protozoa and microcopepods (Kršinić and Grbec, 2002). Data for larger zooplankton are scarce and often deal only with a restricted group or species. In fact, some groups included in the present study have not been investigated in the Adriatic for more than 20 years. Polychaetes, for example, were last studied by Zei (Zei, 1956), and Ctenophora, Pteropoda and Heteropoda by Gamulin (Gamulin, 1979). More recent macroplankton data in the deep South Adriatic are available for hydromedusae (Benović and Lučić, 1996), calycophorae (Gamulin and Kršinić, 2000) and chaetognaths (Batistić, 1999). Some of these studies addressed the vertical distributions of the species, but no attention was paid to differentiating life-history stages. Such life-history data, in fact, are not common for the Mediterranean Sea at all, although a large amount of data, particularly relating to vertical distribution, is available for larger zooplankton in the western basin [e.g. (Franqueville, 1971; Laval *et al.*, 1989; Sardou and Andersen, 1993; Sardou *et al.*, 1996; Andersen *et al.*, 1998)].

The present study addresses this deficiency by documenting the species composition and vertical distribution of gelatinous invertebrate zooplankton of the deep South Adriatic. Particular attention is given to the life-history stages of the most frequently encountered species. The influence of abiotic and biotic factors on the vertical distribution of these groups is examined.

METHOD

Sampling and laboratory procedures

Plankton samples were collected at a deep-sea station (Figure 1) located on the northern edge of the South Adriatic Pit (42°20′N, 17°43′E, maximum depth 1242 m), 24 nautical miles offshore, during five cruises: April 21, September 17 and November 25, 1993; February 27 and June 17, 1994. Samples were collected at night (between sunset and sunrise) on the first cruise; those from all other cruises were taken during the day.

Vertical hauls were made with a Nansen opening–closing net (113 cm diameter, 380 cm length and 250 μm mesh size) in the following layers: 0–50, 50–100, 100–200, 200–300, 300–400, 400–600 and 600–1000 m. The volume of filtered sea water was calculated on the basis of a test that used a low-speed flowmeter (General Oceanics). Samples were preserved in a 2.5% formaldehyde–seawater solution buffered with $CaCO_3$.

Temperature and salinity profiles (0–1000 m) were determined using a CTD multisonde (SEA Bird Electronics Inc., USA). Water samples were taken with 5 L Niskin bottles at 0, 5, 10, 20, 50, 75, 100, 200, 300, 400, 600 and 1000 m depths. Dissolved oxygen was determined by the Winkler method and oxygen saturation (O_2/O_2') was calculated from solubility of oxygen in sea water as a function of temperature and salinity (Weiss, 1970; UNESCO, 1973). Phytoplankton
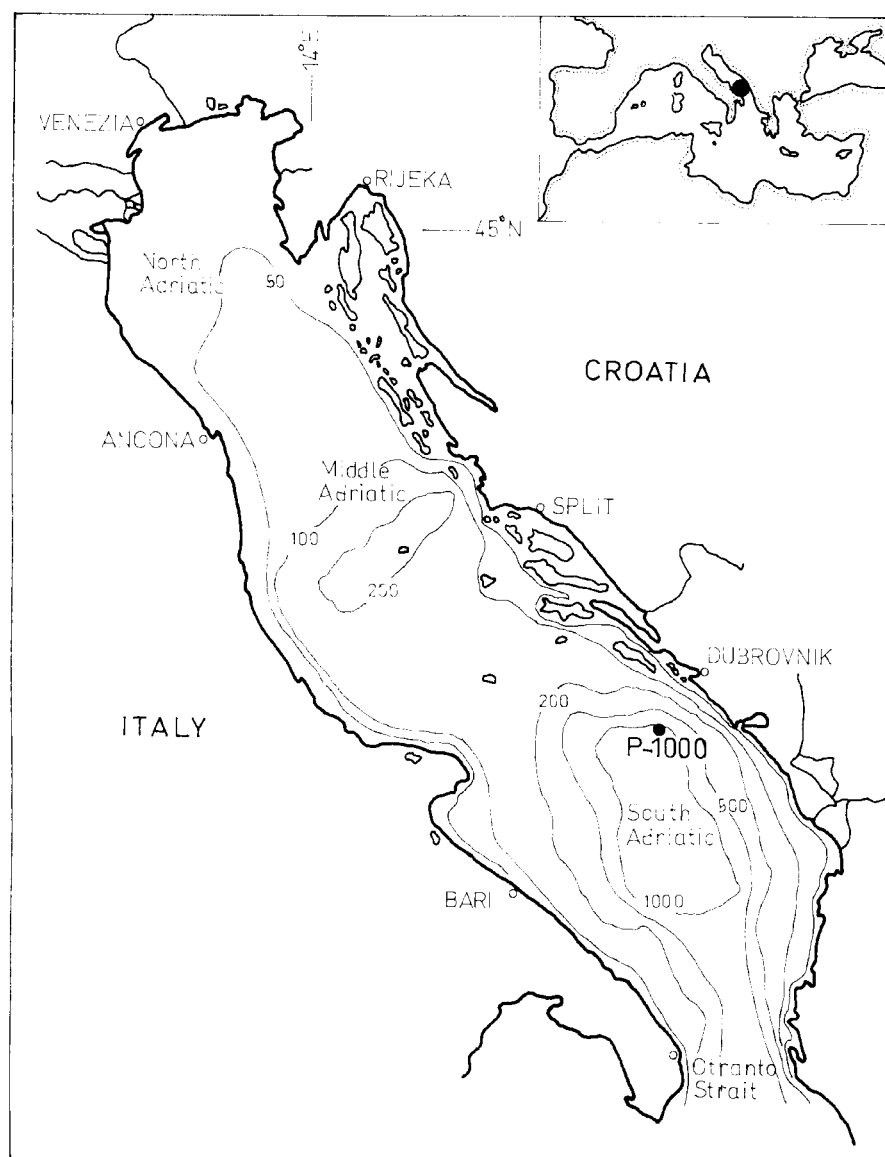

Fig. 1. Location of sampling station.

biomass, as chlorophyll (Chl) *a*, was determined to 300 m from 0.5 dm^3 subsamples filtered through Whatman GF/F glass-fibre filters and stored at $-20°$C. Filtered samples were homogenized and extracted in 90% acetone for 24 h at room temperature (Strickland and Parsons, 1972). Chl *a* was determined fluorometrically using a Turner TD-700 Laboratory Fluorometer (Sigma) calibrated with pure Chl *a*.

Taxonomic identification and counting of individuals were performed with a Zeiss stereomicroscope at ×25 and ×40 magnification. All samples were completely analysed. Abundance of all groups is presented in terms of the number of specimens per square metre (ind. m^{-2}).

