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Bathymetric distribution of medusae in the open waters of the middle and south Adriatic Sea during spring 2002

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Twenty-eight species of hydromedusae and one scyphomedusa were collected from the middle and south Adriatic in Spring 2002. Haliscera bigelowi was recorded for the first time in the Adriatic Sea and Dicodonium adriaticum for the southern Adriatic. The cosmopolitan species Rhopalonema velatum, Aglaura hemistoma and Persa incolorata averaged 88% of total medusan abundance. The Mediterranean species Rhabdoon singulare and Solmissus albescens were numerous at the deeper stations. These species were found either in the southern or in middle Adriatic, and their abundance is greater than in other regions of the Mediterranean Sea. Species diversity and abundance generally were highest in the upper 200 m and decreased with depth. Diel vertical migration patterns included some species that nocturnally sought shallower or deeper layers, and some species migrated in both directions. A few species did not show any vertical migration. Although light likely triggers vertical movements, data suggest that foraging strategies also influence the vertical migration of medusae.

INTRODUCTION

The first account of hydromedusae of the Adriatic Sea comes from the Gulf of Trieste (Will, 1844). Further results originate mostly from the shallow north Adriatic, but some studies were also done in deep waters of the middle and south Adriatic (Benović, 1976). The most comprehensive published data have been provided by Benović and Bender (Benović and Bender, 1987), Benović and Lučić (Benović and Lučić, 1996) and Purcell *et al.* (Purcell *et al.* 1999). These mainly describe species composition and seasonal or geographical distribution of hydromedusae collected by vertical or oblique plankton net tows. Only two papers address vertical distribution: one considers diel vertical migration of *Solmissus albescens* and the other the bathymetric distributions of several other species (Benović, 1973, 1976).

Medusae are often important predators in marine ecosystems, but clear evidence of their impact on the population structure of their zooplankton and fish prey is ambiguous (Purcell, 1997). A more complete understanding of their effect requires information on their biology and ecology. One important aspect of their population ecology is their bathymetric distribution and diel vertical migration. Although vertical migrations of many potential prey species, mostly zooplanktonic crustaceans, have received significant attention (Vinogradov, 1997), there is much less data for medusae (Benović, 1973; Mills, 1983; Roe *et al.*, 1984; Andersen *et al.*, 1992; Pages and Gili, 1992; Sardou *et al.*, 1996; Vinogradov and Shushkina, 2002).

Medusae, mostly those of the metagenetic orders Anthomedusae and Leptomedusae that have alternating pelagic (hydromedusa) and bottom dwelling (hydroid) phases, are likely to be sensitive to environmental changes. Substantial changes of the medusan fauna documented in the northern Adriatic Sea (Benović *et al.*, 1987) have led to the hypothesis that repopulation of this region occurs by the introduction of populations from the middle and southern Adriatic (Benović, 1991; Benović and Lučić, 1995). This replenishment was not unexpected, owing to the general circulation pattern of the Adriatic (Orlić *et al.*, 1992) that facilitates the northward transport of southern populations and the rather constant environmental conditions of the more southern areas (Gačić *et al.*, 2001) that provide a stable source population. This results in a constant hydromedusan fauna (Benović and Lučić, 1996), as well as in the introduction of species that supplement the composition of the north Adriatic zooplankton community (Benović *et al.*, 2000).

Thus, by comparing all data collected from the middle and south Adriatic in Spring 2002, we have introduced

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and tested hypotheses of persistence of bathymetric distributions and daily vertical migrations of hydromedusae and the possible ingression of new species into the Adriatic Sea. It is expected that our data of hydromedusan population, which consist mainly of holoplanktonic species, would demonstrate stability of the hydromedusan fauna in the oligotrophic ecosystem of the southern and middle Adriatic.

METHOD

Study area

The Adriatic Sea is conveniently divided into three separate regions. The north is a relatively broad, shallow basin with depths <50 m. This makes it particularly susceptible to the cold winds common in this area in winter (Gačić *et al.*, 2001). Further, as it contains the mouth of the Po River, it is influenced by industrial discharge originating in northern Italy.

In contrast, the southern Adriatic is the deepest area, with depths down to ~1200 m, and has the more stable environmental conditions year round. It also serves as a source of deep-water formation and thus participates in the broader circulation of the Mediterranean (Gačić *et al.*, 2001).

The middle Adriatic, with depths reaching 280 m in the Jabuka Pit, is a transition area between the shallow north and the deep south. The 170 m deep Palagruza Sill separates it from the southern Adriatic (Fig. 1).

The general circulation pattern features inflow of Ionian Surface Water and Levantine Intermediate Water northward along the eastern coast and southward outflow along the western coast of surface water and deep, dense water from the middle and southern Adriatic, formed seasonally, into the eastern Mediterranean (Orlić *et al.*, 1992). The surface circulation of the southern Adriatic is a gyre that partially isolates the middle Adriatic from the influence of the open Mediterranean. These patterns, of course, strongly influence the distribution of the Adriatic plankton (Kršinić and Grbec, 2002).

