Distribution and Abundance of Calycophores (Siphonophora, Calycophorae) in the Mediterranean and Adriatic Sea

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With 5 figures and 7 tables

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Abstract. The paper presents data on the distribution of calycophores in the open Mediterranean waters based on samples collected during the R/V "Atlantis II" cruise in May-June 1969, as well as the first data on the distribution and quantity of nectophores and gonophores in the coastal and open Adriatic waters. The following species were numerically important in the eastern Mediterranean: Eudoxoides spiralis, Bassia bassensis, Sulculeoaria chuni, Lensia campanella, and Diphyes dispar. In the western part of the study area, however, calycophores were found in low numbers. The presence of the immigrating Atlantic forms, Muggiaea atlantica and Lensia subtiloides, was also registered. Among 22 Adriatic calycophores, numerically important were: Muggiaea kochi, Lensia subtilis, Sphaeronectes gracilis, and S. irregularis. Other species were rarely found and mainly distributed in the Otranto Strait and the Southern Adriatic Pit.

Problem

In the middle of the nineteenth century, knowledge of the Mediterranean calycophores was poor and based mainly on material collected by means of primitive fishing gear. A smaller species, *Muggiaea kochi*, was first described on the basis of material from the Bay of Trieste (WILL, 1844). As early as 1851, Vogt (1851) presented the first data on calycophores obtained from areas off Nice and Villefranche. Kölliker (1853) and Sars (1857) reported on calycophores from the Messina region, Kefferstein & Ehlers (1861) for Naples.

The first extensive investigations of siphonophores in the open Mediterranean were carried out by the "Thor" expedition in the summer of 1908 and winter of 1910; as many as nineteen species were recorded (BIGELOW & SEARS, 1937).

During the last few decades, the data on calycophore ecology has mainly derived from coastal Mediterranean waters (Cervigon, 1958; Kinzer, 1965; Vives, 1966; Carré, 1966; Patriti, 1964; Ianora et al., 1981). Alvarino (1974)

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mentions some species from the open Levantine waters yet provides no quantitative data.

Early data on Adriatic siphonophores may be found in the plankton studies by Busch (1851), Claus (1876), Graeffe (1875, 1884), Cori & Steuer (1901), STIASNY (1910, 1911), CAR & HADŽI (1914a, b), GRANDORI (1910), BABIĆ (1913), and SZÜTS (1915).

The first extensive descriptive study of Adriatic siphonophores was carried out by Moser (1917). It was based on the plankton material collected during the summer cruise by the research vessel "R. Virchow" from Istria to Dubrovnik and by the "Najade" in the southern Adriatic. Gamulin (1948) recorded eleven calycophore species in the middle Adriatic insular area in the summer of 1939. The investigations of the vertical distribution of the zooplankton near Dubrovnik provided first data on calycophores of the southern Adriatic. They contributed considerably to the knowledge of seasonal vertical distribution patterns and mean day-night species depth levels; they also pointed to the dependence of the day-night levels on cloudy weather during the day and on moonlight during the night (Hure, 1955, 1961).

The calycophore distribution along the eastern Adriatic coast was calculated based on samples taken during three one-year studies near Split, Hvar, Vis, Rovinj and at two stations near Dubrovnik, where sixteen calycophore species were recorded and their distribution from north to south and offshore studied (GAMULIN, 1979). Important data for the Jabuka Pit region were also reported by ROTTINI (1966). Furthermore, ten siphonophores were registered during a one-year investigation of the shallow northern Adriatic down to 50 m depth (ROTTINI & GAMULIN, 1969).

During the period May-June 1969, research was carried out in the open waters of the Mediterranean from Rhodos to Gibraltar by the R/S "Atlantis II".

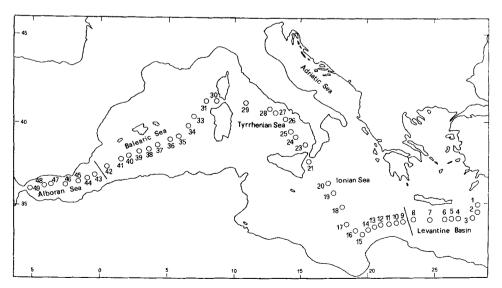


Fig. 1. R/S "Atlantis II" cruise from Rhodos to Gibraltar: 11 May to 3 June, 1968. Stations are those where oblique hauls were made from 200 m to surface.