Life-history stages of chaetognaths were classified according to Thomson's criteria, which are based on ovary development (Thomson, 1947). Developmental stages for males of *Sagitta decipiens* were determined as follows: testes visible, Stage I; seminal vesicles present, Stage II; seminal vesicles full, Stage III. Juveniles of the most numerous hydromedusae were distinguished according to standard criteria (Bouillon, 1993), primarily the presence or absence of gonads. Standard criteria were used to distinguish non-transparent juvenile pteropods (Rampal, 1975; Bandel and Hemleben, 1995) and polychaetes (Fauvel, 1923; Zei, 1956). Abundance of calycophorae was expressed according to the number of nectophores (polygastric) of each species.

The weighted mean depth (WMD) in the water column of the most numerous species was calculated as:

$$WMD = \Sigma(n_i \times z_i \times d_i)/\Sigma(n_i \times z_i)$$

where d_i is the midpoint of the depth interval of sample i, z_i is the thickness of the stratum and n_i is the number of individuals per unit of area (ind. m^{-2}) at that depth.

Margalef's species richness index *D* was used to analyse diversity changes among layers:

$$D = S - 1/\log \mathcal{N}$$

where *S* is the number of species and $\mathcal{N}$ is the total number of individuals.

The Kruskal–Wallis test was used to test differences in the mean position of different chaetognath stages in the water column.

Vertical variation of the most abundant species was analysed using cluster analysis (15 species × 5 cruises × 7 layers). The Bray–Curtis similarity coefficient was used as a measure of distance (Legendre and Legendre, 1983).

RESULTS

Environmental conditions

The 0–50 m layer was thermally stratified, but inverse stratification was observed in February 1994 (Figure 2).
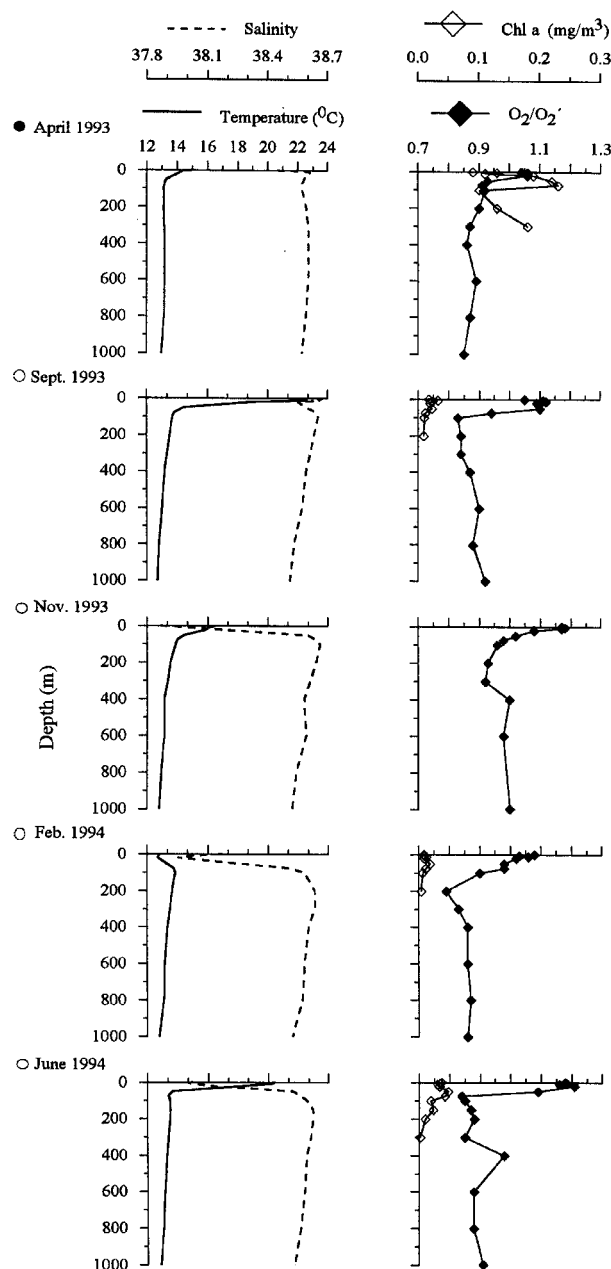

Fig. 2. Basic hydrographic parameters and Chl *a* at station P-1000.

The maximum temperature, 22.5°C, was found at the surface in September, when the thermal gradient was 3.61°C/10 m. The 100–1000 m layer was stable with temperatures between 12 and 13°C.

Salinity ranged between 37.87 and 38.66 in the upper 20 m, with an average of 38.48 ± 0.22. The minimum was found in November. Below 20 m, salinity remained between 38.50 and 38.60 (Figure 2).

Oxygen saturation was between 0.79 and 1.21, with an average of 0.97 ± 0.11. Profiles during all seasons indicated

good aeration in the 0–50 m layer ($O_2/O_2' > 1.0$), with a maximum of 1.21 in July 1994 at 20 m (Figure 2). The oxycline was mostly between 50 and 75 m depth. There were no notable oxygen variations below the oxycline. The range was 0.79–1.0, with average 0.89 ± 0.05.

Chl *a* concentrations were between 0.001 and 0.230 mg m^{-3} (average 0.054 ± 0.066). The highest concentration (≥ 0.09 mg m^{-3}) was found in April 1993. During that cruise, a significant increase in Chl *a* was observed between 100 and 300 m (Figure 2). Chl *a* concentrations and hydrographic data are in accordance with previous data from open South Adriatic waters (Artegiani *et al.*, 1996; Jasprica *et al.*, 2001).

Abundance and vertical distribution of the investigated groups

In general, the abundance of all groups was high in the upper 100 m and decreased conspicuously with depth (Table I). Either chaetognaths or pteropods dominated

Table I: Abundance (ind. m^{-2}) and vertical distribution of the investigated groups

Cruise	Depth (m)	Hydromedusae	Calycophorae (nect. m^{-2})	Ctenophora	Heteropoda	Pteropoda	Polychaeta	Chaetognatha
● April 1993	0–50	47	18	1		2412	9	198
	50–100	45	6			413	36	93
	100–200	136	8			72	43	184
	200–300	8	1			30	29	96
	300–400	8	1			10	47	45
	400–600	18	2			12	22	80
	600–1000	4	5			1	3	12
○ September 1993	0–50	92	9		3	80	11	188
	50–100	24				42	1	95
	100–200	17	30			30		182
	200–300	2				9	1	127
	300–400	15				3	1	48
	400–600	4					2	60
	600–1000		12			3		14
○ November 1993	0–50	35	7	2	6	56	19	562
	50–100	24	2			2	2	193
	100–200	12	2			1	1	167
	200–300	6	3			2	1	121
	300–400		1			2	2	59
	400–600	1	2			2	3	69
	600–1000	12	10			3		12
○ February 1994	0–50	32	76		1	6		370
	50–100	15	9			8	4	884
	100–200	18	23			5	8	259
	200–300	3	3			3		78
	300–400	18				2	3	42
	400–600	2					4	38
	600–1000	4	4					4
○ June 1994	0–50	450	35			1269	2	642
	50–100	62	6			418	2	420
	100–200	37	20			10	8	195
	200–300	12				1		106
	300–400	16				1	8	97
	400–600	17	4			2	22	70
	600–1000	4	10			1	23	28

