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Calycophorae (Siphonophora) in the open waters of the central and southern Adriatic Sea during spring 2002

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Twenty species of calycophoran siphonophores were identified from the central and south Adriatic Sea in spring 2002. Highest abundance and species diversity were noted at the deepest stations in the south Adriatic. Highest total abundance was found in the upper 100 m. The dominant species above 100 m were *Lensia subtilis*, *Eudoxoides spiralis* and *Sphaeronectes gracilis*, none of which showed diel migration. The first two species correlated significantly with the vertical abundance of microzooplankton, and the last with that of copepods. The most abundant species in the 100–400 m layer was *Lensia meteori*, whereas *Lensia conoidea* and *Chlausophyes ovata* were most abundant below 400 m.

INTRODUCTION

Siphonophores are often abundant macrozooplankton (Boucher & Thiriot, 1972; Longhurst, 1985; Haddock et al., 2005) and function as important predators (Purcell, 1981; Mills, 1995; Silguero & Robinson, 2000; Kršinić & Njire, 2001). Understanding their role in planktonic food webs naturally requires information on their biology and ecology, including spatial and temporal aspects of their vertical distribution.

Seasonal and spatial distributions of 24 calycophoran siphonophores in the Adriatic Sea have been reported (see Gamulin & Kršinić, 2000), but these data are mostly based on daytime sampling. Information on vertical distributions and diel migrations is lacking, as generally is the case in the Mediterranean Sea (Carré & Carré, 1993). The present study contributes to the baseline information of the vertical distribution and diel migrations of calycophoran siphonophores in the oligotrophic central and southern Adriatic Sea during spring 2002. This period coincides with the annual peak of crustacean zooplankton (Hure et al., 1980; Kršinić, 1998), the calycophore's main prey. Because of the limited number of observations and the general problems of sea dynamics and patchy distribution of plankton, we have to treat our results with some caution.

MATERIALS AND METHODS

Plankton samples were collected at seven stations in the central and south Adriatic (Figure 1) during spring 2002 'Medusa' cruise (25 May–06 June). Stations are representative for both biological and hydrological aspects of the pelagic ecosystem of the Adriatic Sea (Hure et al., 1980; Gačić et al., 2001; Benović et al., 2005).

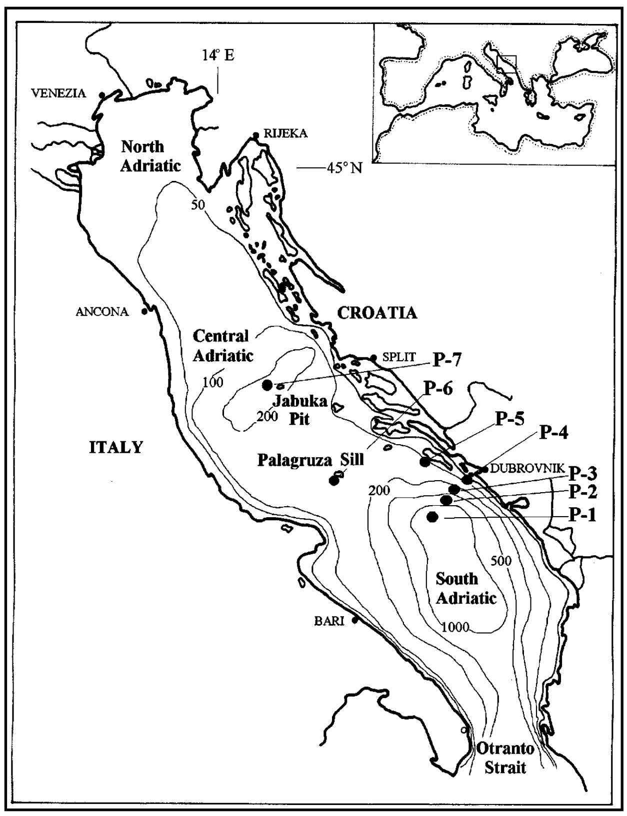

Figure 1. Map of sampling area in the central and south Adriatic Sea.