Sampling

Plankton were collected in the middle and southern Adriatic (Fig. 1, Table I) during the spring 2002 Medusa cruise (25 May to 6 June) by R/V *Naše More* of the Polytechnic of Dubrovnik and with participation of researchers from Providence College (Rhode Island, USA), Dauphin Island Sea Lab (Alabama, USA), Stazione Zoologica (Naples, Italy) and the Marine Station (Piran, Slovenia).

All zooplankton samples were collected by vertical hauls with a Nansen opening–closing net at the following depth intervals: 0–50, 50–100, 100–200, 200–400, 400–600, 600–800 and 800–1000 m. The same intervals were applied, within the limits of the bottom depth, at all stations. Microzooplankton samples were made only during the day, and with a 53 μm mesh, 65 cm diameter net; mesozooplankton were sampled at both day and night at four deep stations with a 200 μm mesh, 113 cm diameter net. Average hauling speed was 0.5 m s^{-1}. Samples were preserved in a 2.5% formaldehyde–seawater solution buffered with $CaCO_3$.

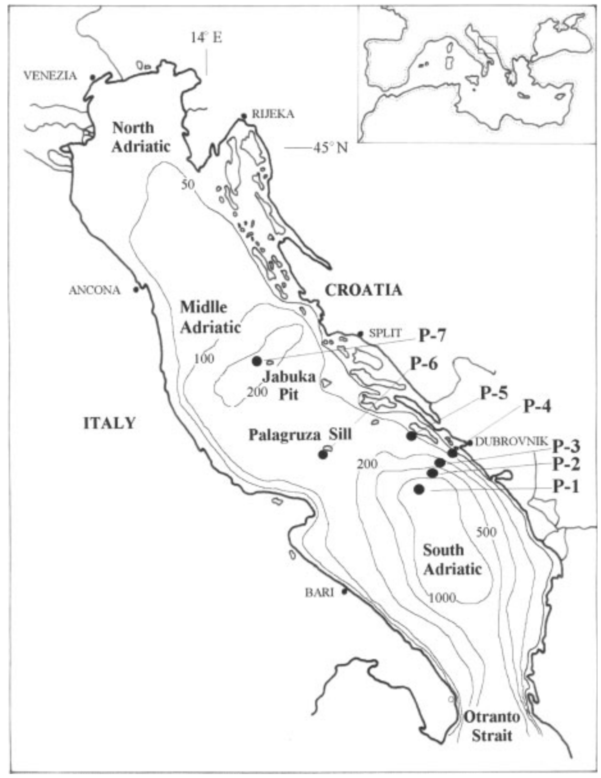

Fig. 1. Map of sampling area in middle and south Adriatic Sea.

All medusae and mesozooplankton identifications were performed using an Olympus SZX 9 stereomicroscope. For microzooplankton, a LEICA DMLB inverted microscope was used at magnifications of ×100 and ×400.

Medusae were counted from total samples. Subsamples performed by Folsom plankton splitter (1/16 to 1/32 of the total sample) were used to count microzooplankton and mesozooplankton.

Temperature, salinity, oxygen saturation and chlorophyll measurements were made in layers from 0 to 200 m with a CTD package consisting of an SBE25 CTD (SeaBird, Inc.), a Wetstar Fluorometer (Wetlabs, Inc.) and a CStar Transmissometer (Wetlabs, Inc.).

Moonlight intensity was not measured; only general stages—waxing, crescent and new—were noted (Table I).

Pearson correlation coefficients were used to compare daily vertical population densities between medusae species and microzooplankton groups and mesozooplankton copepods.

Table I: Stations, depth to bottom, moon phase and time of sampling during the Medusa 1 cruise in middle and south Adriatic, May–June 2002

Code	Description	Position (φ, λ)	Depth (m)	Moon	Date	Hauling time (h)
P-1	South Adriatic Pit	42°11′ N	1100	Waxing	31 May	2200–0320 (night)
		17°42′ E			1 June	1330–1630 (day)
P-2	South Adriatic Pit	42°22′ N	850	Crescent	4 June	2130–0120 (night)
		17°50′ E			5 June	0800–1130 (day)
P-3	South Adriatic Pit	42°27′ N	330	Crescent	3 June	2200–0010 (night)
		17°57′ E			4 June	0830–1100 (day)
P-4	Lokrum Island	42°37′ N	120	—	5 June	1300–1325 (day)
		18°06′ E				
P-5	Mljet Island	42°44′ N	110	—	26 May	1345–1420 (day)
		17°24′ E				
P-6	Palagruza Sill	42°28′ N	184	—	31 May	1530–1720 (day)
		16°21′ E				
P-7	Jabuka Pit	43°06′ N	270	New	30 May	1245–1745 (day)
		15°07′ E			31 May	0220–0400 (night)

RESULTS

Environmental conditions

Highest temperatures were found from the surface to 5 m, with a range of 19.6°C (P-7) to 21.0°C (P-4). The minimum, 11.1°C, was found at 200 m at P-7. Average temperature varied little between stations, with the only noticeable decrease found in the 100–200 m layer at stations P-6 and P-7 (Table II). Salinity ranged from 38.04 (P-4, 0.5 m) to 38.80 and averaged 38.77 ± 0.11 for all depths. Oxygen saturation was high at all stations. A noticeable decrease in the average was recorded only at station P-2 (Table II). The highest chlorophyll *a* (Chl *a*) concentrations were found between 50 and 100 m (Table II) and ranged from 0.122 μg L^{-1} (P-6) to 0.072 μg L^{-1} (P-1).