The water column depth sampled was 0–1000 m in seven layers.
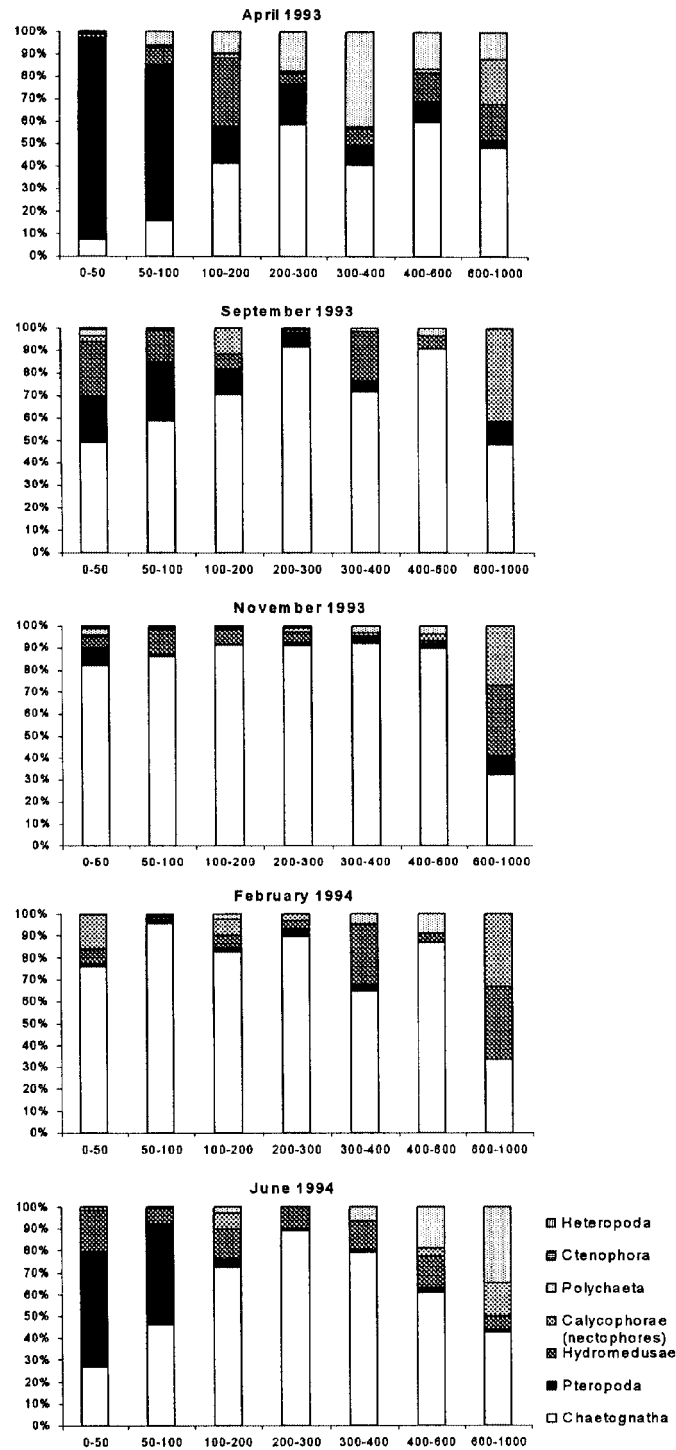○ = day; ● = night.

Fig. 3. Percentage occurrence of investigated groups in the different layers from the surface to 1000 m depths during five cruises (April 1993 is the only night sample).

the 0–50 and 50–100 m layers (Figure 3). In September and November 1993, and February 1994, chaetognaths made up 50–96% of all groups in these layers. In April 1993 in both of these layers and June 1994 in the 0–50 m layer, pteropods were more prevalent (53–90% of total). In June 1994 in the 50–100 m layer, both groups occurred in about equal abundance (~46%). Of other groups, only hydromedusae made a significant contribution to

total abundance, but this rarely exceeded 20% and lasted only for restricted periods (Figure 3).

Below 100 m, the contribution of chaetognaths was very significant, while the relative percentage of pteropods was lower, mostly <10% (Figure 3). In the deepest layer (600–1000 m), there was an increased percentage of hydromedusae and calycophores, as well as polychaetes during the spring cruise.

Species composition

Fifty-seven species were identified: 11 hydromedusae, 13 calycophores, 3 ctenophores, 3 heteropods, 10 pteropods, 8 polychaetes and 9 chaetognaths (Table II). The pteropod *Desmopterus papilio* and the heteropod *Protatlanta mediterranea* were recorded for the first time in the Adriatic Sea. *Desmopterus papilio* were found in November 1993, and *P. mediterranea* in February 1994, in the 50–100 m layer.

A maximum of 38 and a minimum of 24 species were found during November and September 1993, respectively. The species richness index varied between 0.74 and 3.77 (Table III). Higher values were found in April, September and November in the 0–50 m layer, and in February and June 1994 in the 100–200 m layer. Although not very dramatic, there was an apparent variability in species richness throughout the water column.

Table II: List of registered species

	● April 1993		○ Sept. 1993		○ Nov. 1993		○ Feb. 1994		○ June 1994	
	A	B	A	B	A	B	A	B	A	B
Hydromedusae										
*Euphysa aurata		+								
*Bythotiara murrayi				+						
*Obelia sp.					+			+		
*Clytia hemisphaerica	+				+					
*Liriope tetraphylla					+					
Aglaura hemistoma	+		+				+		+	+
Persa incolorata		+			+	+	+	+		+
Rhopalonema velatum	+	+	+	+	+	+	+	+	+	+
*Solmundella bitentaculata	+				+					
*Solmaris leucostyla								+		
Solmissus albescens	+	+		+	+	+		+		+
Calycophorae										
*Hippopodius hippopus										+
*Lensia conoidea	+	+		+	+	+	+	+	+	
*L. multicristata		+								
*L. fowleri				+						+
L. subtilis	+		+		+		+	+	+	
L. meteori		+		+		+		+	+	+
Muggiaea kochi	+				+		+		+	
*Chelophyes appendiculata	+		+							
*Clausophyes ovata				+		+		+		+
*Eudoxoides spiralis							+			
*Sphaeronectes gracilis			+		+				+	
*S. gamulini							+			
*Abylopsis tetragona			+			+	+			
Ctenophora										
*Callianira bialata	+									
*Pleurobrachia rhodopis	+								+	
*Beroe ovata	+									