Vertical hauls were made with a Nansen opening–closing net, traditionally used in Adriatic zooplankton research (Hure et al., 1980; Kršinić, 1998; Batistić et al., 2004). Tows were performed in the following depth intervals: 0–50, 50–100, 100–200, 200–400, 400–600, 600–800, and 800–1000 m. The same intervals were used—adjusted according to the maximum bottom depth—at all stations (P-1 to P-7).

Microzooplankton samples were only taken during the day, and these with a 53-μm mesh, 65-cm diameter Nansen net; mesozooplankton were sampled both day and night at the deepest stations with a 200-μm mesh, 113-cm diameter Nansen net. Average hauling speed was 0.5 m s^{-1} for both nets. Samples were preserved in a 2.5% formaldehyde–seawater solution buffered with $CaCO_3$.

Temperature, salinity, oxygen saturation, and chlorophyll-*a* (Chl-*a*) were measured from 0 to 200 m, at every 0.5 m, with a CTD package consisting of a SBE25 CTD (SeaBird, Inc.), a Wetstar Fluorometer (Wetlabs, Inc.), and a CStar Transmissometer (Wetlabs, Inc.).

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

Calycophoran nectophores were counted from total samples and abundance was expressed according to the number of nectophores (polygastric only) per 10 m^3 of each species. Sub-samples (1/16 to 1/32 of the total sample) were used to count microzooplankton and mesozooplankton. Results are expressed as number of individuals per m^3 (no. ind m^{-3}).

The weighted mean depth (WMD) of species presence was calculated as: $WMD = \sum(n_i \times z_i \times d_i)/\sum(n_i \times z_i)$,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 (nectophores 10 m^{-3}).

Margalef's species richness index *D* was used to characterize diversity: $D = S\text{-}1/\log N$, where *S* is the number of species and *N* is the total number of individuals.

Vertical variation was analysed by cluster analysis, and the Bray–Curtis similarity coefficient was used as measure of distance (Legendre & Legendre, 1983).

Diel differences in vertical population densities between siphonophores and both microzooplankton groups and mesozooplankton copepods were compared with Pearson correlation coefficients.

RESULTS

Environmental conditions

Highest temperatures were found from the surface to 5 m, with a range of 19.60°C (P-7) to 21.00°C (P-4). A thermocline was formed below 15 m, with values less than 18°C at all stations. In the 50–100 m layer temperature ranged from 14.40°C (P-2) to 15.60°C (P-4), and in the 100–200 m layer from 11.10°C (P-7) to 14.60°C. Salinity variations were slight, ranging from 38.04 (Station P-4 at surface) to 38.90 (Station P-7 at 50 m). Mean salinity value was 38.77 ±0.11 for all stations and depths. Oxygen saturation above 100 m was higher than 88% at all stations. The highest Chl-*a* concentrations were between 50 to 100 m and ranged from 0.072 μg l^{-1} (P-1) to 0.122 μg l^{-1} (P-6). More detailed information on hydrographic parameters and Chl-*a* are described in Benović et al. (2005).

Microzooplankton and mesozooplankton

Microzooplankton abundance was highest between 50 and 100 m (Figure 2), corresponding to the maximum chlorophyll concentration. Copepod nauplii were the most numerous group down to 100 m, followed by calanoid copepodites, cyclopoid copepodites, and tintinnids. Poecilostomatoid copepodites dominated between 400 and 600 m. These represented between 67% (P-1) and 91% (P-2) of total abundance.

Copepods accounted for 74% (P-1) to 90% (P-7) of total mesozooplankton, with greater numbers recorded in the upper 100 m layers during both day and night (Figure 2).

More details on microzooplankton and mesozooplankton composition are given in Benović et al. (2005).