Table II: Average values of hydrographic parameters and Chl a in middle and south Adriatic Sea, Medusa 1 cruise, May–June 2002

	P-1	P-2	P-3	P-4	P-5	P-6	P-7
Layer 0–50							
Temperature (°C)	17.3 ± 1.9	18.0 ± 2.1	17.8 ± 2.1	17.6 ± 2.1	17.8 ± 1.8	17.7 ± 1.9	17.5 ± 1.2
Salinity	38.77 ± 0.02	38.77 ± 0.05	38.69 ± 0.20	38.60 ± 0.30	38.53 ± 0.18	38.72 ± 0.08	38.68 ± 0.11
Oxygen (%)	92 ± 1	91 ± 3	92 ± 1	89 ± 9	91 ± 2	92 ± 1	92 ± 1
Chl *a* (μg L^{-1})	0.070 ± 0.002	0.082 ± 0.002	0.074 ± 0.003	0.078 ± 0.004	0.089 ± 0.008	0.079 ± 0.007	0.077 ± 0.006
Layer 50–100							
Temperature (°C)	15.3 ± 0.1	14.7 ± 0.2	14.9 ± 0.2	15.3 ± 0.1	15.2 ± 0.1	15.1 ± 0.2	14.9 ± 0.2
Salinity	38.81 ± 0.02	38.81 ± 0.01	38.83 ± 0.01	38.79 ± 0.01	38.73 ± 0.01	38.82 ± 0.03	38.79 ± 0.01
Oxygen (%)	92 ± 1	88 ± 4	92 ± 1	92 ± 1	93 ± 0	90 ± 0	92 ± 0
Chl *a* (μg L^{-1})	0.072 ± 0.033	0.110 ± 0.009	0.105 ± 0.015	0.089 ± 0.004	0.110 ± 0.006	0.122 ± 0.011	0.101 ± 0.012
Layer 100–200							
Temperature (°C)	14.9 ± 0.2	14.2 ± 0.1	14.4 ± 0.1			13.4 ± 1.2	12.4 ± 1.2
Salinity	38.85 ± 0.01	38.79 ± 0.01	38.81 ± 0.02			38.70 ± 0.09	38.60 ± 0.10
Oxygen (%)	92 ± 1	74 ± 5	93 ± 0			83 ± 5	89 ± 4
Chl *a* (μg L^{-1})	0.071 ± 0.002	0.081 ± 0.012	0.075 ± 0.006			0.086 ± 0.011	0.072 ± 0.004

Refer to Table I and Fig. 1 for an explanation of geographical positions.

Zooplankton general distribution

Microzooplankton

Microzooplankton was most abundant between 50 and 100 m (Fig. 2), corresponding with the maximum chlorophyll concentration. Two peaks occurred: 7987 ind m^{-3} at P-6 and 6472 ind m^{-3} at P-1. At other stations, surface concentrations were decreased and ranged from 2212 ind m^{-3} (P-4) to 4139 ind m^{-3} (P-3). Abundance typically decreased from the surface to bottom. Copepod nauplii were the most numerous group down to 100 m at deeper stations and contributed >50% to total microzooplankton abundance. Poecilostomatoids dominated between 400 and 600 m, representing 91% (P-2) and