A great number of additional zooplankton samples were collected seasonally in the open-sea and coastal regions of the Adriatic between 1973 and 1976. In this paper we present the first quantitative and horizontal distribution data on the calycophores.

Material and Methods

The May-June 1969 cruises by the research vessel "Atlantis II" of the Woods Hole Oceanographic Institution were carried out in the open Mediterranean from Rhodos to Gibraltar. Oblique plankton hauls were made at forty-nine stations (Fig. 1) with a 75 cm net diameter, a mesh netting of 333 µm,

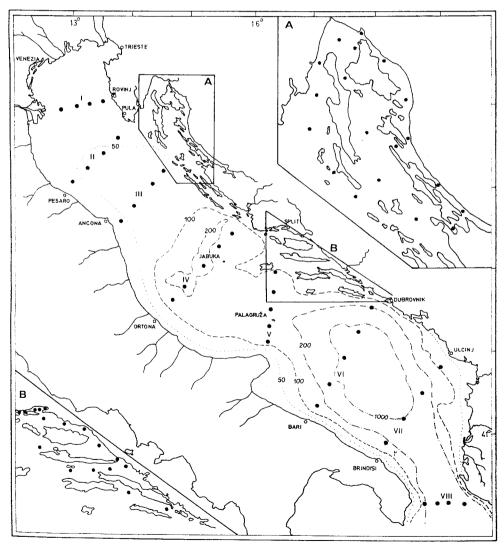


Fig. 2. Location of sampling stations in the Adriatic Sea during the cruises of the "A. Mohorovičić", "Vila Velebita" (A), and "Baldo Kosić" (B).

and a length of 300 cm. A 250 metre long wire cable equipped with lead weights was dropped into the sea; this enabled the net to sample down to 150 m depth and each haul to last thirty minutes. Horizontal tows with a Bongo net were used to sample the deep-sea form *Clausophyes ovata* from 600 to 2000 m depth. The entire catch was examined and the data represent the total number of calycophores per sample.

The present report also covers the entire open Adriatic waters, the more closed Kvarner region, and the middle Adriatic insular area.

The Adriatic samples were taken with vertical tows from the bottom to the surface with a $250 \,\mu m$ mesh net (length $350 \,cm$, mouth diameter 100 and $113 \,cm$).

The investigations in the Kvarner region were carried out in 1973/74 by the research vessel "Vila Velebita" of the Center for Marine Research of the Institute "Ruder Bošković". Samples were taken at 18 fixed stations (Fig. 2 a) with a 100 cm diameter net.

The middle Adriatic cruises were carried out seasonally throughout 1973/74 by the research vessel "Baldo Kosić" of the Biological Institute, Dubrovnik. Samples were taken at 17 fixed stations (Fig. 2b) with a 100 cm diameter plankton net.

The investigations in the open Adriatic waters were performed in 1974–1976 by the research vessel "Andrija Mohorovičić" along 8 transversal profiles at 35 fixed stations (Fig. 2). The samples were taken with an open 113 cm diameter Nansen net. Hydrographic and basic plankton data were published in the Reports and Results, 1982 issued by the Hydrographic Institute JRM, Split.

The plankton material was preserved in 2.5% neutralized formaldehyde. The neritic species were counted from the subsamples of $\frac{1}{10}$ or $\frac{1}{10}$ of the original sample volume, whereas for the open sea species the entire catch was examined.

Results

Calycophores from open Mediterranean waters

The calycophore fauna differed considerably between the eastern and western Mediterranean, with marked differences being observed in certain study areas. Only ten species were recorded in the Alboran Sea, up to seventeen species in the Ionian Sea. The oceanic *Muggiaea atlantica* and *Lensia subtiloides* were found only in the western Mediterranean. *Abylopsis tetragona* and *Chelophyes appendiculata* were also characteristic of this region. One of the smallest forms, *Sphaeronectes gamulini*, was registered only in Gibraltar – to date its westernmost record (Tables 1 and 2).

