ISSN: 0001-5113 AADRAY	ACTA ADRIAT., 52(2): 159 - 172, 2011	UDC: 597.556.333.7: 593.1 (262.16)

A short-term investigation of diel vertical migrations of the calycophoran Siphonophora in the open south Adriatic Sea (July 2003)

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Morning, midday, evening and night repetitive sampling was used to demonstrate calycophoran diel vertical migration (DVM) at a fixed station in the oligotrophic southern Adriatic Sea at 8 depth intervals. Of 20 calycophoran species collected, most of them inhabited layers of specific temperature and light intensity, and migrated during the night. The deep species Kephyes ovata *is primarily non-migratory. Typical nocturnal movements to the surface were recorded for Lensia conoidea and* Sphaeronectes koellikeri. Lensia subtilis *and* Eudoxoides spiralis *migrated toward the surface in the evening but sank deeper at night.* Lensia meteori *and* Lensia fowleri *reached upper layers at midday. The DVM of* Sphaeronectes irregularis *was irregular and independent of diel light patterns. Though low in numbers, some calycophorans were found above the thermocline at night. For mesopelagic species, however, higher summer surface temperatures proved an effective barrier to migration above 100 m. Thus, certain species could be represented as key species of planktonic cnidarian assemblages found within a certain depth range. Though not homogenous, and while some undertake nocturnal migrations in both directions, all are interrelated by preferences of bathymetric distribution and specific DVM behavior.*

Key words: Cnidaria, PAR, jelly plankton, vertical distribution, Mediterranean Sea

INTRODUCTION

Calycophoran siphonophores are widely-distributed colonial marine cnidarians known from all depths (PUGH, 1999). Despite their important predatory role in planktonic food webs (*see* PURCELL, 1997), their gelatinous consistency and fragility render them difficult to collect by conventional trawl gear; they are consequently easy to ignore (PUGH, 1984; HOSIA & BÅMSTEDT, 2008). Their tendency to break into numerous pieces often makes it particularly challenging to obtain reliable quantitative estimates of their abundance. As a result, they generally are under-represented in plankton investigations. There are, for example, relatively few studies on calycophoran diel vertical migration (MOORE, 1953; MUSAYEVA, 1976; CASANOVA, 1980; PUGH, 1977; 1984, 1999; MACKIE *et al*., 1987; LAVAL *et al*., 1989; PAGÈS & GILLI, 1991; ANDERSEN *et al*., 1992; SARDOU & ANDERSEN, 1993; MAYCAS *et al*., 1999).

Diel vertical migrations (DVM) are undertaken by a wide range of zooplanktonic taxa and probably represent the biggest daily animal migration in term of biomass on Earth (HAYS, 2003). Of the many factors proposed to explain this behavior (e.g. hydrographic variables, feeding activities, predator avoidance, reproduction), the change in light intensity at dusk and dawn seems to be the major controlling factor (e.g. PUGH, 1984; FRANK & WIDDER, 2002; GRAHAM *et al*., 2001; LUČIĆ *et al*., 2009).

The present work reports data for calycophoran siphonophores collected over 96 h during the morning, midday, evening, and night at an open-water station in the oligotrophic south Adriatic. The goal was to elucidate the species composition of migrators and their DVM behavior. Particular focus was placed on the hypothesis that calycophoran DVM is influenced considerably by hydrographic features and light intensity. During our investigation a sharp thermocline was formed at a depth of 14 m and salinity was generally high throughout the water column. This work expands on the description of medusan DVM over the same period and at the same station (LUČIĆ *et al*., 2009), with the aim being to understand the importance of planktonic cnidarians in deep oligotrophic ecosystems. Detailed results of irradiance, PAR, temperature, salinity, chlorophyll, as well as micro- and mesozooplankton composition, abundance and DVM are described by LUČIĆ *et al*. (2009).

MATERIAL AND METHODS

Calycophoran siphonophores were sampled at a single station (~ 1200 m depth) in the southern Adriatic Sea (41° 44’ N, 17° 52’ E) from July 22 to July 28 (Fig. 1). The sampling program was interrupted from midday 25 July to the morning of 27 July owing to inclement weather (Table 1). Nineteen sample series (152 vertical hauls) were collected with a Nansen opening-closing net (200-μm mesh, 113-cm diameter) within the following depth intervals: 0-15 (above the thermocline), 15-50, 50-100, 100-200, 200-400, 400-600, 600-800, and 800-1200 m. Five sample series were taken during the morning, four at midday, four during the evening, and six at night (Table 1).

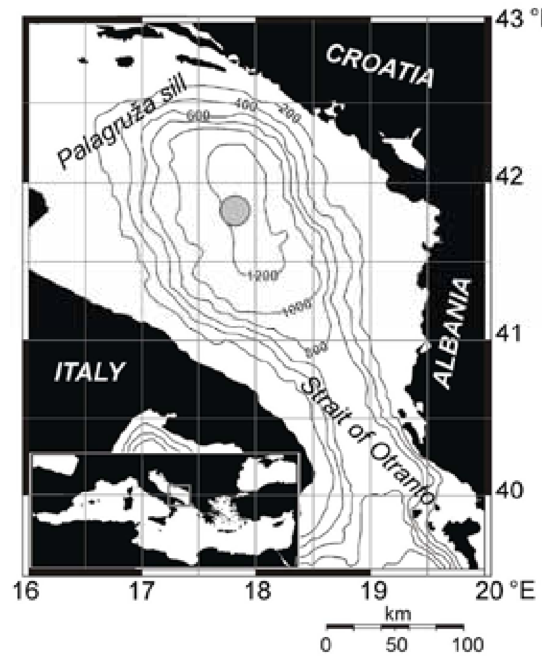

Fig 1. Location of the sampling station in the southern Adriatic, July 2003

The average hauling speed of all tows was 0.5 m s^{-1}. Samples were preserved in a 2.5% formalin-seawater solution buffered with $CaCO_3$. Species identification was performed with an Olympus SZX 9 stereomicroscope. Calycophoran anterior nectophores were counted from total samples and abundance was expressed according to the number of nectophores per 10 cubic meters of each species.