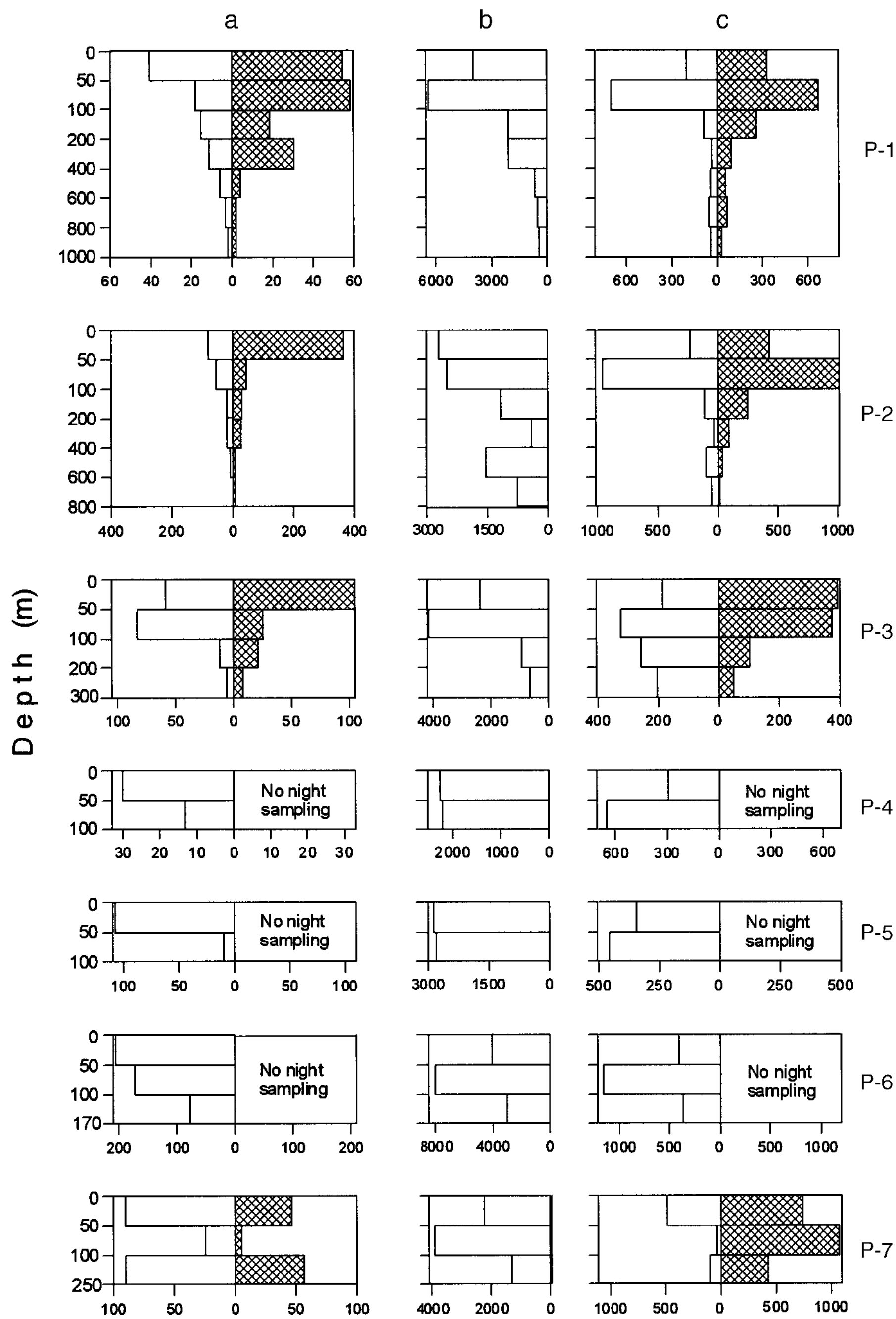

Fig. 2. Vertical distribution of (**a**) medusae (number of individuals 10 m^{-3}), (**b**) microzooplankton and (**c**) copepods (number of individuals m^{-3}) in middle and south Adriatic. Open bars, day samples; hatched bars, night samples.

67% (P-1) of total copepodite abundance. At the shallower stations (P-4, P-5 and P-6), copepod nauplii and copepodites were present in equal proportions. The greatest number of tintinnids was found at the surface of the deepest stations: 901 ind m^{-3} at P-1 and 532 ind m^{-3} at P-2.

Significantly positive correlations ($n = 33$, $r = 0.75$–0.83, $P < 0.003$) between the vertical distribution of tintinnids, nauplii and the copepodites of calanoids and cyclopoids were noted only at the deeper southern stations. This confirms the higher surface concentrations of these groups.

Mesozooplankton

Mesozooplankton occurred in greater numbers in the two upper layers during the day and night (Fig. 2). A maximum of 1273 ind m^{-3} was noted at P-6 in the 50–100 m layer. Pronounced differences between day and night population densities were noted only at Jabuka Pit. Moreover, significant correlations between day and night vertical distribution of total mesozooplankton abundance were noted at two deep stations ($n = 33$, $r = 0.95$–0.96, $P < 0.001$). Copepods dominated, ranging between 74% (P-1) and 90% (P-7) of the total mesozooplankton. At all stations, the most abundant species was *Oithona plumifera*, followed by *Ctenocalanus vanus* and *Clausocalanus jobei*. In addition, *Paracalanus parvus* was abundant at shallower areas and *Clausocalanus pergens* and *Clausocalanus paululus* in the surface layers at deep stations. In general, beneath 200 m, cyclopoids were the most numerous, while between 400 and 600 m depths, poecilostomatoid copepods dominated. Under 600 m depths, the calanoid *Temoropia mayumbaensis* was also abundant.

Medusae

In total, 28 species of hydromedusae and one of scyphomedusa (*Paraphyllina intermedia*) were collected. Anthomedusae and Trachymedusae, each represented by nine species, were the most diverse. Leptomedusae were represented by six species and Narcomedusae by four (Table III).

Haliscera bigelowi, collected at P-1, is the first record of this species in the Adriatic. Only the cosmopolitan species *Aglaura hemistoma* and *Rhopalonema velatum* were present at all stations. The deep stations P-1 and P-2 had the greatest species richness (18 and 13 respectively), while other stations were less diverse, with a minimum of three species at P-4.