The species characteristic of the eastern Mediterranean are: Eudoxoides spiralis, Bassia bassensis, Sulculeolaria chuni, Lensia campanella, and Diphyes dispar. They contributed 95–100% to the total number of nectophores here. The large species D. dispar was registered at all the stations in the Levantine basin and the Ionian Sea. Markedly dominant in the eastern Mediterranean were the species L. subtilis, E. spiralis, and B. bassensis, which, with as many as 13 190 nectophores, contributed 80% to the total nectophores. These species formed 59% of the total nectophores in both basins. L. subtilis had a maximum number of nectophores in the Tyrrhenian and Ionian seas, E. spiralis in the eastern Mediterranean.

Clausophyes ovata was found only between 600-2000 m depth, with anterior and posterior nectophores; it contributed 61.6% to the total nectophores in Bongo net samples. This species is widespread throughout the Mediterranean and is most abundant in the Balearic and Alboran regions.

2. Calycophores from the Adriatic Sea

Our investigations in the open Adriatic waters revealed 22 species (Table 3). The highest species diversity (21) was noted during the September-October 1974 cruise, the lowest (15) in June 1976 (Table 4). As regards the species composition the Adriatic may be divided into: 1. the northern Adriatic (profiles I-III); 2. the middle Adriatic (profiles IV-V) including the western and eastern stations of the southern Adriatic; 3. the southern Adriatic and Strait of Otranto (profiles VI-VIII). A particularly rich calycophore population in the Strait of Otranto and the deep southern Adriatic waters was noted in spring. During our investigations, the immigration of species northwards was more pronounced in spring and winter, although the pattern differs from year to year; this depends mainly of the incoming current, which in winter and early spring proceeds northwards from the Mediterranean along the eastern Adriatic coast (Buljan & Zore-Armanda, 1976; Vučak et al., 1982).

The average annual nectophore number for all the calycophores (calculated for 1 m² surface) along the profiles of the open Adriatic waters are presented in Table 3. The species with the broadest distribution range and highest numerical importance were M. kochi, L. subtilis, S. gracilis, and S. irregularis, which we designated the "A group"; the other calycophores, including the open and deepsea species, was termed the "B group". The "A group" calycophores were ubiquitous in the Adriatic (Fig. 3). The highest average seasonal numbers were registered in the Kvarner region, the middle insular area, the western coast of Istria, from the Ortona to Bari area, as well as in the western part of Palagruža Sill. In the other parts of the Adriatic, within the 1000 m isobath, these species were less abundant and more uniformly distributed. The lowest values were recorded at the deep-sea stations of the southern Adriatic and the Strait of Otranto. The dominance of neritic species along the continental shelf was pronounced; M. kochi alone contributed from between 57 % to 87 % to the total amount of nectophores (Table 5). S. gracilis only occasionally ranked second in importance numerically; in the Kvarner region it comprised 42% of the total nectophore number. The "B group" species were most abundant in the South Adriatic Pit and the Strait of Otranto; they were absent north of the profile Ancona-Lošinj (Fig. 4).

The seasonal distribution of nectophore numbers is represented in Fig. 5. During the April-May cruise, these values in the open Adriatic waters typically ranged from 50 to 500 indiv. · m⁻². The lowest values were recorded in spring and summer in the northern Adriatic at stations directly influenced by the Po river. Therefore, salinities below 37% may exert a negative influence on calycophores. High calycophore numbers were occasionally recorded in warmer seasons in the middle and southern parts of the western Adriatic coast and in the western part of the Palagruža Sill.

Table 1. Calycophore distribution in the western Mediterranean during the R/S "Atlantis II" cruise.

			All	boran S	Sea						
No. of station:	49	48	47	46	45	44	43	42	41	40	39
Hippopodius hippopus								3			
Sulculeolaria quadrivalvis											
S. turgida											
S. chuni											
Diphyes dispar											
Lensia conoidea	1	1									
L. fowleri											
L. subtilis		4			17	2	8	7	10	11	9
L. subtiloides	2	5	3	13	12	13	11	7	5	4	
L. campanella											
L. meteori		3	4	3	7		3	9	3		
Muggiaea kochi	1	5	1	4		2		3	3	1	
M. atlantica	9	47	32	36		3	5	۱,3		1	
Chelophyes appendiculata	15	1	10	9	12	29	15	7	16	26	9
Eudoxoides spiralis											
Sphaeronectes gracilis		1									
S. gamulini		1									
Abylopsis tetragona	12	105	31	400	34	132	45	35	3	13	29
Bassia bassensis											

Table 2. Calycophore distribution in the eastern Mediterranean during the R/S "Atlantis II" cruise.