Two CTD probes were used to measure temperature and salinity twice daily. The Idronaut 316 probe was used to 1200 m and the SeaBird OC25 probe, equipped with a Wetlabs FLUO sensor, above 200 m. Chlorophyll concentrations were calculated from fluorescence with software provided by Seabird. The probes are

Table 1. Temporal sequence of sampling in the south Adriatic, July 2003

Data	Sampling period (hours)
22 July	19:30-22:50
23 July	01:30-04:00
23 July	06:25-09:50
23 July	11:30-15:00
23 July	16:00-18:40
23 July	21:25-23:30
24 July	00:25-03:45
24 July	06:00-09:00
24 July	11:35-13:45
24 July	17:30-20:30
25 July	00:15-03:45
25 July	06:00-09:00
27 July	23:45-03:05
27 July	05:55-09:00
27 July	11:45-15:00
27 July	17:30-20:30
28 July	00:00-03:10
28 July	05:50-08:45
28 July	13:00-16:15

accurate to 0.01 °C, 0.003 salinity units, and 0.5 m depth.

Light was measured daily to 90 m at 0600, 1200, and 1800 (local time) with a profiling radiometer (PRR800 Biospherical Instruments Inc.) at 14 wavelengths (340 – 710 nm) in addition to measurements of PAR (Photosynthetic Available Radiation) attenuation (400-700 nm). Assuming the same water properties in deep waters as in the euphotic layer, the log-line for PAR was extrapolated, prolonging the PAR attenuation profile with the same slope until 1200 m.

Representative calycophoran species within a depth layer were determined according to their frequency of occurrence (percentage) and relative abundance in all samples. The weighted mean depth (WMD) of all representative species was calculated as:

$$\text{WMD} = \ (n_i\, z_i\, d_i)/ \ \ (n_i\, z_i)$$

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 within each depth layer (10 m^{-3}).

RESULTS

Vertical distribution and DVM of the most frequent and abundant calycophores

Of the twenty calycophoran species collected, the most frequent and abundant were *Eudoxoides spiralis* and *Lensia subtilis* (Table 2). Among the less numerous, though frequently occurring, species were *Lensia meteori* and *Lensia conoidea*, followed by *Sphaeronectes koellikeri*, *Sphaeronectes irregularis*, *Lensia fowleri* and *Kephyes ovata*.

Table 2. Average abundance (No. ind. 10 m^{-3}) of calycophoran siphonophores collected in the southern Adriatic Sea, July 2003

Species/depth layer	0-15 m	15-50 m	50-100 m	100-200 m	200-400 m	400-600 m	600-800 m	800-1200 m
Hippopodus hippopus	0.04±0.19	0.12±0.30	0.04±0.13	0.03±0.14				
Vogtia pentacantha					0.01±0.02	<0.01±0.01		<0.01±0.02
Sulculeolaria turgida		<0.01±0.01						
Sulculeolaria chuni	0.13±0.40	0.06±0.17	0.04±0.18	0.02±0.09				
Lensia conoidea				0.06±0.19	0.43±0.48	0.58±0.37	0.88±0.56	0.9±0.32
Lensia multicristata				0.01±0.16	0.01±0.19			
Lensia fowleri				0.23±0.32	0.35±0.49	0.07±0.14		
Lensia subtilis	0.33±0.83	0.32±0.24	4.69±3.33	0.39±0.78	0.01±0.04	<0.01±0.02		
Lensia campanella			0.04±0.19	0.01±0.04	0.01±0.04			
Lensia meteori				7.86±5.84	1.54±1.53	0.41±0.77	0.05±0.08	0.01±0.02
Lensia subtiloides				0.05±0.22	0.04±0.18	<0.01±0.92		
Muggiaea kochi	0.05±0.09							
Chelophyes appendiculata		0.07±0.21						
Eudoxoides spiralis	0.30±0.62	2.33±4.01	3.49±2.90	1.58±2.30	0.06±0.23	0.01±0.03	0.02±0.04	0.01±0.02
Sphaeronectes koellikeri	0.90±1.32	1.21±1.32	3.17±6.73	0.19±0.37				
Sphaeronectes irregularis		0.47±0.87	2.32±1.96	0.99±1.55	0.23±0.43	0.01±0.02		
Sphaeronectes fragilis		0.03±0.14		0.02±0.06	0.03±0.07		0.03±0.12	
Kephyes ovata							0.04±0.08	0.26±0.28
Abylopsis tetragona	0.01±0.05	0.01±0.02						
Bassia bassensis	0.01±0.05	0.02±0.35	0.10±0.32	0.07±0.23				

Eudoxoides spiralis was found in all depth layers, with higher values below the thermocline to 200 m depth (Fig. 2). Daily WMD data show the bulk of the population between 68 and 134 m (Table 3). Slight and irregular migrations toward upper layers were noted in the evening and at night, during which some specimens were found above the thermocline. The maximum abundance was 18 nectophores 10 m^{-3}.