(Continued)

Table II: Continued

	●April 1993		○Sept. 1993		○Nov. 1993		○Feb. 1994		○June 1994	
	A	B	A	B	A	B	A	B	A	B
Heteropoda										
Atlanta peroni			+		+					
Protatlanta mediterranea							+			
Firoloida desmaresti					+					
Pteropoda										
Limacina inflata	+		+	+	+	+	+	+	+	+
L. trochiformis	+				+					
Creseis virgula					+		+		+	
Hyalocylix striata					+					
Clio cuspidata			+	+		+				+
C. pyramidata		+			+		+	+		
Cavolinia inflexa					+					
Peraclis reticulata	+	+							+	+
Cymbulia peroni	+	+	+	+		+		+	+	
Desmopterus papilio					+					
Polychaeta										
Tomopteris helgolandica	+				+			+		
T. elegans								+		
Callizonella lepidota					+		+			
Callizona nasuta					+					
Pelagobia longicirrata	+	+	+		+			+	+	+
Sagitella kowalevskii		+		+	+	+	+	+	+	+
Travisiopsis lanceolata			+		+			+		
Typhloscolex muelleri		+								+
Chaetognatha										
Sagitta enflata	+		+		+		+		+	
S. minima	+	+	+	+	+		+	+	+	+
S. setosa	+				+		+		+	
S. serratodentata	+		+		+		+			
S. bipunctata	+									
S. decipiens		+		+	+	+	+	+		+
S. lyra	+	+	+	+	+	+	+	+	+	+
S. hexaptera							+			
Krohnitta subtilis		+			+	+		+		+
No. of species in both layers	33		24		38		32		27	

A = 0–100 m; B = below 100 m.
*Less abundant species (<15 ind. m^{-2}). ○ = day; ● = night.

Vertical distribution of the main species

With the exception of calycophorae, the vertical distributions of the most numerous species and their life-history stages are presented in Figures 4–6. Regarding calycophorae, only nectophores were calculated; gonophores were rare owing to difficulty in their determination. Other species (Table II) appeared irregularly or were not abundant enough in the samples to allow detailed description of their vertical distribution. It must also be noted that ctenophores may have been underestimated: owing to their rather fragile constitution, the relatively 'rough' treatment of standard plankton collection techniques used in this study may have rendered many unidentifiable.

Table III: Variability in species richness

Layer (m)	●April 1993	○Sept. 1993	○Nov. 1993	○Feb. 1994	○June 1994
0–50	**2.81**	**1.81**	**3.77**	1.60	1.65
50–100	1.84	1.21	1.52	1.46	1.74
100–200	2.13	1.26	1.71	**2.79**	**2.49**
200–300	1.60	1.21	1.63	0.90	1.26
300–400	1.91	1.67	1.67	1.83	1.47
400–600	1.69	1.33	2.22	1.64	1.98
600–1000	2.06	1.10	2.29	0.74	1.77

The highest values are shown in bold.

Hydromedusae

Aglaura hemistoma and *Rhopalonema velatum* were most abundant in the upper 100 m (Figure 4). Both also occurred from 100 to 200 m, although usually with low abundance. *Rhopalonema velatum* abundance was highest in this layer only in April 1993. Adults and juveniles of both species were found in the same layer (Figure 4; Table IV). *Persa incolorata* has a wider vertical distribution, from 50 to 1000 m, but generally it was most abundant from 100 to 200 m. Life-history stages showed a difference in their vertical position in the water column (Table IV). Juveniles occurred mostly from 50 to 200 m, and adults predominated below 100 m (Figure 4). *Solmissus albescens* was found in the upper layers in the sole night sample. During the day, *S. albescens* was deeper, mostly from 100 to 1000 m (Figure 4). Adults were usually distributed deeper than the juveniles by day. On the contrary, in the only night sample, that of April 1993, adults were found in the upper layers, 0–50 and 50–100 m, while juveniles never reached the surface layer (Figure 4; Table IV).

Calycophorae

Lensia subtilis and *Muggiaea kochi* were most abundant in the upper 100 m (Tables II and IV). *Muggiaea kochi* was never found deeper, but *L. subtilis* was collected at 100–200 m in February 1994 (1 nectophore m^{-2}). A maximum of 35 and 36 nectophores m^{-2} were registered in February 1994 in the surface layer for *L. subtilis* and *M. kochi*, respectively. The abundance of both species during other cruises was mostly <15 nectophores m^{-2}, but these species also dominated the 0–100 m layer, contributing >60% of total calycophoran abundance (see Table I). *Lensia meteori* was most abundant from 100 to 200 m (Tables II and IV), with a maximum of 30 nectophores m^{-2} in September 1993. During other cruises, *L. meteori* was also the dominant calycophoran species in that layer, contributing >65% of total nectophores, even though no more than 15 nectophores m^{-2} were ever found (see Table I). *Clausophyes ovata* abund-

ance was low (Table II), but is the only species found to inhabit exclusively layers below 400 m.

Pteropoda

Limacina inflata was most numerous at 0–100 m, and it also was found in deeper layers, particularly in September 1993 (Figure 5A). Juveniles were evident in the upper layers in all samples, including the only one taken at night (April 1993); this sole night-time sample was the only one to feature both stages in the surface layer (Figure 5A; Table IV). Depending upon the season, *Cymbulia peroni* dominated different layers (Figure 5A; Table IV). When juveniles appeared in the plankton, they concentrated in the upper layers (0–50 and 50–100 m). Very high densities of juveniles (1193 ind. m^{-2}) were found in the 0–50 m layer in June 1994. Adults were found below 100 m, mostly from 100 to 400 m (Figure 5A; Table IV). *Peraclis reticulata* was collected throughout the water column in April 1993 and June 1994. The highest abundance was found from 0–50 and 50–100 m, respectively (Figure 5A). Almost all specimens were juveniles. Adults were found from 50 to 200 m, though very rarely (<5 ind. m^{-2}). Less than 30 ind. m^{-2} were found in layers below 200 m.

Polychaeta

Pelagobia longicirrata was recorded from the surface to 1000 m (Figure 5B). Depending on the cruise, this species dominated different layers. Juveniles were observed during all cruises except in February 1994, always at shallower depths than adults (Figure 5B; Table IV).