								Ioni	an Sea
No. of stations:	21	20	19	18	17	16	15	14	13
Hippopodius hippopus	. 17	5	2	48	59	19	65	33	63
Sulculeolaria quadrivalvis		3			1	1	2		
S. turgida			2		2	1	3		2
S. chuni	9	34	13	25	1	8	17	4	16
Diphyes dispar	1	5	1	1	1		1	2	
Lensia conoidea	1								
L. fowleri	7								
L. subtilis	136	304	176	166	45	106	248	280	112
L. subtiloides									
L. campanella	9	31	27	83	144	96	73	21	146
L. meteori									
Muggiaea kochi	52	72		8					
M. atlantica								1	
Chelophyes appendiculata	4	10	9	3	16	1	2	24	10
Eudoxoides spiralis	208	550	690	400	356	195	470	700	370
Sphaeronectes gracilis						1			
S. gamulini									
Abylopsis tetragona	40	200	49	51	82	27	65	42	64
Bassia bassensis	8	57	72	43	112	82	168	16	96

Mediterranean siphonophores

Numbers represent numerical abundance per haul.

			Sea	henian	Tyrrl									ic Sea	Balear
total	23	24	25	26	27	28	29	30	31	33	34	35	36	37	38
179	14	8	9	73	4	41	15			8		3	1		
3					2						1				
12				3		1	. 8								
19	8				1	8							2		
0															
23			3		1	1		3	12						
0															
2364	512	112	265	128	110	136	184	194	89	190	216	43	47	56	14
78												2			1
58				37		21									
80	8		17		23										
187						25	56	81	5						
174	25								2	3		3	3	1	1
960	41	54	115	112	24	51	47	17	33	125	92	18	24	35	23
313	49	33	19	16	12	25	19		11	16	47	35	11	8	12
1															
1															
1420	32	25	41	17	31	53	15	8	7	32	83	96	12	33	96
103	24	27	17		4	31									

Numbers represent numerical abundance per haul.

					_	I	_evantii	ne basin	1			
12	11	10	9	8	7	6	5	4	3	2	1	total
25	15	16	3	25	31	96	9	1	5	1	17	555
1				1				2				11
1	1		1	1	1			1	1	5	1	28
19	17	25	32	29	23	49	25	7	48	26	6	433
		2	17	5	6	31	15	9	8	12	1	118
									1	2		4
												7
57	49	5	16	27	138	96	64	28	16	6	33	2108
												0
105	49	17	41	19	32	27	17	59	9	7	62	1074
				9								9
				ļ								132
												1
3	24	3	17	6	15	16	7	11	9	18	25	233
340	410	325	320	84	210	380	84	96	144	92	136	6563
				1								1
				ļ								0
49	40	16	8	1								734
104	162	88	92	136	530	1050	820	172	320	270	120	4518

Table 3. The average annual nectophore numbers along the profiles of the open Adriatic waters $(n \cdot m^{-2})$; + < 1.

			Adri	atic oper	ı-sea pro	files		
Group A species	I	II	III	IV	v	VI	VII	VIII
Muggiaea kochi	340	237	279	322	314	158	106	97
Lensia subtilis		1	16	73	131	109	65	34
Sphaeronectes gracilis	1	5	19	85	22	11	16	17
S. irregularis			34	11	13	7	7	10
Group B species								
Rosacea cymbiformis								+
Hippopodius hippopus					+	+	+	2
Vogtia pentacantha						+	+	3
Sulculeolaria turgida						+	+	+
S. quadrivalvis						+	+	+
S. chuni				+	+	+	+	+
Lensia conoidea						4	1	3
L. multicristata						+	+	3
L. fowleri						5	4	3
L. campanella						+		+
L. meteori				8	4	72	44	46
Chelophyes appendiculata				+	1	6	2	9
C. ovata						+	+	+
Eudoxoides spiralis				5	7	10	14	14
Sphaeronectes gamulini				+	+	+	+	+
S. fragilis						+	+	+
Abylopsis tetragona				+	1	4	7	20
Bassia bassensis				+			+	+