Lensia subtilis was found from the surface down to 600 m, with the higher values below the thermocline to 100 m depth (Fig. 3). The maximum abundance was 13 nectophores 10 m^{-3}. Daily WMD data showed that most of the population varied from 43 to 82 m (Table 3). A slight movement toward the surface was noted in the evening, and migrations in both directions were commonly observed during the night.

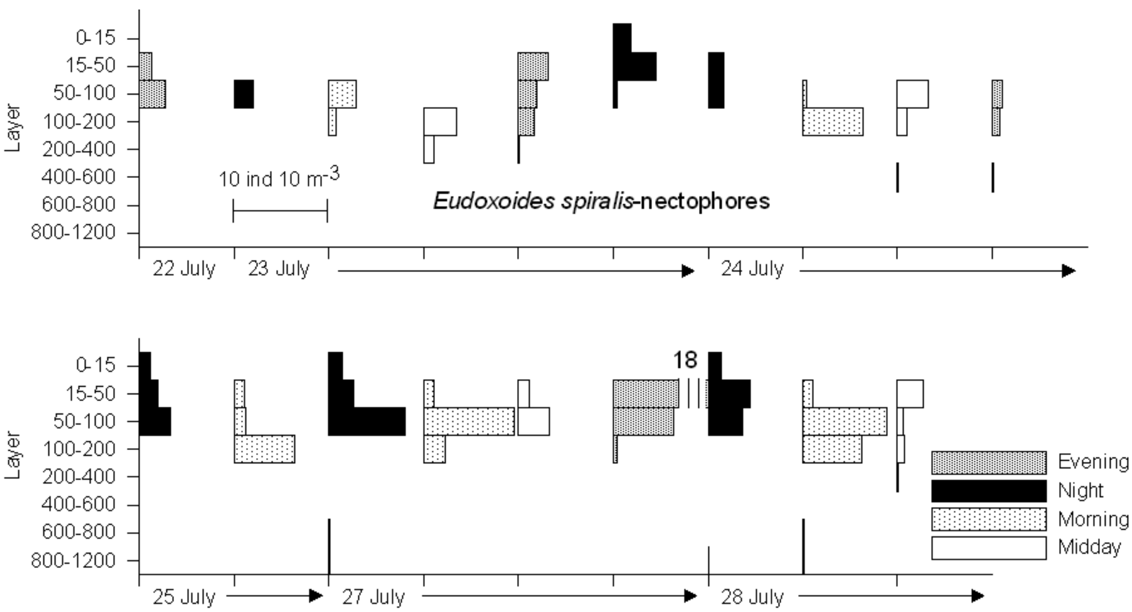

Fig. 2. Diel vertical migration of Eudoxoides spiralis in the southern Adriatic Sea, July 2003. Each unit between ticks along the x-axis represents 10 nectophores per 10 m3, and the arrows represent sampling dates.

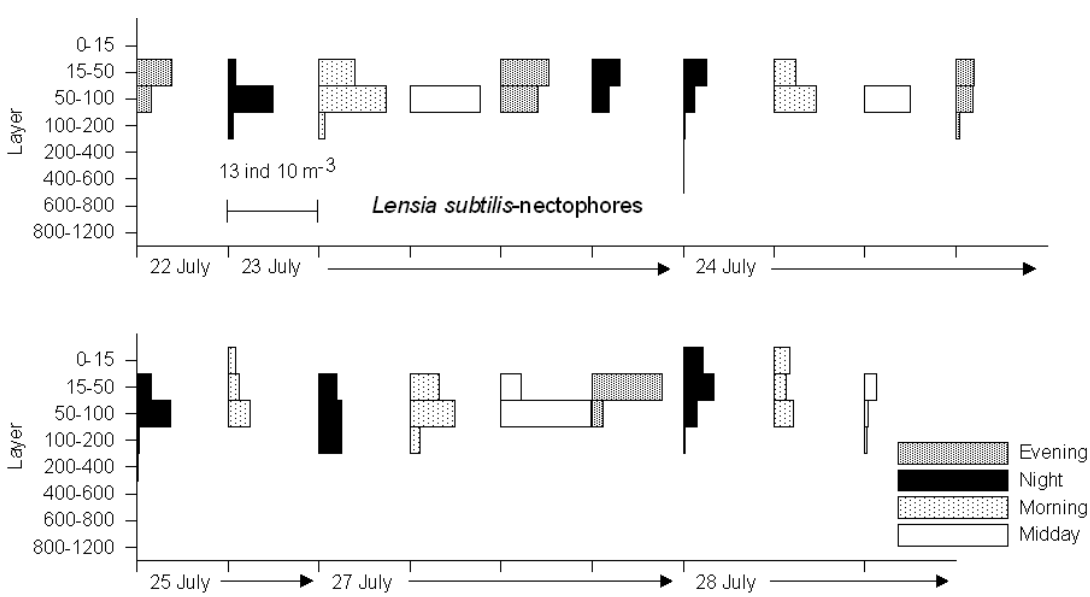

Fig. 3. Diel vertical migration of Lensia subtilis in the southern Adriatic Sea, July 2003. Each unit between ticks along the x-axis represents 13 nectophores per 10 m3, and the arrows represent sampling dates

Table 3 The weighted mean depth (WMD) and sampling depth ranges (SDR) of most common calycophoran siphonophores calculated from data obtained at different day time and from all data collected in the southern Adriatic Sea, July 2003