Chaetognatha

Sagitta enflata was found mainly to 50 m, and *Sagitta minima* to 100 m (Figure 6). All developmental stages of both species were found together in the same layers. *Sagitta lyra* was registered throughout the water column. The younger stages of *S. lyra* were distributed largely within the upper layers. Adults inhabited deeper layers (below 300 m), but in very low abundance, generally <10 ind. m^{-2} (Figure 6).
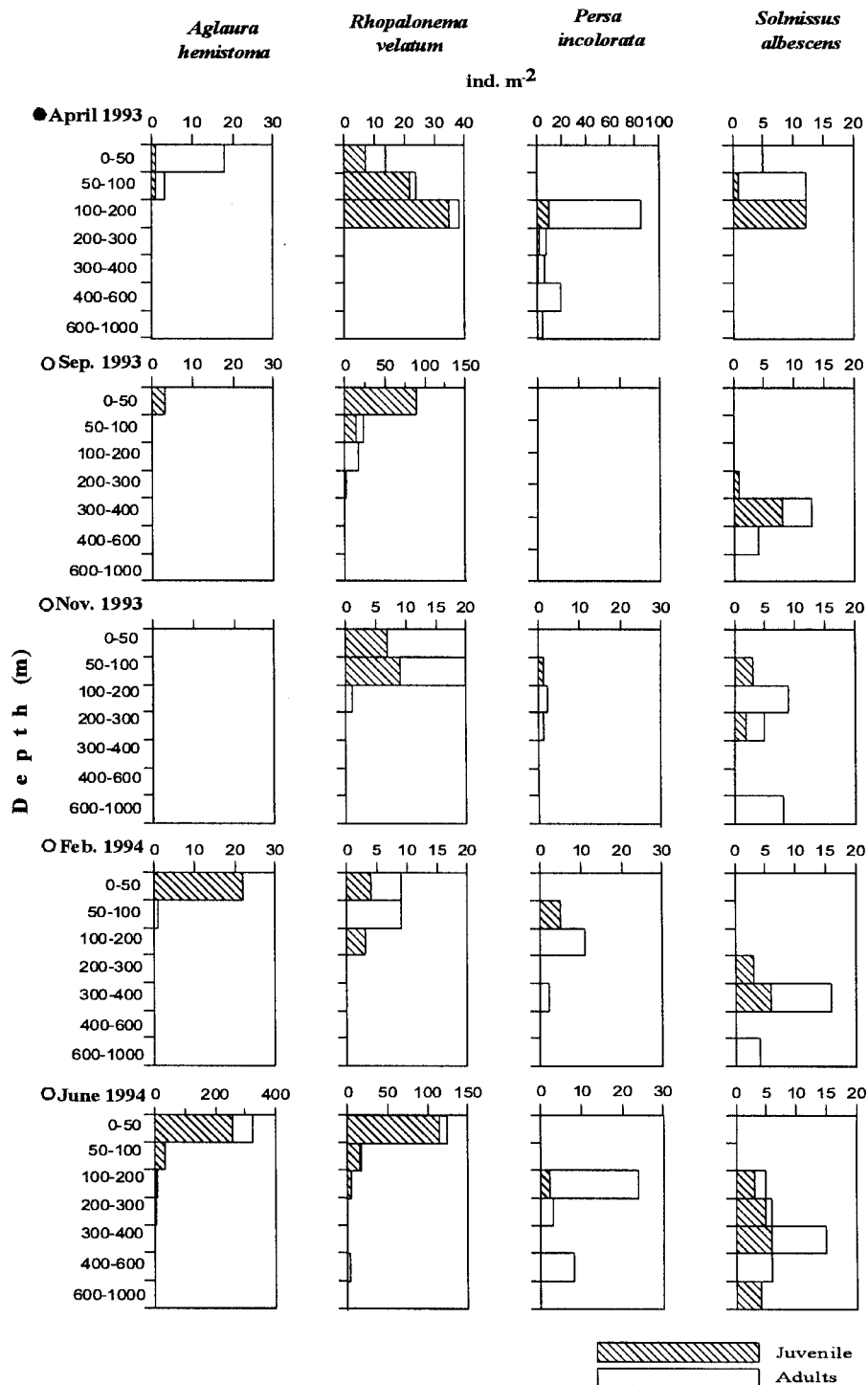
Fig. 4. Vertical distribution of the most abundant hydromedusan species and their life stages. ● = night; ○ = day.

Sagitta decipiens also showed a wide vertical distribution; however, it was found only rarely in the upper 100 m, and this only in November 1993 and February 1994 (Figure 6). The presence of older stages of *S. decipiens* increased with depth (Figure 6; Table IV). According to a Kruskal–Wallis test, the vertical mean positions (WMD) in the water column of the four developmental stages of both species were significantly different ($P < 0.05$).
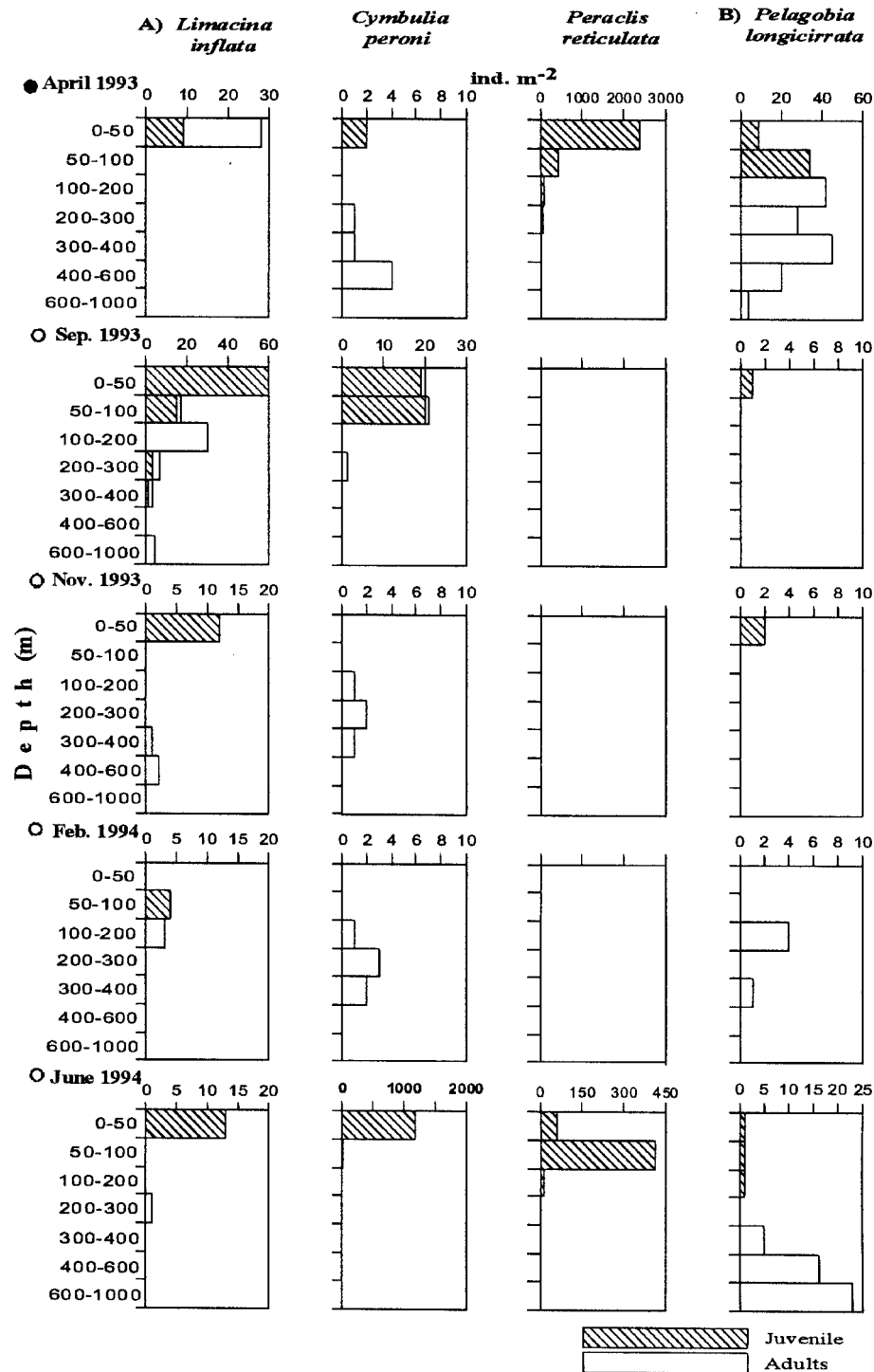
Fig. 5. Vertical distribution of the most abundant (**A**) pteropod and (**B**) polychaete species and their life stages. ● = night; ○ = day.