The bulk of the medusae were in upper layers, but they were present at all depths, although with a distinct diel pattern (Table IV). *Rhopalonema velatum* was the most abundant, averaging 55% of the total. *Aglaura hemistoma* contributed 25% and *Persa incolorata* 8%. Among other species, *Solmaris leucostyla*, *Rhabdoon singulare*, *Liriope tetraphylla* and *S. albescens* altogether contributed ~7%. All other species occurred at densities of 1–3 ind 10 m^{-3}. Among them, *Dicodonium adriaticum*, *Corymorpha nutans*, *Zanclea costata*, *Podocoryne carnea*, *Podocoryne minuta*, *Leuckartiara octona*, *Laodicea undulata*, *Obelia* spp., *Clytia* spp., *Helgicirrha shultzei* and *Eutima gracilis* are metagenetic coastal species; *Oceania armata*, *Amphinema dinema*, *Octophialucium funerarium*, *H. bigelowi*, *Geryonia proboscidalis*, *Arctapodema australis*, *Rhopalonema funerarium*, *Sminthea eurygaster*, *Solmundella bitentaculata* and *Cunina globosa* are pelagic mid-water species; and *P. intermedia* is a deep-water species.

Vertical distribution and diel migrations of the most abundant medusae species

Rhopalonema velatum

Rhopalonema velatum, the most abundant medusa, was found at all stations (Fig. 3). Highest values were found at the surface during the night, with a maximum of 358 ind 10 m^{-3} at P-2. Records from a variety of stations indicate that the abundance of *R. velatum* generally decreased with depth (Fig. 3). There was a clear difference between day and night vertical abundances, indicating a pattern of diel vertical migration. This was most evident at deep stations P-1 and P-2. During the day, *R. velatum* generally was limited to depths >100 m; during the night, the bulk of the population still was found largely within the surface layers, although some fraction did descend to as deep as 1000 m. A higher average number of individuals found in night samples was noted at P-1, P-2 and P-3.

The vertical distribution of *R. velatum* correlated significantly with tintinnid abundance at the open southern Adriatic stations ($n = 20$, $r = 0.81$–0.98, $P < 0.01$). At P-2 and P-3, pronounced correlations also were established with nauplii vertical distributions ($n = 20$, $r = 0.81$–0.99, $P < 0.01$). At the middle Adriatic and coastal stations, significant correlations were not established with any micro- or mesozooplankton groups.

Aglaura hemistoma

Aglaura hemistoma was found at all stations in the layers of 0–100 m only (Fig. 3) and was more numerous at shallow stations. In general, the highest values were noted at the surface, with the maximum abundance of 77 ind 10 m^{-3} at P-7 during daylight. Only at this station was a considerable difference between day and night samples noted.

Daily vertical distribution of *A. hemistoma* significantly correlated with tintinnids ($n = 20$, $r = 0.78$–0.95, $P < 0.01$) and copepod nauplii ($n = 20$, $r = 0.63$–0.93, $P < 0.05$), consistently at the deepest southern Adriatic area only.

Table III: Species list of medusae found in middle and south Adriatic Sea, Medusa 1 cruise, May–June 2002

	Species	Stations						
		P-1	P-2	P-3	P-4	P-5	P-6	P-7
	Anthomedusae							
1	*Dicodonium adriaticum*		+					
2	*Rhabdoon singulare*	+	+	+		+		
3	*Corymorpha nutans*						+	+
4	*Zanclea costata*							+
5	*Oceania armata*	+	+					
6	*Podocoryne carnea*		+			+		
7	*Podocoryne minuta*						+	
8	*Amphinema dinema*	+	+					
9	*Leuckartiara octona*					+		
	Leptomedusae							
10	*Laodicea undulata*	+		+		+		
11	*Obelia* spp.						+	
12	*Clytia hemisphaerica*		+			+		+
13	*Octophialucium funerarium*	+						
14	*Helgicirrha shultzei*						+	
15	*Eutima gracilis*	+			+		+	
	Trachymedusae							
16	*Haliscera bigelowi*	+						
17	*Geryonia proboscidalis*	+						
18	*Liriope tetraphylla*					+		+
19	*Aglaura hemistoma*	+	+	+	+	+	+	+
20	*Arctapodema australis*	+						
21	*Persa incolorata*	+	+	+			+	+
22	*Rhopalonema funeranium*	+						
23	*Rhopalonema velatum*	+	+	+	+	+	+	+
24	*Sminthea eurygaster*	+	+					
	Narcomedusae							
25	*Solmundella bitentaculata*	+	+	+		+		
26	*Solmaris leucostyla*	+					+	
27	*Cunina globosa*						+	
28	*Solmissus albescens*	+	+	+				
	Scyphomedusae							
29	*Paraphyllina intermedia*	+	+					
	Number of species	18	13	7	3	9	10	7

Refer to Table I and Fig. 1 for an explanation of geographical positions.

Persa incolorata

Persa incolorata was found only <100 m (Table IV; Fig. 3), with the greatest population densities in night samples at P-7 (85 ind 10 m^{-3}) and day samples at P-6 (52 ind 10 m^{-3}). This species was always more abundant at mid-depths but was considerably less common at southern stations (P-1, P-2 and P-3). The obvious difference in concentrations between day and night samples indicates daily vertical migrations that spread animals into deeper layers during the night.

Significant correlations were not established with either micro- or mesozooplankton.