	Morning		Midday		Evening		Night		All data
	WMD	SDR	WMD	SDR	WMD	SDR	WMD	SDR	WMD
Lensia conoidea	642	200-1200	739	200-1200	651	200-1200	691	100-1200	677
Lensia fowleri	346	100-600	198	100-400	276	100-600	303	100-600	289
Lensia meteori	224	100-800	178	100-800	247	100-800	224	100-1200	219
Lensia subtilis	66	0-200	70	15-200	43	15-200	82	0-600	67
Eudoxoides spiralis	133	0-1200	134	15-600	68	15-600	84	0-1200	110
Sphaeronectes koellikeri	65	0-200	74	15-200	61	0-200	36	0.-200	68
Sphaeronectes irregularis	179	15-600	120	15-400	109	15-400	127	0-400	138
Kephyes ovata	970	800-1200	1000	1000-1200	981	800-1200	1000	800-1200	983

Specimens were found above the thermocline in only three samples, and never at midday.

Lensia meteori was found from 100 m depth to the bottom. Daily WMD data show that it was the most common between 178 and 297 m (Table 3), but higher values usually were in the 100 - 200 m layer (Fig. 4). Maximum abundance was 27 nectophores 10 m^{-3}. Sinking below 600 m was frequent, especially at night when specimens were collected near the bottom.

Daily WMD data for *Lensia conoidea* showed that most of the population occupied a depth of about 650 m (Table 3). During the day, the bulk of the population was deeper (737 m). Specimens were rarely found above 200 m, and these only during the evening and at night (Fig. 5). The maximum, two nectophores 10 m^{-3}, was found during the morning of July 24.

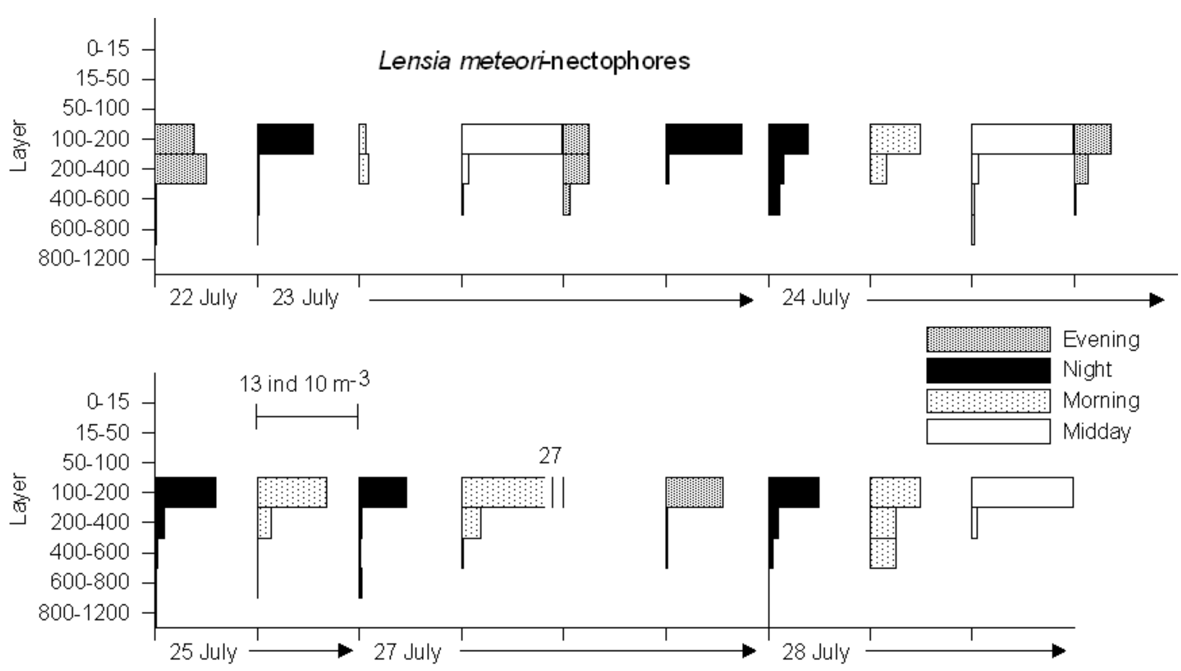

Fig. 4. Diel vertical migration of Lensia meteori in the southern Adriatic Sea, July 2003. Each unit between ticks along the x-axis represents 13 nectophores per 10 m3, and the arrows represent sampling dates