Table 4. Distribution of calycophore species in the Adriatic Sea during seasonal cruises of the "Andrija Mohorovičić" 1974–1976.

profiles total number	1	П	III	IV	V	VI	VII	VIII	
of stations	4	4	4	4	5	5	4	4	total
SeptOct., 1974	1	1-2	2–4	3–6	5–8	6-13	4-11	10–15	21
April-May, 1975	1-2	1-3	4–5	4–6	6-7	6-11	6-10	7–11	17
February, 1976	1	1–4	4	56	4–6	4-8	4–6	5-10	16
June, 1976	1–2	1–2	3-4	4–7	4–8	7–10	4-12	10	15
total	3	4	6	12	11	20	20	22	

Table 5. The percentage of dominant species in the total number of nectophores.

	open Adriatic	Kvarner region	island area of middle Adriatic
Muggiaea kochi	64	57	87
Lensia subtilis	16	+	5
Sphaeronectes gracilis	6	42	5
Sphaeronectes irregularis	3	+	2
other species	11	1	1

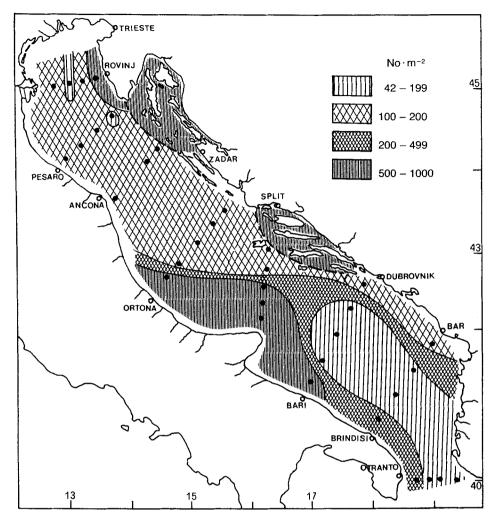


Fig. 3. The distribution of the average number of nectophores for the dominant species: *M. kochi, L. subtilis, S. gracilis,* and *S. irregularis* in the Adriatic Sea.

Discussion

As many as forty calycophore species have been reported from the Mediterranean to date (TOTTON, 1965). The "Atlantis II" expedition recorded twenty species, but seven deep-sea forms reported by BIGELOW & SEARS (1937) were not found, probably because samples were only taken from the surface down to a 150 m depth. In addition, the plankton mesh (333 µm) did not retain the majority of small calycophores such as the genus *Sphaeronectes*. During the "Thor" expedition (BIGELOW & SEARS, 1937), the species *C. appendiculata*, *A. tetragona*, and *B. bassensis* were outstandingly dominant and contributed

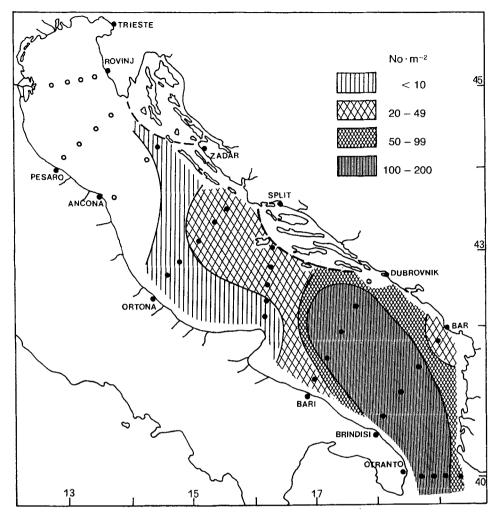


Fig. 4. The distribution of the average number of nectophores for "B group" species in the Adriatic Sea.

78.3% to the total nectophores. On the other hand, this expedition did not record three rather common eastern Mediterranean species M. kochi, L. subtilis, and L. meteori. During the "Atlantis II" expedition, L. subtilis and M. kochi were almost ubiquitous in western Mediterranean and Ionian waters. These were the first records of these species in open Mediterranean waters.