Calycophores

Twenty species of calycophores were collected. Highest species diversity was at deep Stations P-1 and P-2, and the lowest at the most northerly Station P-7 (see Table 2). Species richness varied with depth (Table 1). It was similar at P-1 and P-2 in the 0–50 m layer in day and night samples, but in lower layers it was generally higher at night. At all deep stations highest values were in the 100–200 m layer, except during the day at Station P-3 when these were in the 200–400 m layer. Richness varied little at shallow Stations P-4 and P-5.

Highest total abundance was found in the surface layers at deep southern stations and decreased below 100 m (Figure 2). A maximum of 275 nectophores 10 m^{-3} was recorded in the 0–50 m layer at Station P-2 during the night.

Cluster analyses identified two groups among the 20 calycophoran species. The first 'Group' is composed of species distributed mainly in the 0–50 and 50–100 m layers: *Bassia bassensis*, *Chelophyes appendiculata*, *Sphaeronectes gamulini*, *Muggiaea kochi*, *Lensia campanella*, *Muggiaea atlantica*, *Sphaeronectes irregularis*, *Hippopodius hippopus*, *Sphaeronectes gracilis*, *Lensia subtilis*, and *Eudoxoides spiralis*.

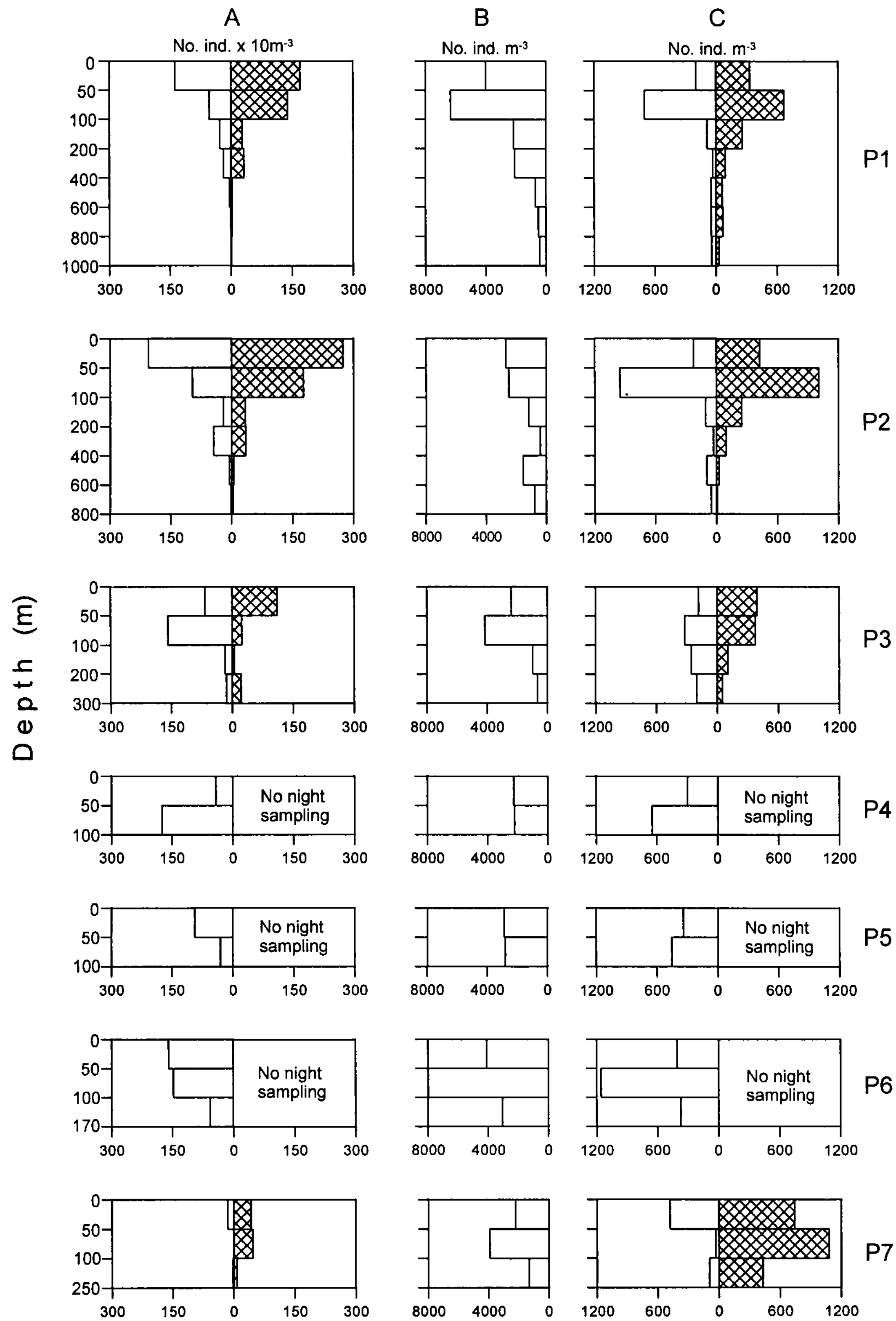