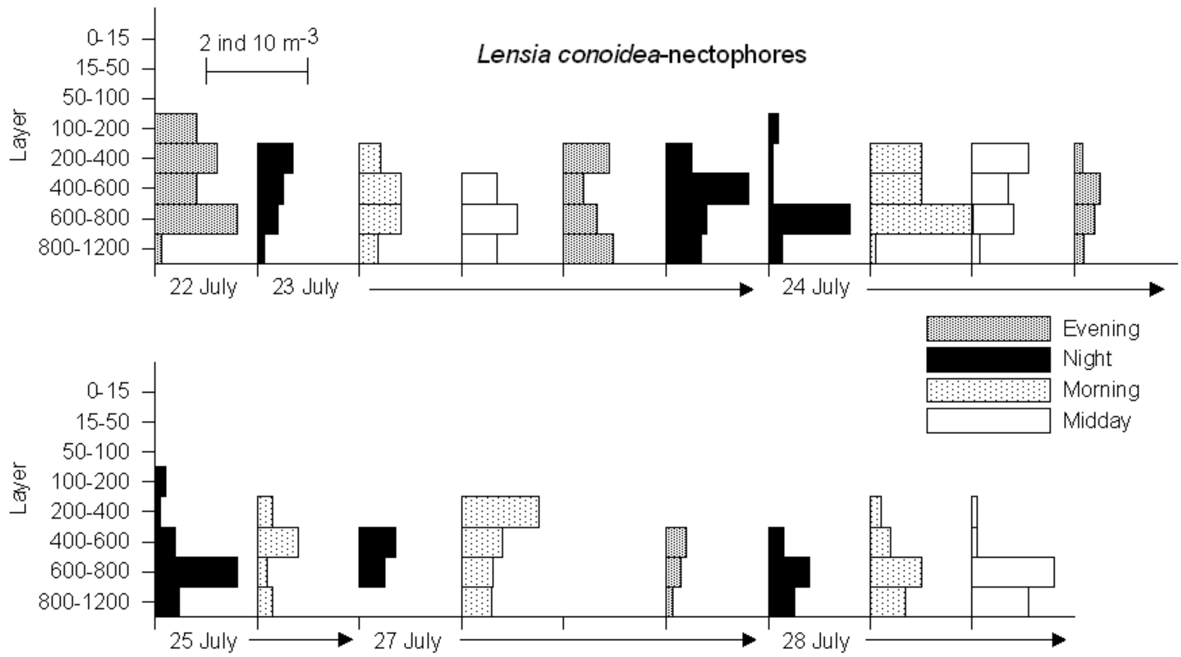

Fig. 5. Diel vertical migration of Lensia conoidea in the southern Adriatic Sea, July 2003. Each unit between ticks along the x-axis represents 2 nectophores per 10 m3, and the arrows represent sampling dates

Most of the *Sphaeronectes koellikeri* calycophorans were found above 100 m (Fig. 6). Daily WMD data show that they were common between 36 and 74 m (Table 3). During midday, this species often aggregated in the 50 - 100 m layer. The highest values of 17 and 26 nectophores 10 m^{-3} were found on July 23 and July 27, respectively.

The calycophoran *Sphaeronectes irregularis* occupied the layer from 15 to 600 m. The

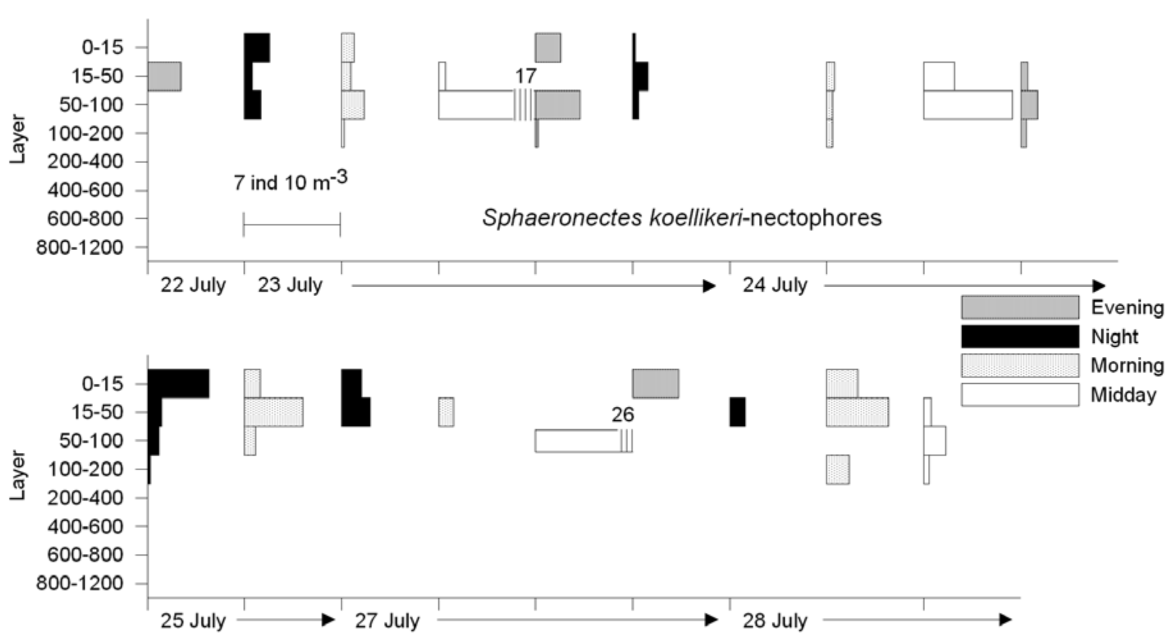

Fig 6. Diel vertical migration of Sphaeronectes koellikeri in the southern Adriatic Sea, July 2003. Each unit between ticks along the x-axis represents 7 nectophores per 10 m3, and the arrows represent sampling dates