Cluster analysis

Two groups may be identified from an analysis of the 15 most abundant species (Figure 7). One, composed of *Aglaura hemistoma, R. velatum, M. kochi, L. subtilis, S. enflata* and *S. minima*, is distributed mainly in the 0–50 and 50–100 m layers. The other is made up of species with wide vertical distributions.
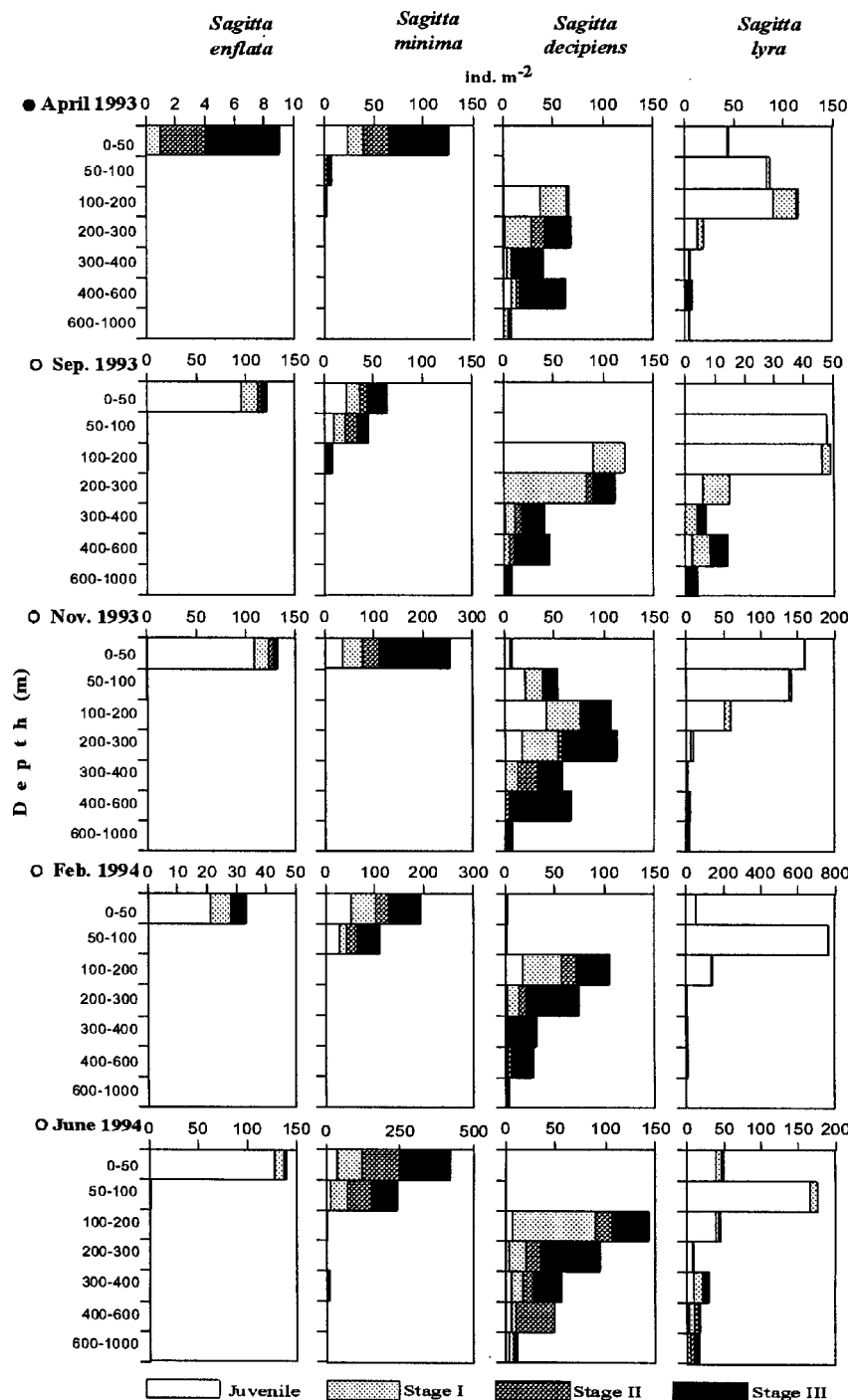
Fig. 6. Vertical distribution of the most abundant chaetognath species and their life stages. ● = night; ○ = day.

DISCUSSION

Species composition

All hydromedusae (Benović and Lučić, 1996), calyco-phorae (Gamulin and Kršinić, 2000), polychaetes (Zei, 1956) and chaetognaths (Gamulin and Ghirardelli, 1983) have been recorded previously in the Adriatic Sea. The pteropod *D. papilio* and the heteropod *P. mediterranea*, however, were found for the first time in the Adriatic Sea. *Desmopterus papilio* is common in the tropical Atlantic and Indian Oceans (Rampal, 1975) and has been

reported in the western Mediterranean (Franc, 1949; Rampal, 1975). *Protatlanta mediterranea* was reported first in the Mediterranean by Issel, who found it in the Straits of Messina (Issel, 1915). Di Geronimo also found large deposits of their shells in the sediment of the Ionian Sea (Di Geronimo, 1970). It may be significant that both *D. papilio* and *P. mediterranea* were observed in winter and late autumn, periods of stronger inflow of Mediterranean water to the South Adriatic (Orlić *et al.*, 1992). During this same time, *D. papilio* was observed at the coastal station near Dubrovnik, which lies on the same transect as the deep-sea station and is directly influenced by open-sea waters (Batistić, 1999).