The presence of *D. dispar* at all stations in the Levantine basin and the Ionian Sea agrees with the findings of ALVARINO (1974); this indicates a possible immigration of this species from the Red Sea and the Indian Ocean. Its presence in the western Mediterranean may be explained by its immigration from the Atlantic (Moser, 1917; BIGELOW & SEARS, 1937).

The markedly greater quantity of nectophores found in the eastern (16529) versus the western Mediterranean (5975) is due to differences in productivity

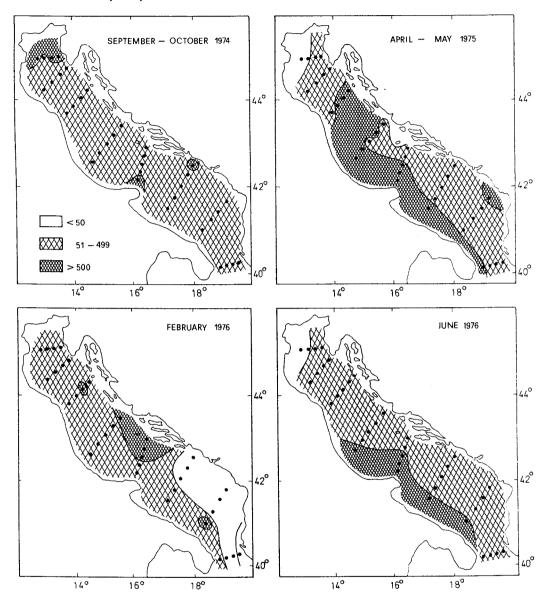


Fig. 5. The seasonal distribution of total nectophores according to the "A. Mohorovičić" cruises in the Adriatic Sea.

patterns. The "Atlantis II" data show that the plankton biomass was considerably higher in the eastern than in the western Mediterranean (average 598 versus 313 mg) (ŠTIRN, 1973).

Our investigations in the open Adriatic waters failed to confirm the presence of only one species, *Lilyopsis rosea* (previously reported by Moser, 1917). In the northern, shallow part of the Adriatic (maximum depth: 50 m), 8 calycophores have been reported (ROTTINI & GAMULIN, 1969), whereas in the waters

off Rovinj, 16 species (Gamulin, 1979) were found. Rottini (1966) collected 16 species in the Jabuka Pit region. In the vicinity of Dubrovnik, Hure (1955) registered 10, Gamulin (1979) 16 species. The variable number of species reported by different authors for the same area may be attributed to the different collection methods used. In order to obtain comparable data on the quantitative/qualitative calycophore distribution patterns in the Adriatic, the present samples were all taken by the same type of plankton net with the same mesh size; only vertical hauls were carried out.

The water currents in the Adriatic are presumably an important factor influencing the quantitative distribution of calycophores in the Adriatic. According to Student's t-test, the differences in quantity between the western and eastern Adriatic were significant, presumably due to the incoming NW-directed flow along the eastern and the outgoing one along the western Adriatic coast. The outgoing current is considerably richer in calycophores than the incoming water masses; this mainly enriches the western Ionian waters. In contrast, 24% more of the "B group" species immigrate into the Adriatic than flow out. The transversal current along the Palagruža Sill is presumably an important factor regulating the spreading of calycophores from the east to the west and vice versa.

Our data on calycophore distribution are based only on the nectophore samples. However, data do exist reporting higher quantities of gonophores during the seasonal cruises of the "A. Mohorovičić" (Gamulin, 1982). Although it has been recognized that gonophores are indispensable for accurately assessing the importance of calycophores in the Adriatic Sea, they have rarely been taken into consideration due to their difficult determination. In our plankton samples, gonophores were constantly more abundant than nectophores. With respect to gonophore abundance, it may be concluded that the calycophores of the "A group" reproduce year round and most intensively over spring and summer. The correlation data for the nectophores and gonophores according to season for all study areas are presented in Table 6. The coefficients

Table 6.	The seasonal	correlation	analysis data	a for the	nectophores (n	.) and the	e gonophores (g.) for a	all study
areas.									