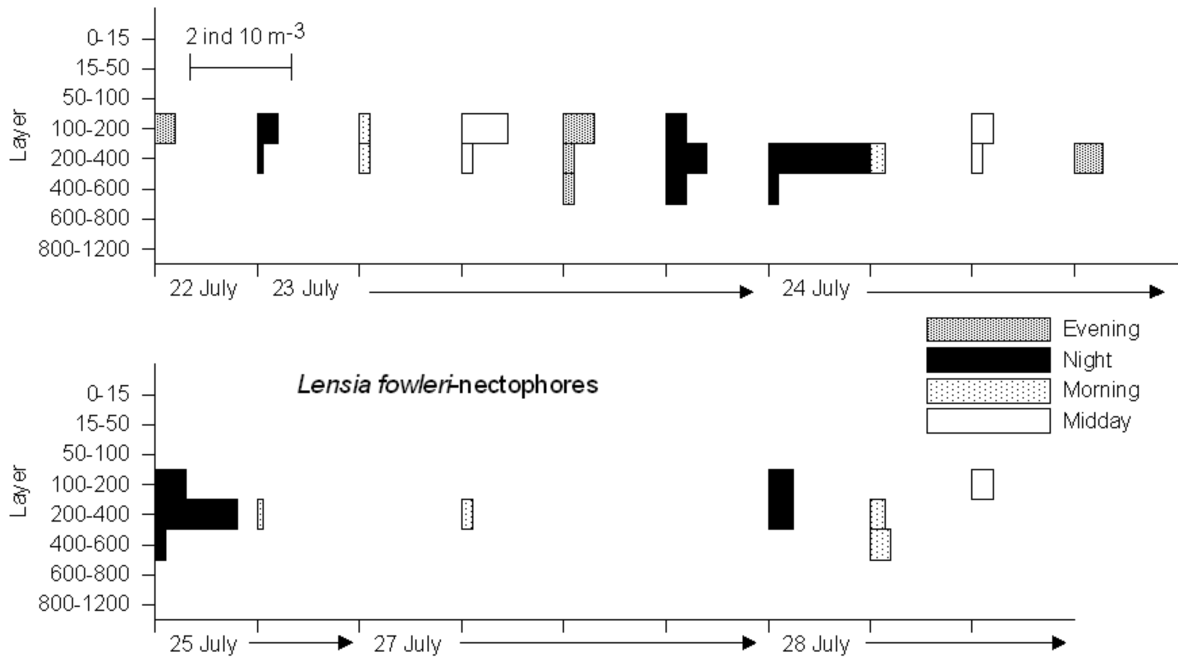

Fig. 7. Diel vertical migration of Lensia fowleri in the southern Adriatic Sea, July 2003. Each unit between ticks along the x-axis represents 2 nectophores per 10 m3, and the arrows represent sampling dates

maximum abundance was 7 nectophores 10 m^{-3}. The DVM of this species was irregular and independent of daily light patterns. WMD data show that it was most commonly found between 109 and 179 m (Table 3).

According to the WMD calculations, the greatest DVM was noted for the species *Lensia fowleri* (148 m). Daily WMD data suggest an atypical vertical distribution of this species: It migrates to the upper layer by midday (198 m) and descends at night, with the deepest penetration of 346 m reached in the morning (Table 3). The maximum abundance of two nectophores 10 m^{-3} was in the 200-400 m layer at night on July 28 (Fig. 7)

Daily WMD data for the calycophoran *Kephyes ovata* showed that most of the population permanently resided below 800 m (Table 3) and rarely migrated to the upper layer. The maximum abundance was one nectophore 10 m^{-3}.

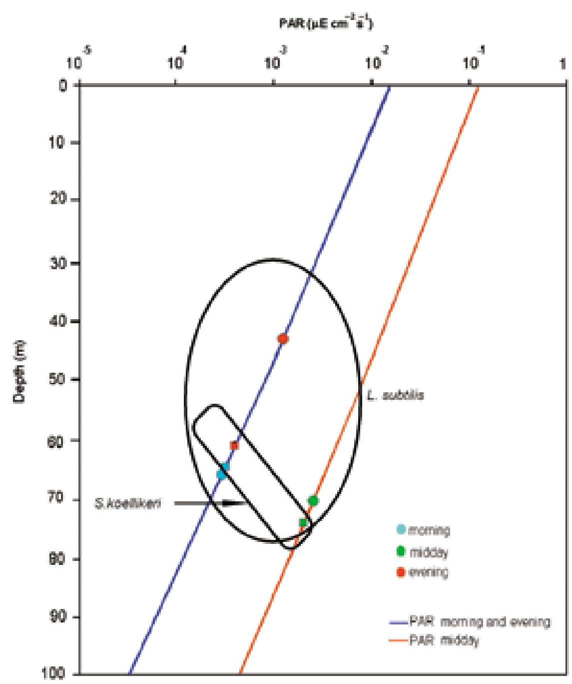

Fig. 8. Extrapolated average depth PAR light intensities at midday (red curve), morning and evening hours (blue curve), and weighted mean depth (WMD) positions of the most frequently occurring and abundant calycophores above 100 m depth (black circles or rectangles). Colored spots indicate calycophoran WMD position at different times (blue = morning; green = midday, red = evening)

Relationships between calycophoran siphonophores and environmental factors

Muggiaea kochi was found exclusively above the thermocline. The thermocline was not

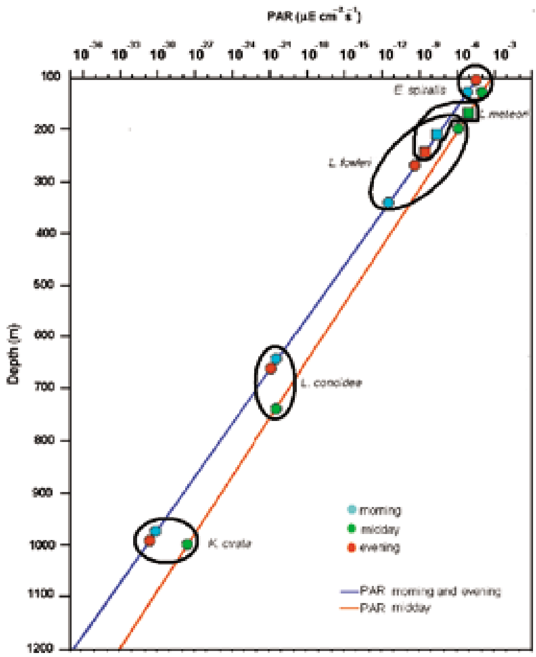

Fig. 9. Extrapolated average depth PAR light intensities at midday (red curve), morning and evening hours (blue curve), and weighted mean depth (WMD) positions of the most frequently occurring and abundant calycophores from 100 to 1200 m depth depth (black circles or rectangles). Colored spots indicate calycophoran WMD position at different times (blue = morning; green = midday, red = evening)