Certain features of the polychaete data differ from those collected earlier in the open South Adriatic. In particular, the rather uncommon species *Pelagobia longicirrata* (Zei, 1956; Požar, 1972) was frequent, especially in April, when it dominated in the whole water column. From April to September 1996, this species was the most abundant polychaete at the coastal station near Dubrovnik (Batistić, 1999). *Pelagobia longicirrata* is widely distributed in the Atlantic Ocean (Pleijel and Dales, 1991) and has been identified in the western Mediterranean (Fauvel, 1923; Pinca and Dallot, 1995), though data on its abundance and distribution in the Mediterranean are rare. In fact, very little is known of its biology elsewhere (Fernández-Álamo, 1996).

A rare pteropod in the Adriatic Sea, *P. reticulata* (Rampal, 1975; Gamulin, 1979), was the dominant pteropod in the epipelagic layer in spring. It is thermophilic,

Table IV: Weighted mean depth (WMD, m) of the most abundant species and their life stages

	● April 1993	○ Sept. 1993	○ Nov. 1993	○ Feb. 1994	○ June 1994
Hydromedusae					
Aglaura hemistoma					
Adult	35	/	/	75	60
Juvenile	50	25	/	25	35
Rhopalonema velatum					
Adult	85	105	60	60	30
Juvenile	125	35	55	80	40
Persa incolorata					
Adult	330	/	185	180	290
Juvenile	180	/	75	75	150
Solmissus albescens					
Adult	60	440	360	630	405
Juvenile	150	340	120	320	550
Calycophorae					
Lensia subtilis	40	25	25	25	30
L. meteori	150	150	200	165	140
Muggiaea kochi	25	/	25	40	40
Pteropoda					
Limacina inflata					
Adult	25	170	470	150	250
Juvenile	25	60	25	75	25
Cymbulia peroni					
Adult	460	150	250	320	/
Juvenile	25	50	/	/	25
Peraclis reticulata					
Adult	/	/	/	/	90
Juvenile	70	/	/	/	80
Polychaeta					
Pelagobia longicirrata					
Adult	360	/	/	190	480
Juvenile	65	25	25	/	100

(Continued)

Table IV: Continued

	● April 1993	○ Sept. 1993	○ Nov. 1993	○ Feb. 1994	○ June 1994
Chaetognatha					
Sagitta enflata					
Juvenile	/	75	30	25	25
Stage I	25	80	25	25	25
Stage II	25	75	25	25	25
Stage III	25	75	25	25	25
Sagitta minima					
Juvenile	25	40	25	40	40
Stage I	40	50	25	40	50
Stage II	30	70	25	40	50
Stage III	30	80	30	45	40
Sagitta decipiens					
Juvenile	260	150	120	160	250
Stage I	350	255	160	185	276
Stage II	330	380	240	270	410
Stage III	460	500	300	360	405
Sagitta lyra					
Juvenile	150	155	90	90	95
Stage I	170	370	160	247	438
Stage II	180	460	350	342	605
Stage III	500	740	673	435	690

/ = no specimens found; ○ = day; ● = night.

known from the Atlantic Ocean, and has been found in large quantities in the Indian Ocean (Rampal, 1975). According to the same author, the presence of *P. reticulata* in the Alboran and Aegean seas may indicate two populations with different origins.

Several authors have commented on other such significant changes in the zooplankton of the South Adriatic. For example, a newly recorded species, *Muggiaea atlantica* (Gamulin and Kršinić, 2000), became the dominant calycophore in spring and summer 1995 at the South Adriatic offshore station (Batistić, 1999); the dominant species of tintinnids has changed (Kršinić, 1998); and a new incoming medusa, *Haliscera bigelowi* (A. Benović, personal communication), has been reported.

It is tempting to explain these broad changes in the structure of the Adriatic planktonic ecosystem by invoking the results of physical oceanographic research that reveal important changes in the water masses of the Eastern Mediterranean (Malanote-Rizzolli *et al.*, 1999; Civitarese and Gacic, 2001). That is, as these water masses influence those of the Adriatic, any changes in their formation may be at least partly responsible for the documented changes in the Adriatic zooplankton. It is, however, very important to exercise caution in this regard, as the biological data required to establish any

such causal relationship are currently insufficient. Data presented herein contribute essential baseline information that should aid in evaluating this connection.

Vertical distribution

All groups investigated in this study were more abundant in the upper 100 m and decreased with depth. This same pattern has been observed for zooplankton in other parts of the Mediterranean (Weikert and Trinkaus, 1989; Pancucci-Papadopoulou *et al.*, 1992; Mazzocchi *et al.*, 1996). The important contribution of chaetognaths found here is consistent with reports from other parts of the Mediterranean (Scotto di Carlo *et al.*, 1984; Pancucci-Papadopoulou *et al.*, 1992; Mazzocchi *et al.*, 1996), as well as with those from other regions (Bone *et al.*, 1991). Pteropods seem to be characterized by variability of abundance: they may occur temporarily in very high numbers, then disappear from the plankton altogether (Rampal, 1975). For example, Mazzocchi *et al.* found great variability in the horizontal and vertical abundance of pteropods in the eastern Mediterranean, particularly in the Sicily Channel and near Rhodes (Mazzocchi *et al.*, 1996). In our work, the highest abundance occurred in April 1993 and June 1994 in the euphotic zone (0–100 m), coincident with the highest Chl *a* concentrations. They also occurred below 100 m, especially
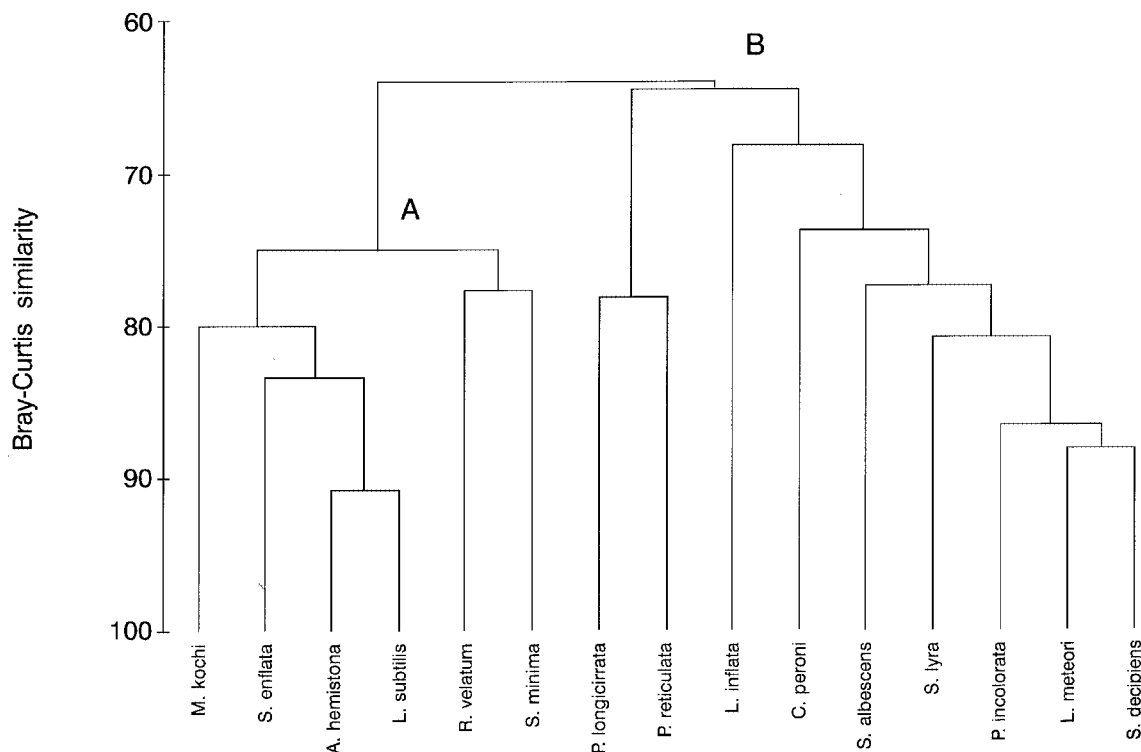
Fig. 7. Cluster analysis of the distribution of the most abundant species.