Rhabdoon singulare

The only abundant anthomedusan was *R. singulare* (Fig. 3). It occurred at a maximum of 13 ind 10 m^{-3} in the

Table IV: Species day (d)–night (n) depth distribution, Medusa 1 cruise, May–June 2002

	Species	Depth layer (m)						
		0–50	50–100	100–200	200–400	400–600	600–800	800–1000
	Anthomedusae							
1	*Dicodonium adriaticum*		n					
2	*Rhabdoon singulare*		d n	d n	d n	n		
3	*Corymorpha nutans*		d	n				
4	*Zanclea costata*		d					
5	*Oceania armata*	n	n	d n	n	n		
6	*Podocoryne carnea*		d	d				
7	*Podocoryne minuta*	d						
8	*Amphinema dinema*			n	d n	d n		
9	*Leuckartiara octona*		d		d			
	Leptomedusae							
10	*Laodicea undulata*		d		d			
11	*Obelia* spp.	d						
12	*Clytia hemisphaerica*	d	d n	n	n			
13	*Octophialucium funerarium*				n	n	n	
14	*Helgicirrha shultzei*	d		d				
15	*Eutima gracilis*	d n						
	Trachymedusae							
16	*Haliscera bigelowi*						d	
17	*Geryonia proboscidalis*	n						
18	*Liriope tetraphylla*	d n	d					
19	*Aglaura hemistoma*	d n	d n					
20	*Arctapodema australis*					d	d	
21	*Persa incolorata*			d n	d n	d n	d n	
22	*Rhopalonema funeranium*				n			
23	*Rhopalonema velatum*	d n	d n	d n	d n	n	n	n
24	*Sminthea eurygaster*		n	d	d n	d		
	Narcomedusae							
25	*Solmundella bitentaculata*	n	n		n			
26	*Solmaris leucostyla*	d	d	d n				
27	*Cunina globosa*	d						
28	*Solmissus albescens*	n	n	n	d n	d n	d n	n
	Scyphomedusae							
29	*Paraphyllina intermedia*						n	d n

50–200 m layer at deep southern Adriatic stations at night. This species was never present within the 0–50 m layer, and its vertical migration pattern showed nocturnal movement only to 600 m. Few individuals were found at any shallow station.

There were no significant correlations with either micro- or mesozooplankton.

Solmissus albescens

The large mesopelagic narcomedusa, *S. albescens*, was present only at southern Adriatic stations (Fig. 3). During the day, this species aggregated between 400 and 600 m depth, with a maximum of 6 ind 10 m^{-3}. The daily distribution at station P-1 was between 400 and 1000 m, and at station P-2 between 200 and 600 m. Its night-time distribution at P-1, during the waxing phase of the moon, was from the surface to 1000 m; at P-2, during crescent moon, from 100 to 800 m; and at P-3, again during crescent moon, within the 200–300 m layer, for one sample only.

The daily vertical distribution of *S. albescens* significantly correlated with poecilostomatoid copepods