a barrier for most surface species: *Hippopodius hippopus*, *Sulculeolaria chuni, Lensia subtilis*, *Eudoxoides spiralis, Sphaeronectes koellikeri*, *Abylopsis tetragena* and *Bassia bassenensis*. These species were found at least once above the thermocline, mainly in samples collected during the morning and at night.

There was a change in the slope of the relationship between the logarithm of light intensity and depth for PAR. Lines between the surface and 40 m depth values show similar slopes for the different daily light regimes, but from 40-90 m the slope is somewhat higher for the morning/ evening values. Extrapolation to conditions at 1200 m was based on changes in light intensity below 40 m depth to the lowest measured layer. The two lines define the daily intensity range at the particular depth (Figs. 8 and 9).

The vertical distributions of calycophorans nectophores suggest clear species-specific differences for preferred light intensities. The WMD position of common species (Table 3) along extrapolated PAR curves (Fig. 8 and 9) illustrates a range of preference for different light intensities during the daily incidence maximum: *Lensia subtilis* (10^{-8} to 0.05511), *Sphaeronectes koellikeri* (10^{-8} to 0.05516), *Eudoxoides spiralis* (10^{-37} to 0.05511), *Lensia fowleri* (10^{-20} to 0.0005), *Lensia meteori* (10^{-25} to 0.0005), *Lensia conoidea* (10^{-37} to 10^{-6}) and *Kephyes ovata* (10^{-37} to 10^{-25}). *Sphaeronectes irregularis* was present from 10^{-20} to 0.05516, but its DVM was independent of the daily light pattern and was not included in Fig. 8 and 9.

DISCUSSION

Of the 24 calycophore species known for the Adriatic Sea (GAMULIN & KRŠINIĆ, 2000), twenty were found during this study. In general, species composition did not differ considerably from previous investigations of the deep southern Adriatic (GAMULIN & KRŠINIĆ, 1993; BATISTIĆ *et al*., 2004; LUČIĆ *et al*., 2005). The cyclonic gyre, which is well-established in this region (GAČIĆ *et al*., 2002), is probably responsible for maintaining a relatively constant composition of the plankton community, including gelatinous taxa. The rather stable environmental conditions over the study period suggest that a coherent system was sampled (MOROVIĆ *et al.*, 2006; LUČIĆ et al., 2009)

Total nectophore densities, less than those noted in spring 2002 (see LUČIĆ *et al*., 2005), are still among the highest reported for the open sea (PARTITI, 1964; PUGH, 1984; GILI & PAGÈS, 1987; GILI *et al*., 1988; PAGÈS & GILLI, 1991; ANDERSEN *et al*., 1992; CARRÉ & CARRÉ, 1993; LO & BIGGS, 1996; BUECHER, 1999; GAMULIN & KRŠINIĆ, 1993; GASCA, 1999; THIBAULT-BOTHA *et al*., 2004; PALMA & SILVA, 2006; HOSIA & BÅMSTEDT, 2008). Our results affirm that *Eudoxoides spiralis* and *Lensia subtilis* are the most numerous species in the open south Adriatic, where they represent a considerable fraction of the total abundance of gelatinous zooplankton.

The high predation rate of siphonophores on zooplankton plays an important role in the pelagic food web (PURCELL, 1981, 1982, 1997; PURCELL & KREMER, 1983; MILLS, 1995; PUGH, 1999) and may contribute to defining trophic structure (PAGÈS *et al.*, 2001). Most calycophores have small gastrozooids and consume only small zooplankton (PURCELL, 1981). Production and maturation of some species correlate with prey availability (PURCELL, 1982; SILGUERO & ROBINSON, 2000). Above 200 m, high calycophoran abundance coincides with the highest density of copepods and their developmental stages (*see* LUČIĆ *et al.*, 2009). Though less numerous, calycophoran fauna is usually well established in the mesopelagic and is linked nutritionally with the deep-sea micro- and mesozooplankton that permanently inhabit the southern Adriatic (KRŠINIĆ, 1998; KRŠINIĆ & GRBEC, 2002; LUČIĆ *et al.*, 2009).

The first investigation of diel differences in calycophoran bathymetric distribution in the southern Adriatic (LUČIĆ *et al.*, 2005) indicated a dependence of some species on daily light intensity changes. The present data support this observation and, owing to the finer scale of temporal sampling, offer additional details of calycophoran diel vertical patterns.

The most common calycophorans exhibited substantial variations of depth range: *Eudoxoides spiralis* (0-1200), *Lensia conoidea* (100-1200), *L. meteori* (100-1200), *L. subtilis* (0-600), *Sphaeronectes irregularis* (0-600), *L. fowleri* (100-600), *Kephyes ovata* (800-1200) and *S. koellikeri* (0-200). WMD calculations showed that these species do not perform extensive DVM, as noted for medusae (LUČIĆ *et al.*, 2009). Thus, the bulk of the population for a defined species usually inhabited layers characterized by the preference for light of a particular intensity.