in April 1993. This may be explained by the unusual increase in Chl *a* in the 100–300 m layer at that time, which may be related the abundance of small diatoms and other nanophytoplankton (<20 μm) cells (Jasprica, 1994). A similar phenomenon has been observed in other parts of the Eastern Mediterranean (Pancucci-Papadopoulou *et al.*, 1992).

In general, the vertical distributions of species studied in this work are similar to those reported previously for the Mediterranean Sea (Andersen *et al.*, 1998). Most of the earlier studies, however, employed a 500 μm mesh, through which juvenile specimens would pass uncollected. Thus, those investigations did not distinguish life-history stages.

Cluster analysis suggests two groups of species. The first (A) consists of those for which all life-history stages were confined mainly to the upper 100 m. Oxygen saturation in this layer was always >1.0 and, as may be expected, temperature and salinity variations were greatest. This zone is also characterized by an ample supply of food, inasmuch as it has the highest levels of phytoplankton, copepods (Hure *et al.*, 1980) and microzooplankton (Kršinić, 1998). Species with this distribution pattern include *A. hemistoma*, *R. velatum*, *L. subtilis*, *M. kochi*, *S. enflata* and *S. minima*. A similar pattern for these species has been reported previously in the South Adriatic (Benović and Lučić, 1996; Batistić, 1999; Gamulin and Kršinić, 2000).

The second group (B) is composed of species with wide vertical distributions. In this group, *P. incolorata*, *L. meteori* and *S. decipiens* had the highest level of similarity. These species occur mainly below 100 m, with the main population between 100 and 300 m. This zone naturally has very low annual oscillations in temperature and salinity, and lower oxygen concentrations, though the water is still well aerated. These species temporarily 'invade' the subsurface layer (50–100 m), while they occur in the surface layer (0–50 m) only after winter mixing of the water column.

The vertical distributions of *P. incolorata* may be explained by reproductive events. It may be assumed that adults inhabiting deeper layers migrate to the upper layers for breeding. Older stages of *S. decipiens* also occurred at greater depth. This is similar to the pattern observed by Kehayias *et al.* in the East Mediterranean (Kehayias *et al.*, 1994). The most frequent prey size taken by *S. decipiens* is <0.8 mm (Batistić *et al.*, 2003), and small copepods dominated layers occupied by *S. decipiens* (Kršinić, 1998), with higher numbers in layers in which their juveniles were found.

The other species belonging to group B are distributed throughout the water column: *S. albescens*, *L. inflata*, *P. reticulata*, *C. peroni*, *P. longicirrata* and *S. lyra*. The distribution of these species was influenced by the vertical position of the dominant life-history stages in the water column

and thus depends on their biological cycle. (As adults of *P. reticulata* were found only very rarely, no information is available on its ontogenetic segregation.) Excluding *S. albescens*, the juveniles of these species always occupied the surface and subsurface layers, while adults were usually found deeper. This suggests a different tolerance of different life stages to environmental conditions.

The distribution of *S. albescens* exhibited diel periodicity, as reported by many authors (Sardou *et al.*, 1996). The number of adult *S. albescens* increased with depth during the day; in the only night sample (April 1993), they were found in the upper 100 m. Juveniles were deeper. This suggests that reproduction occurred in deeper layers, after which juveniles migrated upward, but never reached surface layers. Sardou *et al.* observed that only part of the population reached shallow depths at night, but their data did not distinguish between juveniles and adults (Sardou *et al.*, 1996).

Contrary to other cruise dates, both juveniles and adults of *L. inflata* were in the surface in April 1993, indicating an upward nocturnal migration of adults. Rampal made a similar observation in the Western Mediterranean (Rampal, 1975). The vertical distribution of *C. peroni* showed a clear seasonal difference linked to the appearance of juveniles. According to Rampal, adults occurred in deeper layers during non-breeding periods; during the breeding period, they migrated towards the upper layers (Rampal, 1975).

The polychaete *P. longicirrata*, as well as the chaetognath *S. lyra*, also displayed ontogenetic vertical distributions, with juveniles in upper layers. Similar distributions of *S. lyra* have been reported for the eastern (Kehayias *et al.*, 1994) and western (Furnestin, 1962) Mediterranean. As suggested by several authors [e.g. (Sullivan, 1980; Feigenbaum, 1991)], juveniles seek the upper layers owing to the higher food levels and better opportunity for selecting suitable prey found therein. Copepods, the main prey of chaetognaths, were most abundant in the upper 100 m layer (the maximum abundances of calanoid copepods and small copepod assemblages were 700 and 2300 ind. m^{-3}, respectively), and their abundance decreased conspicuously between the 100 and 1000 m depths in the South Adriatic Pit (Kršinić, 1998; Batistić *et al.*, 2003).

According to the data presented herein, the vertical distributions of second group species may suggest a combination of different life-history strategies (where they reproduce), different food preferences and different environmental tolerances.

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