		"Andrij x ± S		orov n	ičić" T		"Baldo Kosić" x ± SD	n	г		"Vila Velebita" x ± SD	n	r
SeptOct. 1974	n. g.	350.1 ± 424.5 ±	324.9 409.3	34	0.900*	July 1973	775.5 ± 506.8 1227.5 ± 744.8	17	0.913*	August 1973	75.7 ± 74.0 96.7 ± 79.5	15	0.841*
April-May 1975	n. g.	412.3 ± 1053.0 ±	235.8 778.4	35	0.749*	November 1973	158.0 ± 111.3 546.7 ± 380.4	17	0.902*	November 1973	180.7 ± 84.2 301.3 ± 129.9	18	0.647*
February 1976	n. g.	245.0 ± 508.9 ±	228.1 435.0	34	0.846*	February 1974	347.8 ± 308.1 976.1 ± 849.8	17	0.957*	February 1974	330.8 ± 156.3 1066.4 ± 684.9	18	0.539*
June 1976	n. g.	447.0 ± 829.9 ±	544.6 1081.0	34	0.964*	May 1974	211.4 ± 141.6 704.2 ± 465.2	17	0.933*	May 1974	320.5 ± 206.5 775.8 ± 543.4	17	0.799*
										August 1974	879.7 ± 463.5 1278.6 ± 682.2	17	0.885*

P < 0.01 (*); $\bar{x} \pm SD = \text{mean} \pm \text{standard deviation}$; n = number of samples; r = correlation coefficient.

Table 7. The correand copepods dur	•	• '			ophores, gonophores, 1.
	August	November	February	Mav	August

	August	November	February	May	August
'Vila Velebita" n	17	18	18	17	18
r	0.612	0.578	0.312	0.490 `	0.418
	(*)	(**)	(n.s.)	(**)	(n.s.)
"Baldo Kosić" n	17	17	17	17	
r	0.781	- 0.125	0.753	0.795	
	(*)	(n. s.)	(*)	(*)	

P < 0.05 (**); P < 0.01 (*); n = number of samples.

of correlation are positive and noticeably high, ranging from r = 0.539 to r = 0.964. The 1% significance level indicates a significant positive correlation between nectophores and gonophores.

Studies into the feeding of siphonophores have been initiated only recently, accompanied by intensive investigations on the functioning of food webs in the sea along with breeding experiments under laboratory conditions (Purcell, 1981 a, b; Purcell & Kremer, 1983). Siphonophores are carnivorous, and ingest different zooplankton species depending on gastrozooid size. The smaller species feed mainly on nauplii and copepods, whereas the larger calycophores and physonectans prey on copepods, decapod larvae, chaetognaths, as well as on fish larvae. No data exist on this topic for the Adriatic. No correlation was observed between all the persons of calycophores and the copepods from the same open Adriatic plankton samples (Hure et al., 1980; Hure, 1982); this is presumably due to markedly different calycophore and copepod vertical distribution patterns, as well as to pronounced day-night copepod migrations. The day and night samples taken during the "A. Mohorovičić" cruises revealed notable differences between copepod and calycophore quantities (Table 7). In contrast, the fact that only day samples were taken in the Kvarner region and in the insular and coastal part of the middle Adriatic may account for the significant correlation determined for most of the samples.

Summary

This paper presents data on calycophores found in samples taken during the R/S "Atlantis II" cruise from Rhodos to Gibraltar in May–June 1969, the seasonal cruises along the eastern Adriatic coast in 1973/74, and those in the open Adriatic waters in 1974–1976.

In the eastern Mediterranean the species *E. spiralis*, *B. bassensis*, *S. chuni*, *L. campanella*, and *D. dispar* were numerically important. In contrast, calycophores were not as abundant in the western Mediterranean. However, the presence of the immigrating Atlantic forms *M. atlantica* and *L. subtiloides* was registered.

In the Adriatic Sea as many 22 species were found; the most widespread and numerically important were M. kochi, L. subtilis, S. gracilis, and S. irregularis.

The dominant species *M. kochi* contributed from 57 to 87% to the total number of nectophores. Other species were rarely present or of smaller quantitative importance and were mainly distributed in the Otranto Strait and the South Adriatic Pit; north of the Ancona–Lošinj profile these forms were not registered at all.

A statistically significant positive correlation between the quantity of nectophores and sexual persons of gonophores was determined. Gonophores were more abundant than nectophores throughout the study period. They were especially numerous during the warmer months.

Acknowledgements

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