Figure 2. Vertical distribution of (A) calycophores (nectophores 10 m^{-3}); (B) microzooplankton; and (C) copepods (ind m^{-3}) in the central and south Adriatic. Open bars, day samples; hatched bars, night samples.

The second 'Group' species, mainly distributed below 100 m depth, resolves into two separate 'Subgroups'. One consists of *Sphaeronectes fragilis*, *Lensia fowleri*, *Lensia multicristata*, *Sulculeolaria chuni*, *Lensia meteori*, *Abylopsis tetragona*, and *Vogtia pentacantha*, with the main population between 100 and 400 m. The other consists of *Clausophyes ovata* and *Lensia conoidea*, with the majority of specimens below 400 m.

Lensia subtilis, *Eudoxoides spiralis* and *Sphaeronectes gracilis* were found at all stations. They were mainly in the upper 100 m, where they accounted for up to 39%, 33%, and 9% of total calycophoran abundance, respec-

Table 1. *Variability in species richness throughout the water column.*

Station	P-1		P-2		P-3		P-4	P-5	P-6	P-7	
Layer (m)	Day	Night	Day	Night	Day	Night	Day	Day	Day	Day	Night
0–50	1.22	0.97	1.13	1.07	0.71	1.06	1.61	1.32	1.38	1.13	1.07
50–100	1.15	2.03	1.75	2.32	0.79	0.94	1.55	1.46	1.40		0.52
100–200	2.43	2.43	2.65	3.41	1.05	2.32			2.48	2.40	1.99
200–400	1.38	1.45	1.59	2.27	2.24	0.97					
400–600	0.78	1.72	1.84	2.46							
600–800		1.05	0	1.82							
800–1000											