The deep species *Kephyes ovata*, previously known as *Clausophyes ovata* and reclassified by PUGH (2006), is primarily non-migratory. Typical nocturnal movements to the surface layers were recorded for *Lensia conoidea* and *Sphaeronectes koellikeri*, previously known as *Sphaeronectes gracilis* and reclassified by PUGH (2009). *Lensia subtilis* and *Eudoxoides spiralis* migrated toward the surface during the evening. During the night they sank deeper.

Lensia meteori and *L. fowleri* reached upper layers at midday. Such behaviour could be explained by foraging strategies, which vary among planktonic cnidarians (PURCELL, 1981, 1982, 1997; MILLS, 1995), or by avoidance of predators and competitors. For example, the midday WMD of *L. meteori* and *L. fowleri* calculation coincided with the upper borderline of the vertical distribution of narcomedusa *Solmissus albescens* (LUČIĆ *et al.*, 2009) which is known to feed on other gelatinous animals (RASKOFF, 2002).

The DVM of *Sphaeronectes irregularis* was irregular and independent of diel light patterns. This is contrary to the results of LUČIĆ *et al.* (2005) when, in spring, this species was regularly found in upper layers. The finer scale of temporal sampling (6-h intervals) in the current study certainly permits more detailed insight into this calycophoran DVM. However, it should be kept in mind that the higher summer temperatures of the upper layers can also be expected to influence the diel vertical pattern of this species.

Of other frequent and abundant calycophorans, *Lensia subtilis* and *Sphaeronectes koellikeri* were rarely found above the thermocline and never at midday.

The vertical distribution of some less abundant calycophores, i.e. *Hippopodius hippopus*, *Sulculeolaria chuni*, *Abylopsis tetragona* and *Bassia bassenensis*, seemed unaffected by temperature stratification. *Mugiaea kochi* was only found above the thermocline. PAGÈS & GILI (1991) noted that the thermocline probably acted as a boundary for the calycophoran DVM at an offshore station off the northern coast of Namibia. At dusk, however, the urge to feed was sufficiently strong for individuals to breach this boundary and enter the surface layer.

Some calycophoran species are adapted exclusively to the lower temperatures typical of deep water throughout the year. The higher temperatures found in surface layers during the summer thus represent an effective physiological barrier for these species. The mesopelagic species *Lensia meteori, L. conoidea*, and *L. fowleri* that could be found in upper layers at night (ALVARIÑO, 1971; PUGH, 1974, 1984; ANDERSEN *et al.*, 1992; GAMULIN & KRŠINIĆ, 2000) were noted only below 100 m during this study. Some of these species are also epipelagic at high latitudes and mesopelagic at low latitudes (PUGH, 1977; MACKIE *et al.*, 1987; HOSIA *et al.*, 2008) The short-term sampling program implemented in this study reveals important relationships between calycophoran DVM and controlling environmental variables, such as temperature and light intensity. Thus, certain species could be represented as key species of planktonic cnidarian assemblages found within a certain depth range. Though not homogenous, and while some undertake nocturnal migrations in both directions, all are interrelated by preferences of bathymetric distribution and specific DVM behavior. These patterns are important for understanding the role of planktonic cnidarians in the marine ecosystem.

ACKNOWLEDGEMENTS

This work was supported by the Ministry of Science Education and Sport of the Republic of Croatia (Project No. 275-0982705-3047), by the Slovenian Research Agency (Program P1-0237), and the USA-Croatia Cooperation in Science and Technology (Project NSFOCE 0623508).

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Received: 27 September 2010
Accepted: 19 September 2011

Kratkoročno istraživanje dnevnih vertikalnih migracija kalikofora (Siphonophora) u otvorenim vodama južnog Jadrana (srpanj 2003.)

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SAŽETAK

Istraživanje dnevne vertikalne migracije (DVM) kalikofora obavljeno je na jednoj postaji u oligotrofnom južnom Jadranu neprekidnim uzimanjem uzoraka unutar 8 dubinskih slojeva tijekom jutra, sredine dana, popodneva i noći. Od 20 zabilježenih vrsta kalikofora, glavnina obitava unutar slojeva karakteristične temperature i dnevnog intenziteta svjetlosti, a migriraju noću. Duboka vrsta *Kephyes ovata* nije migratorna. Tipične noćne migracije prema gornjim slojevima su zabilježene za vrste *Lensia conoidea* i *Sphaeronectes koellikeri*. Sifonofore *Lensia subtilis* i *Eudoxoides spiralis* migriraju prema površini u večernjim satima, a noću tonu dublje, dok su *Lensia meteori* i *Lensia fowleri* nađene u višim slojevima tijekom sredine dana. DVM vrste *Sphaeronectes irregularis* bile su nepravilne i neovisne o dnevnoj promjeni intenziteta svjetlosti. Manji broj vrsta kalikofora nađen je tijekom noći iznad sloja termokline, a za mezopelagične vrste, 100 m dubine bila je gornja migratorna granica. Stoga, kalikofore mogu predstavljati ključne vrste zajednice planktonskih žarnjaka unutar pojedinih dubinskih raspona. Premda nisu homogene i neke vrste obavljaju migracije u oba smjera, povezane su s preferiranjem određene dubinske raspodjele i specifičnim dnevnim vertikalnim migracijama.

Ključne riječi: žarnjaci, PAR, želatinozni plankton, vertikalna raspodjela, Sredozemno more