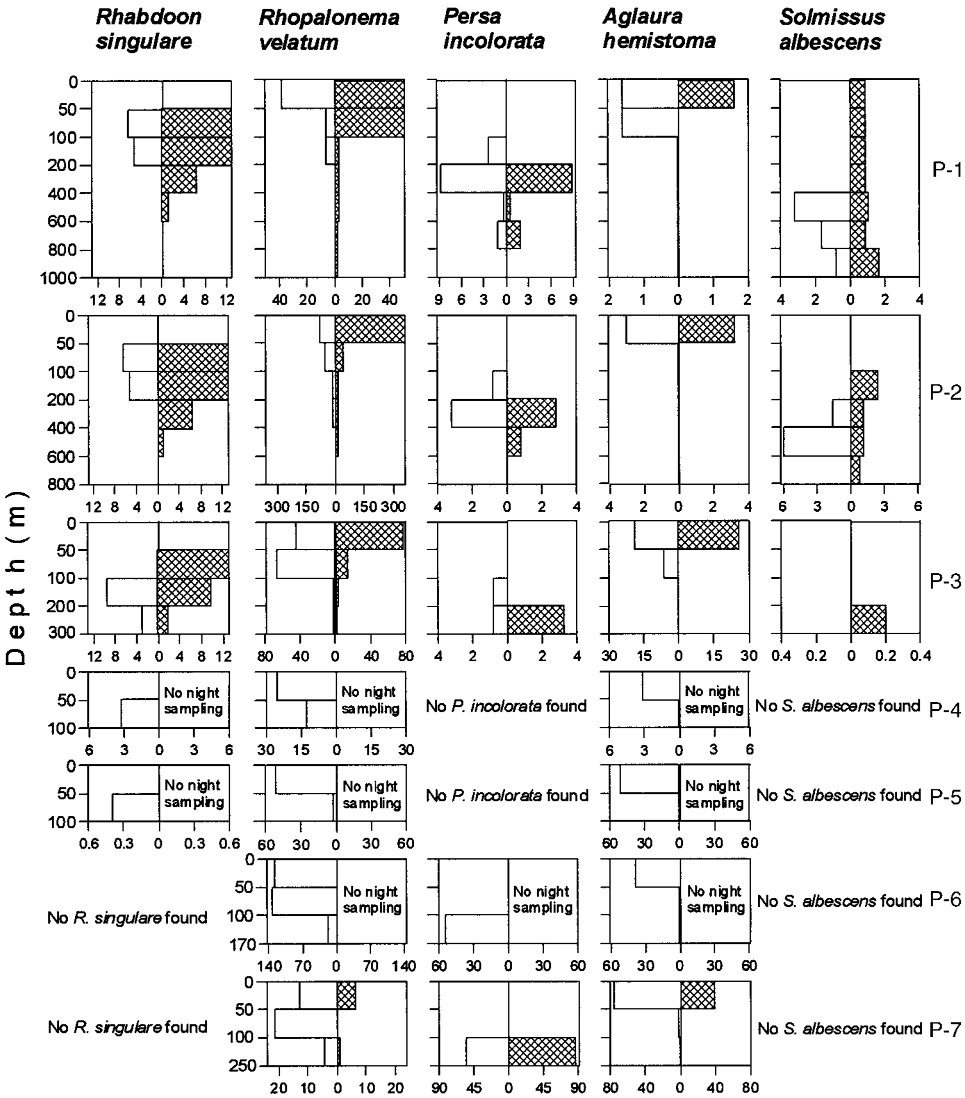

Fig. 3. Day–night vertical distribution of dominant medusae species (number of individuals 10 m^{-3}) in the middle and south Adriatic. Open bars, day samples; hatched bars, night samples.

($n = 16$, $r = 0.78$–0.84, $P < 0.05$). Other large-scale carnivore organisms occupied layers that coincided with the greatest daily population densities of this species. These included Poecilostomatoid copepods, *Nematoscelis megalops* (Euphausiacea) and *Chauliodus sloani* (Pisces).

Liriope tetraphylla

This species was found only at P-5 and P-7. It was present in surface layers of P-5, with a maximum of 32 ind 10 m^{-3}, in both day and night samples at the surface and at 50–100 m only during the day.

Solmaris leucostyla

This species was most abundant in the two uppermost layers of P-6: 37 ind 10 m^{-3} in 0–50 m, and 38 ind 10 m^{-3} in 50–100 m. A few individuals were found at the surface of P-1 during both day and night.

DISCUSSION

Species composition and abundance

Of the 29 medusa species collected in this work, *H. bigelowi*, found at deep-sea station (P-1), was recorded for the first time in the Adriatic Sea. This species is known from the Atlantic and Indian Oceans and also has been noted in the western Mediterranean (Gili and Pages, 1987; Mills *et al.*, 1996). It is probably a recent invader of the Adriatic, as are certain other planktonic cnidarians (Kršinić and Njire, 2001).

Haliscera bigelowi is typically bathypelagic (Kramp, 1959). Fragments of *Haliscera*-like trachymedusans reported from deeper layers of Northeast Atlantic (Roe *et al.*, 1984) support the bathypelagic origins of this species. The present work further supports the bathypelagic origin of *H. bigelowi*, as it was found in the 600–800 m depth interval, as reported by Mills *et al.* (Mills *et al.* 1996).

All other species found here have been recorded previously in the open waters of the Adriatic Sea (Benović and Lučić, 1996), but *D. adriaticum* was found for the first time in the southern Adriatic. This species has been previously collected in the northern Adriatic, and its occurrence in the south is likely due to transport by surface currents (Orlić *et al.*, 1992). It is uncertain whether these two species are truly adapted to the conditions of the middle and southern Adriatic, and so are able to establish stable populations, or whether these occurrences are purely accidental (Benović and Lučić, 2003).

The greatest diversity of medusae was at the deep stations P-1 and P-2. Compared with earlier observations, this differed only in terms of the presence of metagenetic species (Babnik, 1948; Benović and Lučić, 1996). Of those species that regularly occurred in samples, five—*O. funerarium*, *A. australis*, *S. eurygaster*, *S. albescens* and *P. intermedia*—are characteristic of the deep southern Adriatic Sea. None of these was ever found in shallower areas. It is noteworthy that, until now, the deep-water species *P. intermedia* was found only once in the Adriatic Sea (Neppi, 1922: as *Paraphyllina rubra*); and the surface species *G. proboscidalis* and *C. globosa* were found only in early investigations (Graeffe, 1884; Neppi, 1922).

The composition of medusans in the deep south and in the shallower areas of the Adriatic Sea is stable. Only a small number of species of low abundance were found close to the coast and in the shallower middle Adriatic, a finding contrary to that of Gili *et al.* (Gili *et al.* 1988). Typical coastal species such as *C. nutans*, *Z. costata*, *P. minuta*, *Clytia hemisphaerica*, *H. shultzei* and *E. gracilis* were probably transported either from nearby coastal waters or from the north Adriatic via transverse currents (Poulain and Cushman-Roisin, 2001).

The rather low number of metagenetic species in the middle Adriatic suggests dramatically lower medusae numbers in the shallow north (Benović *et al.*, 1987). The hypothesized repopulation of the north Adriatic by medusan species from open waters of middle and south areas (Benović and Lučić, 1995) could not occur, as these areas are permanently populated only by holoplanktonic pelagic species that are unlikely to adapt to the environment of the shallow north Adriatic. The clearest evidence of this is the case of *P. incolorata*, the greatest population densities of which were found at middle Adriatic (P-6 and P-7) in deeper layers where the lowest temperatures were recorded. This species is also found frequently in the north Adriatic, but during winter (Benović and Lučić, 1996). The association of these species with cold-water layers has been observed previously (Goy, 1987; Buecher and Gibbons, 1999).