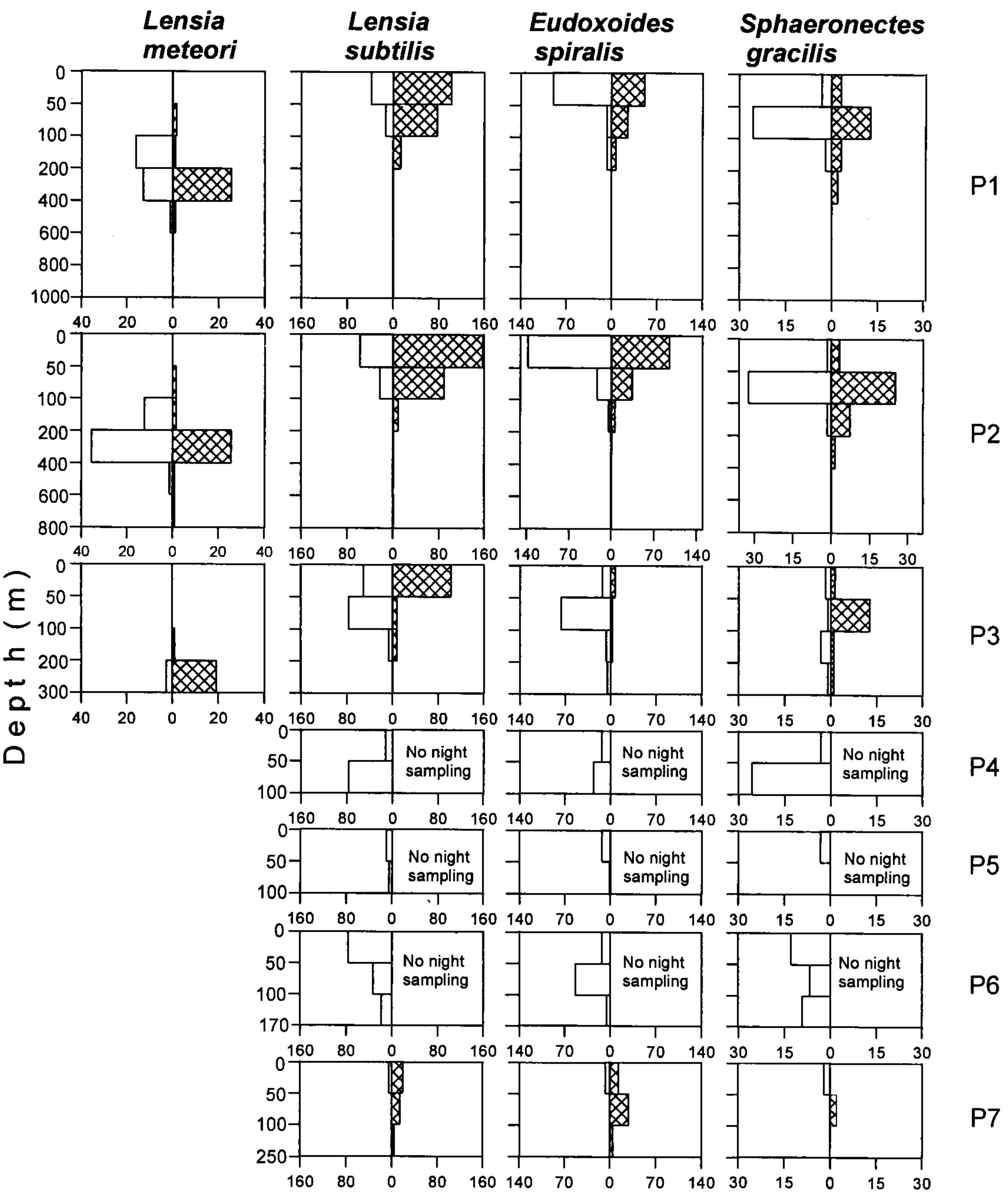

Figure 3. Day–night vertical distribution of dominant calycophores (nectophores 10 m^{-3}) in the central and south Adriatic. Open bars, day samples; hatched bars, night samples.

Table 2. *Weighted mean depth (WMD, m) at day and night.*

Station	P-1		P-2		P-3		P-4	P-5	P-6	P-7	
Species	Day	Night	Day	Night	Day	Night	Day	Day	Day	Day	Night
Hippopodius hippopus	125	125	110	100	75	25	70	35	70	50	65
Vogtia pentacantha		150	300	150							
Lensia subtilis	40	60	40	50	65	40			70	50	60
L. campanella	25	40	45	40			60	25	55		
L. conoidea		695	565	520							
L. fowleri	250	300	445	340	150	150					
L. meteori	250	295	281	315	250	250			142		
L. multicristata	210	235	250	200	250	250					
Muggiaea kochi							50	35	35	25	25
M. atlantica	25	75	25	75	75	25	70	45	85		
Sphaeronectes gracilis	75	120	80	115	125	80	70	25	100		
S. irregularis	205	50	200	50	75	75	75		102		43
S. fragilis	77	215	120	215	250	142					
S. gamulini	75	75	75	75			75			185	185
Eudoxoides spiralis	30	46	35	50	95	50	60	25	75	25	75
Chelophyes appendiculata		75	75	85	250	25			250	185	185
Sulculeolaria chuni	395	450	420	410							
Abylopsis tetragona			130	195							
Clausophyes ovata			700	600							
Bassia bassensis		25	25	25					142		

tively. The highest values were at Station P-2: 157, 138, and 32 nectophores 10 m^{-3}, respectively (Figure 3). The vertical distributions of *L. subtilis* and *E. spiralis* correlated significantly with the abundance of tintinnids (N=47; r=0.84, P<0.001 and r=0.86, P<0.001, respectively) and copepod nauplii (N=47; r=0.62, P<0.01 and r=0.61, P<0.01). *Sphaeronectes gracilis* correlated significantly with calanoid copepodites (N=47; r=0.67, P<0.01), calanoid copepods (N=47; r=0.88; P<0.001), and juvenile appendicularians (N=47; r=0.61; P<0.01).

Of other species in the upper 100 m, higher abundances were found for *Hippopodius hippopus* and *Muggiaea kochi* at Station P-6 with the maximum for each being 26 nectophore 10 m^{-3} in the surface layer, and *M. atlantica* reached an abundance of 36 nectophore 10 m^{-3} in the 50–100 m layer.

No marked differences between day and night mean vertical positions were observed for most of the first 'Group' species (Table 2). Only *Sphaeronectes irregularis* exhibited upward movement at the deepest stations during the night. Similar behaviour was found for *Chelophyes appendiculata*, but only at Station P-3.

The most abundant species in the 100–400 m layer was *Lensia meteori*. This was found only at deep southern stations (Figure 3), where it contributed to 51% of total calycophores. The bulk of the population was at 200–400 m, with the highest number — 36 ind 10 m^{-3} — sampled at Station P-2 during the day (Table 2 and Figure 3). The obvious difference in concentrations between day and night samples shows that part of the population spread out shallower and deeper in the water column during the night. Significant correlations were not established with either micro- or mesozooplankton.

Lensia conoidea and *Clausophyes ovata* dominated below 400 m, contributing more than 90% to total calycophores. Among less-abundant species inhabiting deeper layers, *Vogtia pentachantha*, *Sphaeronectes irregularis*, and *C. ovata* showed upward movements during the night, while *S. fragilis* went deeper (Table 2).

DISCUSSION

Of the 24 calycophores species known for the Adriatic Sea (Gamulin & Kršinić, 2000), 20 were found during this investigation. As usual, highest species diversity was noted at the two deepest stations, but the highest total number found in the same area contradicts some previous works in the Mediterranean (Gili et al., 1998) and Adriatic Sea (Gamulin & Kršinić, 1993). This is probably a consequence of the deep water niche and specific ring circulation patterns of the South Adriatic (Gačić et al., 2001) that could accumulate plankton species in this area. Calycophore densities in the surface layers (0–100 m) at these stations are among the highest reported for open-sea environments (Gili et al., 1987, 1988;

Andersen et al., 1992; Carré & Carré, 1993; Bucher, 1999; Gamulin & Kršinić, 2000; Batistić et al., 2004). The low number of specimens cited in other work may be due to larger-mesh nets (>200 μm) being used allowing smaller specimens to escape.

Earlier data suggest that *Muggiaea kochi* and *Lensia subtilis* were the most numerous calycophores in the Adriatic Sea (Gamulin & Kršinić, 1993). However, Gamulin & Kršinić (2000), have noted recent changes in the Adriatic's calycophore populations, with only *L. subtilis* as the predominant species in both coastal and open waters. This is consistent with the present findings.

In addition to an increase in *Lensia subtilis*, numbers of *Eudoxoides spiralis* and *Sphaeronectes gracilis* are also present in higher quantities than previously reported in the open waters of the Adriatic and Mediterranean Seas (see Gamulin & Kršinić, 2000); further, there are lower numbers of *Muggiaea kochi*. Slightly higher numbers of *M. kochi* at Station P-7 as well as two other species (*Hippopodius hippopus*, *M. atlantica*) probably results from their transport by surface currents originating in the northern Adriatic (Gačić et al., 2001). *Muggiaea atlantica*, after invading the Adriatic Sea (Kršinić & Njire, 2001), seems to be established permanently in the open waters of the northern Adriatic (D. Lučić, unpublished data).