In studying the composition of medusae in the open waters of the middle and southern Adriatic (Benović and Lučić, 1996), only Benović and Bender (1986) provide quantitative data, such as the number of individuals per square metre. The highest values, <500 ind m^{-2}, were in the surface layer. Previous investigations only reported total numbers of individuals per sample. These results thus do not permit comparisons among studies of the relative concentrations or abundance of medusae with those of other zooplankton.

The present work found pronounced medusa abundance in the 0–100 m layer, which is coincident with high concentrations of Chl *a*, microzooplankton and mesozooplankton. In general, Chl *a* concentrations and hydrographic data are in accordance with previous data from middle and open south Adriatic waters (Gačić *et al.*, 2001). This is consistent with previously established spring patterns in the open Adriatic Sea (Hure *et al.*, 1980; Kršinić, 1998; Batistić *et al.*, 2004) and in the Mediterranean (Razouls and Thiriot, 1968; Benović and Bender, 1986, 1987; Gili *et al.*, 1988). Medusae densities found in surface layers (362 ind 10 m^{-3} at P-1 and 206 ind 10 m^{-3} at P-6) are among the greatest reported for open-sea environments (Gili *et al.*, 1988; Pages and Gili, 1991, 1992; Andersen *et al.*, 1992; Seguera-Puertas, 1992; Pages *et al.*, 1996; Buecher and Gibbons, 1999; Morales-Suárez *et al.*, 1999; Nicholas and Frid, 1999; Gibbons and Buecher, 2001).

Communities of planktonic cnidarians are frequently dominated by a few highly adaptable species (Gili *et al.*, 1988). The most important of these in the present study were the cosmopolitan species *R. velatum*, *A. hemistoma* and *P. incolorata* and the Mediterranean species *R. singulare* and *S. albescens*. *Rhopalonema velatum* and *A. hemistoma* are surface and subsurface species found both nearshore and in the pelagic environment. *Persa incolorata* and *R. singulare* are subsurface and mesopelagic species, while *S. albescens* include mesopelagic and bathypelagic species association. *Haliscera bigelowi* and *P. intermedia* are typically bathypelagic and show no vertical migration.

Vertical distribution

Foraging strategies vary among hydromedusae (Mills, 1981; Madin, 1988; Costello, 1992; Colin *et al.*, 2003). For example, most pelagic cnidarians appear to feed continuously, but some exhibit diel feeding activity (Purcell, 1997). These and other trophic interactions between hydromedusae and their microplanktonic prey may thus explain some of the differences observed in their vertical distributions (S. Colin, personal communication).

Thus, the greatest abundances of *R. velatum* and *A. hemistoma* were in layers in which potential prey were at maximal abundance. At night, however, part of the *R. velatum* population was in deeper layers, while *A. hemistoma* was constantly at the surface. At the deep-sea stations, there was a correlation between abundance of these species and their principal microplanktonic prey: tintinnids and copepod nauplii. On the contrary, no such correlation was found in shallow coastal and mid-Adriatic areas, as the concentration of prey was relatively high throughout the entire water column.

Rhabdoon singulare and *P. incolorata* both seek deeper layers at night. This may be a response to the downward migration of its zooplanktonic prey (Hure and Scotto di Carlo, 1969; Kršinić, 1998), or it may be a strategy for avoiding large predators that occupy the surface layers at night. The most important vertical migrant was a typical Mediterranean species, *S. albescens*. There is ample evidence that confirms that its core population is found within 400–600 m during the day and that it migrates toward the surface at night (Kramp, 1924; Pell, 1938; Benović, 1973; Mills and Goy, 1988; Andersen *et al.*, 1992; Sardou *et al.*, 1996). Most authors do not report it in surface layers (0–100 m), perhaps because they do not consider the effect that moonlight can have on its behaviour. *Solmissus albescens* is associated with a constant low light intensity; during the afternoon, it rises to upper levels and at night, during full moon, it remains <100 m (Benović, 1973). In complete darkness, specimens again seek shallower depths. For example, we found *S. albescens* at the surface at night during a waxing moon (P-1), but were absent during a crescent moon (P-2). A novel characteristic of this medusa is that from the daily core population (Benović, 1973) some specimens migrate nocturnally into both shallower and deeper layers, a behaviour found also in some non-medusan carnivores of the same mesopelagic community (Poecilostomatoid copepods, *N. megalops* and *C. sloani*; D. Lučić, unpublished data).

Open-water medusae of the middle and southern Adriatic generally have remained constant throughout the period over which the Adriatic has been investigated, and the rather low diversity and abundance of most species probably is sustained by the influence of the subtropical conditions of the Mediterranean Sea (Kramp, 1959). These medusae, particularly the holoplanktonic species, apparently exhibit regular diel vertical migrations and are well adapted to the environment and food resources of the open Adriatic Sea. Local environmental factors such as temperature, salinity and vertical currents apparently do not exert significant influences on their migratory activity.

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