Cluster analysis suggests two groups of species. The first 'Group' is confined mainly to the upper 100 m, where oxygen saturation was always greater than 1.0 and, where seasonal variations in temperature and salinity were greatest (Gačić et al., 2001). This zone is also characterized by an ample supply of food, inasmuch as it has the highest Chl-*a*, microzooplankton, and copepod concentrations. Reports from previous research in the Mediterranean Sea (see Gamulin & Kršinić, 2000; Batistić et al., 2004) and elsewhere (Pugh, 1974, 1984; Pagès & Gili, 1991; Pagès et al., 2001) support our results.

Lensia subtilis and *Eudoxoides spiralis* dominated the surface layers. Their vertical distributions correlated significantly with tintinnids and copepod nauplii. That of *Sphaeronectes gracilis* correlated with calanoid copepodites, calanoid copepods, and juvenile appendicularians. Calycophores feed mainly on copepods and their development stages (Purcell, 1981, 1982; Pagès et al., 2001). Smaller gastrozooids of *L. subtilis* and *E. spiralis* may prefer small-size prey. Gastrozooids of *S. gracilis* (0.8 mm long), however, prefered larger prey, mostly copepods (Purcell, 1981; Purcell & Kremer, 1983). Siphonophores feed throughout the day and night wherever prey organisms are most abundant (Purcell, 1981). This may partly explain the high abundance of calycophores in epipelagic layers, and the fact that some species migrate toward the surface at night.

Only *Sphaeronectes irregularis* showed clear nightly movement to the upper layers at the deepest stations. For *Chelophyes appendiculata*, different patterns of diel migration have been reported in the Mediteranean Sea. For example, Patriti (1995) did not observe diel vertical migrations for this species, but Sardou et al. (1996) found that it performed weak migrations, and Andersen et al. (1992) reported that it ranged from 100 to 450 m during the day and was distributed in the upper 75 m at night. The behaviour of these siphonophores in coastal waters, however, is different from that offshore (Buecher, 1999). The present study found irregular day/night positions of *C. appendiculata*, with high densities in upper layers at Station P-1 and P-2, and near the bottom at shallower stations. Only at Station P-3 was a pronounced difference in day/night position recorded.

The second 'Group' is composed mainly of species distributed below 100 m depth (Figure 3). This zone naturally has very low annual oscillations in temperature and salinity and lower oxygen concentrations, though it is still well aerated (Gačić et al., 2001).

The bulk of the population of *Lensia meteori* the predominant species in the mid-water layer was distributed between 200 and 400 m. During the night, some specimens appeared to spread out in the water column toward both surface and deeper layers. A few reports on their bathymetric distribution confirm these observations (see Gamulin & Kršinić, 2000). The vertical distribution of this mid-depth species, as well as that of the deep-sea species *Clausophyes ovata* and *L. conoidea*, might be related to the microzooplanktonic poecilostomatoids and protozoans that permanently inhabit these layers of the southern Adriatic (Kršinić, 1998). Moreover, increased food production in the surface layers will lead to increased food supply at all depths, whether via vertical migration or the downward settlement of organic matter.

Results of this investigation, as well as those of Benović et al. (2005) on medusae, confirm the importance of planktonic cnidaria in the Adriatic pelagic community in terms of their diversity, abundance, and trophic relationships. Although there appears to have been a change in the predominant calycophore species in this area, this may have had little effect on the trophic structure of the Adriatic planktonic ecosystem, as the replacement species functions at the same trophic level. This is in accordance with environmental changes and biological succession of zooplankton species at the same trophic level in the Mediterranean and elsewhere (see Buecher, 1999), and this has implications for the stability of material flow in Adriatic plankton communities.

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